AN ABSTRACT OF THE DISSERTATION OF

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Title: The Biology and Ecology of Weeping Alkaligrass (*Puccinellia distans*) and Nuttall's Alkaligrass (*Puccinellia nuttalliana*).

Abstract approved:

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Weeping alkaligrass (*Puccinellia* distans) and Nuttall's alkaligrass (*Puccinellia nuttalliana*) infest Kentucky bluegrass seed fields of eastern Oregon. Weeping alkaligrass is an introduced species from Eurasia, whereas Nuttall's alkaligrass is native to semi arid environments of western North America. These species are often referred to collectively as 'alkaligrass'; however, for farmers of eastern Oregon, there is concern as to which species may prove to be more troublesome. Germination experiments conducted to determine the seed biology attributes of the two species revealed that both species exhibit relatively long afterripening characteristics and viable seed for at least 1 year when dry stored. Once adequately afterripened, weeping alkaligrass had greater germination at most temperature combinations, in particular at constant temperatures. Weeping alkaligrass also was more tolerant of extreme high

temperatures, as well as drought and salt conditions. Field experiments exploring the fitness of these two species on sodic versus normal soil types, found that weeping alkaligrass benefited from normal soil conditions growing larger and producing up to 4 times the seed. Weeping alkaligrass also was able to adjust to a lower solute potential under sodic soil conditions, and maintain a higher relative water content under normal soil conditions. For both species, a strong inhibitor to plant establishment was competing vegetation. Observational studies revealed that depressional areas increased the likelihood of establishment of both species. While Nuttall's alkaligrass was positively associated with exchangeable sodium and negatively associated with exposed mineral soil, weeping alkaligrass exhibited the traits of a resource generalist, its abundance being negatively associated with competing vegetation. Results of a 2-year competition study comparing both species of alkaligrass with Kentucky bluegrass indicated that in year 1 Kentucky bluegrass grew slower than Nuttall's alkaligrass, and to a lesser extent weeping alkaligrass. Yet, by year 2, the average Kentucky bluegrass plant was vastly larger than either of the alkaligrasses, in particular weeping alkaligrass. As well, during the first year of establishment, Kentucky bluegrass biomass was equally reduced by both species of alkaligrass more so than by itself. Results from the second year indicate that Kentucky bluegrass had much higher survival rates than the two species of alkaligrass, especially weeping alkaligrass. In year 2, the original planting density of Kentucky bluegrass was the strongest indicator of potential biomass for all three species. In a comparison between year 1 and year 2 biomass, it was apparent that while weeping alkaligrass exhibited high levels of mortality, the original planting densities strongly impacted the year 2 biomass accumulation of both Kentucky bluegrass and Nuttall's alkaligrass. In conclusion, the traits of having wide ranging suitable germination conditions, a more dynamic phenotypic plasticity, increased fitness under agriculturally productive soils, traits of a resource generalist and lingering effects on the growth of both Nuttall's alkaligrass and Kentucky bluegrass, may make the introduced weeping alkaligrass a species of greater concern than the native Nuttall's alkaligrass for farmers of eastern Oregon.

The Biology and Ecology of Weeping Alkaligrass *(Puccinellia distans*) and Nuttall's Alkaligrass (*Puccinellia nuttalliana*)

by

Catherine S. Tarasoff

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Catherine S. Tarasoff, Author

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Dustin Larson contributed to the preliminary literature review and project design.

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The Biology and Ecology of Weeping Alkaligrass *(Puccinellia distans*)
and Nuttall's Alkaligrass (*Puccinellia nuttalliana*)

CHAPTER 1

General Introduction

Control of grassy weeds can be difficult in grass seed production due to the difficulty of selectively removing the weeds from the crop. Although grassy weeds compete with the crop species for nutrients and water, perhaps of equal importance is that weedy grass seeds contaminate the harvested grass seed crop. Weed seed contaminants can result in a substantial reduction in seed quality, resulting in lower market values.

Kentucky bluegrass (*Poa pratensis*) seed is a crop of primary importance in the Grande Ronde Valley of Eastern Oregon (Union County). Approximately 90% of grass seed crops in Union County are grown under contract with seed companies as certified seed[1]. In 2003, in Union County, there were 4,795 certified acres in Kentucky bluegrass, representing approximately 43% of the certified grass seed production for that area (Oregon State University, 2003). Due to alkaligrass' seed size, it is exceedingly difficult to clean out of Kentucky bluegrass and is one the most common weed seed contaminants. Alkaligrass (*Puccinellia spp.*) was reported in 8% of samples compiled by the Oregon State University Extension Service in 2000[1]. Preliminary field visits and plant identification confirmed that the majority of seeds

[1] Personal communication with Darrin Walenta – Field Crops Agent, Union County, Oregon State University.

identified as 'alkaligrass' were either weeping alkaligrass or Nuttall's alkaligrass, two species similar in appearance with different origins.

Weeping alkaligrass, a naturalized species, is suspected to have been introduced to North America from Eurasia, at the turn of the century (Cusick, 1982). From here, the plant probably traveled westward to eastern Oregon. Ironically, one of the earliest collections of weeping alkaligrass was in Ohio in 1968 in a seeding of Kentucky bluegrass (Cusick, 1982). Nuttall's alkaligrass is native to North America.

The best plan for weed management should start with an understanding of characteristics associated with establishment and competition of each species. Hence, farmers of the Grande Ronde Valley managing crops infested with either species of alkaligrass may need information such as an understanding of the basic biology, plant and soil associations, and competitive traits of these two species.

Both species are considered to be among the most saline tolerant C_3 plants (Harivandi et al., 1983; Macke and Ungar, 1971; Mintenko et al., 2002; Salo et al., 1996; Ashraf et al., 1985 etc.) with weeping alkaligrass perhaps more salt tolerant than Nuttall's alkaligrass (Salo et al., 1996; Moravcova and Frantik, 2002). Nuttall's alkaligrass has been documented on saline depressions (Macke and Ungar, 1971), and along saline lake margins (Brotherson, 1987). Weeping alkaligrass has also been documented in saline depressions (Piernik, 2003), as well as, along heavily salted roadsides (Davis and Goldman, 1983; Garlitz, 1992) and ruderal areas (Moravcova and Frantik, 2002). It is these species' salinity tolerance, in particular Nuttall's alkaligrass that has garnered the majority of research attention. Both Nuttall's alkaligrass and weeping alkaligrass are facultative halophytes (Macke and Ungar, 1970; Moravcova and Frantik, 2002; Beyschlag et al., 1996), as neither species requires salt to complete its lifecycle. Unfortunately, a conclusive classification system for halophytes has not been agreed upon; therefore, the definition of a facultative halophyte described above will be used. Macke and Ungar (1971), found slightly increased germination rates for Nuttall's alkaligrass when grown at $^{-}4$ bars versus all other treatments. Moravcova and Frantik (2002) documented marginally higher germination rates for weeping alkaligrass when subjected to 0.25 and 0.5% NaCl. Similarly, both species can tolerate low levels of salinity with either no effect or improved effect on seedling growth form or rate. Haravandi et al. (1983b) witnessed no significant difference in weeping alkaligrass when grown in tap water versus a 25% solution of sea water (EC_w = 11.8 mmhos/cm). Similarly, Macke and Ungar (1970) showed a marked increase in shoot and root growth for Nuttall's alkaligrass when grown at $^{-}4.0$ bars. Unfortunately, parallel studies for both species end at germination and early growth rates across gradients of salinity. Continuing studies into germination, dormancy, plant ecology, plant physiology and competitive attributes are limited to either one or the other species.

Although Macke and Ungar (1971) cite alternating temperatures of 20/5 C as optimal for Nuttall's alkaligrass, this has not been verified through experimentation. However, Moravcova and Frantik (2002) have documented optimal germination temperatures for weeping alkaligrass of 30/15 C. Dormancy, or after ripening requirements of weeping alkaligrass was also studied by Moravcova and Frantik (2002) and they found that germination rates increased with storage duration up to a maximum of nearly 100% germination after 90 days. They suggest that this species has non-deep physiological dormancy i.e. embryos lack sufficient growth potential to overcome the inhibiting effects of the palea and lemma (Baskin and Baskin, 1998). Whether or not Nuttall's alkaligrass exhibits the same fluctuating temperature preferences and dormancy attributes has not been documented. As well, data on moisture requirements for germination of both species are lacking in the literature. This information would help to determine which micro-climatic conditions might prohibit the establishment and/or survival of these two species.

Establishment and successful invasion of a species, however, is not dictated by germination and dormancy alone. Factors limiting establishment of any species are its interactions with biotic and abiotic site characteristics. Although field observations by various researchers (Dodd et al., 1964; Macke, 1969) indicate that the soils upon which Nuttall's alkaligrass naturally occur are alkaline (median pH = 8), perhaps the presence of weeping alkaligrass versus Nuttall's alkaligrass is actually the effect of an interaction of various site conditions within these harsh environments. Brotherson (1987) described the habitat of Nuttall's alkaligrass as having an average pH of 8.47, high levels of calcium, magnesium, sodium and potassium; and low levels of phosphorous, iron and zinc. He generally describes soil and associated vegetation, but does not attempt to derive any predictive correlations between the presence of Nuttall's alkaligrass and its associated soil characteristics. Currently, there is no documentation which links soil characteristics, spatial conditions, and competing plant species to the abundance of weeping alkaligrass and Nuttall's alkaligrass within the Grande Ronde Valley of eastern Oregon. Interestingly, Nuttall's alkaligrass and weeping alkaligrass do not commonly grow in mixed communities (Personal observation). Therefore, an understanding of which ecological niche each species occupies would be useful to predicting potential infestations.

Once a species has established in an area, an understanding of basic plant biology such as phenological development is useful for management and possible control. Phenological development of both species has been loosely outlined (Macke and Ungar, 1971; Martin and Cooper, 1976; and Schwarz and Redmann, 1989). Generally speaking, seeds of both species germinate in the spring with flowering occurring in May/June and seed ripening in June/July depending on climatic conditions. However, a detailed description of phenological development, growth rates, and potential seed production of these two species under differing field conditions has yet to be documented for populations in the Grande Ronde Valley. Because there appears to be community segregation, a description of phenological development may aid in early species identification.

In Schwarz and Redmann's research (1989), they eluded that Nuttall's alkaligrass may be utilizing a salinity avoidance mechanism in its ability to survive in these harsh environments. Nuttall's alkaligrass is considered a 'non-salt accumulator' by some (Guy et al., 1986), yet a 'salt accumulator' by others (Sessoms, 2004). To date the presence of salt glands is unknown, however, it does have the ability to tolerate site conditions with remarkably high salt concentrations (Schwarz and Redmann, 1989; Brotherson, 1987). Halophytes in general have been documented to express optimal growth rates at around 200 mol m^{-3} (Munns et al., 1983). However, previous research confirms that Nuttall's alkaligrass does not flower at water potentials below -2.4 MPa (Guy et al., 1986).

Although most plants experience reduced photosynthesis as a function of increasing salinity, salt-tolerant plants differ from salt-sensitive ones in having a low rate of toxicity from salt ions due to a low rate of Na^+ and Cl^- transport to leaves combined with the ability to compartmentalize these ions in vacuoles of older leaves. The result of these tolerating characteristics is an ability to minimize salt toxicity in the young actively photosynthesizing leaves (Munns, 2002; Tattini et al., 2003). A well understood mechanism of salt tolerance within halophytic species is a general 2-phase reaction to increasing salinity stress. In the first phase, the plant experiences osmotic stress through what is referred to as 'physiological drought' associated with low external water potentials (Hester et al., 2001). In the second phase, toxic ions are diverted away from the salt sensitive cytoplasms and shunted into the vacuoles of older leaves (Tattini et al., 2003; Alarcon et al., 1999). Halophytic plants will then accumulate organic solutes such as proline (Maggio et al., 2000), glycine betaine (Munns, 2002), and mannitol (Tattini et al., 2003) into the cytoplasm to balance the increased osmotic potential of the vacuole (Maggio et al., 2000; Munns, 2002), maintain turgor pressure and a favorable water potential gradient for water uptake (Warne et al., 1990). When the vacuoles can no longer sequester toxic ions, the leaf experiences necrosis (Mühling and Läuchi, 2001; Munns, 2002). Thus, it is the older leaves which experience salt toxicity (Munns, 2002). If the plant cannot maintain a positive production of young healthy, photosynthesizing leaves to counterbalance the loss of old necrotic leaves then net photosynthesis becomes negative. However, if a plant is able to *avoid* high levels of salt then the 2-phase reaction described above may not be so consequential to the overall plant survival.

Finally, distribution of these plants may simply be due to differing competitive abilities. The competitive interaction of crop versus weed is mute within the saline environments of the Grande Ronde Valley as Kentucky bluegrass does not establish within these harsh environments (personal observation, 2001). However, of increasing concern to Kentucky bluegrass farmers is the potential for either species of alkaligrass to 'move out' of the saline areas and into agriculturally productive areas. Therefore, competitive exclusion may be the limiting factor in alkaligrass establishment outside of saline areas.

Historically, replacement or additive design studies have been utilized extensively to study the effect of density of one species on the growth of another species (Radosevich et al., 1997). However, neither replacement series nor additive designs attempt to explain the effect of both density and frequency on the growth of an individual (Firbank and Watkinson, 2003) interspecifically or intraspecifically. By the early 1960s, deWit (1960) and others were advocating the use of addition series experiments where in a matrix combination of a variety of densities and frequencies of both species are analyzed. The addition series experiment derives a 'competition coefficient', which measures the effect on one species of a unit change in the density of the opposing species relative to a unit change in the density of itself (Connolly et al., 2001).

Another limitation associated with competition studies is the short time frame under which competition is studied. Most competition studies, whether the species are annuals or perennials, analyze plant parameters over one growing season (Sher, 2000; Shainsky and Radosevich, 1992). A 1-year time frame is suitable for annuals; but, competition dynamics within a perennial community may vary greatly over a 2 year period. No competition studies have been found to date which study perennial species over a 2-year period. As well, most studies rate final harvest biomass as the indicator of 'competitive success'. However, multiple measurements over the course of the study would allow for an assessment of each species relative growth rates as a function of interspecific and intraspecific competition over time. Although European studies reported weeping alkaligrass as weakly competitive when grown with the highly competitive tall grass *Elymus repens* (Ryel et al., 1996), there is no literature studying the competitive abilities of either weeping alkaligrass or Nuttall's alkaligrass when grown intraspecifically, with each other, or with the species of concern in the Grande Ronde Valley - Kentucky bluegrass (*Poa pratensis*).

The objectives of the studies described here in were to study the seed biology, developmental characteristics, plant to soil associations of these two species, as well as their competitive characteristics to assess which species may be of greater concern for Kentucky bluegrass farmers of the Grande Ronde valley of eastern Oregon. Specific seed biology studies were to evaluate the loss of dormancy during afterripening in combination with dormancy breaking treatments and the effect of temperature on germination following adequate afterripening; and to assess the ionic effects of NaCl on Kentucky bluegrass, weeping alkaligrass, and Nuttall's alkaligrass germination under optimal conditions of 10/15 C (Moravcova and Frantik, 2002; Tarasoff et al., 2006) and supra-optimal temperature conditions. An assessment of the species plant to soil association was conducted to determine how the local scale distribution of weeping alkaligrass and Nuttall's alkaligrass may be related to soil and topographical attributes as well as vegetation community dynamics. Following the natural niche distribution study, the two species were grown in sodic versus normal soil types without competition to assess potentially unique developmental characteristics through a description of their life-history and fitness characteristics; and an examination of their plant-water relations. Lastly, the two species were grown in pairwise matrices with Kentucky bluegrass and each other to evaluate the potential for either alkaligrass species to establish and compete with Kentucky bluegrass in the agriculturally productive soils of eastern Oregon.

CHAPTER 2

Afterripening requirements and optimal germination temperatures for Nuttall's alkaligrass and weeping alkaligrass

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Abstract

In the Grande Ronde Valley of eastern Oregon, two perennial grass species in the genus *Puccinellia*; *Puccinellia distans* (L.) Parl. (weeping alkaligrass) and *Puccinellia nuttalliana* Hitchc. (Nuttall's alkaligrass), are weeds of *Poa pratensis* (Kentucky bluegrass) grass seed production fields. Weeping alkaligrass is introduced from Eurasia; whereas Nuttall's alkaligrass is native to the region. These two species were studied to determine dormancy attributes and optimal temperature conditions for seed germination. Results from the current studies indicate that both species have a high level of embryonic dormancy immediately following seed harvest, which is primarily eliminated through dry storage (afterripening) and an incubation temperature of 20 C. Following adequate afterripening, a prechill treatment of 5 days at 5 C had an inconsistent effect on germination of weeping alkaligrass ($P = 0.012$ in 2002, 0.156 in 2003) and improved germination of Nuttall's alkaligrass over both years ($P < 0.0001$). The afterripening requirement for weeping alkaligrass was more than 90 days, whereas Nuttall's alkaligrass required more than 180 days. Following adequate afterripening, both species had rapid and well synchronized germination at fluctuating temperatures of 30/10 C given unlimited moisture conditions. Given these results, it is unlikely that seeds of either species would germinate in eastern Oregon during the summer months. The data predict a long viability period under dry storage for both species. Weeping alkaligrass and Nuttall's alkaligrass should exhibit a rapid well synchronized germination in the spring as observed in the field.

Introduction

Weeping alkaligrass and Nuttall's alkaligrass are weeds within Kentucky bluegrass grass seed production fields in the Grande Ronde Valley of eastern Oregon. Both perennial grass species typically occupy sites with high pH soils throughout North America (Brotherson, 1987; Hughes, 1972; Macke and Ungar, 1971). Weeping alkaligrass, an introduced species from Eurasia, is widespread across moist, more or less alkaline environments of North America (Hitchcock, 1971), whereas Nuttall's alkaligrass, native to North America, occupies moist, usually alkaline soils from Wisconsin to British Columbia, south to Kansas, New Mexico, and California (Hitchcock, 1971). Both species are considered to be among the most saline tolerant C_3 grasses in North America (Ashraf et al., 1986; Harivandi et al., 1983a; Macke and Ungar, 1971); with weeping alkaligrass perhaps more salt tolerant than Nuttall's alkaligrass (Moravcova and Frantik, 2002; Salo et al., 1996).

Kentucky bluegrass seed is a crop of primary importance in the Grande Ronde Valley of Eastern Oregon (Union County). Approximately 90% of grass seed crops in Union County are grown under contract with seed companies as certified seed[1]. In 2004, in Union County, there were 2,428 harvested hectares of Kentucky bluegrass which represented 34% of Oregon's total production (Oregon State University, 2005). It is well documented that weeds compete with the crop species for limited resources such as nutrients, water, and sunlight. However, of greater importance for grass seed producers is that weedy grasses such as alkaligrass contaminate the harvested grass seed crop resulting in reduced seed quality, and a reduced market value. For Kentucky bluegrass seed producers of eastern Oregon, control of these grassy weeds can be difficult due to the complexity of selectively controlling grass weeds in grass seed crops.

An understanding of a plant's dormancy and germination is a primary step toward a better understanding of its biology, ultimately adding to the development of effective control strategies. Seed dormancy is an adaptation which prevents the germination of newly dispersed seed and, based on the length and type of dormancy, may help to preserve a supply of seed in the soil seed bank. Farmers need to understand the potential for seed bank persistence due to seed dormancy attributes which controls the timing of germination to maximize the probability of seedling survival (Meyer et al., 1990). Understanding the dormancy attributes of weeping alkaligrass and Nuttall's alkaligrass could help land managers to predict the possible longevity of an infestation.

Afterripening requirements of weeping alkaligrass were studied by Moravcova and Frantik (2002). They found that percent germination increased after 90 days of dry storage duration up to a maximum of nearly 100% germination. However, in their experiment, dormancy breaking treatments such as chilling and potassium nitrate were not tested. Field observations by Macke and Ungar (1971) documented that these species are likely to germinate the spring following a winter chill. Macke and Ungar (1971) cited alternating temperatures of 20/5 C as optimal for Nuttall's alkaligrass germination; however, this was not verified through experimentation. Moravcova and Frantik (2002) documented the optimal temperature combination for germination of weeping alkaligrass at 30/15 C; however, this experiment only reported final percent germination at 12 fluctuating temperature combinations and 6 constant temperatures, but not germination over time.

In order to determine the overriding effect of afterripening, chilling and temperature on dormancy, it was necessary to investigate the effect of dormancy breaking treatments in combination with afterripening. To evaluate optimal temperatures for germination of nondormant seeds, a wider range of temperatures was tested, especially extreme high and low temperatures that are common within the shallow layers of soil (top 2.5 cm) of eastern Oregon where summer temperatures can reach upward of 40 C (Figure 1.1).

This paper presents the results and interpretation of two experiments studying the loss of dormancy during afterripening in combination with dormancy breaking treatments and the effect of temperature on germination following adequate afterripening.

Materials and methods

Factors regulating loss of dormancy during afterripening

An afterripening experiment was conducted to study the loss of seed dormancy in the species Nuttall's alkaligrass and weeping alkaligrass. Nuttall's alkaligrass and weeping alkaligrass seeds were collected from multiple distinct sites within a large acreage in the Grande Ronde valley at the 'Imbler Site' (45°29′15.9″ N, 117°56′4″ W) July 8, 2002. In 2003, the 'Imbler site' was removed from grass seed production, thereby eliminating the 2002 collection site. Therefore, weeping alkaligrass was collected in the same manner previously described at 'Market Ln' site (45°22′57.5″ N, 117°54′37.7″ W) and Nuttall's alkaligrass at 'Hull Ln' (45°26′57.8″ N, 117°56′22.1″

W); both species were collected on July 29, 2003. Seeds were hand-thrashed, sorted, and air-dried at 20 C for 5 days. Seeds were afterripened for 10, 30, 90, 180 and 365 days after harvest (DAH). All seeds were surface sterilized for 20 s with a 5% solution of bleach and triple rinsed. At each afterripening date, fifty seeds of each species were counted onto 2 layers of germination paper placed in a 9 cm diameter petri dish. Treatment options used at each germination time were a wet pre-chill for 5 days at 5 C versus no pre-chill and, an incubation fluid of potassium nitrate (20 mM) or de-ionized water combined with a germination temperature of 20 C or 30 C (Hoffman Manufacturing Inc. Albany, OR).

All possible combination options for each species resulted in eight treatments in a 2 by 2 by 2 factorial arrangement with each petri dish assigned to a treatment in a completely randomized design. Each treatment combination was replicated 4 times and the protocol was identical for both species. Pre-chilled treatments were wetted prior to placing seeds into the pre-chill chamber. Seeds were germinated under dark conditions except limited exposure to ambient light conditions as necessary to count germinated seeds on days 3, 7, 14 and 21. Seeds were considered germinated when the coleoptile was 2 mm long and a radicle was present. Germinated seeds were removed from the petri dish as they were counted. At day 21, the remaining ungerminated seeds were counted and recorded to allow accurate calculation of percent germination. Due to the small seed size, accurate tetrazolium tests could not be conducted but by day 21 most ungerminated seeds were soft to the touch and moldy. Differences in probability of germination between treatments were analyzed using the logistic link function (PROC GENMOD, SAS v.9.1). Logistic regression considers the probability of germination as a function of each seed's response to the treatment calculated by the fraction of germinated seeds in relation to the total number of seeds in a Petri dish. Many forms of psuedoreplication occur during the study of seed germination through the lack of true replication of each independent treatment (Morrison and Morris, 2000). Logistic regression calculates the probability of germination by assuming all seeds in a given Petri dish are subjected to the same conditions.

Effect of temperature on germination of nondormant seed

Nuttall's alkaligrass and weeping alkaligrass seeds were collected from the Grande Ronde Valley at the 'Imbler Site' July 8, 2002 and open air dried at 20 C for 18 months to ensure adequate afterripening. All seeds were surface sterilized for 20 s with a 5% solution of bleach and triple rinsed. Following the bleach treatment, 200 seeds were placed on two layers of germination paper which was placed on top of 80 ml (0.5 cm deep) of sterilized 20-grit silica sand in an 8 cm by 8 cm plastic germination box. The silica sand was wetted to maximum holding capacity to provide a buffer against dessication and water puddling. After wetting, all seeds were pre-chilled for 48 hrs at 5 C.

Following the pre-chill treatment, each germination box was randomly assigned to one of 32 temperature combinations located on a two-way thermogradient plate (Larsen et al., 1973). The germination boxes were placed on the thermogradient plate in a checkerboard pattern resulting in daytime/nighttime temperature combinations of approximately: 5/5, 5/15, 5/25/, 5/35, 10/10, 10/20, 10/30, 10/40, 15/5, 15/15, 15/25, 15/35, 20/10, 20/20, 20/30, 20/40, 25/5, 25/15, 25/25, 25/35, 30/10, 30/20, 30/30, 30/40, 35/5, 35/15, 35/25, 35/35, 40/10, 40/20, 40/30, and 40/40 C. The experiment was a completely randomized design with 200 sample seeds per treatment. The experiment was repeated. The thermogradient plate required approximately 2 hr of heating and cooling to the specific temperature. No specific photoperiod was used and seeds were exposed to ambient indoor lighting conditions. Temperature of each treatment was measured by a copper-constantan thermocouple at 15 s intervals and the data averaged over 10 min using a datalogger (CR 10, Campbell-Scientific Inc., Logan, UT) attached to a multiplexer (AM 16/32, Campbell-Scientific Inc., Logan, UT).

Germinated seeds were counted and removed 3, 6, 9, 12, 15, and 18 days after the experiments were initiated. Seeds were considered germinated when the coleoptile was 2 mm long and a radicle was present. On day 18, the remaining ungerminated seeds were counted. Differences in probability of germination among treatments were analyzed using logistic link function (PROC GENMOD, SAS v.9.1).

Results and Discussion

Factors regulating loss of dormancy during afterripening

Unequal variances in germination between 2002 and 2003 prevented data combination for weeping alkaligrass. Although the germination values of weeping alkaligrass were lower in 2002, and the data could not be combined, the trends were similar between years. Nuttall’s alkaligrass had acceptable variances in germination between years and therefore the data was combined.

<u>Weeping alkaligrass</u>

Incubation temperature was the most important factors affecting germination across both years (Table 2.1). Total germination was greatest in 2002 with an incubation temperature of 20 C combined with 365 days of afterripening (55% ± 19.0%). There was no significant difference between seeds given a pre-chill treatment (51% ± 8%) and those than were unchilled (55% ± 19.0%). The effect of the interactions of afterripening, temperature and pre-chill treatments varied by year (Table 2.1). In 2002, the afterripening, temperature, and pre-chill treatments improved germination of weeping alkaligrass (Table 2.1). In 2002, weeping alkaligrass seed dormancy was beginning to decline by 90 DAH with 29% ± 11% of the seeds germinated with 20 C and a pre-chill treatment (Figure 2.2A).

In 2003, interactions between temperature and afterripening, and afterripening and chill were significant ($P < 0.0001$). Therefore, germination was improved with temperatures of 20 C or a chill treatment combined with afterripening, but not all three. Although in 2003, weeping alkaligrass seeds began to lose dormancy by 10 DAH (Figure 2.2B), not until 90 DAH did the seeds exhibit higher germination values 81% ± 4%. In 2003, weeping alkaligrass was able to germinate at incubation temperatures of 30 C with a pre-chill treatment and 90 and 180 DAH; however by 365 DAH the seeds were no longer able to germinate at 30 C, regardless of a pre-chill treatment (Figure 2.2B) possibly due to embryonic death. While pre-chilling improved germination in both years at 90 DAH, its effect was reduced over time and was inconsistent between 2002 and 2003 (Table 2.1). Overall, there did appear to be a dormancy breaking effect of pre-chilling for weeping alkaligrass at 90 DAH regardless of year. However, for both years by 180 DAH the pre-chill treatment marginally and inconsistently improved germination values. Weeping alkaligrass did not respond to the solution of 20mM potassium nitrate (KNO_3) in either year (Table 2.1). The results for weeping alkaligrass are consistent with the findings of Moravcova and Frantik (2002) and indicate that while afterripening is the most important factor relating to loss of dormancy, afterripening combined with suitable temperatures of 20 C are necessary for non-dormant seeds to germinate.

Nuttall's alkaligrass

Under no circumstances was Nuttall's alkaligrass able to germinate at 30 C (Figure 2.2C) nor did this species respond to the potassium nitrate treatment (Table 2.1).

Pre-chill treatments were highly significant in germination response in Nuttall's alkaligrass (Table 2.1) as this species consistently responded to the chilling treatment with higher germination values (Figure 2.2C). Germination response to the pre-chill treatment increased linearly with length of afterripening. The increased germination from 90 DAH to 365 DAH indicates a gradual loss of dormancy through afterripening which was stimulated via a pre-chill treatment.

While Nuttall's alkaligrass began to exhibit dormancy breaking at 90 DAH with 20 C and a pre-chill treatment (11% $\pm$ 4%), higher germination values were not noted until 180 DAH (31% $\pm$ 5%) with the same treatment combinations (Figure 2.2C). Within Nuttall's alkaligrass, germination increased linearly, and at a greater rate, with afterripening when a pre-chill treatment was combined with an incubation temperature of 20 C. Although the precise dormancy breaking mechanisms associated with chilling treatments are not clearly understood, the effects of low temperatures on plant cells generally result in an overall decrease in metabolic rates, a qualitative change in metabolism, a structural change in membranes (i.e., lipid composition) (Hara et al., 2003), and changes in hormone abundance such as gibberellin (Yamauchi et al., 2004) and abscisic acid (Ali-Rachedi et al., 2004). While the effect of low temperatures (chilling) on germination is species specific and interrelated with other environmental factors such as light, salinity, moisture, and/or oxygen to name a few (Silvertown, 1980), embryonic development, or afterripening, is known to influence the overall effect of temperature on germination (Baskin and Baskin, 1998). Therefore, it is not surprising that both species demonstrated increased germination when they were adequately afterripened, given a pre-chill treatment and subjected to an incubation temperature of 20 C. Germination responses to various KNO_3 concentrations appears to be inconsistent within the literature (Adkins and Adkins, 1994; Larsen et al., 1973), with no particular rate providing optimum germination across species (Adkins and Adkins, 1994; Mekki and Leroux, 1991). It is apparent that the rate of KNO_3 required to break dormancy is highly dependant upon the species being studied and was not significant within this study.

Germination Rate

Rate of germination was not altered or improved with any of the dormancy breaking treatment combinations (Table 2.2). At 365 days of afterripening both species had the least amount of dormancy remaining, therefore any germination stimulation as a result of the treatments should be apparent. For both species, after

365 days of afterripening, regardless of treatment, the majority of germination occurred between day 3 and day 7 after treatment (Table 2.2).

Effect of temperature on germination of nondormant seed

The germination data for both species were assessed for equal variance between runs. Variability was not found to be significant ($P \leq 0.05$ at $\alpha = 0.05$), therefore 2002 and 2003 data were combined prior to analysis. To accommodate the quadratic relationship between temperature and germination, the independent variables of daytime and nighttime temperatures were squared and incorporated into the logistic regression analysis (PROC GENMOD, SAS v.9.1). Due to the large number of treatment combinations, germination rate is presented as a figure created using mathematical interpolation formulae within GIS software (Figure 2.3) (Tarasoff et al., 2005). Not surprisingly, the interaction of daytime and nighttime temperature was found to affect germination for both species ($P \leq 0.05$ at $\alpha = 0.05$) as both species benefited from fluctuating temperatures. Rates of germination were slightly slower at temperature combinations involving the extreme high and low temperatures as well as at constant temperatures (Figure 2.3).

Similar to the afterripening results, regardless of temperature, most germination occurred by day 9 (Figure 2.3). Germination was less than 20% for all treatment combinations for both species at day 3 (data not shown); as well, germination at day 18 was the same as day 15 for all treatment combinations for both species (data not shown).

Although both species germinated across a variety of temperature combinations, in general, weeping alkaligrass had higher germination at most temperature combinations, in particular at constant temperatures. For weeping alkaligrass, greater than 80% germination occurred on day 6 at the optimal temperature combinations of a daytime temperature of 30C with a nighttime temperature of 10-15 C. Although Nuttall's alkaligrass was less vigorous, greater than 80% germination occurred on day 6 with daytime temperatures between 25-30 C combined with nighttime temperatures of 10-15 C.

In the Grande Ronde Valley of eastern Oregon, high summer soil temperatures are associated with dry soil conditions (Figure 2.1). However, average soil temperature conditions throughout the summer should be suitable to initiate some germination in both species. Therefore, because neither species emerges in the summer (personal observation), it is likely that the combination of adequate afterripening and soil moisture are more critical for germination than specific temperature requirements.

Conclusion

Weed seeds with short afterripening periods and concentrated germination flushes and emergence should be easier to control than those with long afterripening periods and drawn out germination characteristics. Both species of alkaligrass exhibit relatively long afterripening characteristics making control and prevention of alkaligrass seed bank development more difficult for land managers. As well, seeds of either species of alkaligrass will remain viable for at least 1 year within dry stored Kentucky bluegrass. Newly establishing Kentucky bluegrass fields could be subjected to competition from either species due to their ability to germinate at low temperatures allowing for the establishment of dense monocultures early in the season. Early establishment by either species of alkaligrass would limit resources available for the development of other plant species, an obvious competitive advantage.

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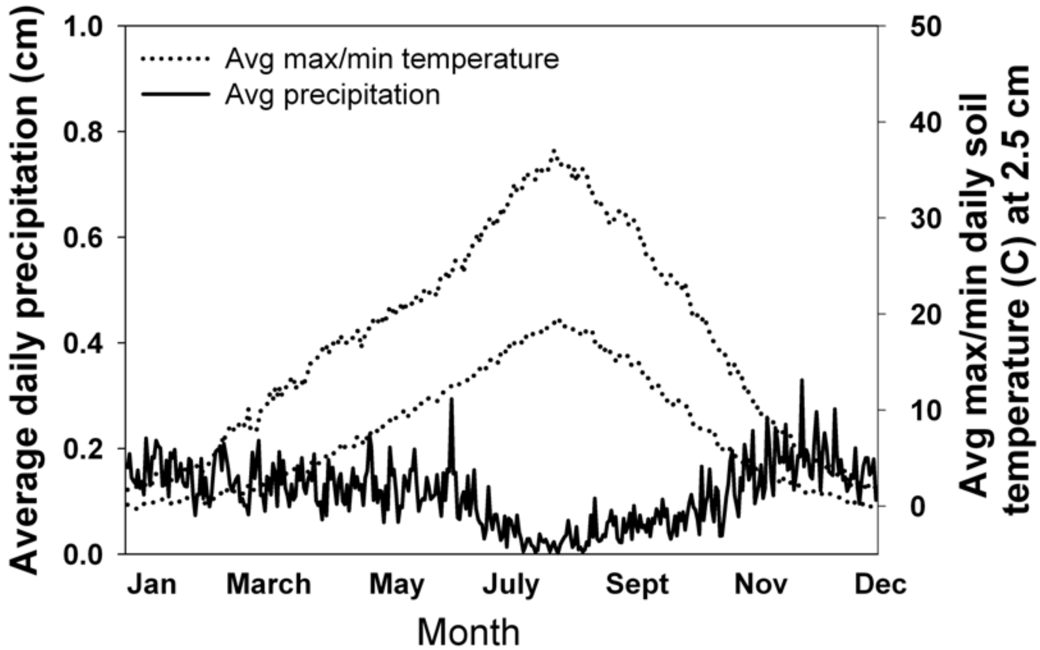

Figure 2.1 - Twenty year average daily maximum and minimum soil temperatures at 2.5 cm depth with 20 year average daily precipitation.

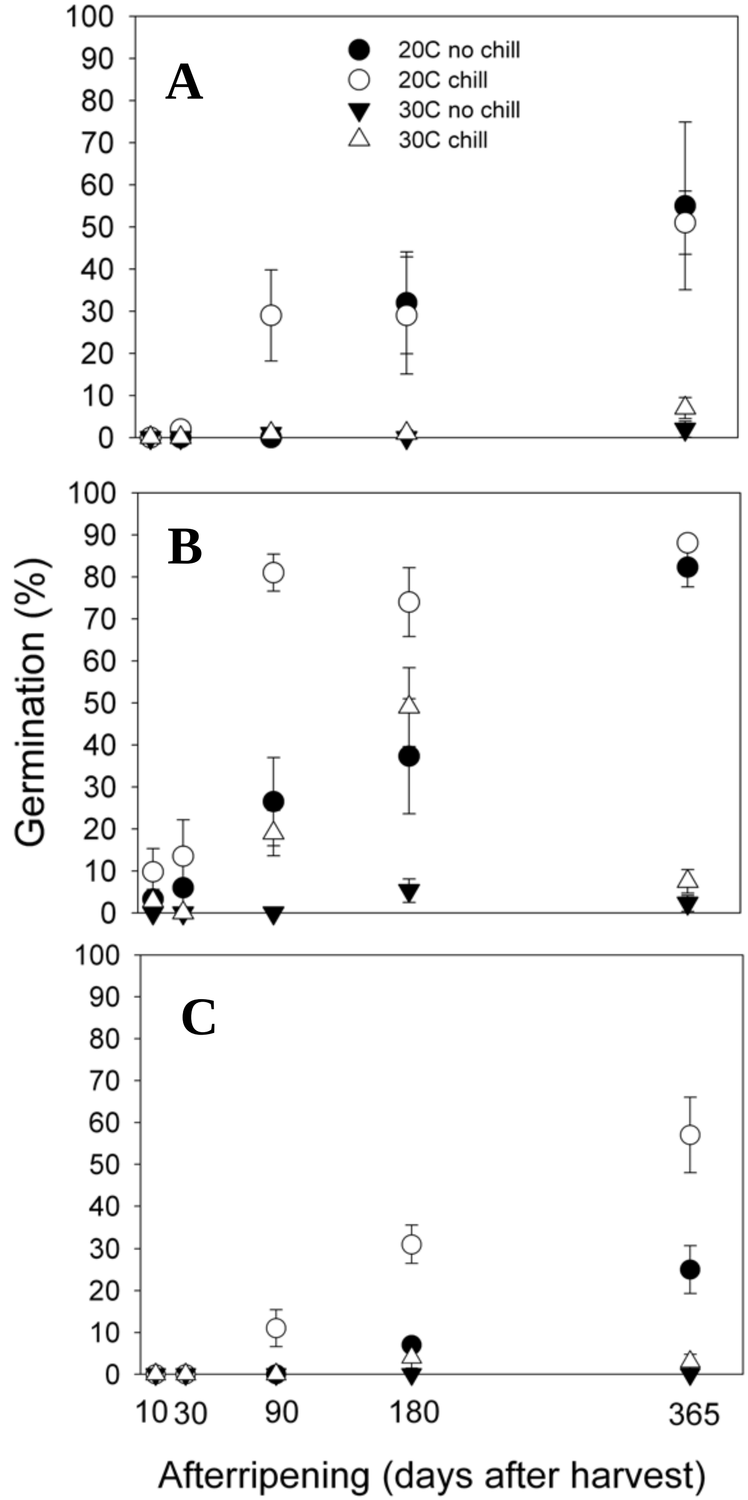

Figure 2.2 - Effect of afterripening, chill and germination temperature on germination at day 18 for weeping alkaligrass in 2002 (A), 2003 (B), and Nuttall’s alkaligrass 2002 and 2003 data combined (C).

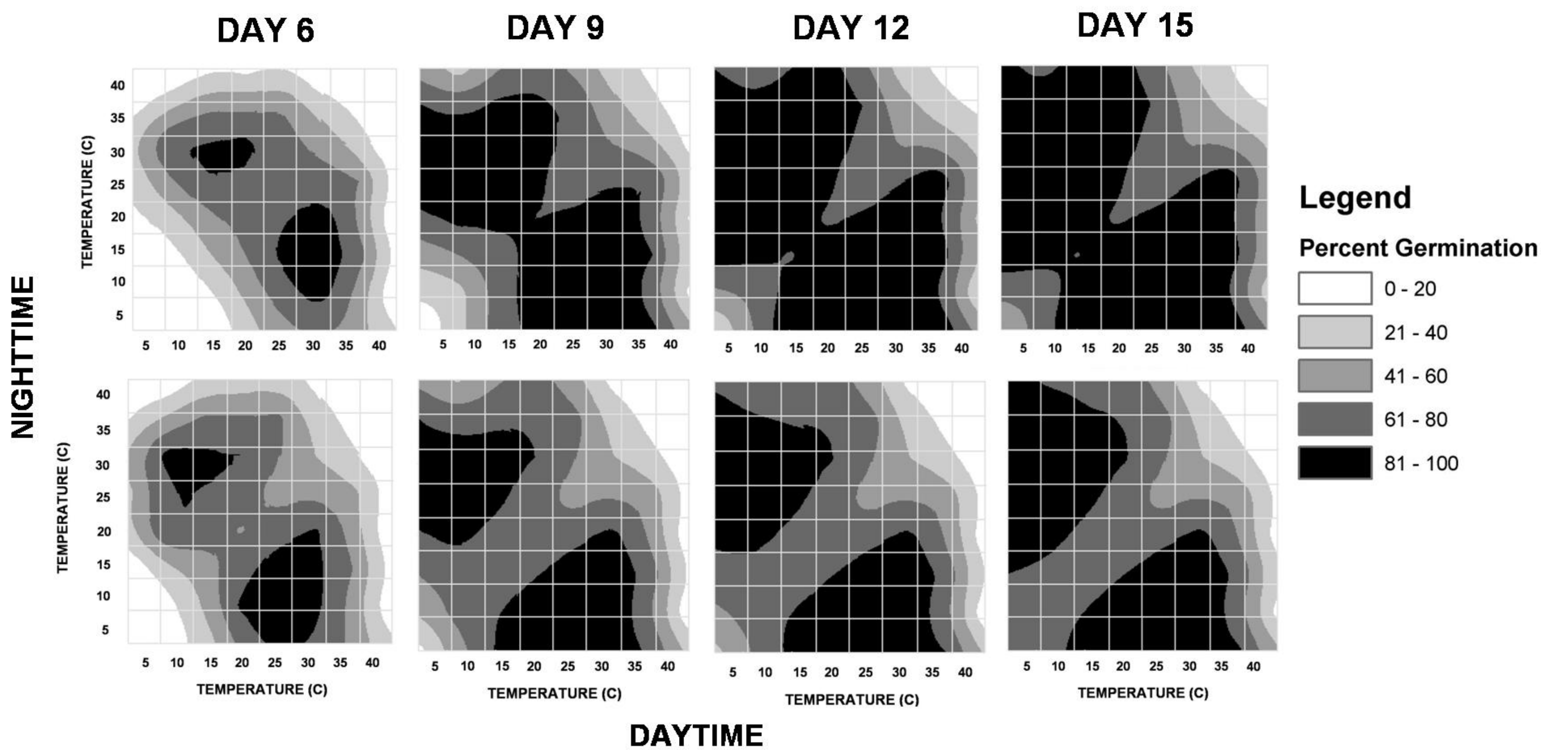

Figure 2.3 - Germination over time of weeping alkaligrass (A) and Nuttall's alkaligrass (B) from day 6 to day 15 at various daytime and nighttime temperature treatment combinations.

Table 2.1. Statistical results of logistic regression analysis of afterripening data for weeping alkaligrass (2002 and 2003 separately), and Nuttall's alkaligrass (2002 and 2003 combined).

Species	Year	Treatment **	F value	P
weeping alkaligrass	2002	Afterripening	$F_{4,120} = 4.67$	<0.001
		KNO_3	$F_{1,120} = 1.63$	0.202
		Temperature	$F_{1,120} = 13.16$	<0.001
		Chill	$F_{1,120} = 6.24$	0.012
		Afterripening *Temp	$F_{4,120} = 1.35$	0.248
		Afterripening *Chill	$F_{4,120} = 1.38$	0.238
weeping alkaligrass	2003	Afterripening	$F_{4,120} = 97.5$	<0.0001
		KNO_3	$F_{1,120} = 0.76$	0.383
		Temperature	$F_{1,120} = 247.47$	<0.0001
		Chill	$F_{1,120} = 2.01$	0.156
		Afterripening *Temp	$F_{4,120} = 28.86$	<0.0001
		Afterripening *Chill	$F_{4,120} = 9.30$	<0.0001
Nuttall's alkaligrass	2002/3	Afterripening	$F_{4,280} = 36.82$	<0.0001
		KNO_3	$F_{1,280} = 0.96$	0.327
		Temperature	$F_{1,280} = 116.75$	<0.0001
		Chill	$F_{1,280} = 48.70$	<0.0001
		Afterripening *Temp	$F_{4,280} = 40.2$	<0.0001
		Afterripening *Chill	$F_{4,280} = 8.3$	<0.0001

** Unlisted treatment combinations were not significant at $\alpha = 0.05$.

Table 2.2. Germination at 3, 7, 14, and 21 days after treatment (d AT) with 365 days of afterripening for weeping alkaligrass (2002 and 2003 separately) and Nuttall's alkaligrass (2002 and 2003 combined).

			Percent Germination (± 95% CI)			
Species	Year	Treatment	3 d AT	7 d AT	14 d AT	21 d AT
Weeping	2002	20 C + Chill	0	65 (6.6)	89 (4.3)	89 (4.3)
		20 C no Chill	0	17 (5.2)	33 (6.5)	33 (6.5)
		30 C + Chill	0	4 (2.7)	4 (2.7)	4 (2.7)
		30 C no Chill	0	0	0	0
Weeping	2003	20 C + Chill	0	85 (4.9)	91 (4.0)	91 (4.0)
		20 C no Chill	0	72 (6.2)	82 (5.3)	82 (5.3)
		30 C + Chill	0	5 (3.0)	5 (3.0)	5 (3.0)
		30 C no Chill	0	2 (1.9)	2 (1.9)	2 (1.9)
Nuttall's	2002/3	20 C + Chill	0	44 (6.9)	45 (6.9)	45 (6.9)
		20 C no Chill	0	14 (4.8)	16 (5.1)	16 (5.1)
		30 C + Chill	0	1 (1.4)	1 (1.4)	1 (1.4)
		30 C no Chill	0	0	0	0

CHAPTER 3

Extreme Ionic and Temperature Effects on Germination of weeping alkaligrass, Nuttall's alkaligrass, and Kentucky bluegrass

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Abstract

Within the Grande Ronde valley of eastern Oregon, the introduced species weeping alkaligrass and the native species Nuttall's alkaligrass, two of the most salt tolerant C_3 grasses found in arid and semi-arid environments of western North America occur. The seeds of both species occur as weeds and subsequent grass seed contaminants within Kentucky bluegrass seed fields in eastern Oregon. Two separate germination experiments were conducted to better understand the seed germination biology of these two species compared to Kentucky bluegrass under negative water potentials and high temperature conditions. Results of these studies indicate that weeping alkaligrass is the most drought and salt tolerant of the three species, germinating at osmotic potentials of -2.0 MPa. Dry seeds of weeping alkaligrass are particularly resistant to high temperatures with no difference in germination at temperatures below 50 C, indicating that seed viability under non-irrigated field conditions should be unaffected by high soil temperatures. Under soil temperature conditions as high as 40 C, moist Kentucky bluegrass seed had the highest germination rates, indicating that this species should benefit from irrigation more than the other two species.

Introduction

Although a conclusive classification system for halophytes has not been agreed upon; halophytes are generally distinguished from glycophytes by their ability to tolerate saline conditions (Miller and Doescher, 1995). Early in the literature, a halophyte was defined as a plant that was able to grow in an environment with more than 0.5% NaCl (Chapman, 1942). However, since early definitions, there have been many sub-classes and alternate categories of halophytes including euhalophytes, those that grow optimally in 0.5% NaCl or greater versus miohalophytes, those that are found in habitats with greater than 0.5% NaCl, but who's optimal growth occurs when NaCl is less than 0.5% (Baskin and Baskin, 1998). Other categories include facultative halophytes, those that do not require salt to complete their life cycle versus obligate halophytes, those that do require salt to complete their life cycle (Macke and Ungar, 1971).

Two of the most salt tolerant C_3 grasses commonly found in arid and semi-arid environments of western North America: *Puccinellia distans* (weeping alkaligrass) and *Puccinellia nuttalliana* (Nuttall's alkaligrass) (Ashraf et al., 1986; Harivandi et al., 1983a; Macke and Ungar, 1971) occur within the Grande Ronde valley of eastern Oregon. Both species are commonly referred to as alkaligrass and have both been defined as facultative halophytes (Macke and Ungar, 1970; Moravcova and Frantik, 2002; Beyschlag et. al. 1996). Generally, these two species occupy moist, alkaline to somewhat alkaline soil conditions (Hitchcock, 1971), often occupying distinct alkaline patches unsuitable to most crop species. Weeping alkaligrass, a naturalized species, is suspected to have been introduced to North America from Eurasia at the turn of the century in the vicinity of Michigan (Cusick, 1982). From Michigan, the plant probably traveled westward to eastern Oregon. Nuttall's alkaligrass is native to North America.

These two species pose a problem for *Poa pratensis* (Kentucky bluegrass) seed farmers of the Grande Ronde Valley in eastern Oregon through seed contamination. The seeds of both alkaligrass species are almost identical to Kentucky bluegrass making them exceedingly difficult to remove during the cleaning process. Alkaligrass seed was reported as a contaminant in 8% of Kentucky bluegrass samples submitted for certification by Oregon State University Extension Service in 2000[1].

In arid and semi-arid environments, water availability is the most important factor affecting the distribution, growth and survival of plants (Brown, 1995). In the arid environments of eastern Oregon, the water deficit may be due to either insufficient moisture in the soil, creating negative matric potential, or due to the presence of excessive soil water solutes, resulting in a negative osmotic potential (Taiz and Zeiger, 1991), or both. Drought and salinity are major factors which reduce crop yields worldwide.

Increasing salinity generally reduces germination in most species due to two processes: an osmotic effect due to increasing soil solutes and an ionic effect due to toxic ion uptake and accumulation (Ungar, 1991). Uncoupling the ionic from the osmotic effects of a negative water potential can be challenging. Therefore, researchers often compare the ionic versus osmotic water potential effects on seed germination using two isotonic (equal osmotic potential) solutions created using a non-ionic osmotic medium such as polyethylene glycol (PEG) versus a solution created using salt such as sodium chloride (NaCl). The differences in seed germination between the PEG and NaCl solutions can be attributed to ionic effects (Dodd and Donovan, 1999).

The first stage in seed germination is imbibition, or water uptake, which is affected by seed characteristics and water relations between the seed and substrate (Wester, 1995). The first phase of imbibition is largely a passive process controlled by the high negative matric potential of the dry seed (Wester, 1995). During the second phase of imbibition, water uptake slows and is controlled mostly by osmotic and pressure potentials of the seed; it is during this phase that the major metabolic events occur in preparation for radicle emergence (Wester, 1995). Many researchers have studied the effects of negative water potentials on seed germination and the general result for most species is a negative correlation between germination and matric water potentials (Teulat et al., 2001; Tobe et al., 2004)

The effect of soil solutes, in particular salts, may have the same result on seed germination through a reduction in water availability or toxicity associated with excessive salt absorption. Salinity may affect seed germination by decreasing the ease with which the seeds imbibe water and/or by facilitating the entry of ions in amounts high enough to be toxic and/or reducing the absorption of nutrients through ion imbalances (Romo and Eddleman, 1985). Generally, germination is delayed and reduced when salt stress exceeds a critical level. The level of salinity at which germination is reduced varies with species, genotype, environmental conditions, osmotic potential, and specific ions (Ungar, 1978). Conversely, the accumulation of salt ions by the embryo may function to promote a water potential gradient between the embryo and substrate, making germination conditions more favorable than substrates of similar osmotic potentials without salt (Romo and Eddleman, 1985). Successful germination of Nuttall's alkaligrass under negative water potentials of -1.2 MPa created with NaCl (34% $\pm$ 4.2%) versus ethylene glycol (10% $\pm$ 1.6%) was reported by Macke and Ungar (1971). However, the seeds were germinated in growth chambers with widely fluctuating temperatures of 12 hrs at 5 C (night) and 12 hrs at 20 C (day). The water potential of a solution is affected by temperature such that lower temperatures make the water potential less negative, where as higher temperatures have the opposite effect (Kramer and Boyer, 1995). Earlier work indicated that weeping alkaligrass was able to germinate (50%) in solutions equivalent to 75% sea water (Harivandi et al., 1983a). However, it is difficult to attribute the results to a specific ion or to make cross comparisons to other research as the sea water solution was comprised of twelve ions (Harivandi et al., 1983b). Many Kentucky bluegrass cultivars were studied for salinity tolerance and significant differences in germination existed between them (Horst and Taylor, 1983). Although four solution concentrations of NaCl, ranging from 0.7 to 23.4 dS m^{-1}, were tested by Horst and Taylor, germination results were averaged across all salt concentrations, making the results difficult to interpret. Because of the difficulty in comparing the various methods previously used to study the ionic effects of NaCl on germination it was necessary to study all three species under identical conditions.

Extreme osmotic and ionic conditions are not the only environmental stresses a seed may encounter in arid environments. Within the arid environments of eastern Oregon, where the uppermost layer of soil (top 2.5 cm) can reach temperatures in excess of 50 C (Figure 3.1), extreme soil temperatures also may inhibit seed germination. Although, under natural rangeland conditions high temperatures may never coincide with enough soil moisture to promote seed germination; irrigation would mitigate this obstacle. While properly utilized irrigation enhances crop germination and seedling growth, the benefits to weeping alkaligrass and Nuttall's alkaligrass germination are unknown. This paper presents the results and interpretation of two experiments studying the relative ionic effects of NaCl on Kentucky bluegrass, weeping alkaligrass, and Nuttall's alkaligrass germination, as well as, germination of moist and dry seeds under optimal conditions of 10/15 C (Moravcova and Frantik, 2002; Tarasoff et al., 2006) and supra-optimal temperature conditions.

Materials and Methods

Osmotic Stress

Nuttall's alkaligrass and weeping alkaligrass seeds were hand-collected from the Grande Ronde valley at the 'Imbler Site' (45°29′15.9″ N, 117°56′4″ W) July 8, 2002. Seeds were hand-thrashed, sorted, and air dried at 20 C for 18 months to ensure adequate afterripening. Kentucky bluegrass var. 'Brilliant' seed was supplied by a local seed cleaning facility.

Seeds were surface sterilized with a 5% solution of bleach for 20 s and triple rinsed with de-ionized water. After seed sterilization, an 8 by 8 cm germination box was filled with 50 ml of 20-grit silica sand. Within each box, 10 seeds of one species were placed approximately 1 mm below the surface. Each germination box was randomly assigned to one of 4 osmotic treatments created using either Polyethylene glycol 6000 (PEG) or sodium chloride (NaCl): 0.0, -0.25, -1.0 or -2.0 MPa. The PEG (Michel and Kaufman, 1973) and NaCl (Lang, 1967) treatments were created and were verified using a dewpoint potentiameter WP4 (Decagon, Pullman, WA) at a constant temperature of 20 C. Each germination box was filled to water-holding capacity with one of the treatments (osmotic or ionic) and placed inside an unilluminated germination chamber at a constant temperature of 20 C. Each treatment was replicated 5 times and the experiment repeated. Germinated seeds were counted and removed 3, 9, 15, and 18 days after initiation of the treatment (DAT). Seeds were considered germinated when the coleoptile was 2 mm long and a radicle was present. On day 18, the remaining ungerminated seeds were counted.

Temperature Stress

Seeds of all three species were collected and sterilized following the same procedures previously described.

<u>Temperature stress under moist conditions</u>

Following the sterilization treatment, 25 seeds were placed on top of 2 layers of germination paper wetted to maximum holding capacity in an 8 cm by 8 cm germination box. After wetting, seeds were pre-chilled for 48 h at 5 C. Following the pre-chill treatment, each germination box was randomly assigned to one of 5 temperature treatments: the optimal germination temperature of 10/15 C, and four supra-optimal constant temperatures: 30, 35, 40, and 50 C. Germinated seeds were counted and removed 3, 9, 15, and 18 d after initiation of the treatment (DAT). Seeds were considered germinated when the coleoptile was 2 mm long and a radicle was present. On day 18, the remaining ungerminated seeds were counted. Each treatment was replicated 7 times and the experiment repeated.

Temperature stress under dry conditions

Dry, afterripened seeds of all three species were randomly assigned to one of 4 temperature treatments: 30, 35, 40, and 50 C. The dry seeds were placed in temperature controlled chambers for 18 d. After which, the seeds were removed and 25 seeds were placed on top of 2 layers of germination paper wetted to maximum holding capacity in an 8 cm by 8 cm germination box. At this time, a control treatment of 25 seeds at 10/15 C was initiated. After wetting, seeds were pre-chilled for 48 h at 5 C. All temperature treated seeds were then placed in an unilluminated germination chamber at 10/15 C on a 12hr/12hr cycle. Germinated seeds were counted and removed 3, 9, 15, and 18 days after initiation of the 10/15 C treatment. Germination will be referred to as "rebound germination" as the seeds are rebounding under ideal germination conditions following the heat treatment. Rebound germination occurred under dark conditions except limited exposure to ambient light conditions as necessary to count germination. Seeds were considered germinated when the coleoptile was 2 mm long and a radicle was present. Each treatment was replicated 7 times and the experiment repeated.

Statistical Analysis

All experiments were analyzed for equal variance between runs using the link logit function (PROC GENMOD, SAS v.9.1). No significant differences were found between runs; therefore, the data sets for each experiment were combined. Germination results for all experiments were analyzed as binary response variables and 95% confidence intervals were created and contrasted for the total proportion of germination (Ramsey and Schafer, 2002).

Results and Discussion

Osmotic Stress

Comparisons within species

The comparison of isotonic (same osmotic potential) substrates generated using NaCl or PEG demonstrated that none of the species exhibited ion toxicity and that weeping alkaligrass and Kentucky bluegrass exhibited ion enhancement (Figure 3.2) at 18 DAT. Weeping alkaligrass had greater germination at osmotic potentials of -0.5 (44% ± 9.1 with NaCl versus 14% ± 6.4 with PEG) and -1.0 MPa (22% ± 7.6 with NaCl versus 5% ± 4.0 with PEG) (Figure 3.2B). Kentucky bluegrass benefited from the ionic effects at the moderate osmotic potential of -0.5 MPa, with germination of 28.0% ± 9.9% with NaCl versus 1.5% ± 2.6% when PEG was used (Figure 3.2A). There were no differences among treatments at any of the water potentials for Nuttall's alkaligrass (Figure 3.2C), indicating that this species is unaffected by NaCl ions. These results conflict with those of Macke and Ungar (1971) and may be due to differences in temperature treatments, differences in length of seed afterripening, and/or ecotypic differences between populations. If Nuttall's alkaligrass is able to avoid ion uptake, its mechanisms are yet to be elucidated.

Comparisons between species

At -0.25 MPa, there were no differences among species or treatments. At osmotic potentials of -0.50 MPa (NaCl), weeping alkaligrass germination was greater (21% $\pm$ 12.7%) than Nuttall's alkaligrass and Kentucky bluegrass (16% $\pm$ 13.1). This trend continued at -1.0 MPa (NaCl) where weeping alkaligrass germination was 17.0% $\pm$ 9.2 greater than Nuttall's alkaligrass and 14.6% $\pm$ 9.6 greater than Kentucky bluegrass. There were no differences between Kentucky bluegrass and Nuttall's alkaligrass at any of the osmotic potentials using NaCl (Table 3.1). Although germination of weeping alkaligrass was only 5.0% at -2.0 MPa, it was greater than Kentucky bluegrass which did not germinate at all.

A study of the species' response to increasing negative osmotic potentials created through PEG reveals that there was no difference in drought tolerance between weeping alkaligrass and Nuttall's alkaligrass at osmotic treatments less than 0.0 MPa ($P > 0.05$). However, at osmotic water potential less than 0.0 MPa, weeping alkaligrass and Nuttall's alkaligrass are significantly more tolerant than Kentucky bluegrass (Table 3.1).

Not surprisingly, weeping alkaligrass exhibited both the greatest ion enhancement and drought tolerance. However, quite unexpectedly, Kentucky bluegrass benefited more from the NaCl ions than Nuttall's alkaligrass. Though not yet studied, it is possible that Nuttall's alkaligrass uses a mechanism to avoid ion uptake during seed germination. If this is the case, Nuttall's alkaligrass may rely more on salt avoidance strategies than salt tolerating mechanisms. Given the results of this study, one would expect weeping alkaligrass to be more likely to germinate in the sodic soils of the

Grande Ronde Valley, followed by Kentucky bluegrass and then Nuttall's alkaligrass. In terms of the unexpected response of Kentucky bluegrass to the ionic affects of NaCl, it is possible that while Kentucky bluegrass germination benefits from the ionic affects of NaCl, the drought conditions may be too great for seedling survival and establishment. Field observations indicate that while Kentucky bluegrass can germinate under sodic soil conditions, seedlings often die before the 4-leaf stage.

Germination response to temperature stress

Germination of the seeds under high temperature and moist conditions is referred to as 'moist germination'; where as, the dry treated seed is referred to as 'rebound germination'.

Moist Kentucky bluegrass germination was not affected by any of the temperature treatments until the temperature reached 40 C (Figure 3.3A), at which point germination dropped to 20.0% $\pm$ 7.0%. Rebound germination of Kentucky bluegrass was greater when the dry seeds were subjected to 35 C (49.0% $\pm$ 6.2%). The alternating temperature of 10/15 C was not different from 30 or 40 C ($P > 0.05$). Germination dropped to 20% $\pm$ 4.9% when seeds were subjected to 50 C. At temperatures greater than 30 C, the dry treated seeds had higher germination responses than the moist seeds.

Moist weeping alkaligrass seed had very high germination values at the optimal temperature of fluctuating 10/15 C (80.3% $\pm$ 8.1%) but dropped to approximately 20% for the treatments of 30, 35, and 40 C (Figure 3.3B). Rebound germination of weeping alkaligrass was high, approximately 83 – 91%, and was not affected by temperature until 50 C when germination dropped to 67.5% $\pm$ 5.9%.

Moist Nuttall's alkaligrass seed expressed a bimodal germination response with moderate germination at the optimal temperature combination of fluctuating 10/15 C (58% ± 6%), very little germination at 30 C (4% ± 2%) or 35 C (3% ± 2%), but then germination increased at 40 C (24 ± 5%) (Figure 3.3C). The increase in germination at 40 C in both run 1 and run 2 cannot be explained based on current knowledge. Rebound germination of Nuttall's alkaligrass was significantly higher when dry treated at 30 and 35 C (86.1 ± 4.3% respectively) than 10/15 C (74% ± 5.6%), and all three temperatures had significantly greater germination responses than dry treatments of 40 or 50 C (56% ± 6.2%).

Between species comparisons are outlined in Table 3.2. Generally, weeping alkaligrass exhibited the greatest rebound germination response, followed by Nuttall's alkaligrass and then Kentucky bluegrass. The only exception was at temperatures of 30 and 35 C when there was no difference between weeping and Nuttall's alkaligrass. Moist treated seeds exhibited an opposite response. At optimal temperatures of 10/15 C, weeping alkaligrass had the greatest germination, followed by Nuttall's alkaligrass and then Kentucky bluegrass (Table 3.2). Yet, as temperatures increased to 30 and 35 C, Kentucky bluegrass had the greatest germination, followed by Nuttall's alkaligrass and then weeping alkaligrass (Table 2.2). At 40 C, Nuttall's alkaligrass germinated slightly better than weeping alkaligrass (9.0% ± 7.7%) and there were no differences between other species comparisons. No moist seeds from any of the species germinated at 50 C.

Moist weeping alkaligrass responded more negatively than Nuttall's alkaligrass to high temperature treatments. These results indicate that non-dormant seeds of both species should exhibit low rates of germination under irrigated field conditions if the soil temperatures are above a constant temperature of 30 C. However, even under soil temperature conditions as high as 40 C, Kentucky bluegrass had the highest germination rates, indicating that this species should benefit from irrigation more than the other two species.

Dry non-dormant seeds of weeping alkaligrass are particularly resistant to high temperatures, indicating that seed viability under non-irrigated field conditions should be unaffected by the high soil temperature conditions. Similar results indicate that germination of dry Nuttall's alkaligrass seed should decline only when soil temperatures are greater than 40 C. The significantly lower germination of dry non-dormant Kentucky bluegrass seed than either alkaligrass species indicates that weeping alkaligrass seed should have the greatest germination response to fall precipitation, when rain events coincide with soil temperatures of 10-20 C (Figure 3.1), followed by Nuttall's alkaligrass and then Kentucky bluegrass.

Conclusion

Results from all three studies indicate that for Kentucky bluegrass farmers of the Grande Ronde valley of eastern Oregon, weeping alkaligrass may pose a greater threat than Nuttall's alkaligrass in terms of seed resistance to the extreme soil and environmental conditions of this semi-arid environment.

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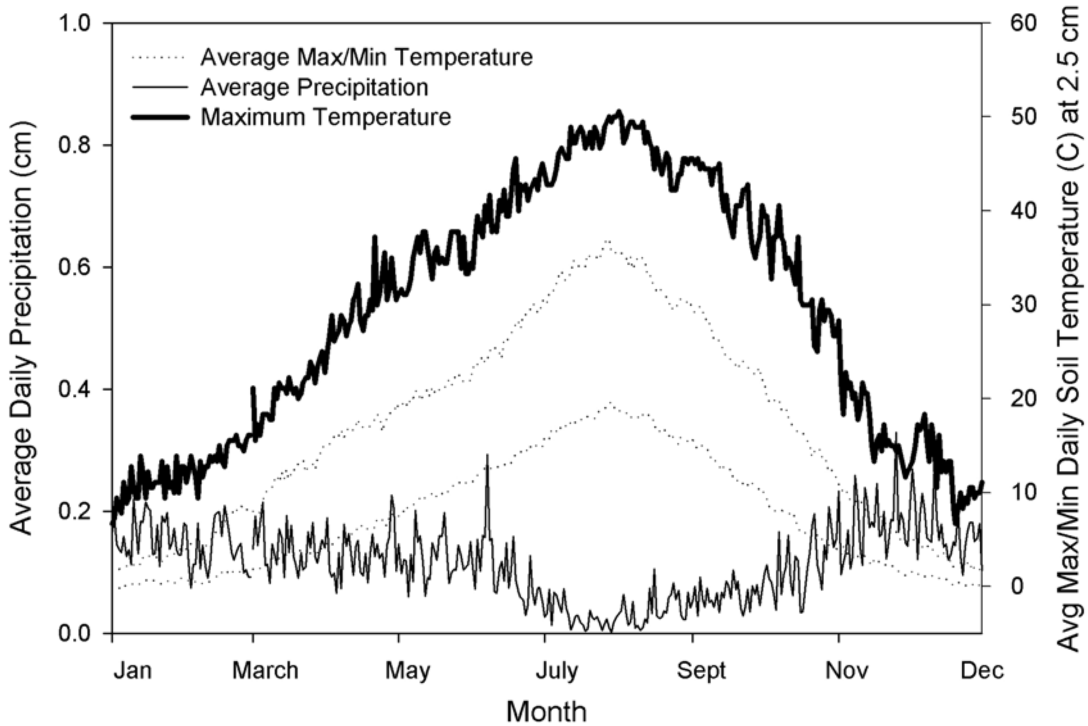

Figure 3.1 - Twenty year average daily maximum and minimum soil temperatures at 2.5 cm depth with 20 year maximum recorded daily temperature and 20 year average daily precipitation

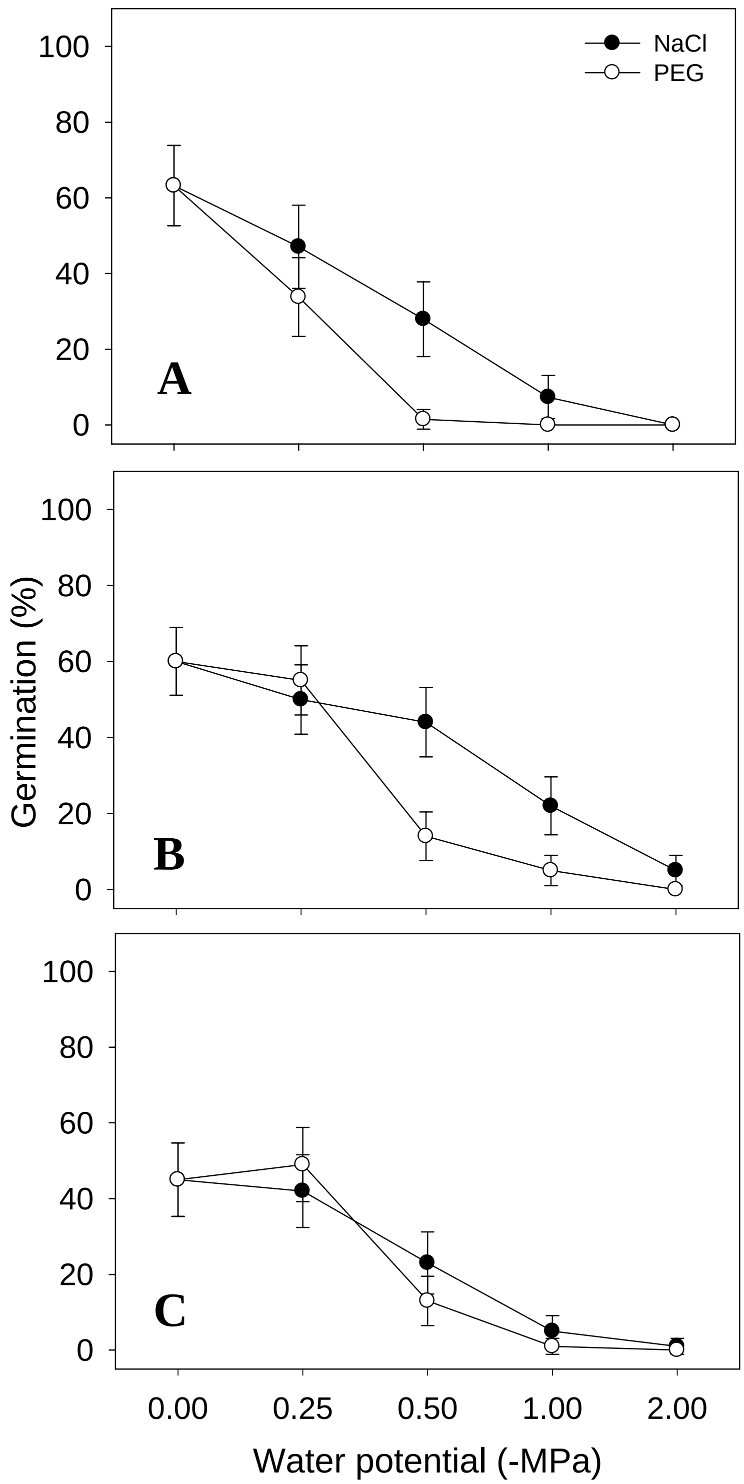

Figure 3.2 - Germination response of Kentucky bluegrass (A), weeping alkaligrass (B), and Nuttall's alkaligrass (C) to negative osmotic potentials created using NaCl versus PEG-6000.

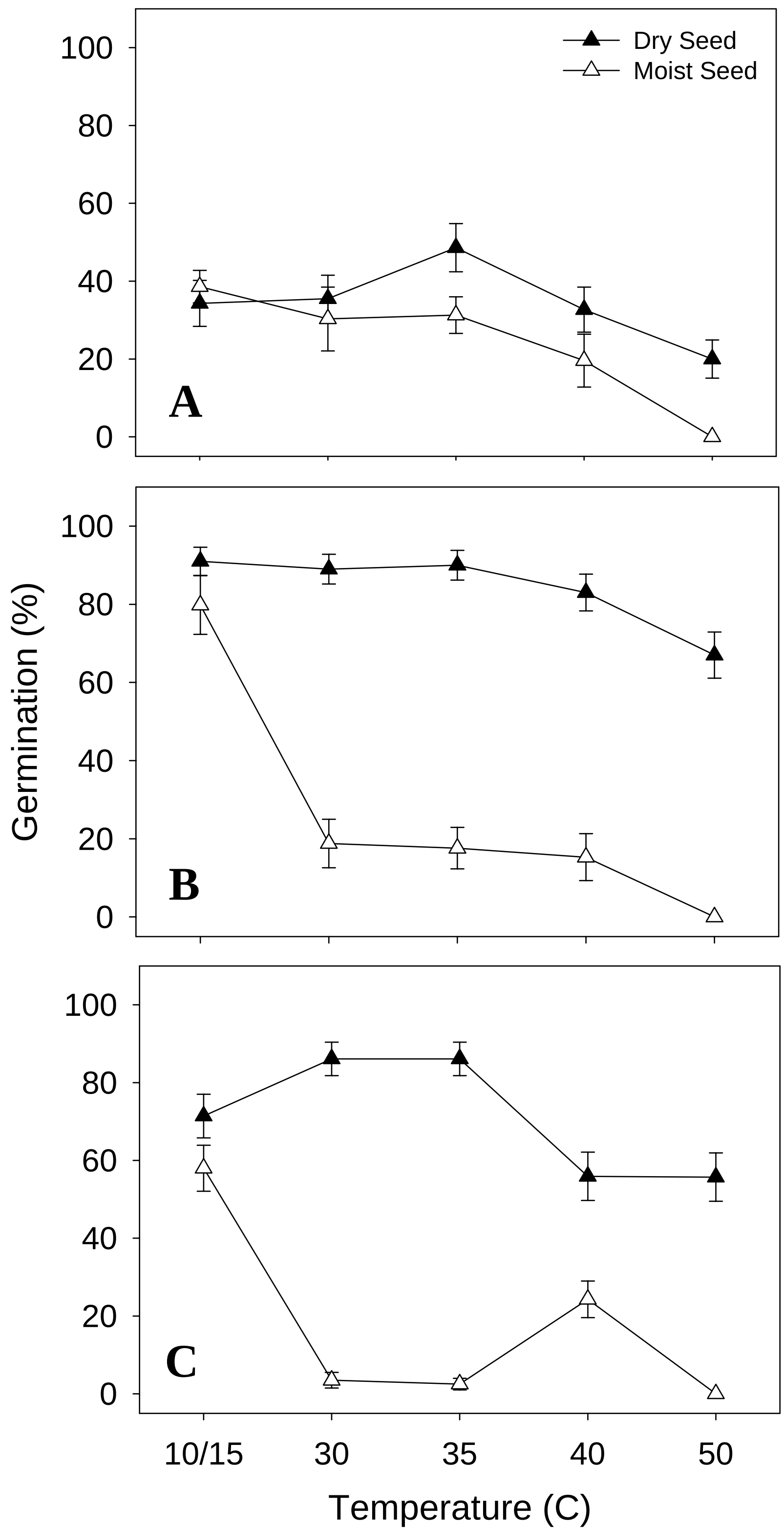

Figure 3.3 - Germination response of Kentucky bluegrass (A), weeping alkaligrass (B), and Nuttall's alkaligrass (C) following temperature treatment of dry versus moist seed.

Table 3.1. Comparison of differences in germination between species for various osmotic potential treatments using NaCl or PEG-6000.

	NaCl		PEG-6000	
Species Comparison	-MPa	% Difference	-MPa	% Difference
Weeping vs. Kentucky	0	-3.2 ± 13.4	0	-3.2 ± 13.4
Weeping vs. Nuttall's	0	15.0 ± 13.7	0	15.0 ± 13.7
Kentucky vs. Nuttall's	0	18.2 ± 13.6	0	18.2 ± 13.6
Weeping vs. Kentucky	.25	2.9 ± 13.8	.25	21.2 ± 13.4
Weeping vs. Nuttall's	.25	8.0 ± 13.7	.25	6.0 ± 13.8
Kentucky vs. Nuttall's	.25	5.1 ± 13.7	.25	-15.2 ± 13.5
Weeping vs. Kentucky	0.5	16.1 ± 13.1	0.5	12.5 ± 7.2
Weeping vs. Nuttall's	0.5	21.0 ± 12.7	0.5	1.0 ± 9.5
Kentucky vs. Nuttall's	0.5	4.9 ± 12.1	0.5	-11.5 ± 7.0
Weeping vs. Kentucky	1.0	14.6 ± 9.6	1.0	5.0 ± 4.3
Weeping vs. Nuttall's	1.0	17.0 ± 9.2	1.0	4.0 ± 4.7
Kentucky vs. Nuttall's	1.0	2.4 ± 6.6	1.0	-1.0 ± 2.0
Weeping vs. Kentucky	2.0	5.0 ± 4.2	2.0	NG[a]
Weeping vs. Nuttall's	2.0	4.0 ± 4.6	2.0	NG
Kentucky vs. Nuttall's	2.0	-1.0 ± 2.0	2.0	NG

[a] NG = No germination of either species

Table 3.2. Comparison of differences in germination between species for various temperature treatments of moist versus dry seeds.

	Dry seeds – Rebound Germination		**Moist seeds - Germination**	
Species Comparison	Temp (C)	% Difference	Temp (C)	% Difference
Weeping vs. Kentucky	10/15	56.7 ± 7.1	10/15	41.2 ± 8.7
Weeping vs. Nuttall's	10/15	19.6 ± 9.4	10/15	21.8 ± 8.8
Kentucky vs. Nuttall's	10/15	-37.1 ± 15.6	10/15	-19.4 ± 9.6
Weeping vs. Kentucky	30	53.5 ± 7.2	30	-11.5 ± 8.4
Weeping vs. Nuttall's	30	2.9 ± 5.8	30	15.3 ± 6.0
Kentucky vs. Nuttall's	30	-50.6 ± 11.2	30	26.8 ± 6.9
Weeping vs. Kentucky	35	41.4 ± 7.3	35	-13.7 ± 8.3
Weeping vs. Nuttall's	35	3.9 ± 5.7	35	15.1 ± 5.7
Kentucky vs. Nuttall's	35	-37.5 ±11.5	35	28.8 ± 6.8
Weeping vs. Kentucky	40	50.3 ± 7.5	40	-4.3 ± 7.4
Weeping vs. Nuttall's	40	27.1 ± 7.8	40	-9.0 ± 7.7
Kentucky vs. Nuttall's	40	-23.2 ± 12.9	40	-4.7 ±12.2
Weeping vs. Kentucky	50	47.0 ± 10.2	50	NG[a]
Weeping vs. Nuttall's	50	11.3 ± 11.3	50	NG
Kentucky vs. Nuttall's	50	-35.7 ± 16.0	50	NG

[a] NG = No germination of either species

CHAPTER 4

Associations between site characteristics and Nuttall's and weeping alkaligrass distribution

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Abstract

Within the semi-arid region of the Grande Ronde Valley of eastern Oregon, two species of alkaligrass, Nuttall's alkaligrass, a native to the region, and weeping alkaligrass, an introduced species from Eurasia, are found within agricultural fields. Both species are considered to be two of the most salt tolerant facultative halophytes in North America and are often associated with areas of low site productivity. Recently, farmers have been concerned over the ability of these two species to colonize a wide array of soil types but have not been able to predict which sites might be at risk for invasion. The results of this study indicate that the strongest inhibitor to plant establishment is a dense cover of competing vegetation. The likelihood of establishment of either species was positively linked to depressional areas. Within infested areas, Nuttall's alkaligrass was positively associated with exchangeable sodium and negatively associated with exposed mineral soil. The introduced species weeping alkaligrass showed traits typical of a resource generalist, establishing on a wide variety of sites and having no clear associations among any of the variables except percent cover of competing vegetation. For farmers of this area, the generalist weeping alkaligrass may prove to be the more problematic than the niche specific Nuttall's alkaligrass. The primary goal for prevention of both species on agriculturally productive sites should be improved crop cover.

Introduction

To explain the factors affecting plant species distribution and abundance studies commonly look for patterns at multiple scales (Carey et al., 1995; Dodd et al., 2002; Martin et al., 2005). While continental and national patterns of species distribution are usually linked to climate (Good, 1931), factors limiting the establishment of a species at the regional or local scale may be determined by a combination of biotic and abiotic site characteristics. It is commonly understood within the study of population biology that the geographic distribution of a species is heterogeneous with the highest abundance often occurring near the center of the species range and the lowest near the margins (Brown, 1984). The question of what is, or are, the strongest determinants of species distribution within a local area lies in the elucidation of site specific ecological patterns or processes. Multivariate techniques are available to aid in the description of ecological patterns which can be related to species distribution and abundance by providing correlative information.

Within the Grande Ronde Valley of eastern Oregon, the distribution at the local scale of two species of alkaligrass: weeping alkaligrass (*Puccinellia distans*) *and* Nuttall's alkaligrass (*Puccinellia nuttalliana*) are of increasing importance to Kentucky bluegrass (*Poa pratensis*) farmers. Weeping alkaligrass is an introduced species from Eurasia, whereas Nuttall's alkaligrass is native to semi-arid environments of North America. Both species are considered to be among the most salt tolerant C_3 grasses in North America (Ashraf et al., 1986; Harivandi et al., 1983a; Macke and Ungar, 1971; Mintenko et al., 2002; Salo et al., 1996) with weeping alkaligrass perhaps more salt tolerant than Nuttall's alkaligrass (Moravcova and Frantik, 2002;

Salo et al., 1996). Nuttall's alkaligrass has been documented on saline depressions (Macke, 1969), and along saline lake margins (Brotherson, 1987). Weeping alkaligrass has also been documented in saline depressions (Piernik, 2003), as well as along heavily salted roadsides (Davis and Goldman, 1993; Garlitz, 1992) and ruderal areas (Moravcova and Frantik, 2002). Both Nuttall's and weeping alkaligrass could be considered facultative halophytes (Beyschlag et al., 1996; Macke and Ungar, 1971; Moravcova and Frantik, 2002), as neither species requires salt to complete its lifecycle.

The soil and habitat associated with Nuttall's alkaligrass have been described as having an average pH of 8.47, high levels of calcium, magnesium, sodium and potassium; and low levels of phosphorous, iron and zinc (Brotherson, 1987). While Brotherson provides a description of sites dominated by Nuttall's alkaligrass, he does not attempt to derive correlations between the presence of Nuttall's alkaligrass and associated soil characteristics.

In order to manage areas for potential risk of alkaligrass establishment, Kentucky bluegrass farmers of the Grande Ronde Valley need to understand what factors are permitting the establishment of either species of alkaligrass through an understanding of the ecological niche(s) that each of these two species occupy. Currently, there is no documentation which links soil characteristics, spatial conditions, and competing plant species to the abundance of weeping alkaligrass and Nuttall's alkaligrass within the Grande Ronde Valley. This paper investigates how the local scale distribution of weeping alkaligrass and Nuttall's alkaligrass may be related to soil and topographical attributes as well as vegetation community dynamics.

Materials and methods

Description of study area

Study sites were located throughout the semi-arid region of the Grande Ronde Valley in Union County of eastern Oregon. The Grande Ronde Valley lies at the center of Union County, near La Grande, stretching approximately 56 km north-south, and 24 km east-west. The Grande Ronde Valley lies within the Blue Mountain Basin ecoregion. The valley fill consists of various Pleistocene deposits of gravels and silts, lacustrine deposits, alluvial fans, and loess from the Columbia Plateau to the north. The lake bed silts are poorly drained and are classified as Haploxerolls, Endoaquolls, and Haplaquolls. The loess deposit regions running from the central valley to its northern edge have deep soils and are classified as Haploxerolls, Argialbolls, and Argixerolis (Clark and Bryce, (eds.) 1997).

The natural vegetation on the terraces and loess hills consists of Idaho fescue (*Festuca idahoensis*), common snowberry (*Symphoricarpos albus*), and Sandberg's bluegrass (*Poa sandbergii*). On the flood plains, tufted hairgrass (*Deschampsia caespitosa*), redtop (*Agrostis gigantea*), and sedges (*Carex spp*.) are associated with wetter soils (Clark and Bryce, (eds.) 1997). Today, most of the valley is farmed and parts of the Grande Ronde River and its tributary streams have been channelized to provide irrigation water to grow hay, commercial grass seed, alfalfa (*Medicago sativa*), and peas (*Pisum spp.*). The climate of the valley is moderated by the marine influence from the West. Precipitation ranges from 32 cm in the dry southern valley to 60 cm at the eastern end of the valley (Clark and Bryce, (eds.) 1997).

In the spring of 2004, the area east of La Grande to Cove and north to Elgin, Oregon (Figure 4.1) was surveyed for alkaligrass (Nuttall's and weeping) infestations. During the survey period, all roads in the survey area were driven, as well farmers and fieldmen were contacted questioned as to incidences of alkaligrass on their land. Because infestations of both species can be very distinct small patches, an infestation was defined as an area having at least 1 plant per m^{-2} over an area of at least 5 m^2. In the spring 2005, 28 randomly chosen sites were sampled for soil chemistry, soil texture, environmental, as well as vegetation parameters (Table 4.1). Most sites were within agriculturally productive fields growing peppermint (*Mentha spp.*), Kentucky bluegrass seed (*Poa pratensis*), wheat (*Triticum aestivum*), barley (*Hordeum spp.*), fescue (*Fesctuca spp.*), or pasture. However, some sites were in ruderal areas such as roadsides and field margins. All fields were sampled from June 23 to July 9, 2005.

Soil analyses were conducted on a bulked sample of four randomly located soil cores within each field site. The soil core represented soil conditions to a depth of 20 cm. A separate 20 cm soil sample was collected and dried at 105 C for 48 hours to determine gravimetric soil moisture content. Soil texture was calculated using the hydrometer method. Before chemical analysis, the samples were air-dried at 65 C and sieved through a 1 mm mesh. The following analyses were performed: pH by the Walkley-Black method; the exchangeable cations sodium, calcium, magnesium, potassium and phosphorous following the procedures outlined by the American Society of Agronomy (Thomas, 1982); extractable boron, copper, manganese, zinc, iron, sulfur using DTPA extraction by ICP (Lindsay and Norvell, 1978); electrical conductivity (EC_w) using the 1:2 dilution method (Gavlak et al., 2001); nitrate (NO^-_3) and ammonium (NH^+_4) via the chromotropic acid method (Gavlak et al., 2001).

Average percent cover of plant species and bare ground was recorded using five 1 m^2 quadrats located randomly throughout the infestation. Plant species were categorized into one of three functional groups Nuttall's alkaligrass/weeping alkaligrass, other weeds, or crop species. Based on a visual assessment, the microtopography of each plot was categorized as either depressional or not.

For each site, a paired plot was located less than 10 m beyond the perimeter of the infestation within the adjacent uninfested area. Within each paired plot, identical site information was collected as per the infested plot.

From the soil chemistry data, calcium:magnesium, sodium:calcium, and sodium absorption ratio (SAR) were calculated for each plot. Soils were classified to map unit based on the United States Department of Agriculture (USDA) soil classification descriptions. Plots were classified as normal, saline, saline-sodic or sodic soils by combining electrical conductivity measurements with SAR and pH (Brady and Weil, 2002).

Statistical Analysis

Principal components analysis (PCA) using the correlation matrix of the environmental variables was used as an investigative tool to determine the primary site characteristics responsible for alkaligrass segregation between the infested versus uninfested sites. Principal components analysis selects several linear combinations that capture the majority of the variation of the multivariate responses (Ramsey and Schafer, 2002). Analysis of the log-likelihood of infestation relating to the categorical variable of slope position (depression versus non-depression) was calculated using logistic regression where the response variable was binary (infested versus uninfested). Within the infested sites, multiple regression using Bayesian Information Criteria (BIC) variable selection, was used to determine the relationship between incremental changes in parametric data and the abundance of weeping and Nuttall's alkaligrass.

Results and Discussion

General Soil Types

Nuttall's alkaligrass sites (infested and uninfested) tended (73% of sites) to occur within the Hot Lake silt loam soil site type. This somewhat poorly drained soil type occurs on old lake basins and valley floors which formed in loess and volcanic ash over diatomaceous sediment (Dyksterhuis and High, 1985). Although this soil is suited to cultivated crops, it is limited by seasonal high water table, poor drainage and a restricted rooting depth. These soils are typically mildly alkaline to strongly alkaline (Dyksterhuis and High, 1985). Included within the Hot Lake silt loam series are small areas of Hot Lake soils which are even more poorly drained. The other soil types were Catherine Silt Loam (2 sites) and La Grande silty clay loam (2 sites). Of the 15 infested sites, 14 were categorized as being sodic, while only 1 infested site was categorized as normal.

Sodic soils are generally considered to be the most troublesome of the salt-affected soils. In terms of soil structure, a high level of exchangeable sodium creates soil dispersion which prevents large pore development, resulting in very poor soil hydraulic conductivity and infiltration (Brady and Weil, 2002). Poor soil structure is compounded by the toxic and nutrient imbalancing effects of sodium. Generally, sodium is toxic to most plants. As well, sodium, and the anion chloride, compete with other beneficial cations, namely potassium and calcium for root uptake and/or shoot transport, and utilization, resulting in nutrient imbalances (Marschner, 2005).

Weeping alkaligrass showed no strong soil site type association. Unlike Nuttall's alkaligrass, weeping alkaligrass was mostly associated with well drained soil types. The strongest site association, at 27% (5 sites), was Alicel loam. The Alicel loam soil series is found on valley terraces, is well drained and is ideal for cultivated crops (Dyksterhuis and High, 1985). Other soil series were Hot Lake silt loam (3 sites), Hoopal fine sandy loam (1 site), Hooly silt loam (2 sites), Catherine silt loam (1 site), and Alicel fine sandy loam (1 site). In contrast to Nuttall's alkaligrass, of the 13 infested sites, 11 were categorized as having normal soils whereas only 2 were sodic.

Descriptive Statistics

Many of the variables did not differ between infested and uninfested sites, nor between Nuttall's alkaligrass and weeping alkaligrass infested sites (Appendix 2).

<u>Nuttall's alkaligrass</u>

Not surprisingly, percent crop cover was much lower in areas infested versus areas uninfested with Nuttall's alkaligrass (Table 4.2). The soil chemistry variable of pH was higher in infested sites than uninfested sites; as were EC, exchangeable sodium, and Ca:Mg ratio. Exchangeable magnesium was lower in infested sites than uninfested; as were the Ca:Na ratio, ammonium, and percent organic matter. The higher ammonium and organic matter could be expected for sites dominated by a dense crop cover. However, the nutrient composition of sites infested with Nuttall's alkaligrass may limit crop establishment.

While sodium is a beneficial mineral nutrient, exposure to high exchangeable sodium concentrations, versus other osmotic salts such as calcium or magnesium, over the long-term creates two major constraints for plant growth. Firstly, ion toxicity associated with excessive uptake of Cl^- and Na^+; secondly, nutrient imbalances associated with the depression of uptake and/or shoot transport, and impaired internal distribution of mineral nutrients (calcium in particular) (Marschner, 2005).

Magnesium is an essential macronutrient and a substantial proportion of total magnesium is involved in the regulation of cellular pH and the cation-anion balance (Marschner, 2005). Magnesium is involved in many enzymatic processes as well as forming the central atom of the chlorophyll molecule; therefore, temporary deficiencies will result in chlorosis and depressed protein synthesis (Marschner, 2005). At permanently insufficient supplies, root development is inhibited which has a considerable impact on mineral acquisition and water uptake. Reduced water and mineral acquisition would negatively affect drought resistance and adaptations to nutrient-poor sites (Marschner, 2005).

As an essential plant nutrient, calcium is vital to the structural integrity of macromolecules, predominantly in the cell walls and at the plasma membrane. While the exchangeable calcium did not vary between infested and uninfested sites the interplay between sodium, calcium and magnesium ratios did. Calcium, among other cations, has been shown to strongly depress magnesium uptake (Marschner, 2005). While high sodium competes with both calcium and magnesium on the cation exchange site. It is difficult to say whether Nuttall's alkaligrass' site tolerance mechanism involves sodium exclusion, sodium adaptations, a low magnesium requirement, or a combination of all three as leaf tissue was not analyzed.

Weeping alkaligrass

Of all the variables, percent crop cover was the only distinguishing variable that separated sites infested versus sites uninfested (Table 4.2). The presence of weeping alkaligrass on sites with soil chemistry similar to those dominated by crop species indicates that perhaps this species is limited more by competitive exclusion than chemical soil characteristics. While it is logical that higher densities of one plant will result in lower densities of a competing species, previous research by Tarasoff et. al. (Chapter 5), indicated that under agriculturally productive soil conditions when grown with Kentucky bluegrass, both Nuttall's alkaligrass and weeping alkaligrass biomass declined drastically from year 1 to year 2 as an effect of competition. Therefore, sites uninfested are at least partially a result of a robust crop cover which provides a strong competitive barrier to establishment.

Nuttall's versus weeping alkaligrass

Trends between sites infested versus uninfested with Nuttall's alkaligrass were similar to sites infested with Nuttall's versus weeping alkaligrass. Soil pH, Na, and the Ca:Mg ratio were higher in Nuttall's alkaligrass infested sites than those infested with weeping alkaligrass, while magnesium, Ca:Na ratio, and organic matter were lower (Table 4.2)

Multivariate analysis

Nuttall's alkaligrass exhibited a strong separation between the infested and uninfested sites (Figure 4.2A) as described by PCA (Table 4.3). Analysis of the data showed that the first factor, a contrast between percent crop cover (crop), Ca:Na, NH_4, Mg, percent organic matter (OM), sand, sodium absorption ratio (SAR), Na, pH, EC, and P accounted for 41.1% of the variance within the data (Table 4.3). The second factor, a contrast between Ca, Mg, OM, pH, NO_3, and NH_4 accounted for 14.6% of the variability. An orthogonal combination of factors 1 and 2 (Figure 4.2B) accounted for a cumulative variance of 55.7%. The first 5 factors, all with eigenvalues greater than 1, accounted for a cumulative 84.2% of the variability. For all contrasts, eigenvalues less than 1 are considered spurious and therefore omitted from the discussion.

Weeping alkaligrass exhibited a less clearly defined separation between the infested verus uninfested sites (Figure 4.3A). The first factor, a contrast between SM, NO_3, P, EC, pH and Na; versus weeds, and Ca:Na accounted for 32.2% of the variance within the data. The second factor, a contrast between crop, pH; versus percent cover of bare ground (bare), weeds, Ca:Na, NO_3, SM, and EC accounted for 19.0% of the variability. A combination of factors 1 and 2 (Figure 4.3B) accounted for a cumulative variance of 51.2%. The first 4 factors, all with eigenvalues greater than 1, accounted for a cumulative 78.4% of the variability.

The contrast between sites infested with Nuttall's alkaligrass versus those infested with weeping alkaligrass exhibited a separation similar to that for sites infested with Nuttall's alkaligrass (Figure 4.4A). Further analysis of the data indicated that the first factor accounted for 36.8% of the variance within the data. The first factor was a contrast between the variables pH, EC, Ca, Ca:Mg, clay, and Na; versus NO_3, NH_4, OM, P, Mg, Fe, sand, weeds, and Ca:Na. The second factor, which accounted for 19.0% of the variability was a contrast between the variables EC, OM, P, Ca, Mg, NH_4 Ca:Na, and clay; versus pH, Ca:Mg, NO_3, sand, weeds, and Fe. A combination of factors 1 and 2 (Figure 4.4B) resulted in a cumulative variance of 51.2%. The first 4 factors, all with eigenvalues greater than 1, accounted for a cumulative 78.4% of the variability.

Logistic Regression

Results from binary data analysis of slope position indicated that the log-likelihood of Nuttall's alkaligrass infesting an area increased by 71% (13% - 91%) when the site was depressional versus not. Findings were similar for weeping alkaligrass where the log-likelihood of weeping alkaligrass infesting a depressional area increased by 69% (16% - 90%). Although site microtopography did not correspond to soil moisture, soil moisture was generally higher for Nuttall's alkaligrass infested (33.43 $\pm$ 5.33) versus uninfested (25.93 $\pm$ 5.18) and weeping alkaligrass infested (33.16 $\pm$ 4.25) versus uninfested (24.82 $\pm$ 4.91) sites. It is not uncommon for depressional areas to act as water receiving sites, accumulating large volumes of water during the spring. At the time of sampling, the water table at all sites was below the sampling depth yet some of the sites had standing water earlier in the season.

Previous field observations have linked both species of alkaligrass with saline depressions (Macke, 1969; Piernik, 2003). In this study, both species were positively associated with depressions, yet the soils of depressions infested with weeping alkaligrass were categorized as normal whereas Nuttall's were sodic. Thus, it is possible that a major factor limiting crop establishment, and thus competition in sites infested with weeping alkaligrass, is the presence of water logging early in the growing season. Most plants species not adapted to waterlogging will develop injury symptoms such as wilting, leaf senescence and epinasty over a period of several days (Drew, 1990).

Multiple Regression

Results of the BIC model selection process revealed that within Nuttall's alkaligrass infested plots, the percent exposure of bare ground and sodium accounted for 47% of the variability (R^2) in percent Nuttall's alkaligrass cover, explained by the model:

$$Y_N = 45.8_{(15.5)} - 0.49X_{i\ (0.25)} + 1.40Y_{i\ (0.82)} \qquad (1)$$

Where Y_N represents the abundance (% cover) of Nuttall's alkaligrass, X_i represents exposed mineral soil (%), and Y_i represents the concentration of exchangeable sodium (meq/100 g). It can be expected that for a 1 unit increase in the percent cover of exposed mineral soil, the cover of Nuttall's alkaligrass will decline by 0.49% (se = 0.25). As well, a 1 unit (meq/100 g) increase in exchangeable sodium will result in a 1.4 unit increase in Nuttall's alkaligrass percent cover (se = 0.82). Therefore, Nuttall's alkaligrass is negatively associated with bare soil yet positively associated with exchangeable sodium salts. The negative association with bare soil indicates that within sites infested with Nuttall's alkaligrass competitive exclusion is not a factor limiting establishment. The positive association with increases in exchangeable sodium indicates that at the plant community level, while Nuttall's alkaligrass is not an obligate halophyte (salt requiring) it is not quite a facultative halophyte (salt tolerating) either.

Percent cover of weeping alkaligrass was not as clearly associated with site characteristics. Within weeping alkaligrass infested plots, the percent cover of other weedy species accounted for 39% of the variability (R^2) in percent cover of weeping alkaligrass as explained by the model:

$$Y_W = 52.3_{(7.4)} - 0.79X_{i\ (0.29)} \qquad (2)$$

Where Y_W represents the abundance (percent cover) of weeping alkaligrass, X_i represents the abundance (percent cover) of other weedy species. Therefore, it can be expected that for a 1 unit increase in the percent cover of other weedy species, the percent cover of weeping alkaligrass will decline by 0.79% (se = 0.29).

Conclusion

The results of our study indicate that, on agriculturally productive soils, for both species of alkaligrass, a strong factor separating infested from uninfested was percent crop cover. However, it is somewhat difficult to determine the precise mechanisms limiting the establishment of the two alkaligrass species within the cropped areas as historical and current weed control practices were unknown.

Sites uninfested with Nuttall's alkaligrass tended to be higher in calcium, organic matter, magnesium, ammonium; and, consequently had greater percent cover of the crop species, than those sites infested with Nuttall's alkaligrass. Infested sites were typically depressions with higher values of the interrelated variables of pH, EC, Na, and Ca:Mg. Within infested sites, Nuttall's alkaligrass displayed a positive association between increasing levels of Na and percent plant cover.

As one might expect from an introduced species, weeping alkaligrass did not exhibit a clear pattern between infested versus uninfested site characteristics. Within infested sites, the strongest factor relating to weeping alkaligrass abundance was the lack of competing weedy vegetation. In general, it was witnessed that weeping alkaligrass followed the pattern of a resource generalist, capitalizing on available resources. A plant that behaves as a resource generalist can be troublesome for farmers as there is little predictability between plant-site associations.

For farmers of the Grande Ronde Valley, the primary management objective should be to maintain a healthy crop cover, wherever possible, to reduce the establishment of both species within productive soils. Within sodic sites, where most crop species cannot establish, farmers should remove all weedy species to prevent seed contamination and transport.

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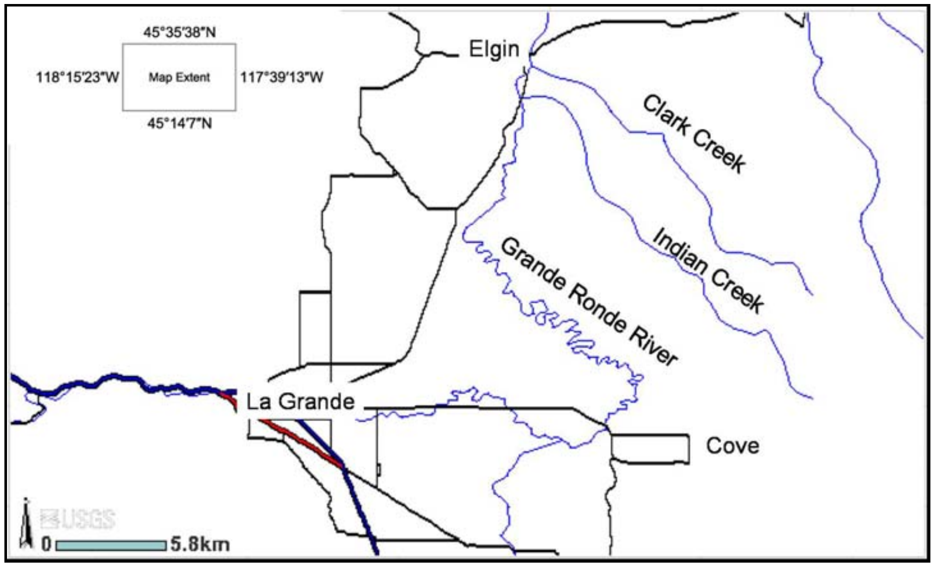

Figure 4.1 – Alkaligrass survey zone encompassing the area north of La Grande to Elgin and east to Cove, Oregon.
(Created from:http://nmviewogc.cr.usgs.gov/viewer.htm)

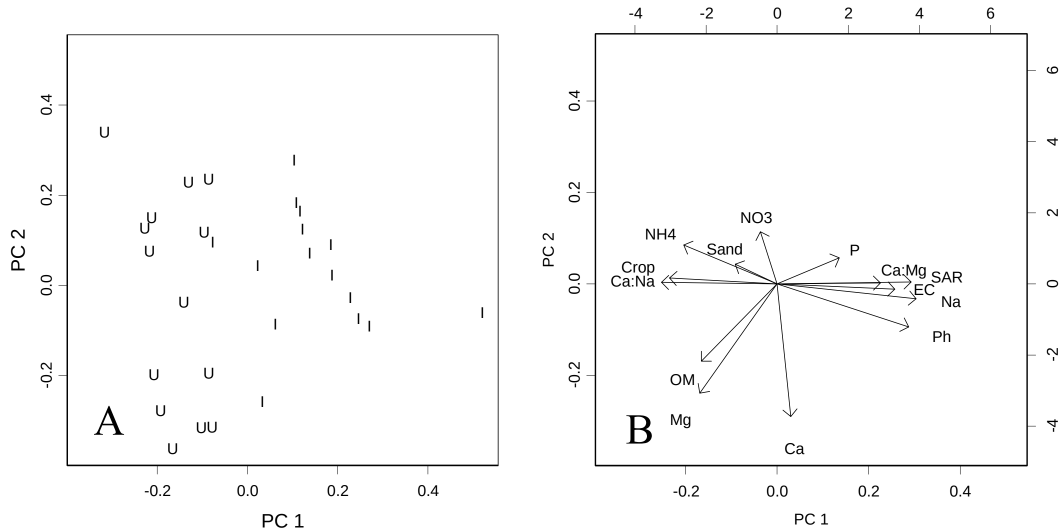

Figure 4.2 – Nuttall's alkaligrass principal components analysis of infested (I) versus uninfested (U) (A) and the soil chemistry variables dominating the separation between the two categories (B).

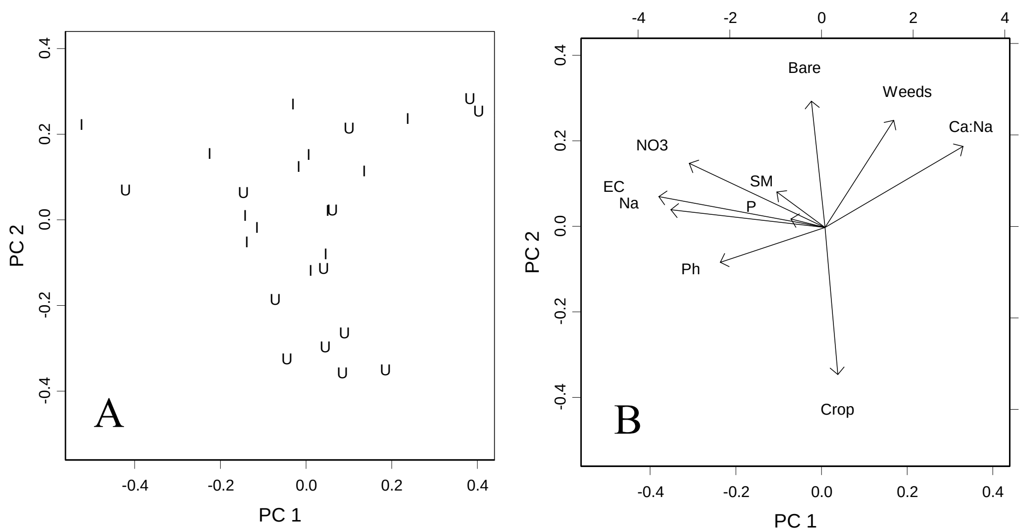

Figure 4.3 – Weeping alkaligrass principal components analysis of infested (I) versus uninfested (U) (A) and the soil chemistry variables dominating the separation between the two categories (B).

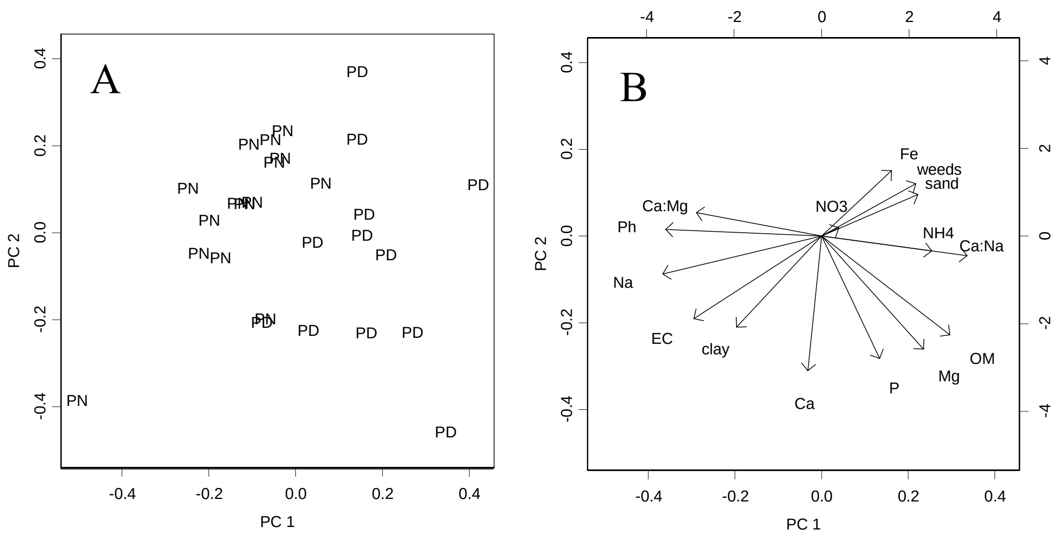

Figure 4.4 – Principal components analysis of sites infested with Nuttall's alkaligrass (PN) versus weeping alkaligrass (PD) (A) and the soil chemistry variables dominating the separation between the species colonization (B).

Table 4.1. Characteristics recorded for each site.

Chemical/Structural		
pH	copper (meq)	sand (%)
electrical conductivity (mmhos)	manganese (meq)	silt (%)
exchangeable sodium (meq)	zinc (meq)	clay (%)
exchangeable calcium (meq)	iron (meq)	organic matter (%)
exchangeable magnesium (meq)	nitrate (#/a)	gravimetric soil moisture content (g/g)
exchangeable potassium (meq)	ammonium (#/a)	
exchangeable phosphorous (meq)	sulfur (meq)	
boron (ppm)		

Spatial/Physical
elevation (m)
slope position (depression versus non-depression)
GPS coordinates

Vegetation
percent cover of weeping alkaligrass
percent cover of Nuttall's alkaligrass
percent cover of crop species
percent cover of other weedy species
percent exposed mineral soil

Table 4.2. Summary of significant soil chemical and physical measurements followed by 95% confidence intervals in brackets.

Characteristic	Nuttall's alkaligrass		Weeping alkaligrass	
	Infested	**Uninfested**	**Infested**	**Uninfested**
Crop cover	14.77 (8.65)*	71.25 (14.20)	14.46 (11.07)*	55.38 (23.73)
OM	2.03 (0.30)*+	3.33 (0.86)	3.53 (0.65)+	3.61 (1.06)
NH_4	27.87 (4.68)*	36.40 (4.54)	32.38 (6.93)	34.23 (8.50)
pH	9.26 (0.24)*+	8.28 (0.30)	8.31 (0.32)+	8.13 (0.34)
EC	1.08 (0.34)*	0.60 (0.17)	0.75 (0.21)	0.61 (0.27)
Na	12.02 (3.81)*+	2.82 (1.12)	3.26 (2.05)	2.31 (1.42)
Ca:Na	3.13 (1.48)*+	12.98 (4.12)	16.21 (7.97)+	22.65 (13.60)
Mg	4.83 (0.74)*+	7.30 (1.23)	7.88 (1.46)+	8.20 (2.92)
Ca:Mg	5.93 (0.94)*+	3.71 (0.52)	3.43 (0.36)+	3.21 (0.51)

* - significant difference between infested and uninfested sites within species

\+ - significant difference between Nuttall's versus weeping alkaligrass infested sites

Table 4.3. Summary of variability and eigenvalues (> 1.0) for Nuttall's alkaligrass, weeping alkaligrass, and the contrast of areas infested with Nuttall's alkaligrass versus weeping alkaligrass from principal components analysis.

Nuttall's alkaligrass				
Factor	Eigenvalue	Variance (%)	Cumulative Eigenvalue	Cumulative Variance (%)
1	5.34	41.1	5.34	41.1
2	1.90	14.6	7.24	55.7
3	1.57	12.1	8.81	67.8
4	1.12	8.6	9.93	76.4
5	1.02	7.8	10.95	84.2

Weeping alkaligrass				
Factor	Eigenvalue	Variance (%)	Cumulative Eigenvalue	Cumulative Variance (%)
1	3.22	32.2	3.22	32.2
2	1.90	19.0	5.12	51.2
3	1.49	14.9	6.61	66.1
4	1.23	12.3	7.84	78.4

Nuttall's versus weeping alkaligrass				
Factor	Eigenvalue	Variance (%)	Cumulative Eigenvalue	Cumulative Variance (%)
1	5.52	36.8	5.52	36.8
2	2.57	17.1	8.09	53.9
3	1.64	11.0	9.73	64.9
4	1.29	8.6	11.02	73.5

CHAPTER 5

Comparative plant responses of weeping alkaligrass and Nuttall's alkaligrass to sodic versus normal soil types

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Abstract

In the Grande Ronde Valley of eastern Oregon, two perennial grass species within the genus *Puccinellia*; *Puccinellia distans* (weeping alkaligrass) and *P. nuttalliana* (Nuttall's alkaligrass), are weeds that occupy distinct sodic soil patches within agriculturally productive fields. These two species were studied to determine if, under non-competitive conditions, either species exhibited attributes that could allow for the movement of populations into productive soils. Both species had high germination on either sodic or normal soil types. Yet, on both soil types, weeping alkaligrass grew larger and produced up to 4 times the number of viable seed than did Nuttall's alkaligrass. Growth rates and seed production of Nuttall's alkaligrass were not affected by soil type; yet, weeping alkaligrass benefited from the normal soil condition through increased biomass accumulation and seed production. While the phenological development of either species was not affected by soil type; weeping alkaligrass was able to continue tiller production through out the growing season whereas Nuttall's alkaligrass ceased tiller development soon after onset of reproduction. Weeping alkaligrass adjusted osmotically to a much lower solute potential (-3.6 MPa) than Nuttall's alkaligrass (-2.3 MPa) under sodic soils. Under normal soil conditions, weeping alkaligrass maintained a higher relative water content (80%) than Nuttall's alkaligrass (60%) at the same osmotic potential of (-2.3 MPa).

Introduction

Puccinellia distans (weeping alkaligrass) and *Nuttall's alkaligrass* (Nuttall's alkaligrass) typically occupy high pH soils throughout North America (Brotherson, 1987; Hughes, 1972; Macke and Ungar, 1971). Weeping alkaligrass, an introduced species from Eurasia, is widespread across arid and saline environments of North America (Hitchcock, 1971). Whereas Nuttall's alkaligrass, a native to North America, occupies most arid regions from Wisconsin to British Columbia, south to Kansas, New Mexico, and California (Hitchcock, 1971). Both species are considered to be among the most salt tolerant C_3 grasses in North America and are often associated with areas of low site productivity (Ashraf et al., 1986; Harivandi et al., 1983a; Macke and Ungar, 1971; Mintenko et al., 2002; Salo et al., 1996). Nuttall's alkaligrass has been documented on saline depressions (Macke, 1969), and along saline lake margins (Brotherson, 1987). Weeping alkaligrass has also been documented in saline depressions (Piernik, 2003), as well as along heavily salted roadsides (Davis and Goldman, 1993; Garlitz, 1992) and ruderal areas (Moravcova and Frantik, 2002). Both Nuttall's and weeping alkaligrass could be considered facultative halophytes (Beyschlag et al., 1996; Macke and Ungar, 1971; Moravcova and Frantik, 2002), as neither species requires salt to complete its lifecycle.

Within the Grande Ronde valley of eastern Oregon, sodic soil deposits, considered to be the most troublesome of salt-affected soils, are commonly found along the valley bottom. Generally, few plants can tolerate the high levels of sodium, hydroxyl, and biocarbonate ions, the poor soil physical structure, and slower permeability of water found within these soils (Brady and Weil, 2002). Sodic soils are typically classified as such when sodium dominates the soluble salts, the pH is greater than 8.5 and the electrical conductivity is less than 4.0 dS/m; whereas ‘normal’ soils, such as those ideal for agricultural production, tend to have a low concentration of soluble salts, of which sodium does not dominate, and a pH of less than 8.5 (Brady and Weil, 2002). While it has been documented that both species are typically found on arid, saline environments (Hitchcock, 1971), it is unknown if either species development is affected either positively or negatively under these growing conditions. In fact, while often undistinguished to species level during the seed certification process, alkaligrass was reported in 8% of Kentucky bluegrass seed certification samples compiled by the Oregon State University Extension Service in 2000[1].

It is not uncommon for species within the same genus to differ markedly in their life history traits such as phenological development (Schuster and De Leon Garcia, 1973), and/or morphological characteristics (Mueller and Richards, 1986). Differences in life history traits may make one species more successful in a given environment, or more adaptable to changing environments, than another species (Rejmanek and Richardson, 1996).

In 1979, Grime introduced a life history theory in an attempt to describe the development of plants, their interaction with the environment and the formation of various community types (Craine, 2005; Grime, 1977; Grime, 1979). Grime felt that the external factors which limited plant production could be classified by two factors, regardless of habitat. The first factor, which is the focus of this study, is described as stress and consists of conditions that restrict plant production, such as limited/excess nutrients, light, water, temperature, etc. Key to Grime's theory is the uncoupling of the competitive effects of other plants on a given species productivity versus non-competitive effects. Clearly, the relative competitiveness of a plant species will vary according to the conditions in which it is growing; and variation in that plant's productivity will arise because different environments favor different plant species.

Therefore, Grime concluded, that all plants have evolved a distinct strategy enabling them to prevail in a given habitat. A plant which flourishes under low stress and low disturbance would have a competitive strategy; one which dominates under high stress and low disturbance would have a stress-tolerant strategy; and, one that flourishes under low stress and high disturbance would be said to have a ruderal strategy. For the purpose of this discussion, differentiation between the three strategies is limited only to the stress-tolerator and competitive life-history characteristics as these relate to a plant's response under stress conditions, as was studied during the experiment. If plants occurring in harsh environments, such as the sodic soils of eastern Oregon, are somehow restricted to these environments due to competitive exclusion, they may flourish under productive agricultural habitats if given the opportunity. Farmers of the area want to know, specifically, which, if either, of the two species of alkaligrass may pose a greater threat of colonization within agriculturally productive sites.

To help answer this question, a three-step experiment was designed which studied developmental characteristics of the two species when grown on sodic versus normal soil types: first, to describe life-history characteristics of each species; second, to examine the plant-water relations of the two species; and third, to characterize both species phenological development.

Materials and Methods

Soil Characteristics

In November 2003, two soil types to be used in the experiment were collected near Imbler, Oregon (45°29′15.9″ N, 117°56′4″ W). These soils were chosen because they represent two extreme soil conditions of the region: unproductive sodic soil versus agriculturally productive ‘normal soil’. To remove any potential soil contaminants such as pathogens and parasites, each soil type was steam autoclaved for 4 hours at 150 C. Soil characteristics for the two soil types are presented in Table 5.1.

Life-history characteristics

<u>Germination</u>

On 28 March 2004 and 19 March 2005, 7.6 L pots were filled with either sodic or normal soil and planted with either 10 weeping alkaligrass or 10 Nuttall’s alkaligrass adequately afterripened (18 months at 21 C) seeds. One day after sowing, all pots were buried to rim level in trenches at the Columbia Basin Agriculture Research Center (CBARC) near Pendleton, OR in a completely randomized design with 24 and 40 replicates of each species by soil type in 2004 and 2005, respectively. Germination counts started following the first sign of emergence and followed on days 4, 7, 14, and 21 after emergence. To prevent severe dessication during establishment, pots were given supplemental watering as needed. On day 23, all seedlings but the centermost were removed prior to beginning measurements of phenology, fitness, water relations, and seed production. After day 23, only the center most plant per pot remained.

Phenology

In 2004 and 2005, 6 and 10 replicates of each species by soil type treatment, respectively, were subjected to leaf development measurements 3 times per week using the Haun Scale (Haun, 1973). Once the plant had progressed into the initial tillering phase, a modified scale originally described by Jensen and Lund (1967) was utilized to describe 6 stages (tillering, jointing, booting, emergence, full inflorescence emergence, flowering, and mature seed) of phenological development based on the primary reproductive culm. *Tillering* was defined as the stage of rapid vegetative growth when the plant produced multiple potentially reproductive culms. *Jointing* was when the first node of the primary reproductive stem appeared above the soil surface. *Booting* was when the inflorescence appeared as a swelling within the leaf sheath of the primary reproductive culm. *Emergence* was when a portion of the inflorescence of the primary reproductive culm was visible. *Full inflorescence emergence* was when the base of the inflorescence of the primary reproductive culm had emerged at least 2 cm from the flag leaf ligule. *Flowering* was when at least 50% of the florets on the main reproductive culm were open. The *mature seed* stage was when seeds were easily removed from the inflorescence of the primary reproductive culm utilizing little mechanical force. A species was considered to be at a phenological stage when more than 30% of the sample units were expressing a given phenological characteristic. In addition to recording the phenological growth stage, tiller number and plant height also were recorded.

Thermal time, based on air temperature and represented by growing degree days (GDD), was used to measure plant development. GDD were calculated using a standard GDD model for C_3 grasses (Ball et al., 2004; Klepper et al., 1988):

$$GDD = [(T_{max} + T_{min})/2] - T_b \qquad (1)$$

where T_{max} and T_{min} are the daily maximum and minimum recorded temperatures and T_b is the minimum temperature at which growth ceases ($T_b = 0$ C).

Biomass partitioning

In 2004 and 2005, 6 and 10 replicates, respectively, were harvested at four phenological development stages (tillering, boot, full inflorescence emergence, and mature seed). Plant height and tiller number were recorded. The above ground biomass and roots were separated at the crown. The roots were thoroughly washed under a low pressure spray. Both roots and above ground biomass were oven dried at 65 C for 72 h

Fitness (seed production)

In 2004 and 2005, the number of emerged inflorescences per plant and the number of spikelets on two representative inflorescences per plant were recorded at the mature seed development stage, to determine potential seed production. It was assumed that weeping alkaligrass averaged 5 seeds per spikelet and Nuttall's alkaligrass averaged 4.5 seeds per spikelet (Hitchcock, 1971). Average seed production was calculated using the formula:

$$SP = F_S * S_I * I_P * S_V \qquad (2)$$

where SP is the average seed production measured as seeds per plant, F_S is the average number of florets per spikelet, S_I is the average number of spikelets per inflorescence, I_P is the average number of inflorescence per plant, and S_V is the average seed viability as determined in 2005 when tetrazolium tests (ISTA, 1996) were conducted on the mature seed harvest.

Plant-water relations

In 2005, at five dates throughout the growing season, 5 random plants of each treatment (species by soil type) were subjected to pre-dawn osmotic potential and relative water content measurements. Osmotic potential and relative water content were measured following established methodology (Jones and Turner, 1978). A vapor pressure osmometer (Model 5520, Wescor, Logan, UT) was used to determine osmolality, which was converted to osmotic potential using the equation:

$$-\pi = -RTCs \qquad (3)$$

where $-\pi$ is the osmotic potential measured in MPa, R is the ideal gas constant (8.31 J $K^{-1}mol^{-1}$), T is the absolute temperature (K) and Cs is the measured osmolality (mOsm/L). Relative water content was calculated using the equation:

$$RWC(\%) = [(FW-DW)/(TW-DW)]*100 \qquad (4)$$

where FW is the fresh weight (g) of the excised leaf samples immediately after harvest, TW is turgid weight (g) of the excised leaf sample after floating for 16 h in de-ionized water at 20 C under photosynthetically active radiation, and DW is the dry weight (g) of the leaf sample after being oven dried at 65 C for 48 h. Water potential analysis using the Scholander pressure bomb method was attempted but the data could not be used as the leaves were too delicate and often destroyed during the pressurization stage.

Statistical Methods

Germination, life history characteristics and osmotic adjustment data for each species within soil type were separated using Tukey's Mean Separation ($\alpha = 0.05$); species by soil type characteristics were separated using ANOVA. Number of tillers (y) was characterized using the sigmoidal regression equation:

$$Y = \frac{a}{1 + e^{-(\frac{x - x_o}{b})}} \qquad (5)$$

where x is the number of growing degree days.

Results and Discussion

Due to the exceptionally wet spring of 2004, there were large differences between year 1 (2004) and year 2 (2005) data. The 20-year average precipitation from May 19 to June 10 for the area is 23.1 mm. During the rapid tillering phase from May 19 to June 10, 2004, the Columbia Basin Agricultural Research Center (CBARC) recorded a total precipitation of approximately 95.5 mm, four times greater than the 20-year average. In 2005, total precipitation from May 19 to June 10 was only 30.6 mm. While the higher precipitation in 2004 did not affect germination or phenological development rates of either species, it did result in greater tillering, overall biomass, and seed production of both species. Therefore, this paper will present year 1 and year 2 data separately when necessary.

Life-history characteristics

Germination

In both years, both species exhibited relatively high rates of germination on both soil types under non-limiting soil moisture conditions. More Nuttall's alkaligrass seeds were likely to emerge in sodic than normal soils ($P < 0.05$) at 4 d after first emergence (AFE). However, the rate of germination was mitigated over time as there was no significant difference between soil types by 7 d AFE when germination was approximately 70% (Figure 5.1). While weeping alkaligrass had a slightly greater germination under normal soil than sodic soil, the differences were not significant ($P = 0.85$). At 7 d AFE, roughly 80% of the seeds had germinated regardless of soil type. While there was a trend towards higher germination in both soil types for weeping alkaligrass than Nuttall's alkaligrass, there was no difference by 21 d AFE ($P = 0.70$).

Phenology

Both species initiated each stage of phenological development after approximately the same accumulation of growing degree day regardless of soil type or year (Figure 5.5 and 5.6). Although, differences in precipitation between the two study years did not affect either species phenological development rates, there were significant differences in number of tillers, therefore, the data are presented separately.

Regardless of soil type, weeping alkaligrass consistently accumulated more tillers throughout the growing season than did Nuttall's alkaligrass (Figures 5.5 and 5.6). In year 1, on normal soils tiller development was not different between the two species. However, on sodic soils while tillering of both species slowed after the flowering stage, tiller production of weeping alkaligrass on sodic soils ($R^2 = 0.95$) slowed less than Nuttall's alkaligrass ($R^2 = 0.96$). In year 2, under normal soil conditions weeping alkaligrass ($R^2 = 0.82$) tiller development was greater than Nuttall's alkaligrass

(R^2 = 0.80). Under sodic soil conditions, tillering of Nuttall's alkaligrass (R^2 = 0.70) appeared to stop once the species initiated the boot stage of development (800 GDD); while tillering slowed in normal soils (R^2 = 0.80) after flowering was initiated (1100 GDD). In both sodic (R^2 = 0.88) and normal (R^2 = 0.82) soil conditions, the tillering rate of weeping alkaligrass slowed marginally after flowering (1100 GDD) but never appeared to stop (Figure 5.6).

Biomass Partitioning

Within each year, significant species by soil interactions were variable for the biomass partitioning data collected. In year 1, the only attribute which had a significant species by soil interaction was the shoot:root ratio ($P = 0.03$). In year 2, a species by soil interaction was significant for the number of tillers ($P=0.002$), and the number of inflorescence ($P=0.003$). Not surprisingly, there generally existed a significant difference in the biomass data between year 1 and year 2; therefore each year's results will presented separately.

Nuttall's alkaligrass by soil type

Differences in biomass accumulation by soil type within each year for Nuttall's alkaligrass was variable and generally not significant by the mature seed harvest (Figures 5.2 and 5.3). Between years, Nuttall's alkaligrass grew taller, produced more tillers, and greater biomass regardless of soil type in year 1 than year 2 ($P < 0.05$) (Figures 5.2 and 5.3).

Puccinellia distans by soil type

Under sodic soil conditions, weeping alkaligrass exhibited more vigorous growth in year 1 than year 2 with greater biomass and tiller accumulation (Figures 5.2 and

5.3). By the mature harvest, total biomass in year 1 and year 2 averaged 12.6 g/plant ($\pm$ 4.1) and 4.3 g/plant ($\pm$ 0.8), respectively. Average tiller development during the same sampling periods was 50 tillers/plant ($\pm$ 20) versus 27 tillers/plant ($\pm$ 7). Yet, at the mature harvest, under normal soils, weeping alkaligrass tiller accumulation, total biomass, shoot biomass, or root biomass between year 1 and year 2 was not different.

In year 2, during the boot ($P<0.001$, df = 9) and emergence stages ($P = 0.03$) of development, plants grown in sodic soils were larger than those grown in normal soils; however, by the mature harvest date, the sodic grown plants were smaller (4.29 $\pm$ 0.8 g/plant) than those grown in normal soils (8.39 $\pm$ 2.8 g/plant) (Figure 5.3). The differences witnessed over time may be attributed to the cessation of root and shoot growth after the emergence stage of development for those plants grown in sodic soils.

<u>Nuttall's alkaligrass versus weeping alkaligrass</u>

After the tillering stage, Nuttall's alkaligrass was taller than weeping alkaligrass ($P < 0.05$) throughout the growing season (Figures 5.2 and 5.3). The difference between the heights of the two species can be seen in the field, where weeping alkaligrass is prostrate and Nuttall's alkaligrass is upright.

In year 1, the species were different in their biomass accumulation across both soil types ($P = 0.004$), however there did not exist a species by soil type interaction ($P = 0.93$) (Figure 5.2). The significant difference between the species may be attributed to the rapid growth rate of Nuttall's alkaligrass on sodic soils at the emergence stage.

In year 2, the species were different in their biomass accumulation across both soil types ($P<0.0001$), however, once again, there did not exist a species by soil type interaction ($P = 0.13$) (Figure 5.3). At the mature harvest, when grown in normal soils, total biomass of weeping alkaligrass was no different (6.64 ± 2.0 g/plant) than Nuttall's alkaligrass (4.0 ± 1.2 g/plant) at the mature harvest date (Figure 5.3).

Fitness (seed production)

Nuttall's alkaligrass by soil type

Inflorescence production by Nuttall's alkaligrass at the mature harvest was unaffected by the different soil types in year 1 ($P = 0.6$) or year 2 ($P = 0.8$). Yet, from year 2 versus year 1, there was a decrease in the average inflorescence per plant on sodic soils ($P = 0.02$), as well as on normal soils ($P<0.0001$) (Table 5.2). Similar trends, though not significant, were observed for average number of spikelets per inflorescence. In 2005, based on tetrazolium tests, there was no difference in seed viability, 75% ± 6.0 versus 73% ± 6.2 for seeds produced under sodic versus normal soil conditions, respectively. Therefore, the calculated average per plant seed production was slightly greater under normal soil conditions in year 1 and slightly greater under sodic soil conditions in year 2 (Table 5.2).

Weeping alkaligrass by soil type

Inflorescence production by weeping alkaligrass at the mature harvest was unaffected by the different soil types in year 1 ($P = 0.50$), yet was significantly higher on sodic soils in year 2 ($P = 0.001$). From year 1 to year 2, there was a decrease in the average inflorescence per plant on sodic soils ($P = 0.01$), yet not on normal soils ($P = 0.10$).

Within each year, soil type did not affect the average number of spikelets per inflorescence. Yet, in year 2, weeping alkaligrass grown in sodic soil conditions did have lowered spikelet production, dropping from 404 ± 44 to 233 ± 53. In 2005, based on tetrazolium tests, the viability of seeds produced under sodic versus normal soil conditions were 76% $\pm$ 5.9 versus 90% $\pm$ 4.0, respectively. Therefore, the calculated average seed production was relatively equal between soil types in year 1 yet nearly double on normal soils in year 2 (Table 5.2).

Nuttall's alkaligrass versus weeping alkaligrass

There were no differences in inflorescence number at the mature harvest between the two species in year 1 when grown on normal soil ($P = 0.32$) or sodic soil ($P = 0.76$) as well as in year 2 (Table 5.2). However, weeping alkaligrass consistently produced more spikelets per inflorescence than Nuttall's alkaligrass under all conditions ($P<0.05$). Therefore, depending on the conditions, weeping alkaligrass produced approximately 2-4 times the average seed yield than Nuttall's alkaligrass.

Both species produced equal or greater biomass under the higher precipitation of year 1 when grown in sodic soil indicating that irrigation may benefit both species. The increase in biomass of Nuttall's alkaligrass on both soil types under the higher rainfall of year 1 indicated that this species may be more limited by available water than sodium salts. No differences in tiller development and biomass accumulation for weeping alkaligrass, when grown on normal soils, between the years indicated that sodium salts rather than water may be the factor limiting growth. Higher relative water contents at the same osmotic potential under normal soil conditions, suggest a greater drought tolerance for weeping alkaligrass than Nuttall's alkaligrass.

The continued tiller development of weeping alkaligrass throughout the growing season may be troublesome for land managers as this species may exhibit indeterminate inflorescence production and continuous seed production. Nuttall's alkaligrass, on the other hand, appears to have determinate inflorescence production which should translate into one seed production event per growing season.

Plant-water relations

When comparing two species, it is important to note that different osmotic potentials may be the product of an inherent difference in the basal osmotic potential (measured at full hydration) of the species. Within this experiment, both species exhibited osmotic potentials of roughly -1.2 MPa at 100% water content which is within the average range for most crop species (Morgan, 1984).

Nuttall's alkaligrass

Nuttall's alkaligrass exhibited a non-linear decline in osmotic water potential and appeared to stop osmotic adjustments when cellular water potential reached -2.0 to -2.5 MPa regardless of soil type (Figure 5.4). The cessation of osmotic adjustments of Nuttall's alkaligrass corresponded to relative water potentials of approximately 85% (Figure 5.4).

Weeping alkaligrass

Under both soils conditions, weeping alkaligrass exhibited a linear relationship between osmotic potential and relative water content. Under sodic soil conditions, weeping alkaligrass was able to osmotically adjust to values of at least -3.5 MPa at relative water contents of less than 60% (Figure 5.4). At relative water contents $\leq$ 87%, weeping alkaligrass had significantly lower osmotic values for the same relative water contents when grown in sodic versus normal soils, indicating osmotic adjustment. In this experiment, weeping alkaligrass did not reach a condition where osmotic adjustment ceased. It is unknown whether the species was adjusting via sodium salts or soluble carbohydrates.

In terms of salt tolerance, Nuttall's alkaligrass did not appear to be affected cellularly by the high levels of sodium salts associated with the sodic soils. This result is not surprising since it had previously been reported that under increasing sodium concentrations, Nuttall's alkaligrass did not take up sodium ions (Harivandi et al., 1982; Harivandi et al., 1983a; Sessoms, 2004). Osmotic adjustments allow the potential for maintaining photosynthesis and growth as the water deficit increases (Turner and Jones 1980), and therefore, tolerance of water stress often involves low osmotic potentials (Morgan, 1984) as observed in weeping alkaligrass. The ability of weeping alkaligrass to osmotically adjust to maintain a higher level of vegetative growth throughout the summer is clearly a competitive advantage.

Conclusion

Historically, most land managers of eastern Oregon have not distinguished between weeping alkaligrass and Nuttall's alkaligrass, simply referring to them commonly as alkaligrass. However, the results of this study indicate that a distinction should be made between the two species as weeping alkaligrass exhibited competitive characteristics versus the stress-tolerator Nuttall's alkaligrass.

Nuttall's alkaligrass did not exhibit strong phenotypic plasticity when subjected to the conditions of the sodic versus normal soils, rather its morphogenetic responses were small in magnitude indicating a reliance on its stress-tolerant characteristics for survival. However, weeping alkaligrass had more competitive attributes, via increased biomass accumulation and seed production in normal soil conditions. According to

Grime's theory (Grime, 1979), in the early stages of plant development under productive habitats, such as the agricultural fields of eastern Oregon, the more competitive weeping alkaligrass would have a tendency to sustain high rates of water and mineral uptake to maintain dry-matter production under stress and to succeed in competition; whereas the stress-tolerant Nuttall's alkaligrass would be outcompeted by more competitive plant species.

In conclusion, for farmers of eastern Oregon, weeping alkaligrass may pose a greater threat in terms of expansion and proliferation in agriculturally productive crop land.

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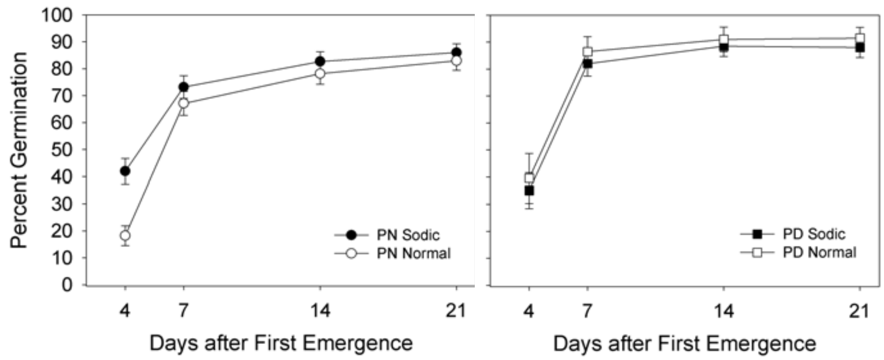

Figure 5.1 – Comparison of Nuttall's alkaligrass (PN) and weeping alkaligrass (PD) germination with 95% confidence intervals when grown on sodic versus normal soil types for combined years.

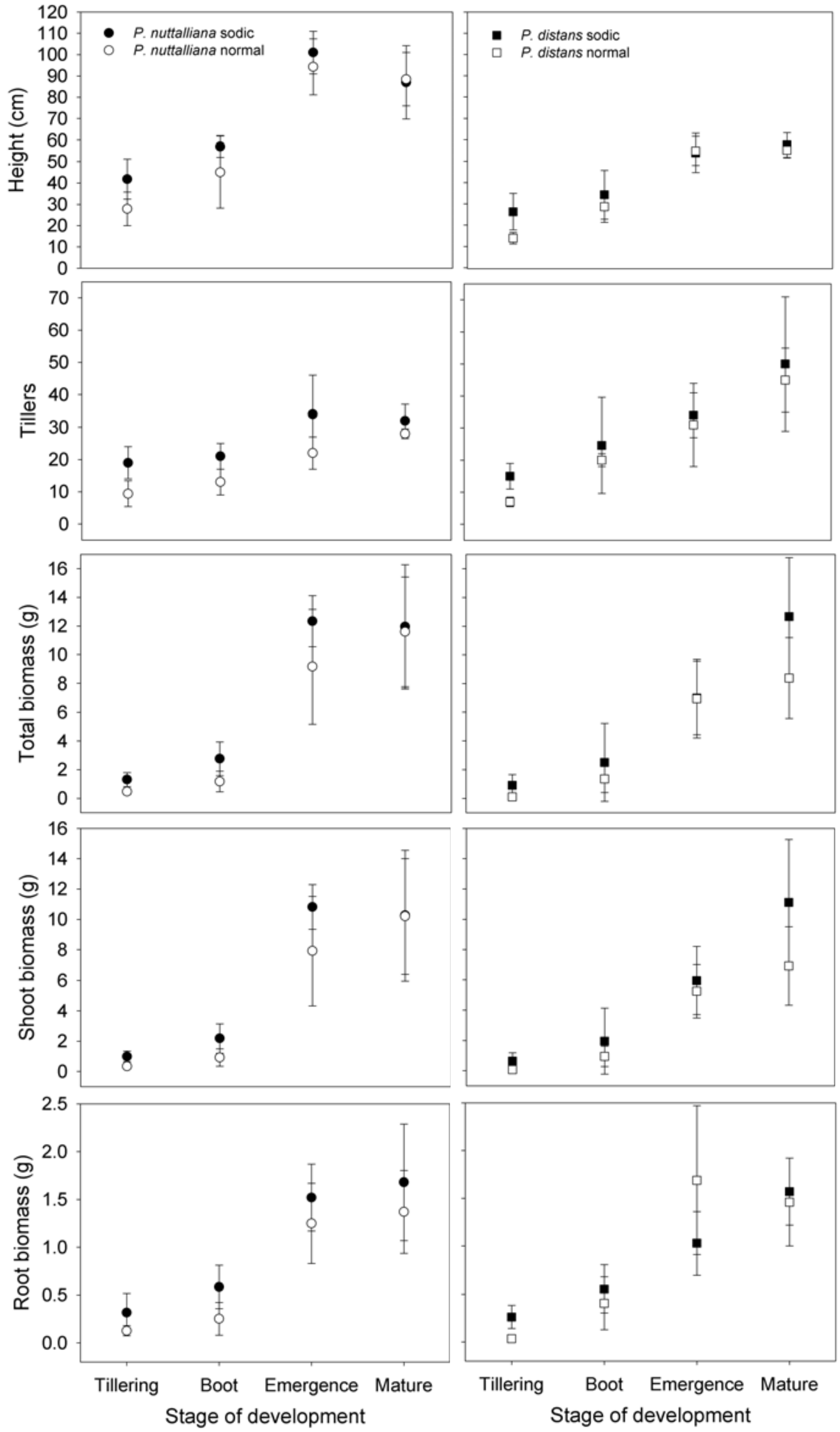

Figure 5.2 – Year 1 comparison of biomass accumulation and partitioning for Nuttall's alkaligrass (*P. nuttalliana*) and weeping alkaligrass (*P. distans*) with 95% confidence intervals when grown in sodic versus normal soil types

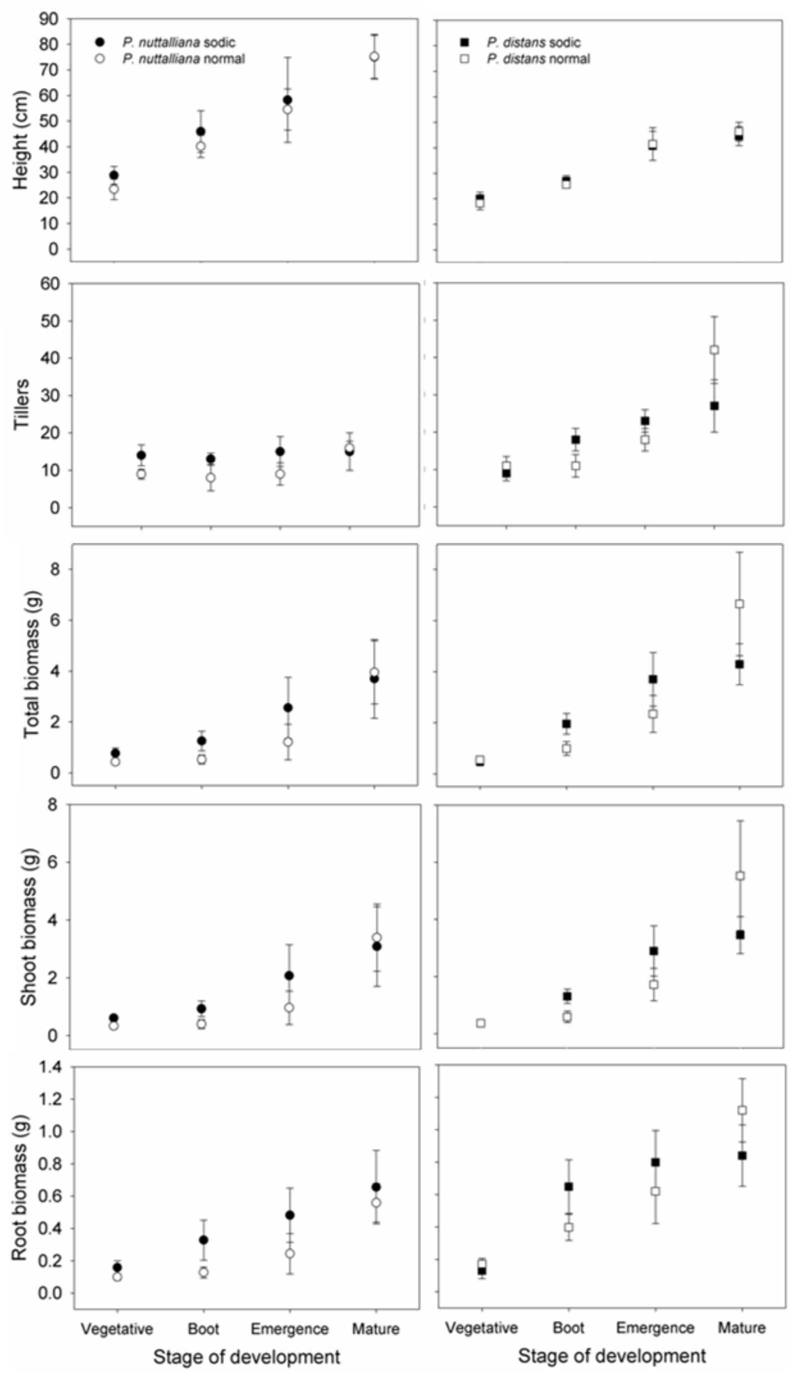

Figure 5.3 – Year 2 comparison of biomass accumulation and partitioning for Nuttall's alkaligrass (*P. nuttalliana*) and weeping alkaligrass (*P. distans*) with 95% confidence intervals when grown in sodic versus normal soil types

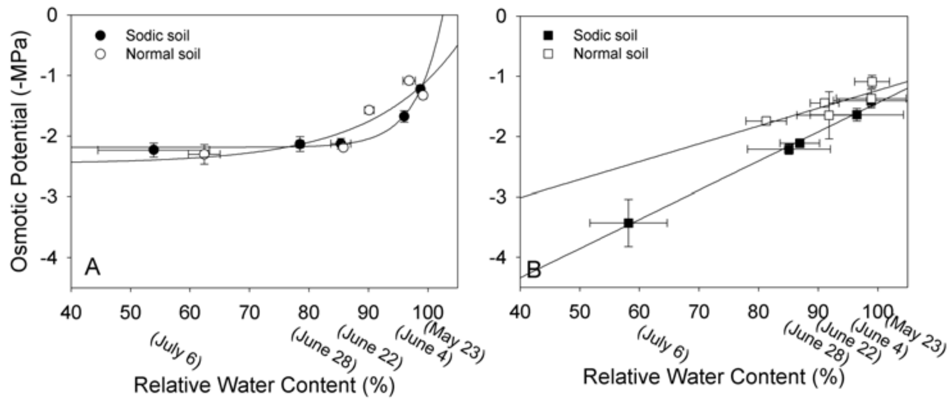

Figure 5.4 – Year 2 comparison of changes in osmotic potential versus relative water content for Nuttall's alkaligrass (A) and weeping alkaligrass (B) with 95% confidence intervals when grown in sodic versus normal soil types. Dates given correspond to sample date and are associated with the sodic soil value for that date.

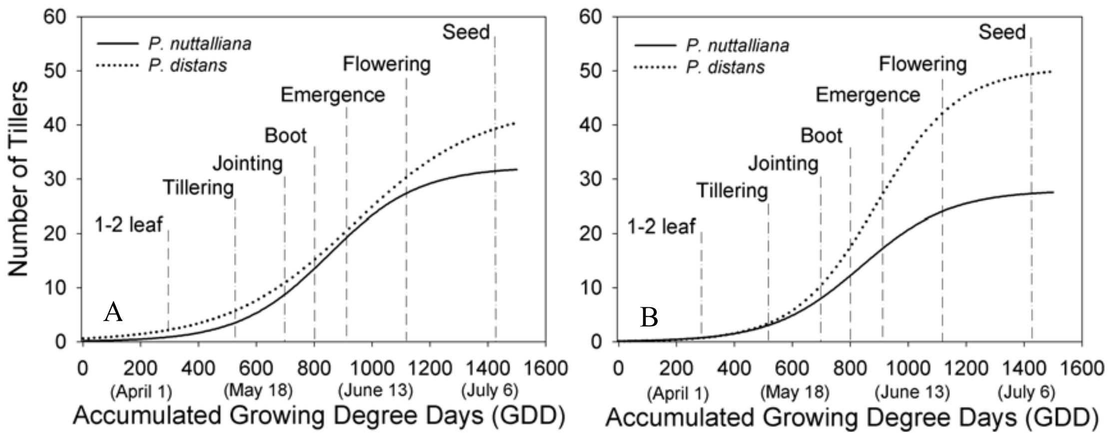

Figure 5.5 – Year 1 comparison of Nuttall's alkaligrass (*P. nuttalliana*) and weeping alkaligrass (*P. distans*) phenological development rates and tiller development based on accumulated growing degree days under normal (A) versus sodic (B) soil types.

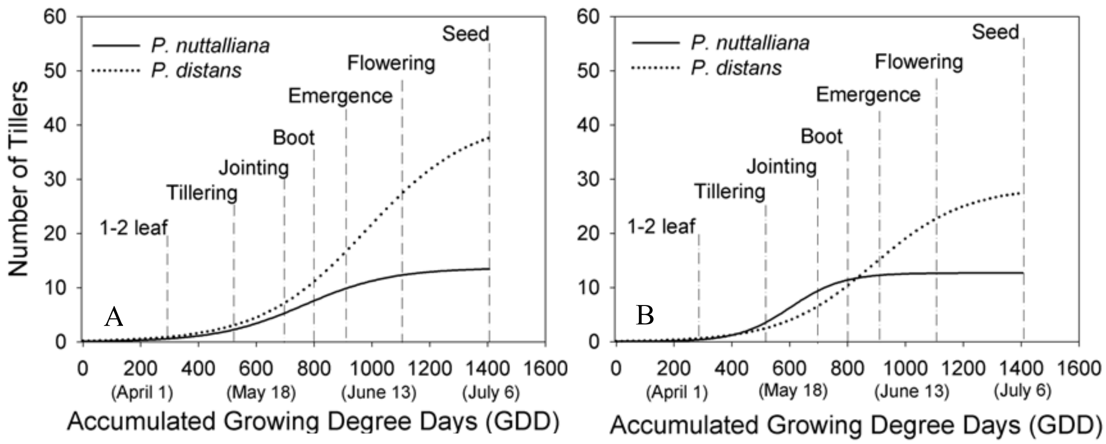

Figure 5.6 – Year 2 comparison of Nuttall's alkaligrass (*P. nuttalliana*) and weeping alkaligrass (*P. distans*) phenological development rates and tiller development based on accumulated growing degree days under normal (A) versus sodic (B) soil types.

Table 5.1. Soil characteristics of the sodic versus normal soil types

Soil Characteristics	Sodic	Normal
pH	9.1	6.0
Ca (meq/100g)	20.0	3.6
Mg (meq/100g)	8.5	0.9
Na (meq/100g)	9.7	0.2
EC (meq/100g)	0.8	0.2
Sand (%)	27.5	83.8
Silt (%)	51.3	7.5
Clay (%)	21.3	8.8
Texture Class	Silt Loam/Loam	Loamy Sand

Table 5.2. Comparison of average inflorescence, spikelet and maximum potential seed production per plant after 1 year of growth for Nuttall's alkaligrass and weeping alkaligrass when grown in sodic verus normal soil types. Average values followed by 95% confidence interval where applicable.
Note: potential seed yield calculated in 2005 using the equation: $SP = F_S{*}S_I{*}I_P{*}S_V$

	Inflorescence/plant			
	Sodic		**Normal**	
	Year 1	Year 2	Year 1	Year 2
Weeping alkaligrass	22 (10)	12 (3)	19 (9)	12 (3)
Nuttall's alkaligrass	21 (9)	12 (4)	23 (2)	11 (4)
	Spikelets/inflorescence			
	Sodic		**Normal**	
	Year 1	Year 2	Year 1	Year 2
Weeping alkaligrass	404 (44)	233 (53)	369 (9)	355 (113)
Nuttall's alkaligrass	175 (55)	138 (49)	176 (78)	140 (48)
	Average Seed Yield/Plant			
	Sodic		**Normal**	
	Year 1	Year 2	Year 1	Year 2
Weeping alkaligrass	33 774	10 625	31 550	19 170
Nuttall's alkaligrass	12 403	5 589	13 298	5 059

CHAPTER 6

Competitive interactions of Kentucky bluegrass, Nuttall's alkaligrass, and weeping alkaligrass in mixed-density pairwise combinations

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Abstract

Mechanisms of interspecific and intraspecific competitive interactions between Kentucky bluegrass (*Poa pratensis*), Nuttall's alkaligrass (*Puccinellia nuttalliana*), and weeping alkaligrass (*Puccinellia distans*) were assessed over a two year period. A matrix of competitive regimes was created consisting of 4 monoculture densities and 16 mixtures of all possible pairwise combinations. Response surfaces and substitution analysis for biomass of the three species were generated within the matrix to evaluate the potential for either alkaligrass species to establish and compete with Kentucky bluegrass in the agriculturally productive soils of eastern Oregon. In year 1, Nuttall's alkaligrass and weeping alkaligrass were similarly more competitive than Kentucky bluegrass, with Nuttall's alkaligrass being slightly more competitive than weeping alkaligrass. In year 2, Kentucky bluegrass was more competitive than either of the alkaligrass species. Nuttall's alkaligrass remained more competitive than weeping alkaligrass. Both alkaligrass species exhibited negative changes in biomass from year 1 to year 2, whereas Kentucky bluegrass biomass increased by nearly 100%.

Introduction

Control of grassy weeds can be difficult in grass seed production due to the difficulty of selectively removing the weeds from the crop. Not only can weeds compete with the grass seed crop for nutrients, water, and sunlight, they can also contaminate the harvested seed crop, resulting in lower market values.

Kentucky bluegrass (*Poa pratensis*) is a seed crop of primary importance in eastern Oregon (Union County). Approximately 90% of grass seed crops in Union County are grown under contract with seed companies as certified seed[1]. In 2003, in Union County, there were 4,795 certified hectares in Kentucky bluegrass, representing approximately 43% of the certified grass seed production for that area (Oregon State University, 2003). In saline areas of Union County, alkaligrass (*Puccinellia spp.*) is a dominant weedy species. The common name 'alkaligrass' actually refers to either one of two species of alkaligrass: *Puccinellia nuttalliana* (Nuttall's alkaligrass) a native grass to the region or *Puccinellia distans* (weeping alkaligrass) an introduced species from Eurasia. Often undistinguished at the species level during the seed certification process, alkaligrass was reported in 8% of Kentucky bluegrass seed certification samples compiled by the Oregon State University Extension Service in 2000[1]. Due to their similar seed size to Kentucky bluegrass, it is exceedingly difficult to eliminate either Nuttall's or weeping alkaligrass during the seed cleaning process.

Both species are considered to be among the most saline tolerant C_3 grasses in North America (Ashraf et al., 1986; Harivandi et al., 1983a; Macke and Ungar, 1971; Mintenko et al., 2002; Salo et al., 1996) with weeping alkaligrass perhaps more salt tolerant than Nuttall's alkaligrass (Moravcova and Frantik, 2002; Salo et al., 1996).

Either, or both, species have been documented to occur on saline depressions (Macke, 1969), along saline lake margins (Brotherson, 1987), along heavily salted roadsides (Davis and Goldman, 1993; Garlitz, 1992) and ruderal areas (Moravcova and Frantik, 2002). Both Nuttall's alkaligrass and weeping alkaligrass are considered to be facultative halophytes (Beyschlag et al., 1996; Macke and Ungar, 1971; Moravcova and Frantik, 2002), as neither species requires salt to complete its lifecycle. In fact, Haravandi et al. (1983b) witnessed no significant difference in weeping alkaligrass growth when grown in tap water versus a 25% solution of sea water ($EC_w = 11.8$ mmhos/cm). Results from unpublished work (Chapter 4) indicate that while phenological development of both species was similar in sodic versus normal soil type conditions, weeping alkaligrass had a greater biomass accumulation in normal soils than sodic soils. Where as, Nuttall's alkaligrass had no significant difference in biomass accumulation under the sodic versus normal soil conditions.

Therefore, it is not surprising that eastern Oregon grass seed producers are concerned over the potential for either species of alkaligrass to expand from their typical sodic habitats and compete with Kentucky bluegrass on agriculturally productive sites. While Kentucky bluegrass is generally regarded as a competitive species (Brown and Munsell, 1945), competitive abilities can vary widely between biotypes (Ahlgren et al., 1945) and cultivars (Eggens, 1982). European studies reported weeping alkaligrass as weakly competitive when grown with the highly competitive *Elymus repens*, possibly due to an intolerance of mowing (Ryel et al., 1996). Nuttall's alkaligrass also has also been documented to be intolerant to mowing (Mintenko et al., 2002). In a turf grass evaluation study, Mintenko et al (2002), found that percent coverage of Nuttall's alkaligrass dropped by 46% from June 1997 to August 2000 when mowed weekly, to a 3.8 cm height, from mid-May to the end of September. Kentucky bluegrass, on the other hand, has been shown to increase its shoot regrowth under moderate mowing height (6.2 cm) and frequency (semiweekly) compared to a non-mowed control (Krans and Beard, 1985). While the growth of all three species has been studied, more or less, under various conditions, there have been no studies of the competitive abilities of either weeping alkaligrass or Nuttall's alkaligrass when grown with Kentucky bluegrass. Farmers of Union County want to know, specifically, which, if either, of the two species of alkaligrass may pose a greater threat to Kentucky bluegrass production.

Historically, replacement or additive design studies have been utilized to study the effect of density of one species on the growth of another species (Radosevich, 1987). However, neither replacement series nor additive designs attempt to explain the effect of both density and frequency on the growth of an individual (Firbank and Watkinson, 1985) interspecifically or intraspecifically. By the early 1960s, deWit (Law and Watkinson, 1987) advocated the use of addition series experiments wherein a matrix combination of a series of densities and frequencies of both species were analyzed.

Another potential limitation often associated with competition studies is the short time frame under which competition is often studied. Most competition studies analyze plant parameters over one growing season (Law and Watkinson, 1987; Shainsky and Radosevich, 1992; Sher et al., 2000) regardless of the life history of the species. A one-season time frame may be suitable for annuals; however, competition dynamics within a perennial community may vary greatly over a longer time period.

For example, Brown and Munsell (1945) found that when seeded in the spring with clovers, or in late summer with pasture mixes, very little Kentucky bluegrass was found in either the summer crop or the following year's harvest. Yet, over a two year period, Kentucky bluegrass provided a larger proportion of the biomass harvested.

The goals of this research project were to study the short (1 year), the longer term (2 years), and the change over time (year 1 to year 2) competitive interactions among three species: Kentucky bluegrass, Nuttall's alkaligrass, and weeping alkaligrass in pairwise matrices to evaluate the potential for either alkaligrass species to establish and compete with Kentucky bluegrass in the agriculturally productive soils of eastern Oregon.

Materials and Methods

Seedlings of each of the three species, weeping alkaligrass, Nuttall's alkaligrass and Kentucky bluegrass were grown under greenhouse conditions near Pendleton, Oregon at the Columbia Basin Agriculture Research Center (CBARC). Three weeks prior to planting, the study site was pre-irrigated and tilled to remove as many weeds as possible and prepare the site for transplanting. The one month old seedlings were transplanted from September 22-24, 2004, in two dimensional matrices of weeping alkaligrass with Nuttall's alkaligrass; weeping alkaligrass with Kentucky bluegrass; and Nuttall's alkaligrass with Kentucky bluegrass. The planting site was located at CBARC on well drained, non saline, productive soils described as coarse-silty mixed, superactive, mesic Typic Haploxerolls (Walla Walla silt loam - cultivated) (Dyksterhuis and High, 1985).

Monocultures of each species were planted at densities of 1, 4, 8, and 16 plants per 0.25 m^{-2}. As well, species mixtures of all possible pair-wise density combinations were planted, resulting in a total of 24 density treatments. To ensure identical spacing between treatment replications, plywood templates were designed and utilized for all planting treatments. To account for possible edge effects, each 0.25 m^2 plot had a 25 cm buffer boundary planted to the same density and proportions as the plot area. The total area associated with each plot was 1 m^2 with a 50 cm alley between plots (Figure 6.1). The experimental design of each pair-wise matrix was a randomized complete block replicated 3 times with 24 plots (treatments) per block, for a total of 72 plots per pair-wise matrix. Prior to planting the study, the above ground biomass of 10 seedlings of each species was harvested and dried for 48 hrs at 65 C to ensure that there were no significant differences between initial seedling size of the three species ($P > 0.05$).

Throughout the course of the study, weed control was maintained through shallow tillage of the alleys and in-plot hand weeding. Plant densities and ratios of weeping alkaligrass and Nuttall's alkaligrass were maintained at the initial densities and ratios planted; however, Kentucky bluegrass was allowed to grow in its sod forming nature. On July 9, 2005, individual plants within each 0.25 m^2 plot were harvested at 5 cm above the soil surface. Plants were oven dried for 48 hrs at 65 C and weighed. At the same time, inflorescence numbers and height of three plants (when present) within each plot were recorded. After harvest, the complete study area was mowed to 5 cm stubble height, residue removed and plants allowed to regenerate without additional water, fertilizer or pesticides. In year 2, on June 20, 2006, the same harvesting and processing procedures were followed as in year 1.

Statistical Analysis

In the analysis of two-species competition data, the number of models which can be fitted to the data is daunting. Models were fit to biomass and inflorescence data for each pair of species in each of the two mixture experiments. After fitting several linear models, the adequacy of each model was evaluated using an assessment of the residuals, the R^2 value, and, by incorporating the law of parsimony, as the ability to biologically interpret model parameters was of primary importance. For all models used, an assessment of the residuals offered no evidence for further evaluation via non-linear modeling (i.e. – the residuals were randomly and uniformly distributed about zero).

Modeling the data

For all three pair-wise experiments, both biomass and inflorescence number per plot were best explained by reduced versions of the full model:

$$\log Y_i = \beta_0 + \beta_1 X_i + \beta_2 Y_i + \beta_3 X_i^2 + \beta_4 Y_i^2 + \beta_5 (X_i Y_i) \qquad (1)$$

where $\log Y_i$ is the log of biomass or inflorescence number of species Y with respect to the density of species X and/or species Y; and the quadratic of the density of species X and/or species Y; and the interaction of the densities of species X and/or Y. For all three pair-wise experiments, height was unaffected by species density or proportions ($P > 0.05$). The results of the models for the biomass and inflorescence data were almost identical. Correlation analysis of the biomass and inflorescence response variables and residuals confirmed that they were highly correlated (>0.98); therefore, only the biomass data will be presented (see Appendix 3 for inflorescence results).

Results and Discussion

Year 1

Visual representation of the biomass data was modeled using 3-dimensional response surface graphs (Figure 6.2). Best fit models with their respective R^2 results are presented in Table 6.1. The interaction of the densities of both species was significant ($P < 0.001$). Therefore, it was not possible to describe the results in terms of main effect competition coefficients because the effect of each species changes with changes in total density. As well, because the data was log transformed for analysis and then back transformed for discussion, the confidence intervals around the mean are often not even. Therefore, where necessary, descriptions of the data within the text are presented with both upper and lower 95% confidence intervals separated by a comma.

Change in biomass across densities and proportions

The interaction term of $\beta_5(X_iY_i)$ was not 0, thus the effect of the two plant densities on yield can not be assumed to be independent; therefore, the biological significance of the interaction term must be interpreted from a graphical representation of the model (Damgaard, 1998). The addition of quadratic terms, where significant, allowed for polynomial curvature of the response variable away from linearity; providing a more accurate representation and interpretation of the data. Figures 6.2 A – F visually represent the best-fit models for each pair-wise comparison as outlined in Table 6.1.

It is apparent from Figures 6.2A and B that weeping alkaligrass and Nuttall's alkaligrass had a much stronger, negative impact on Kentucky bluegrass biomass production than Kentucky bluegrass did on itself regardless of the species combination. Interspecific competitive effects on the biomass of Nuttall's alkaligrass were more pronounced when grown with weeping alkaligrass (Figure 6.2D) than Kentucky bluegrass (Figure 6.2C). The interspecific effects of both weeping alkaligrass and Kentucky bluegrass were stronger than the intraspecific effect of Nuttall's alkaligrass. However, intraspecific competition was more pronounced when Nuttall's alkaligrass was grown with weeping alkaligrass than Kentucky bluegrass. At low densities of weeping alkaligrass, the interspecific effect of competition was more pronounced when grown in combination with Nuttall's alkaligrass (Figure 6.2F) than Kentucky bluegrass (Figure 6.2E). As was witnessed with Nuttall's alkaligrass, the intraspecific effect was stronger when weeping alkaligrass was grown with Nuttall's alkaligrass than Kentucky bluegrass. However, for all species combinations, it is important to note that the effect of competititon, both inter- and intraspecific, often diminished over increasing densities as is shown in Figure 6.2A through F, thus the significant density-dependent interactions.

Generally, it appears from the response surface graphs that weeping and Nuttall's alkaligrass are more competitive than Kentucky bluegrass, though their interspecific affect on each another is greater than their intraspecific affects, respectively. However, as mentioned earlier, the effect of the interaction of increasing densities of both species was very important ($P<0.001$) and should be analyzed in addition to quadratic parameters, where significant.

Change in biomass across densities with the addition of one plant

While response surface graphs present all the data clearly, it is difficult to explain how increasing densities changes the effect of competition. By slicing through the response surface graph, it is possible to create a linear representation which clarifies how the biomass response was affected by increasing densities. There are an abundance of possible 'slices' through the response surface which can be presented. The comparisons presented were the effect on the response species biomass (weeping alkaligrass, Nuttall's alkaligrass or Kentucky bluegrass) at initial densities of 1 through 16 plants per $0.25m^{-2}$ with the addition of just one additional weeping alkaligrass, Nuttall's alkaligrass or Kentucky bluegrass plant (Figure 6.3).

Substitution rates show the percent change in biomass of a species (ex: Kentucky bluegrass) when subjected to a one unit increase in intraspecific (ex: Kentucky bluegrass) versus interspecific competition (ex: Nuttall's alkaligrass or weeping alkaligrass). The graphs in Figure 6.3 indicate that the effect of each additional unit increase diminishes with higher original densities regardless of species. For example, Kentucky bluegrass is more affected by an additional weeping alkaligrass or Nuttall's alkaligrass than an additional Kentucky bluegrass regardless of the initial Kentucky bluegrass density (Figure 6.3A). With an initial density of 6 Kentucky bluegrasses, the addition of 1 Nuttall's alkaligrass resulted in an overall reduction of the average biomass by 17.4% ($\pm$ 3.5%); whereas, the addition of one weeping alkaligrass reduced the average Kentucky bluegrass biomass by 17.3% (+ 3.0, - 2.3%). Therefore, weeping alkaligrass and Nuttall's alkaligrass are equal in their affect on average biomass of Kentucky bluegrass, which is much greater than Kentucky bluegrasses effect on itself. At an initial density of 6 Kentucky bluegrass plants an additional Kentucky bluegrass plant reduced the average biomass by only 3.9% (± 2.0%). Yet, while, weeping alkaligrass and Nuttall's alkaligrass are equal in their effect on Kentucky bluegrass, they are not equal in their effect on each other.

Nuttall's alkaligrass was more affected by an additional weeping alkaligrass than Kentucky bluegrass. For example, with an initial density of 6 Nuttall's alkaligrass plants, the addition of 1 weeping alkaligrass resulted in an overall reduction of the average biomass by 17.3% (+ 3.2, -3.4%); where as, the addition of 1 Kentucky bluegrass resulted in a biomass reduction of 11.6% (+ 1.4, - 1.9%) (Figure 6.3B). At the same initial density of 6 Nuttall's alkaligrass plants, the intraspecific effect of 1 Nuttall's alkaligrass resulted in an average biomass reduction of 16.5% (+ 3.2, - 3.4%).

Given the same initial density of 6 weeping alkaligrass plants, the addition of 1 Nuttall's alkaligrass resulted in an overall reduction of the average biomass by 17.3% (+ 4.0, -4.3%); where as, the addition of 1 Kentucky bluegrass resulted in a biomass reduction of only 9.4% (+ 2.8, - 3.0%) (Figure 6.3C). The intraspecific effect of an additional weeping alkaligrass was a 17.3% (+ 3.2, -3.3%) reduction in average biomass.

Therefore, in year 1, across many densities, an additional Nuttall's alkaligrass was the most likely to reduce biomass production of all three species, followed by weeping alkaligrass and then Kentucky bluegrass.

Year 2

Drastic overwinter mortality occurred between the Year 1 harvest and Year 2 growing season; in fact one complete replication was abandoned due to excessive mortality of all three species. The abandoned replicate was close to a juniper windbreak which we suspect caused an extreme drought condition. Therefore, the remaining two replicates were analyzed in the same manner as Year 1. As well, a presentation of total survival by species is presented.

Comparison of species survival

An assessment of survival of the three species across two replications showed that the lowest survival rates were incurred by weeping alkaligrass, followed by Nuttall's alkaligrass, and lastly Kentucky bluegrass (Figure 6.4). It is also apparent that survival of each species was not dependant upon the species mixture (Figure 6.4). For example, the average percent survival of weeping alkaligrass was 47% ($\pm$ 11%) when grown with Nuttall's alkaligrass versus 34% ($\pm$ 15%) when grown with Kentucky bluegrass. Due to the very high overall percent survival of Kentucky bluegrass, it is not surprising that Kentucky bluegrass survival was not affected by the original planting densities of Nuttall's alkaligrass, weeping alkaligrass or Kentucky bluegrass ($P>0.05$). Nor were the probabilities of weeping alkaligrass survival affected by weeping alkaligrass or Nuttall's alkaligrass planting densities ($P>0.05$). However, the original planting density of Kentucky bluegrass did affect the probability of weeping alkaligrass survival such that an increase of 1 Kentucky bluegrass plant per $0.25m^{-2}$ resulted in a 56% decrease in the probability of weeping alkaligrass survival.

Nuttall's alkaligrass survival was affected by planting densities of Kentucky bluegrass, Nuttall's alkaligrass and weeping alkaligrass (Figure 6.5). The probability of Nuttall's alkaligrass survival from year 1 to year 2 decreased as densities of Nuttall's alkaligrass increased across all species combinations. As well, probabilities of survival were lower when an additional Nuttall's alkaligrass was added at the time of planting versus an additional Kentucky bluegrass ($P<0.05$). The effect of an additional weeping alkaligrass was not different from either an additional Kentucky bluegrass or Nuttall's alkaligrass ($P>0.05$).

Modeling the data

Model selection followed the same procedures as outlined in Year 6.1. Visual representation of the biomass data is modeled using 3-dimensional response surfaces (Figure 6.6A through F). Best fit models with their respective R^2 results are presented in Table 6.2. The species interaction and the quadradic transformation of densities were often significant.

Change in biomass across densities and proportions

In Year 2, there was a definite change in competitive ability of the species analyzed. The results from Table 6.2 and Figure 6.6A and B indicate that at low densities of Nuttall's alkaligrass or Kentucky bluegrass, the biomass of Kentucky bluegrass was more strongly affected by Nuttall's alkaligrass than Kentucky bluegrass (Figure 6.6A). Kentucky bluegrass exhibited a polynomial response when grown with weeping alkaligrass (Figure 6.6B). The polynomial response indicates that Kentucky bluegrass growth increased linearly to a maximum biomass after which the biomass response was a linear decline with increasing densities.

Growth of Nuttall's alkaligrass was equally affected by increases in Kentucky bluegrass or Nuttall's alkaligrass densities when these two species were grown in combination (Figure 6.6C). As well, Nuttall's alkaligrass biomass was equally affected by increases in weeping alkaligrass densities as increases in Nuttall's alkaligrass densities (Figure 6.6D).

Growth of weeping alkaligrass was unaffected by changes in its own original densities (Table 6.2); rather, increases in Kentucky bluegrass resulted in a polynomial decrease (Figure 6.6E). At low Nuttall's alkaligrass densities, increasing weeping alkaligrass densities resulted in a linear decrease in biomass, yet at high Nuttall's alkaligrass densities increasing weeping alkaligrass densities resulted in linear increases in biomass (Figure 6.6F). Increases in Nuttall's alkaligrass resulted in a polynomial decrease in weeping alkaligrass biomass (Figure 6.6F).

It appears from the response surface graphs that, in Year 2, Kentucky bluegrass was more competitive interspecifically than either Nuttall's alkaligrass or weeping alkaligrass. In general, weeping alkaligrass and Nuttall's alkaligrass were almost equal in their interspecific competitive ability. However, as in year 1, the effect of the interaction of increasing densities and polynomial effects should be analyzed.

Change in biomass across densities with the addition of one plant

The graphs in Figure 6.7 indicate that the effect of each additional unit increase did not always diminish with higher original densities, and the responses are not as clear as year 1 results.

Kentucky bluegrass was more affected by an additional weeping alkaligrass than an additional Nuttall's alkaligrass (Figure 6.7A). For example, with an initial density of 6 Kentucky bluegrasses, the addition of one Nuttall's alkaligrass resulted in an overall reduction of the average biomass by 8.0% (+ 2.3, - 2.4%); whereas, the addition of one weeping alkaligrass reduced the average Kentucky bluegrass biomass by 20.3% (+ 6.7, - 7.5%). In year 2, the intraspecific effect of Kentucky bluegrass was strong, reducing the average biomass by 25.9% (+ 7.7, - 8.6%).

It is apparent that Nuttall's alkaligrass was more affected by an additional Kentucky bluegrass than an additional weeping alkaligrass or Nuttall's alkaligrass regardless of species combination (Figure 6.7B). For example, with an initial density of 6 Nuttall's alkaligrass plants, the addition of one Kentucky bluegrass resulted in an overall reduction of the average biomass by 36.0% (+ 10.6, -12.7) versus 22.8% (+ 4.4, - 5.6%) with an additional weeping alkaligrass. The intraspecific effect of Nuttall's alkaligrass was highly variable (Figure 6.7B). At an initial density of 6 plants, there was no difference in average biomass with the addition of one Nuttall's alkaligrass.

Due to high mortality, weeping alkaligrass biomass was difficult to model in year 2. Even with high mortality, the biomass of weeping alkaligrass was more strongly affected by increases in Nuttall's alkaligrass plants or Kentucky bluegrass plants than increases in weeping alkaligrass plants (Figure 6.7C). Given the same initial density of 6 weeping alkaligrass plants, the addition of 1 Nuttall's alkaligrass plant resulted in an overall reduction of the average biomass by 40.1% (+ 13.5, -17.9%), versus a reduction of 41.1% (+13.5, - 15.6%) with the addition of 1 Kentucky bluegrass plant. The addition of 1 weeping alkaligrass plant resulted in highly variable changes over increasing densities.

Generally, the effect of Kentucky bluegrass was greater than either the interspecific or intraspecific effects of weeping alkaligrass or Nuttall's alkaligrass across most densities.

Changes from Year 1 to Year 2

An assessment of percent change in biomass of all three species across all treatment densities indicated that the average Kentucky bluegrass biomass increased by roughly 100% while biomass of both alkaligrass species decreased by almost 100% (Figure 6.8). In the first year, the average biomass of Kentucky bluegrass was less (17.1 g + 4.6, - 3.7 g) than Nuttall's alkaligrass (33.1 g + 10.1, - 6.0 g) but not different from weeping alkaligrass (22.2 g + 4.9, - 5.8). However, in year 2, the average biomass of Kentucky bluegrass was greater (34.5 g + 9.8, - 6.5 g) than either Nuttall's alkaligrass (5.0 g + 3.2, - 2.2 g) or weeping alkaligrass (1.2 g + 1.0, - 0.6 g). Possibly the initial plant densities and species combinations affected the changes in plant biomass.

Modeling the data

Model selection followed the same procedures as outlined in Year 1. Visual representation of the biomass data was modeled using 3-dimensional response surfaces (Figure 6.9). Best fit models with their respective R^2 results are presented in Table 6.3. The interaction of the densities of both species as well as quadradic terms were often significant ($P < 0.05$); therefore, all results will be described in the same manner as Year 1.

Change in biomass across densities and proportions

Changes in biomass from Year 1 to Year 2 were generally positive for Kentucky bluegrass and negative for the two species of alkaligrass (Figure 6.9A through F). The results from Table 6.3 and Figure 6.9A indicate that across all densities of Nuttall's alkaligrass and Kentucky bluegrass, the change in biomass of Kentucky bluegrass was significantly improved (0.04) by the addition of 1 Nuttall's alkaligrass at original planting versus reduced (-0.04) by the addition of 1 Kentucky bluegrass at original planting (Figure 6.9A). Kentucky bluegrass exhibited a polynomial response between the two years when grown with weeping alkaligrass, with high rates of biomass increases between year 1 and year 2 at low densities of weeping alkaligrass (Figure 6.9B).

Nuttall's alkaligrass also exhibited a polynomial response to the initial planting densities of Nuttall's alkaligrass. The impact of Nuttall's alkaligrass densities on changes in biomass were steeper at high densities versus low densities of Kentucky bluegrass (Figure 6.9C). Where as, the effect of Kentucky bluegrass on changes in Nuttall's alkaligrass biomass was more pronounced at low Nuttall's alkaligrass densities rather than high. When grown in combination with weeping alkaligrass, Nuttall's alkaligrass biomass was influenced negatively by additional weeping alkaligrass densities at low Nuttall's alkaligrass densities. Whereas, Nuttall's alkaligrass biomass was influenced positively by additional Nuttall's alkaligrass at high weeping alkaligrass densities (Figure 6.9D).

Changes in biomass of weeping alkaligrass were unaffected by changes in its original densities (Table 6.3) ($P > 0.05$), rather there was a polynomial effect of the original Kentucky bluegrass densities (Figure 6.9E). The relationship between changes in weeping alkaligrass biomass and densities of weeping alkaligrass and Nuttall's alkaligrass was poorly explained by the full model used ($R^2 = 0.25$) (Table 6.3). High variability in the data made it difficult to model the results (Figure 6.9F).

The positive changes in the biomass of Kentucky bluegrass were affected the most by the original planting densities of weeping alkaligrass, followed by Kentucky bluegrass and then Nuttall's alkaligrass.

Nuttall's alkaligrass was negatively affected by increasing Kentucky bluegrass densities across all densities of Nuttall's alkaligrass. Yet, it exhibited mixed responses (both positive and negative) to increasing densities of weeping alkaligrass or Nuttall's alkaligrass; making a general interpretive statement difficult. Changes in biomass of weeping alkaligrass were most negatively affected by original Kentucky bluegrass densities, followed by Nuttall's alkaligrass and then itself. However, as in year 1 and year 2, the effect of the interaction of increasing densities and polynomial effects must be analyzed.

Change in Year 1 to Year 2 biomass across densities with the addition of one plant

Kentucky bluegrass biomass decreased roughly 32% (-12.0, +17.1%) from year 1 to year 2 across all original Kentucky bluegrass planting densities when 1 weeping alkaligrass was added to the mix (Figure 6.10A). Whereas Kentucky bluegrass biomass increased roughly 4.1% (±2.0%) from year 1 to year 2 across all original Kentucky bluegrass planting densities when 1 Nuttall's alkaligrass was added at the time of planting (Figure 6.10A). The intraspecific effect on biomass of Kentucky bluegrass was 8.8% ± 6.0% (Figure 6.10A).

The effect of an additional plant had highly variable results for Nuttall's alkaligrass changes in biomass from year 1 to year 2 (Figure 6.10B). For example, with an initial density of 6 Nuttall's alkaligrass plants, there was no difference in the effect of an additional Kentucky bluegrass (16.1% decrease ± 4.1%) versus an additional weeping alkaligrass (14.3% decrease ± 5.0%). However, the intraspecific effect of an additional Nuttall's alkaligrass plant was highly variable but positive. For example, at an initial density of 6 Nuttall's alkaligrass plants, the addition of one Nuttall's alkaligrass increased its average biomass by 27.4% (+27.0, -22.4%).

Weeping alkaligrass biomass was consistently reduced by 36.9% (-12.4, + 14.5%) across all initial densities with the addition of one Kentucky bluegrass plant. The effect of an additional Nuttall's alkaligrass at an original density of 6 weeping alkaligrass plants, resulted in a 30.0% decrease (± 15.3%) in biomass from year 1 to year 2, yet an additional weeping alkaligrass plant resulted in a 5.8% increase in average biomass (- 8.5 ,+9.1%).

Conclusions

Results of our study indicated that in year 1 Kentucky bluegrass was slower to establish, in terms of biomass accumulation, than Nuttall's alkaligrass, and to a lesser extent weeping alkaligrass. Yet, by year 2, the average Kentucky bluegrass plant was vastly larger than either of the alkaligrasses, in particular weeping alkaligrass.

During the first year of establishment, Kentucky bluegrass biomass was reduced equally by both species of alkaligrass more than by Kentucky bluegrass itself.

Results from the second year indicate that, under the conditions of this study, Kentucky bluegrass was able to out-survive the two species of alkaligrass, especially weeping alkaligrass. In year 2, the original planting densities of Kentucky bluegrass were the strongest indicators of potential biomass for all three species. In a comparison between year 1 and year 2 biomass, it is apparent that while weeping alkaligrass exhibited high levels of mortality, the original planting densities were able to strongly impact the year 2 biomass accumulation of both Kentucky bluegrass and Nuttall's alkaligrass. This indicates that even though weeping alkaligrass mortality was high, there existed a strong residual effect not easily offset by Kentucky bluegrass growth in year 2.

Although unaccountable, the effect of late-season mowing (i.e. – harvest in year 1) may have played a greater role in year 2 biomass of weeping alkaligrass than competition. However, Kentucky bluegrass seed fields are swathed before threshing, thus this procedure may reduce weeping alkaligrass, and to a lesser extent Nuttall's alkaligrass, after the first year.

For Kentucky bluegrass producers of eastern Oregon, competitive effects of both species of alkaligrass are equally damaging in the first year. Diligent weed control is necessary to prevent soil seed bank development and Kentucky bluegrass seed contamination. Alkaligrass plants that escape weed control efforts in the first year could have a difficult time surviving through the Kentucky bluegrass harvesting procedures and into the next growing season. However, while weeping alkaligrass may not survive into year 2, the effects of its density in year 1 may reduce Kentucky bluegrass yields the following year. Therefore, it is hypothesized that weeping alkaligrass will prove to be a greater threat to Kentucky bluegrass production in eastern Oregon than Nuttall's alkaligrass.

The changes in all three species biomass in the second year introduces a point of interest for competition study practitioners. Researchers should consider potential differences in rates of establishment, growth habit, reproductive strategies, among other attributes when designing competition studies.

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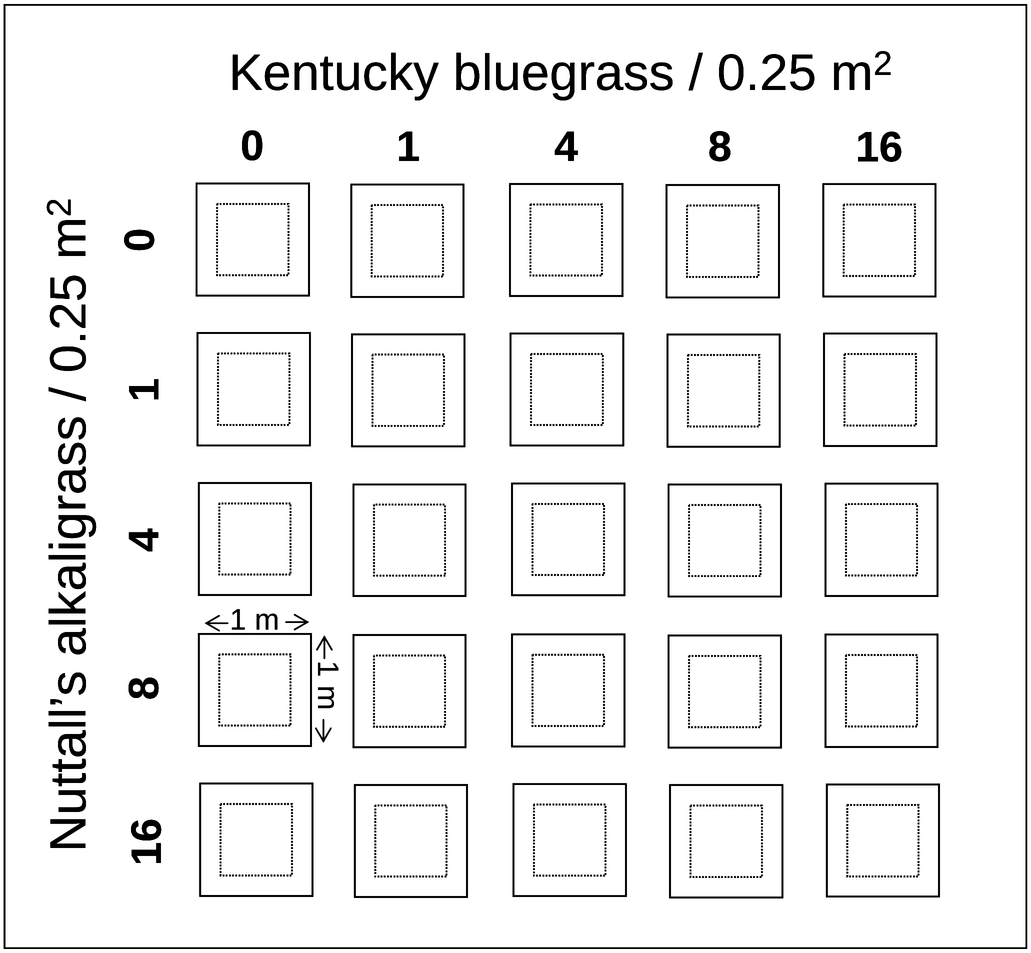

Figure 6.1 – Plot lay-out for one (Kentucky bluegrass vs. Nuttall's alkaligrass) of three two-way combination of species.

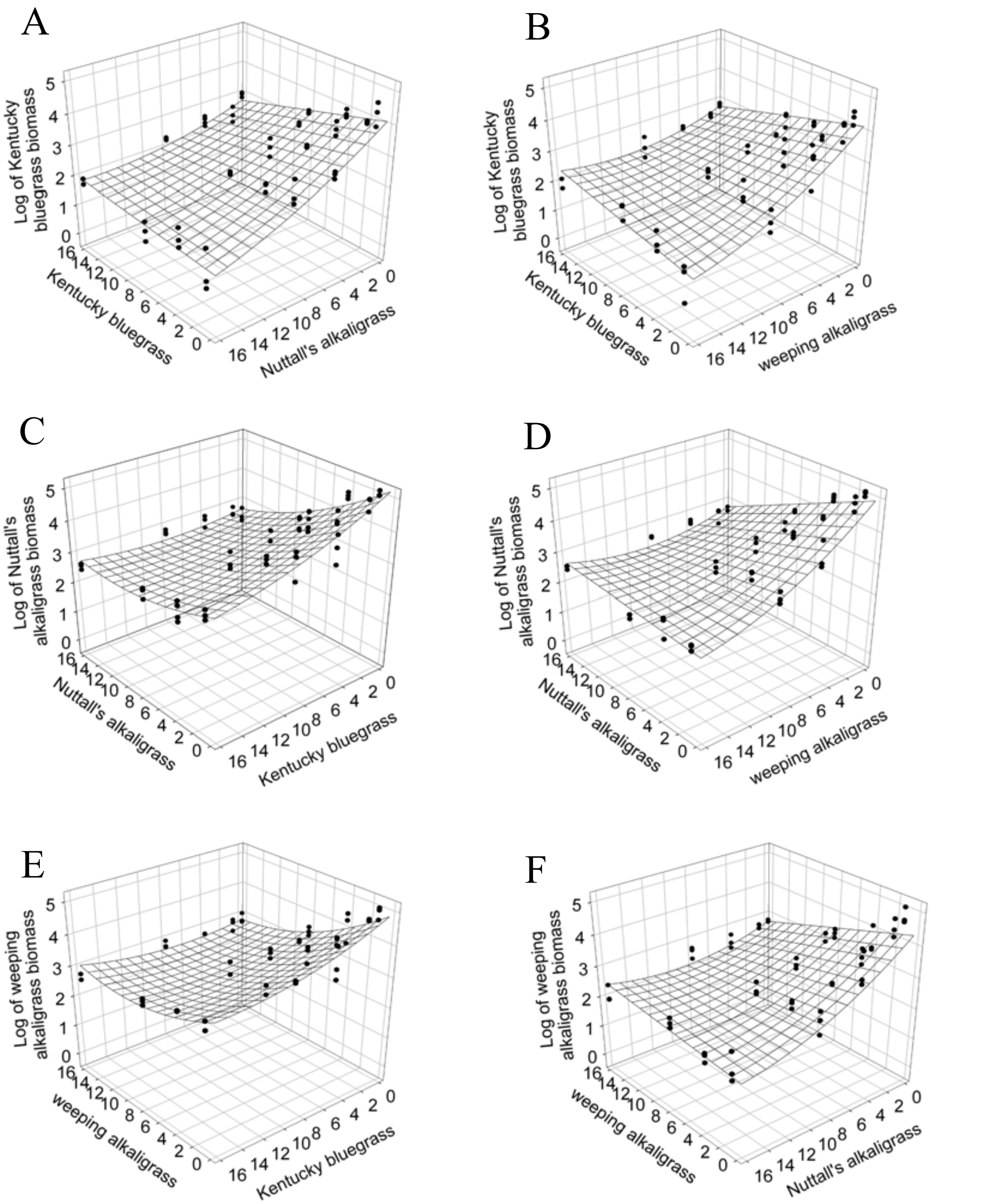

Figure 6.2 – Comparison of competition on the log of biomass of weeping alkaligrass, Nuttall's alkaligrass and Kentucky bluegrass in Year 1. X and Z axes indicate the planting density per $0.25m^{-2}$ of each species respectively.

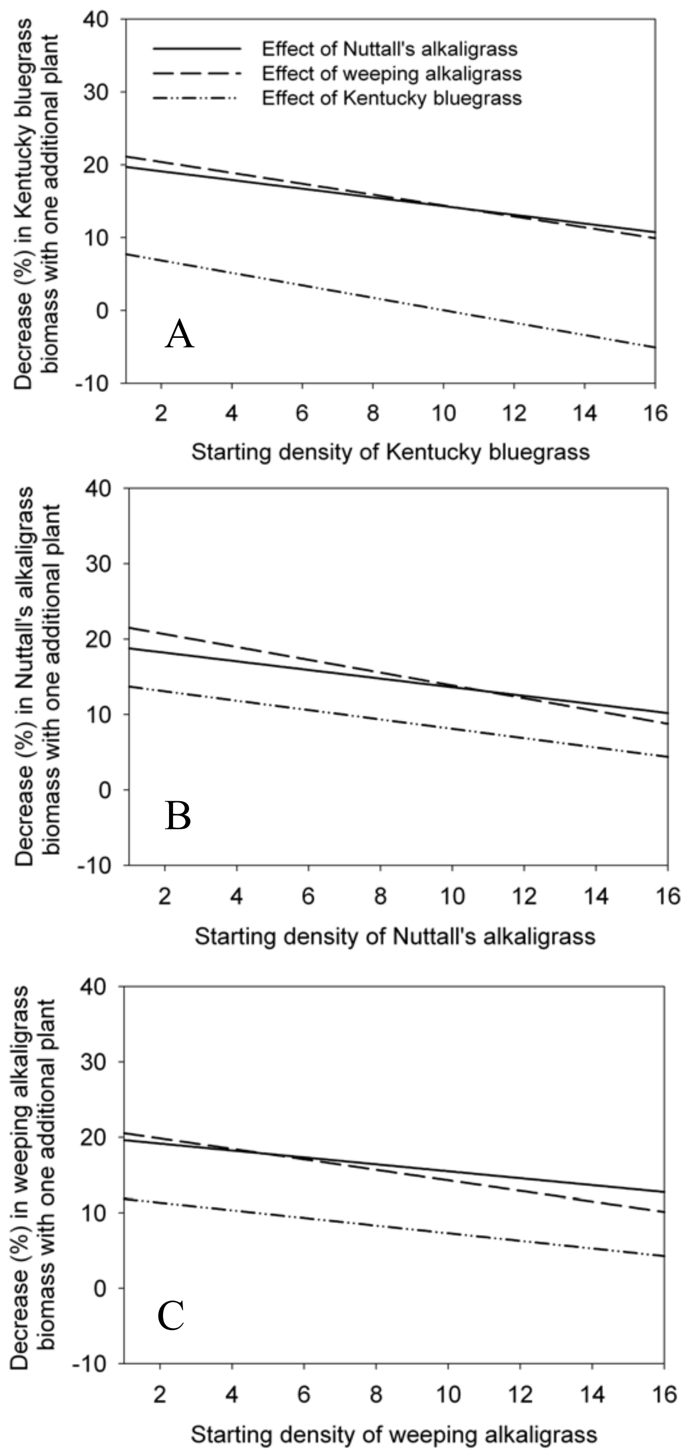

Figure 6.3 – Year 1 change (%) in average biomass of Kentucky bluegrass (A), Nuttall's alkaligrass (B) and weeping alkaligrass (C) at differing initial densities with the addition of one Kentucky bluegrass versus an additional weeping or Nuttall's alkaligrass.

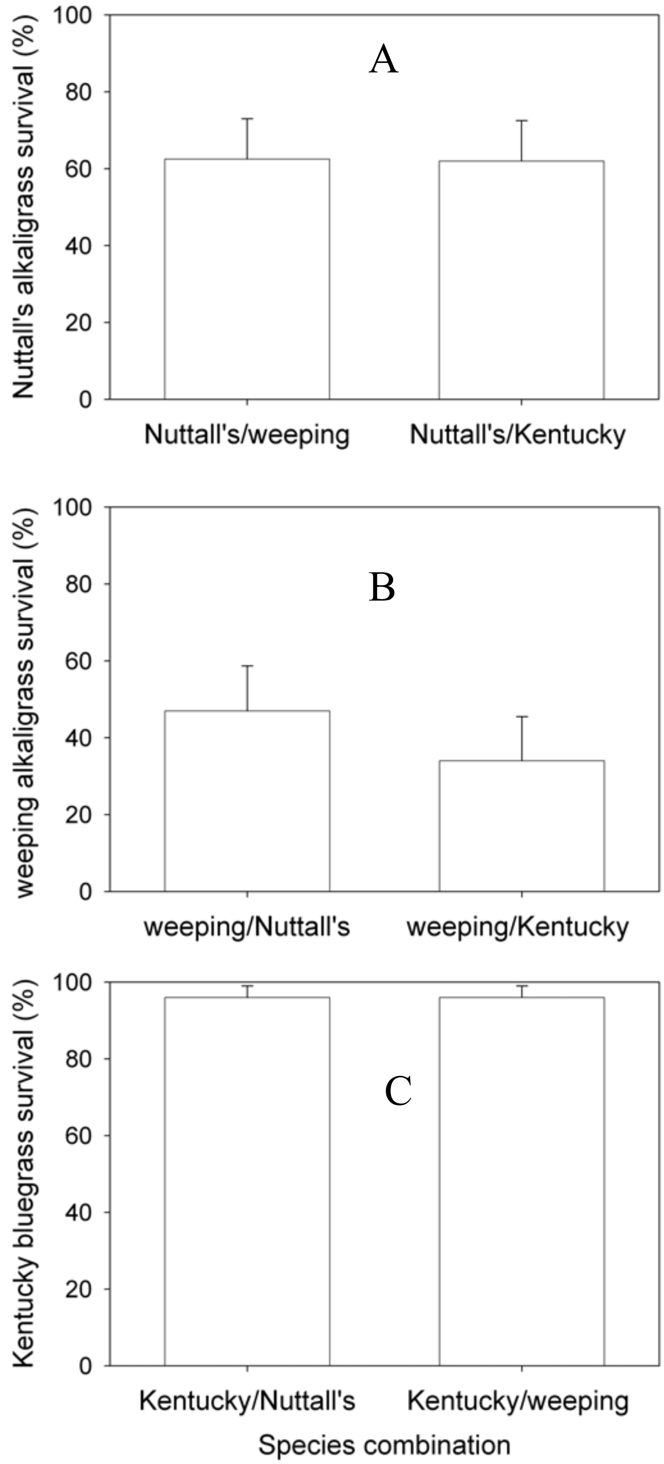

Figure 6.4 – Average percent survival (+ 95% confidence intervals) of Nuttall's alkaligrass (A), weeping alkaligrass (B) and Kentucky bluegrass (C) at Year 2 when grown in two-way combination with each other.

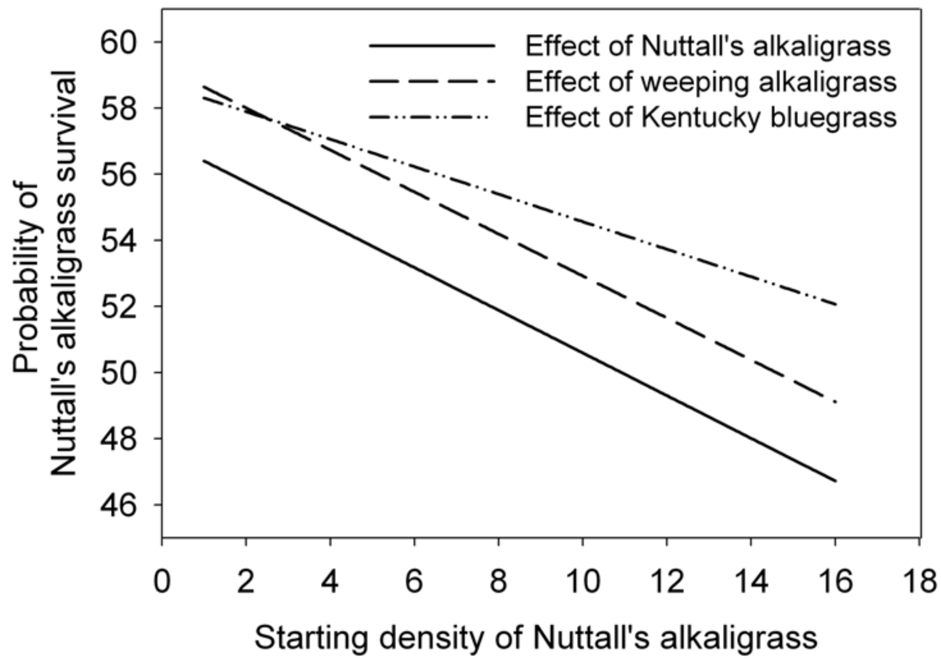

Figure 6.5 – Probability of Nuttall’s alkaligrass survival at various initial densities with the addition of one Kentucky bluegrass, versus an additional weeping alkaligrass or Nuttall’s alkaligrass.

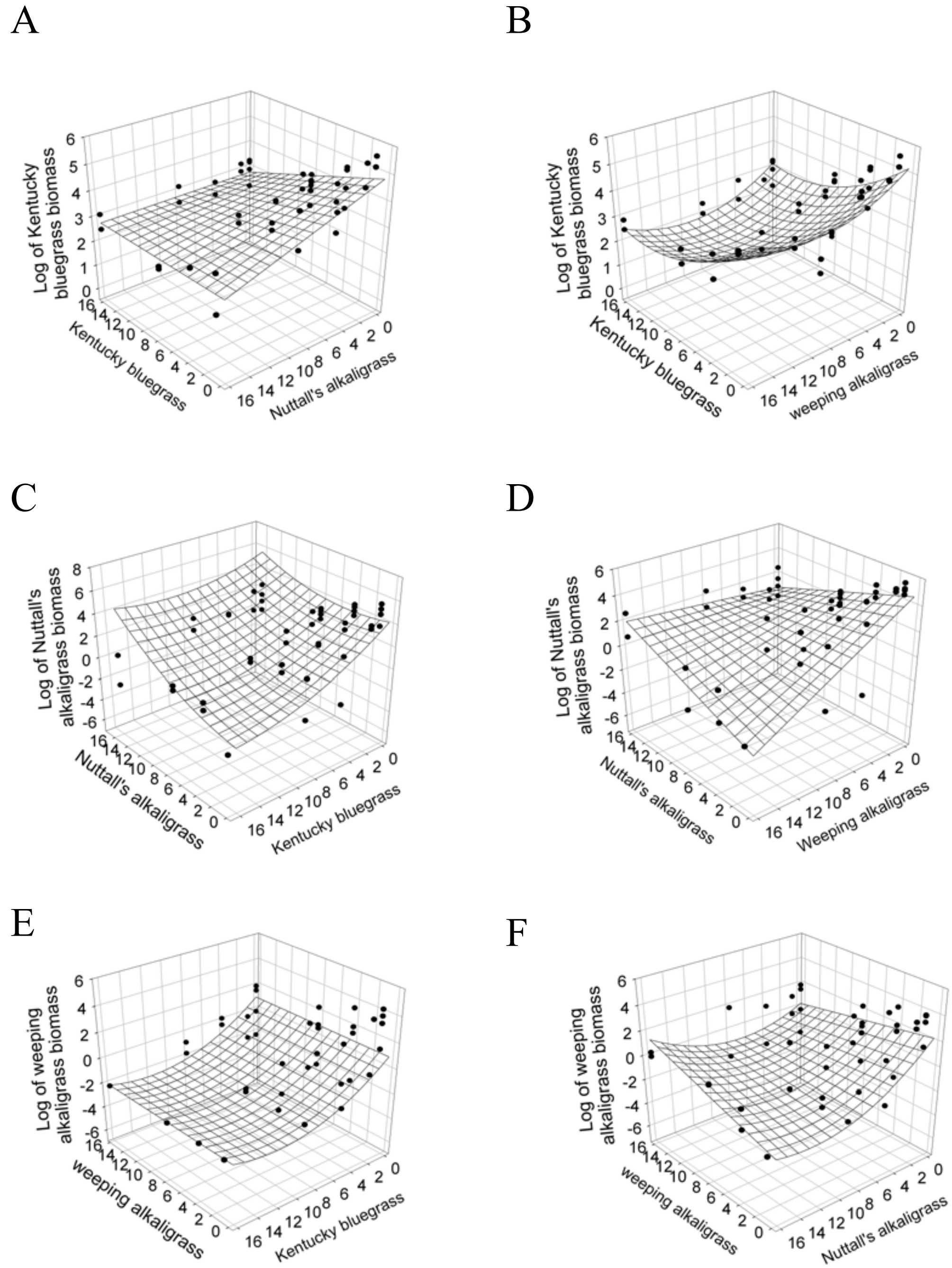

Figure 6.6 – Year 2 comparison of competition on the log of biomass of weeping alkaligrass, Nuttall’s alkaligrass and Kentucky bluegrass.

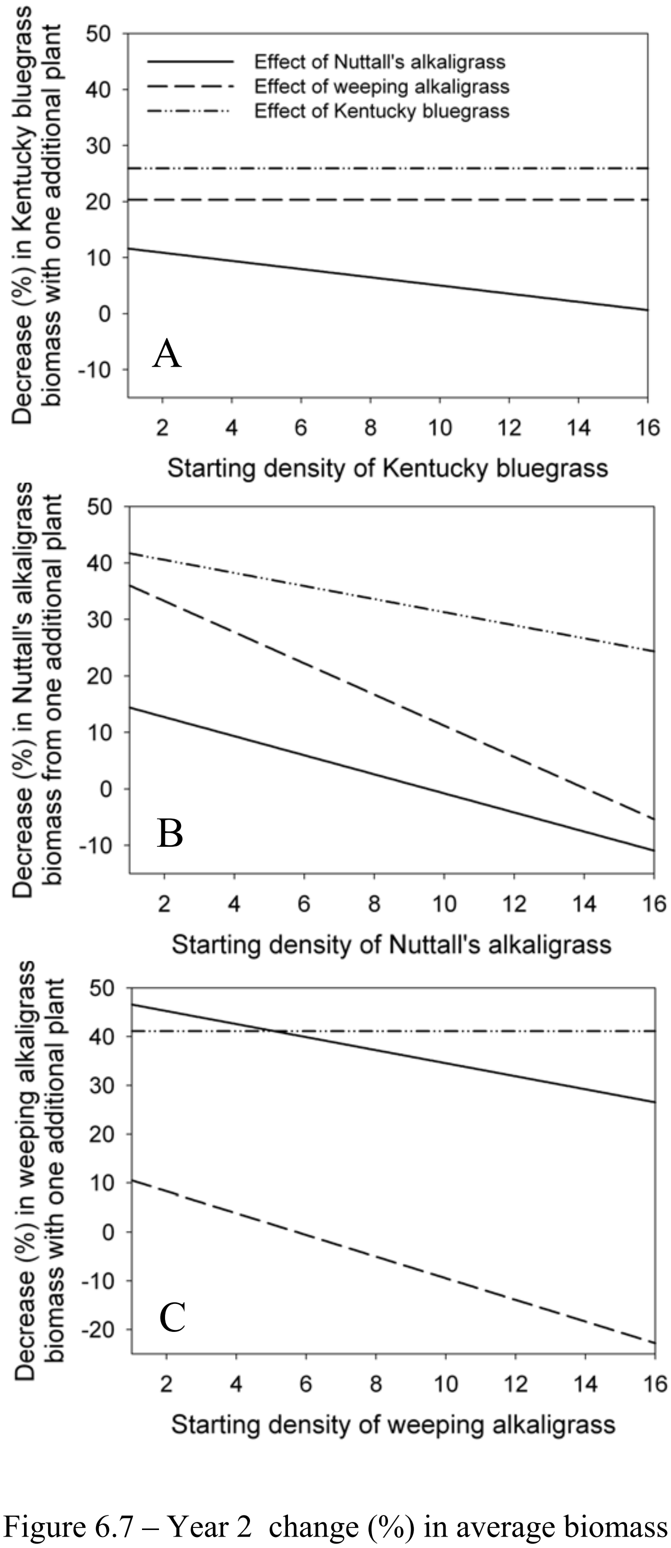

Figure 6.7 – Year 2 change (%) in average biomass of Kentucky bluegrass (A), Nuttall’s alkaligrass (B), and weeping alkaligrass (C) at differing initial densities with the addition of one Kentucky bluegrass versus an additional weeping or Nuttall’s alkaligrass.

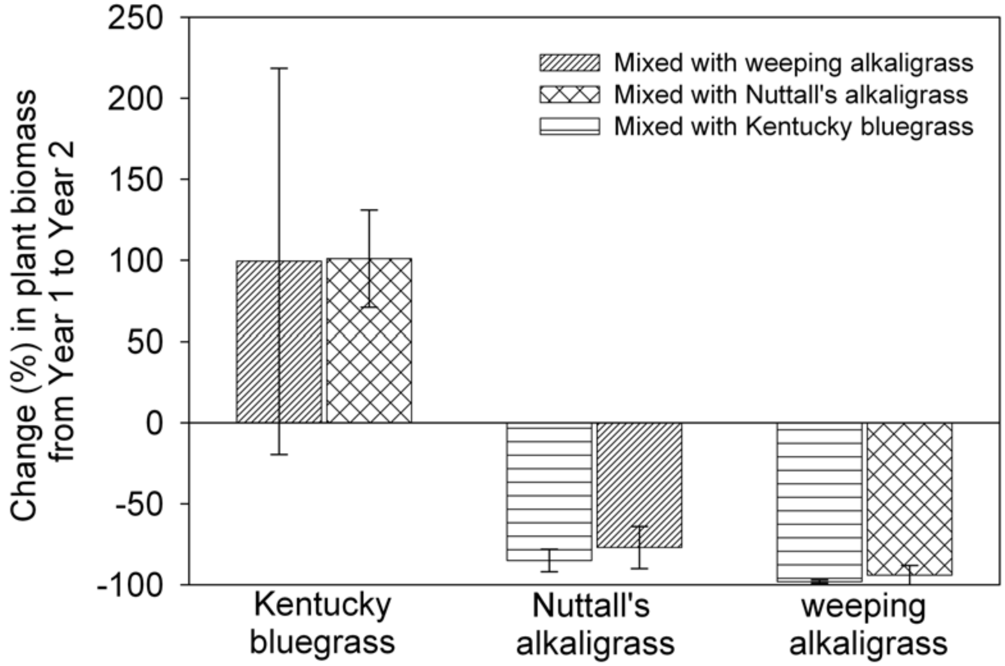

Figure 6.8 – Percent change from year 1 to year 2 of average plant biomass of Kentucky bluegrass, Nuttall's alkaligrass, and weeping alkaligrass (± 95% confidence intervals) across all treatment densities.

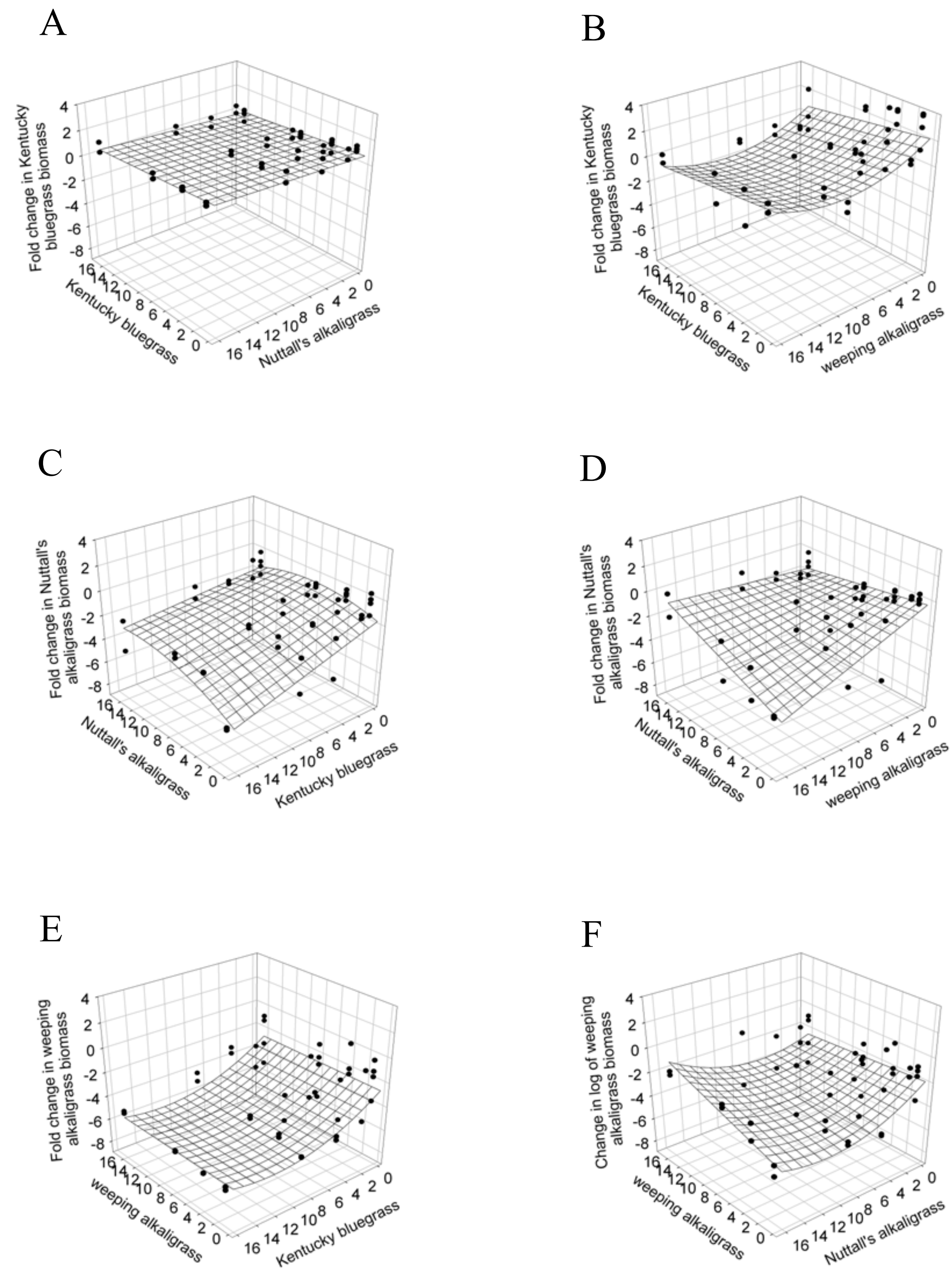

Figure 6.9 – Comparison of competition on the change in biomass from year 1 to year 2 of weeping alkaligrass, Nuttall’s alkaligrass, and Kentucky bluegrass.

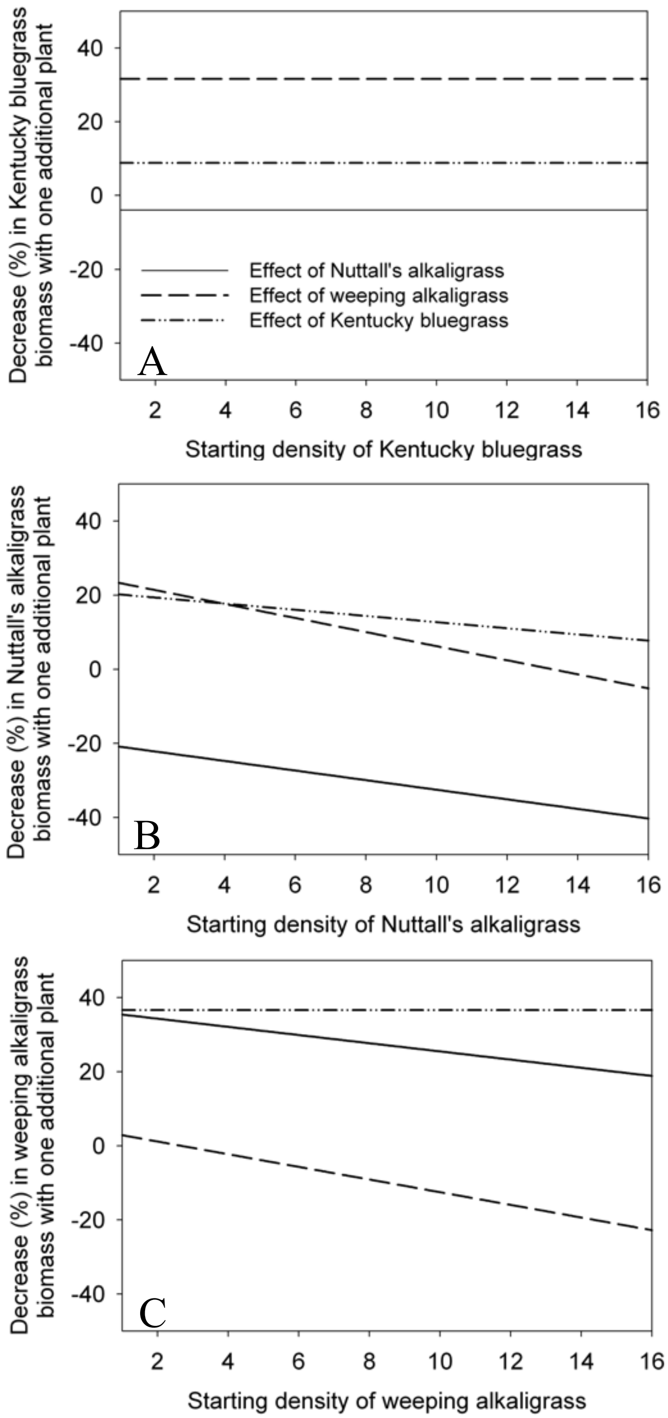

Figure 6.10 – The change (%) in average biomass from Year 1 to Year 2 of Kentucky bluegrass (A), Nuttall's alkaligrass (B), and weeping alkaligrass (C) at various initial densities with the addition of one Kentucky bluegrass, versus an additional weeping or Nuttall's alkaligrass.

Table 6.1. Year 1 best-fit models for average plant biomass (Y) by plot for each species in a two species mixture, where D represents density (plants per plot) of Kentucky bluegrass (D_k), weeping alkaligrass (D_w), and Nuttall's alkaligrass (D_n).

Species Mixture	Variable	Equation	R^2
Kentucky X Weeping alkaligrass			
Kentucky	Biomass	$LogY_k = 4.16 - 0.26D_w - 0.09D_k + 0.006D_w^2 + 0.009D_wD_k$	0.82
Weeping	Biomass	$LogY_w = 4.88 - 0.24D_w - 0.14D_k + 0.007D_w^2 + 0.004D_k^2 + 0.01D_wD_k$	0.87
Kentucky X Nuttall's alkaligrass			
Kentucky	Biomass	$LogY_k = 4.11 - 0.23D_n - 0.09D_k + 0.004D_n^2 + 0.007D_nD_k$	0.90
Nuttall's	Biomass	$LogY_n = 5.22 - 0.24D_n - 0.17D_k + 0.005D_n^2 + 0.003D_k^2 + 0.01D_nD_k$	0.92
Weeping X Nuttall's alkaligrass			
Weeping	Biomass	$LogY_w = 4.33 - 0.10D_w - 0.26D_n + 0.006D_n^2 + 0.008D_wD_n$	0.83
Nuttall's	Biomass	$LogY_n = 4.95 - 0.27D_w - 0.14D_n + 0.01D_wD_n$	0.90

Table 6.2. Year 2 best-fit models for average plant biomass (Y) by plot for each species in a two species mixture, where D represents density (plants per plot) of Kentucky bluegrass (D_k), weeping alkaligrass (D_w), and Nuttall's alkaligrass (D_n).

Species Mixture	Variable	Equation	R^2
Kentucky X Weeping alkaligrass			
Kentucky	Biomass	$LogY_k = 5.22 – 0.27D_w – 0.34D_k + 0.01D_w^2 + 0.01D_k^2$	0.68
weeping	Biomass	$LogY_w = 0.96 – 0.62D_k + 0.03D_k^2$	0.43
Kentucky X Nuttall's alkaligrass			
Kentucky	Biomass	$LogY_k = 4.83 – 0.13D_n – 0.13D_k + 0.01D_nD_k$	0.69
Nuttall's	Biomass	$LogY_n = 4.19 – 0.17D_n – 0.60D_k + 0.02D_k^2 + 0.02D_nD_k$	0.64
Weeping X Nuttall's alkaligrass			
Nuttall's	Biomass	$LogY_n = 4.69 – 0.46D_w – 0.24D_n + 0.03D_wD_n$	0.62
weeping	Biomass	$LogY_w = 2.25 - 0.12 D_w – 0.72D_n + 0.03D_n^2 + 0.02D_wD_n$	0.38

Table 6.3. Best-fit models for change in the log of average plant biomass from Year 1 to Year 2 for each species in a two species mixture, where D represents density (plants per plot) of Kentucky bluegrass (D_k), weeping alkaligrass (D_w), and Nuttall's alkaligrass (D_n).

Species Mixture	Variable	Equation	R^2
Kentucky X Weeping alkaligrass			
Kentucky	Biomass	$\text{Log}Y_k = 2.19 - 0.45D_w + 0.02{D_w}^2 - 0.09D_k$	0.33
weeping	Biomass	$\text{Log}Y_w = -2.61 - 0.52D_k + 0.02{D_k}^2$	0.43
Kentucky X Nuttall's alkaligrass			
Kentucky	Biomass	$\text{Log}Y_k = 0.80 + 0.04D_n - 0.04D_k$	0.45
Nuttall's	Biomass	$\text{Log}Y_n = -1.62 - 0.23D_k + 0.22D_n - 0.01{D_n}^2 + 0.01D_kD_n$	0.54
Weeping X Nuttall's alkaligrass			
Nuttall's	Biomass	$\text{Log}Y_n = -0.24 - 0.28D_w - 0.09D_k + 0.02D_wD_k$	0.42
weeping	Biomass	$\text{Log}Y_w = -1.89 - 0.03\ D_w - 0.52D_n + 0.02{D_n}^2 + 0.02D_wD_k$	0.25

The Biology and Ecology of Weeping alkaligrass *(Puccinellia distans*) and

Nuttall's alkaligrass (*Puccinellia nuttalliana*)

CHAPTER 7

General Conclusions

The results of this study indicate that weeping alkaligrass may prove to be a greater challenge than Nuttall's alkaligrass for land managers of eastern Oregon, especially Kentucky bluegrass farmers.

Both species of alkaligrass exhibit relatively long afterripening characteristics making control and prevention of alkaligrass seed bank development more difficult for land managers. As well, seeds of either species of alkaligrass will remain viable for at least 1 year within dry stored Kentucky bluegrass. Newly establishing Kentucky bluegrass fields could be subjected to competition from either species due to their ability to germinate at low temperatures allowing for the establishment of dense monocultures early in the season. Early establishment by either species of alkaligrass would limit resources available for the development of other plant species, an obvious competitive advantage. However, once adequately afterripened, weeping alkaligrass had greater germination than Nuttall's alkaligrass at most temperature combinations, in particular at constant temperatures; and had a greater tolerance to extreme high temperatures, as well as drought and salt conditions.

Plant development and fitness of the two species varied depending on the environmental conditions and soil type. Weeping alkaligrass appeared to benefit more than Nuttall's alkaligrass to increased precipitation and agriculturally productive soils. The continued tiller development of weeping alkaligrass throughout the growing season may be troublesome for land managers as this species may exhibit indeterminate inflorescence production and continuous seed production. Nuttall's alkaligrass, on the other hand, appears to have determinate inflorescence production which should translate into one seed production event per growing season. Nuttall's alkaligrass growth may be more limited by available water than sodium salts whereas weeping alkaligrass may be more limited by sodium salts rather than water. Higher relative water contents at the same osmotic potential under normal soil conditions, suggest a greater drought tolerance for weeping alkaligrass than Nuttall's alkaligrass.

While both species are able to germinate and grow on a wide variety of soils, observational studies revealed that Nuttall's alkaligrass was positively associated with exchangeable sodium and negatively associated with exposed mineral soil. Weeping alkaligrass exhibited the traits of a resource generalist, as its abundance was negatively associated with competing vegetation.

Results of a 2-year competition study comparing both species of alkaligrass with Kentucky bluegrass indicated that although both species were more competitive that Kentucky bluegrass in year 1, both species also suffered from high mortality, possibly via the harvesting process. Although Kentucky bluegrass had much higher survival rates than the two species of alkaligrass, especially weeping alkaligrass, the original planting densities of weeping alkaligrass strongly impacted the year 2 biomass accumulation of both Kentucky bluegrass and Nuttall's alkaligrass. Therefore, there existed a strong residual effect of year 1 weeping alkaligrass competition not easily offset by Kentucky bluegrass growth in year 2. For Kentucky bluegrass producers of eastern Oregon, competitive effects of both species of alkaligrass are equally damaging in the first year. Diligent weed control is necessary to prevent soil seed bank development and Kentucky bluegrass seed contamination.

Historically, most land managers of eastern Oregon have not distinguished between weeping alkaligrass and Nuttall's alkaligrass, simply referring to them commonly as alkaligrass. The results of this study indicate that these two species should be distinguished early in the growing season and managed accordingly as weeping alkaligrass exhibited traits which may make it more troublesome within agriculturally productive soil conditions, especially if no competition exists.

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APPENDIX 1

Using Geographic Information Systems to present nongeographical data:

An example using 2-way thermogradient plate data

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Abstract

"A picture is worth a thousand words" is a familiar truism which is aptly suited to the dilemma of presenting complex research results involving multiple explanatory variables. An example of such a scenario is the use of two-way thermogradient plates to study optimal germination temperatures and germination over time to answer a variety of biological questions. Two-way thermogradient plates produce a plethora of seed germination data, the value of which quickly becomes obscured in cumbersome tabular data formats. Problems related to comprehensible data presentation can swell when germination over time is incorporated into an experiment. Although somewhat unorthodox, Geographic Information Systems, (GIS) based techniques provide a powerful tool which provides a clear and visually evident presentation of seed germination data to the reader.

Introduction

Studying the variation of a dependent variable as a function of two continuous explanatory variables is a scientific procedure practiced throughout a range of disciplines. Currently, there are a variety of methods, such as tables and three dimensional graphs, which illustrate the effect of the continuous explanatory variables on the dependant variable. For example, one might study the effect of light and sugar concentrations on the density of bacteria colonization over a period of time. The discussion and techniques presented below are for one example: seed germination over time on a two-way thermogradient plate. However, the reader is invited to explore other opportunities with their research to modify and expand upon these techniques.

Thermogradient plates are used by seed biologists in various disciplines to study optimal germination temperatures and germination over time to answer a variety of biological questions (Larsen et al. 1973, Webb et al. 1987, Lodge and Whalley 2002,Young et al. 2003). Thermogradient plates in general do not provide discrete temperature intervals, but rather a gradient of temperatures – usually a result from cold and hot water passing through pipes under the table surface (Larsen 1971). The two-way thermogradient (Figure 1) plate allows researchers to monitor germination responses to alternating temperatures over a time continuum. However, the amount of data produced from a two-way thermogradient plate presents a challenge to the researcher when trying to present the data in an easily comprehensible visual format for publication and/or presentation.

It is generally understood that a researcher has 90 seconds to entice an audience with a poster at professional meetings and less than 2 minutes to convey the complete package of their research (O'Connor 1991, University of Guelph 2003). Given the obvious time limitation for reviewers at professional meetings it is in the researcher's best interest to present their data in a visually striking and easily interpreted format.

Typically, researchers present their data in tabular form (Larsen et al. 1973, Webb et al. 1987, Lodge and Whalley 2002,Young et al. 2003) such as displayed in Table 1. The tabular format allows for the presentation of precise data results including descriptive statistical conclusions, but does not present a visually clear interpretation of the data, especially germination over time intervals, or interpolation beyond the actual data points collected. However, there exists an opportunity to use Geographic Information System (GIS) based techniques to present thermogradient plate data in a visually clear format which utilizes mathematical formulae to interpolate germination beyond the data points collected. This technical note details the steps necessary to create an improved and efficient presentation of two-way thermogradient plate data using GIS.

Method

GIS Application

The primary application of GIS is the presentation and manipulation of spatially related geographical data. In GIS, the XY coordinates represent the intersection of easting and northing meridians on the Earth's surface. A z value can be recorded at the XY intersection, and it can be any count from the number of ants to the percent concentration of nitrogen at the XY intersection. Elevation is a common z value and is used to create a three dimensional image of the spatial relationship between data collected at each XY intersection. However, because it is rarely possible to collect enough X, Y and z values to produce a smooth three dimensional image, researchers use interpolation - the process of using known data points from different spatial locations on the landscape - to create a continuous surface of values (Johnston et al. 2001). The principle underlying spatial interpolation is the First Law of Geography which states that everything is related to everything else, but near things are more related than distant things, or that the zone of influence will decay over distance (Bonham-Carter 1994). It is assumed that as known value locations get farther away from the predicted value location, the spatial autocorrelation will be reduced (Johnston et al. 2001). It is the role of the GIS operator to determine how many known locations, or nearest neighbors, should be used to predict the unknown value. Within the GIS environment there are various mathematical formulae for interpolation including kriging, spline, and inverse distance weighting. Each method has its own set of assumptions and capabilities.

Kriging would the most suitable option for calculating germination values because, 1) it generates values which do not exceed the highest and lowest values, 2) it is good for sample points which are close together and have extreme differences in values and 3) it is well suited for dense, evenly-spaced sample point sets (Johnston et al. 2001). The kriging method uses weighted zone of influence decay rates which are optimized at each interpolation point by considering distance, clustering and spatial autocorrelation (Bonham-Carter 1994). Ordinary kriging was used to create all maps produced in this article. The formula for ordinary kriging used within the ESRI® ArcGIS™ Geostatistical Analyst extension within ArcMap v8.2™ program (ESRI 2002) is (Johnston et al. 2001):

$$Z(s) = \mu(s) + \varepsilon(s) \qquad (1)$$

Where $Z(s)$ is the unknown germination value being predicted for the location s, $\mu(s)$ represents an unknown constant, and $\varepsilon(s)$ is an error term, assumed to be 0.

Just as known elevation values (z value) can be used to interpolate three dimensional images across the landscape, the known germination values (z value) can be used to interpolate potential germination values across the thermogradient plate.

<u>Image Creation Process</u>

Following data collection, a text (.txt) file was created with three columns: X, Y, representing spatial coordinates, and Germ, expressed as a percent value, as the z value. The text file was saved in ASCII format (Table 2). The researcher can use any initial plausible XY coordinate to serve as the 'southwest' corner of the thermogradient plate. However, all ensuing coordinates must be in relation to the first XY coordinate. Because each digit increment in Universal Transverse Mercador coordinates represents 1 meter on the Earth's surface it is an easy coordinate system to use to create an evenly spaced grid of data coordinates, thus creating a surface which is analogous to the landscape-level context typically analyzed within a GIS environment. To ensure accuracy, the data coordinates were spaced in a manner which reflected their actual location on the thermogradient plate (data points). For example, the data points in this example were in a checkerboard fashion and therefore the offset pattern was reflected with similar gaps in the XY spatial coordinates. The text file was imported into ArcMap™ and the XY data was presented. An example of the data points pattern and mean germination values are presented in Figure 2 as graduated symbols. However, a more mathematically complete and visually pleasing presentation of the data can be produced using interpolation.

In ArcMap v.8.2™ Geostatistical Analyst, the data points were presented and then interpolated into a raster using ordinary kriging prediction mapping. The spherical semivariogram model was used incorporating the four nearest neighbors in the search radius. Map properties such as classification classes and color ramp were adjusted. Using the 'draw' tool in ArcMap™, an even grid was created across the surface to represent the general temperature increments on the thermogradient plate. Text and a legend were added and the complete image was exported as a Tag Image File Format (.tiff). These procedures were repeated for each time interval (Figure 3).

Discussion

The goal of research is to effectively translate data into a comprehensible format which will be understood and utilized within the scientific community. Yet, research is a fast-paced environment where information can be overlooked and disregarded if it is not easily understood. Therefore, it is advantageous for researchers to present data in the most visually impressive and simplistic manner.

For over a decade GIS has been well utilized within the geosciences community for presenting visually impressive images of geographical data. However, GIS can be utilized as a tool within other disciplines to present data other than that of a geographic nature. For example, in this paper, GIS allowed for a clear and dynamic presentation of data relating to seed germination over time on a two-way thermogradient plate.

However, GIS users must be aware of and understand the data manipulation that occurs when using an interpolation formula such as kriging. Also, given that the GIS technique discussed in this paper groups germination data into categories (ie: 16-30%, 31-45%) it may be prudent to combine GIS images with a tabular format to ensure a thorough presentation of germination data. Finally, the reader is encouraged to contemplate how the particular GIS techniques discussed in this paper could be incorporated into their data presentation repertoire.

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Figure A1.1 – Example of a two-way thermogradient plate with germination boxes and temperature monitoring thermocouples. Approximate size of plate is $1m^2$.

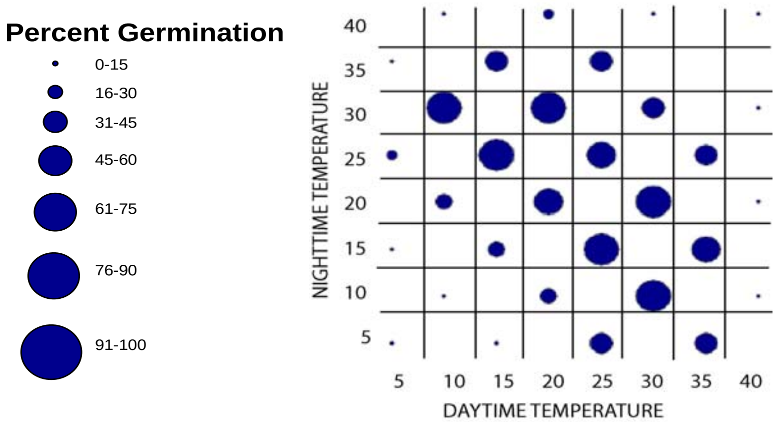

Figure A1.2 – An example of mean germination values represented as graduated symbols for day 6 data.

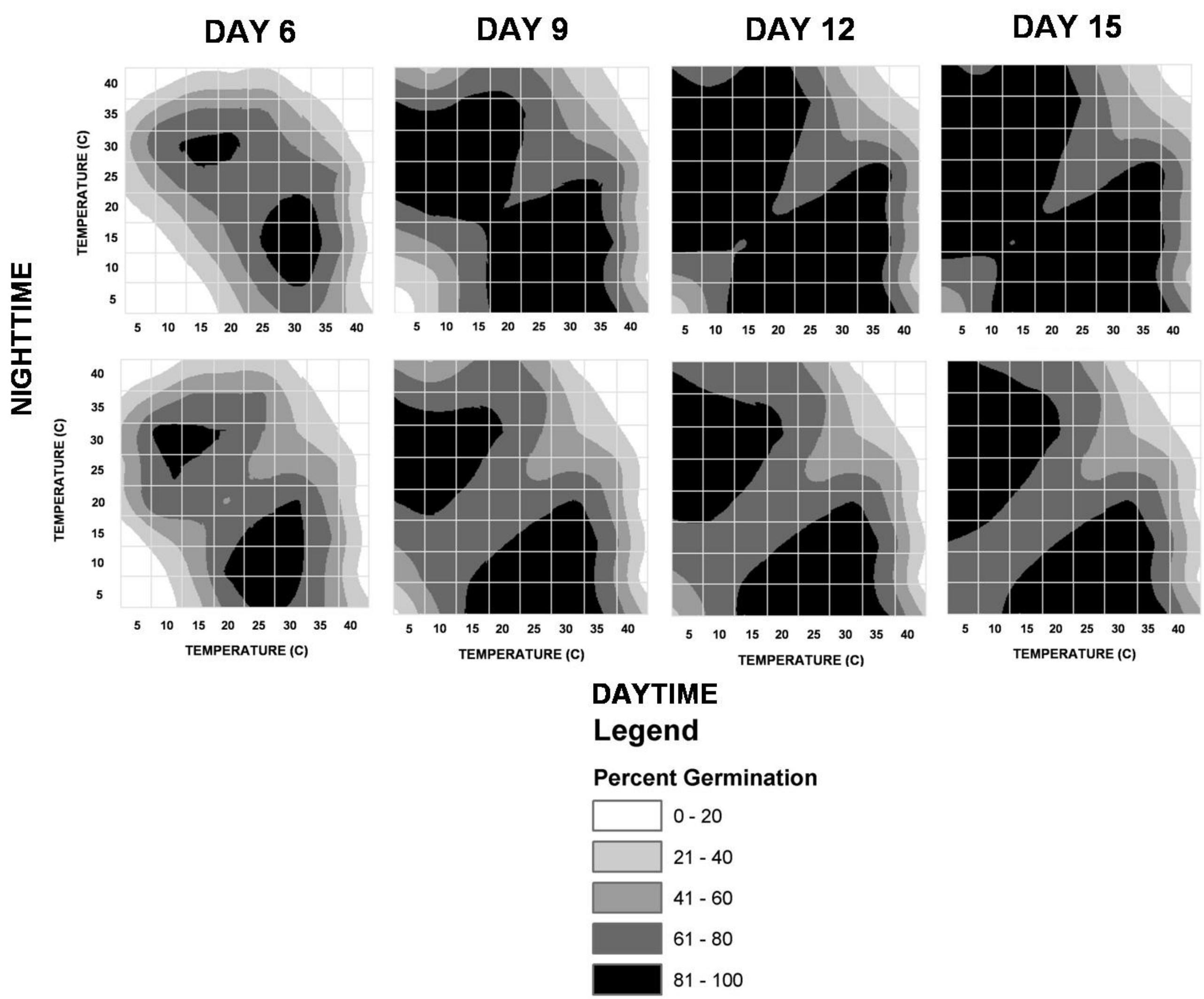

Figure A1.3 – Interplated images of germination over four 3-day intervals using ordinary kriging, including a legend and overlaid grid image.

Table A1.1. Tabular format of the mean germination data presented in Figure 2. Numbers in brackets represent ± 95% confidence intervals for germination values.

	Percent Germination								
		Daytime Temperature (°C)							
Nighttime Temperature (°C)		5	10	15	20	25	30	35	40
	5	0 (0)		2 (2)		53 (7)		48 (7)	
	10		0 (0)		45 (7)		86 (5)		.5 (1)
	15	0 (0)		38 (7)		84 (5)		70 (6)	
	20		32 (7)		68 (7)		88 (5)		0 (0)
	25	26 (6)		80 (6)		65 (7)		61 (7)	
	30		78 (6)		83 (5)		53 (7)		.5 (1)
	35	13 (5)		55 (7)		58 (7)		24 (6)	
	40		0 (0)		15 (5)		4 (3)		0 (0)

Table A1.2. Example of .txt file used to generate eight data coordinates.

Plate Location	X_Coord	Y_Coord	Germ
1	424000	5208000	0
2	424002	5208000	1.5
3	424004	5208000	53
4	424006	5208000	48
5	424001	5208001	0
6	424003	5208001	45
7	424005	5208001	86
8	424007	5208001	0.5

APPENDIX 2

Table A2.1. Summary of average values for soil chemical and physical measurements followed by 95% confidence intervals in brackets.

Characteristic	Nuttall's alkaligrass		weeping alkaligrass	
	Infested	**Uninfested**	**Infested**	**Uninfested**
pH	9.26 (0.24)*+	8.28 (0.30)	8.31 (0.32)+	8.13 (0.34)
EC	1.08 (0.34)*	0.60 (0.17)	0.75 (0.21)	0.61 (0.27)
Na	12.02 (3.81)*+	2.82 (1.12)	3.26 (2.05)	2.31 (1.42)
Ca	27.02 (2.66)	27.08 (5.54)	26.98 (5.37)	24.37 (6.11)
Ca:Na	3.13 (1.48)*+	12.98 (4.12)	16.21 (7.97)+	22.65 (13.60)
Mg	4.83 (0.74)*+	7.30 (1.23)	7.88 (1.46)+	8.20 (2.92)
Ca:Mg	5.93 (0.94)*+	3.71 (0.52)	3.43 (0.36)+	3.21 (0.51)
B	0.016 (0.008)	0.012 (0.005)	0.014 (0.006)	0.014 (0.007)
Cu	0.002 (0.001)	0.001 (0.001)	0.002 (0.001)	0.002 (0.001)
Fe	0.046 (0.022)	0.065 (0.028)	0.054 (0.013)	0.061 (0.039)
K	1.25 (0.61)	1.44 (0.89)	1.49 (0.51)	1.13 (0.35)
NH_4	27.87 (4.68)*	36.40 (4.54)	32.38 (6.93)	34.23 (8.50)
NO_3	137.93 (73.87)	135.87 (70.04)	175.47 (96.24)	103.23 (66.74)
P	30.39 (6.36)	38.11 (30.28)	46.78 (20.65)	31.15 (11.80)
S	0.072 (0.03)	0.068 (0.03)	0.085 (0.036)	0.094 (0.061)
Zn	0.002 (0.001)	0.003 (0.001)	0.004 (0.002)	0.004 (0.001)
Sand	35.52 (5.39)	41.89 (5.47)	41.05 (4.85)	42.92 (6.56)
Silt	49.39 (6.36)	45.60 (4.96)	46.17 (4.44)	43.76 (6.03)
Clay	15.09 (4.90)	12.54 (1.43)	12.78 (1.59)	13.58 (2.37)
Organic matter	2.03 (0.30)*+	3.33 (0.86)	3.53 (0.65)+	3.61 (1.06)
Soil moisture	33.43 (5.33)	25.93 (5.18)	33.16 (4.25)	27.82 (4.91)
Crop cover	14.77 (8.65)*	71.25 (14.20)	14.46 (11.07)*	55.38 (23.73)
Other weeds	5.87 (5.01)	7.93 (10.16)	18.17 (10.85)	16.28 (17.46)
Bare soil	30.87 (12.46)	16.93 (9.47)	31.52 (12.11)	24.23 (18.41)

* - significant difference between infested and uninfested sites within each species
+ - significant difference between Nuttall's versus weeping alkaligrass infested sites

APPENDIX 3

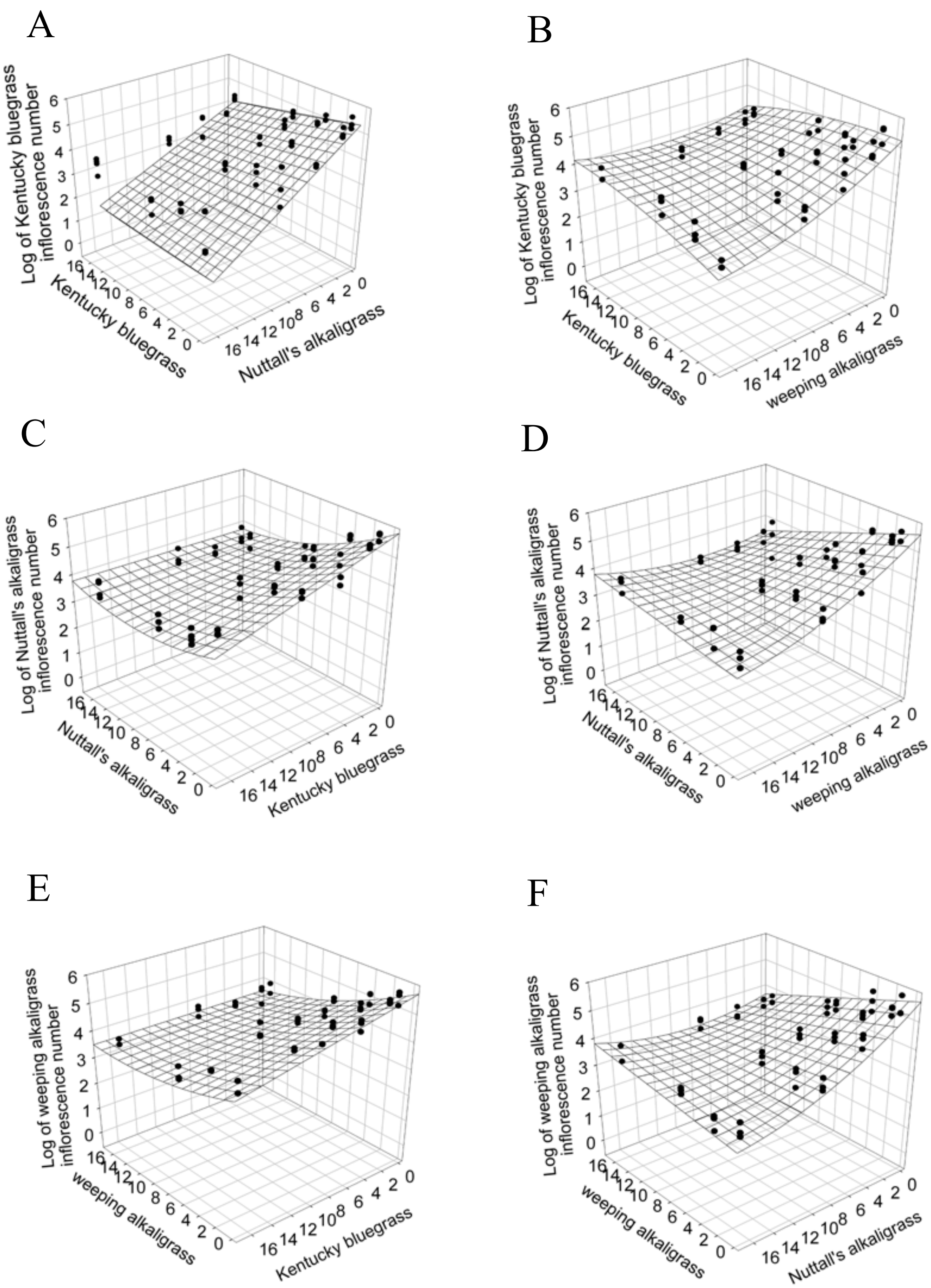

Figure A3.1 – Comparison of competition on the log of inflorescence of weeping alkaligrass, Nuttall's alkaligrass and Kentucky bluegrass in Year 1. X and Z axes indicate the planting density per $0.25m^{-2}$ of each species respectively.

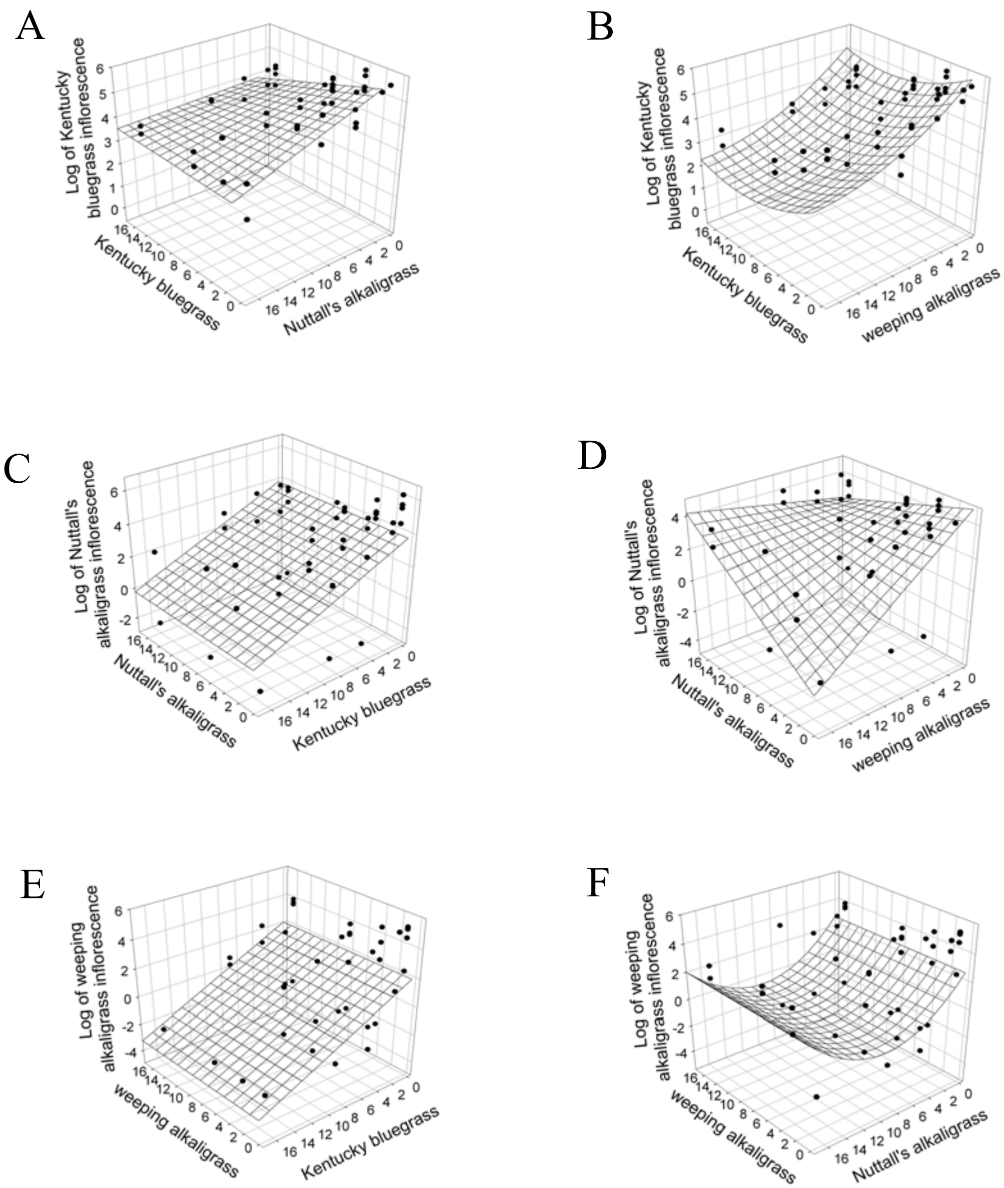

Figure A3.2 – Year 2 comparison of competition on the log of inflorescence of weeping alkaligrass, Nuttall’s alkaligrass and Kentucky bluegrass.

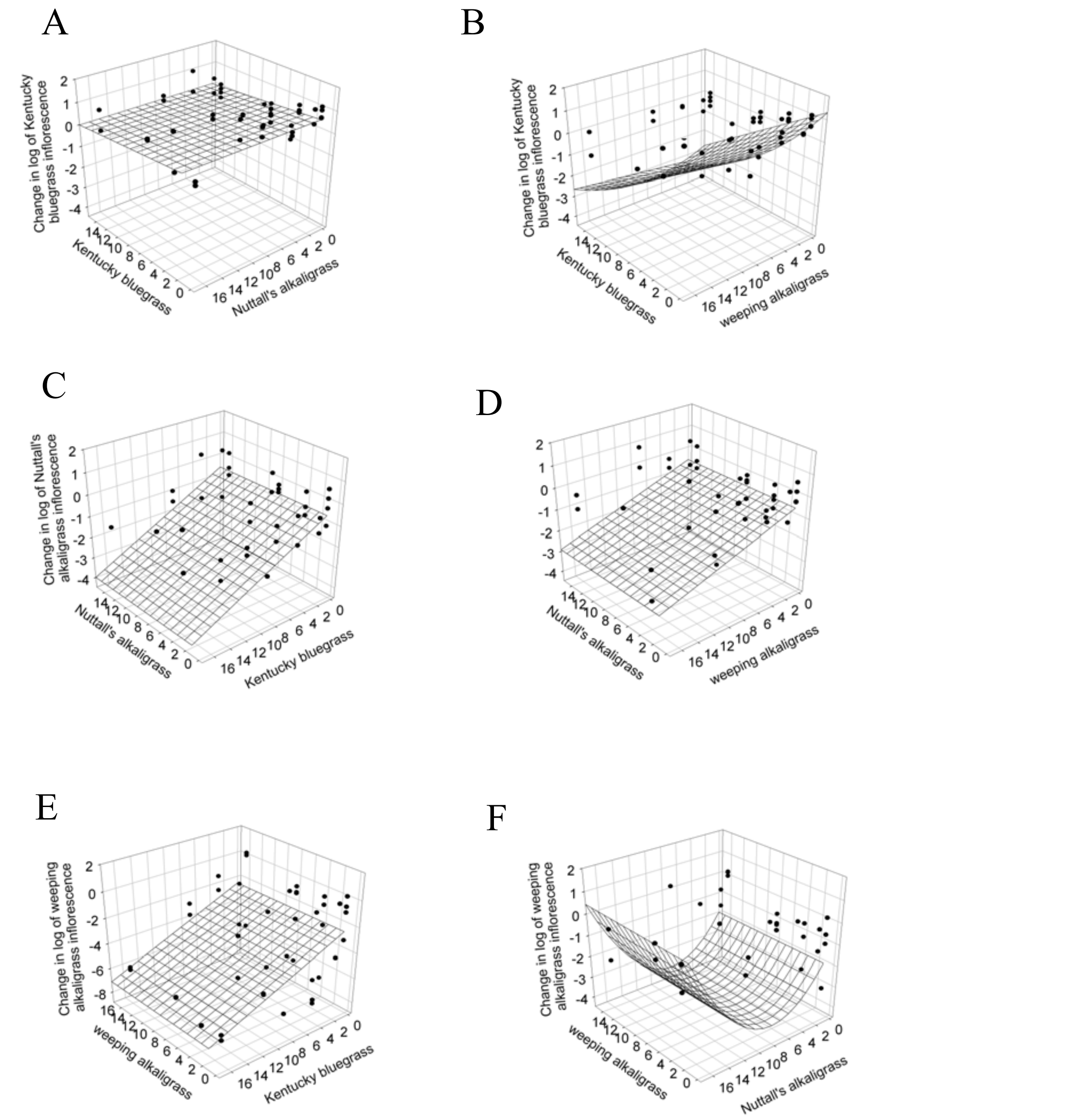

Figure A3.3 – Comparison of competition on the change in inflorescence from year 1 to year 2 of weeping alkaligrass, Nuttall’s alkaligrass, and Kentucky bluegrass.

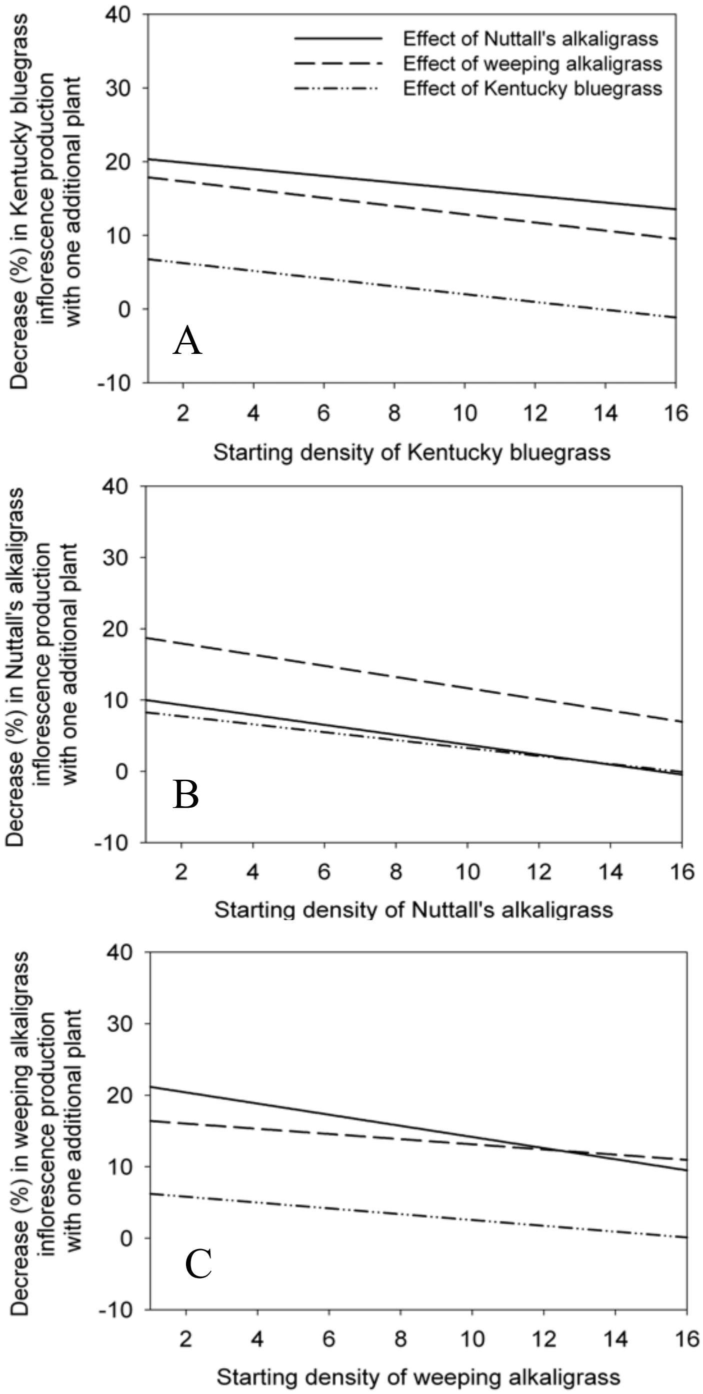

Figure A3.4 – Year 1 change (%) in average inflorescence of Kentucky bluegrass (A), Nuttall's alkaligrass (B) and weeping alkaligrass (C) at differing initial densities with the addition of one Kentucky bluegrass versus an additional weeping or Nuttall's alkaligrass.

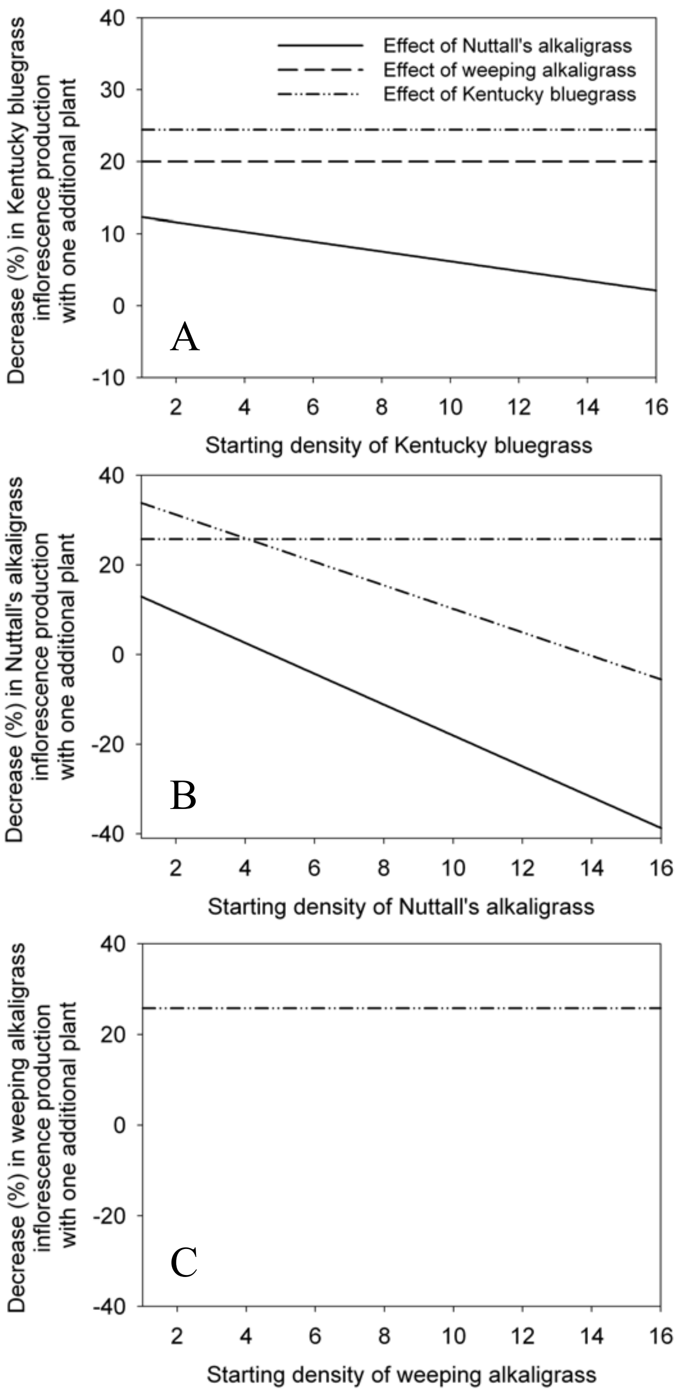

Figure A3.5 – Year 2 change (%) in average inflorescence of Kentucky bluegrass (A), Nuttall's alkaligrass (B), and weeping alkaligrass (C) at differing initial densities with the addition of one Kentucky bluegrass versus an additional weeping or Nuttall's alkaligrass. Note – lines not shown were not significant (α = 0.05).

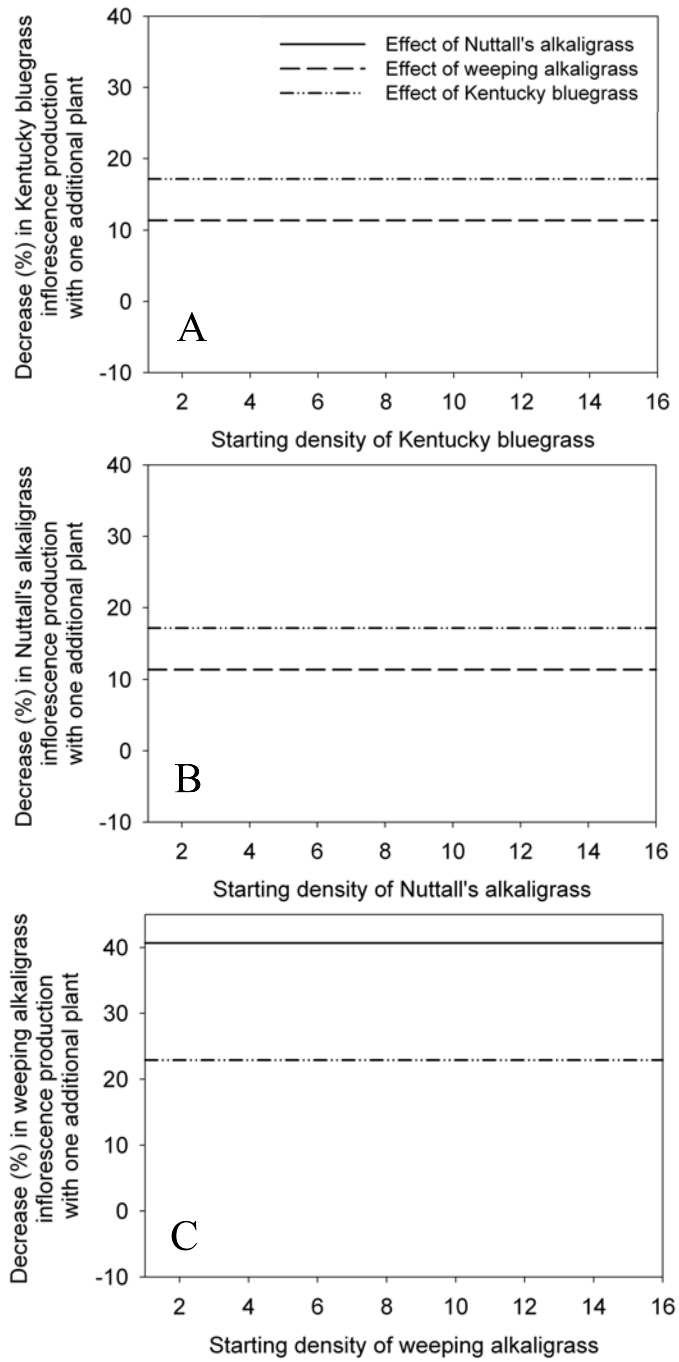

Figure A3.6 – The change (%) in average inflorescence from Year 1 to Year 2 of Kentucky bluegrass (A), Nuttall's alkaligrass (B), and weeping alkaligrass (C) at various initial densities with the addition of one Kentucky bluegrass, versus an additional weeping or Nuttall's alkaligrass. Note – lines not shown were not significant (α = 0.05).

Table A3.1. Year 1 best-fit models for average plant inflorescence (Y) by plot for each species in a two species mixture, where D represents density (plants per plot) of Kentucky bluegrass (D_k), weeping alkaligrass (D_w), and Nuttall's alkaligrass (D_n).

Species Mixture	Variable	Equation	R^2
Kentucky X Weeping alkaligrass			
Kentucky	Inflor	$\mathrm{Log}Y_k = 5.12 – 0.21D_w – 0.004D_k + 0.005D_w^2 – 0.003D_k^2 + 0.007D_wD_k$	0.82
Weeping	Inflor	$\mathrm{Log}Y_w = 5.58– 0.19D_w – 0.07D_k + 0.004D_w^2 + 0.004D_wD_k$	0.87
Kentucky X Nuttall's alkaligrass			
Kentucky	Inflor	$\mathrm{Log}Y_k = 5.36 – 0.24D_n – 0.08D_k + 0.006D_n^2 + 0.005D_nD_k$	0.80
Nuttall's	Inflor	$\mathrm{Log}Y_n = 5.69– 0.22D_n – 0.10D_k + 0.006D_n^2 + 0.006D_nD_k$	0.84
Weeping X Nuttall's alkaligrass			
Weeping	Inflor	$\mathrm{Log}Y_w = 5.51 – 0.11D_w – 0.25D_n + 0.006D_n^2 + 0.009D_wD_n$	0.89
Nuttall's	Inflor	$\mathrm{Log}Y_n = 5.44 – 0.22D_w – 0.12D_n + 0.005D_w^2\ 0.009D_wD_n$	0.81

Table A3.2. Year 2 best-fit models for average plant inflorescence (Y) by plot for each species in a two species mixture, where D represents density (plants per plot) of Kentucky bluegrass (D_k), weeping alkaligrass (D_w), and Nuttall's alkaligrass (D_n).

Species Mixture	Variable	Equation	R^2
Kentucky X Weeping alkaligrass			
Kentucky	Inflor	$\text{Log}Y_k = 6.01 - 0.30D_w - 0.23D_k + 0.01D_w^2 + 0.008D_k^2$	0.77
Weeping	Inflor	$\text{Log}Y_w = 1.99 - 0.30D_k$	0.37
Kentucky X Nuttall's alkaligrass			
Kentucky	Inflor	$\text{Log}Y_k = 5.73 - 0.14D_n - 0.11D_k + 0.007D_nD_k$	0.68
Nuttall's	Inflor	$\text{Log}Y_n = 3.77 - 0.23D_k$	0.33
Weeping X Nuttall's alkaligrass			
Nuttall's	Inflor	$\text{Log}Y_n = 4.95 - 0.42D_w - 0.15D_n + 0.03D_wD_n$	0.45
Weeping	Inflor	$\text{Log}Y_w = 2.68 - 0.74D_n + 0.04D_n^2$	0.19

Table A3.3. Best-fit models for change in the log of average plant inflorescence from Year 1 to Year 2 for each species in a two species mixture, where D represents density (plants per plot) of Kentucky bluegrass (D_k), weeping alkaligrass (D_w), and Nuttall's alkaligrass (D_n).

Species Mixture	Variable	Equation	R^2
Kentucky X Weeping alkaligrass			
Kentucky	Inflor	$LogY_k = 1.11 – 0.16D_w - 0.23D_k + 0.01D_w^2 + 0.01D_k^2$	0.51
Weeping	Inflor	$LogY_w = -2.57 – 0.26D_k$	0.31
Kentucky X Nuttall's alkaligrass			
Kentucky	Inflor	$LogY_k = 0.51– 0.03D_k$	0.08
Nuttall's	Inflor	$LogY_n = -0.67– 0.19D_k$	0.30
Weeping X Nuttall's alkaligrass			
Nuttall's	Inflor	$LogY_n = -0.64 – 0.13D_w$	0.14
Weeping	Inflor	$LogY_w = -2.02 – 0.56D_n + 0.04D_n^2$	0.11