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# Site Characteristics Associated with Nuttall's and Weeping Alkaligrass in Northeastern Oregon

## Abstract

Two species of alkaligrass, Nuttall's alkaligrass (*Puccinellia nuttalliana* [Schult.] Hitch.), a native, and weeping alkaligrass (*Puccinella distans* [Jacq.] Parl.), an introduced species from Eurasia, are found within semi-arid regions of the United States. Recently, land managers have become 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 of invasion. Paired plots comparing site characteristics of infested versus very close, yet uninfested sites were sampled throughout the Grand Ronde Valley, northeastern Oregon. The results of this study indicate that Nuttall's alkaligrass was most commonly associated with sodic soils (73%), whereas 85% of the sites infested with weeping alkaligrass were agriculturally 'normal' sites. In general, Nuttall's alkaligrass was positively associated with sodium; whereas, for weeping alkaligrass, competing vegetation was the only factor affecting establishment and abundance. Weeping alkaligrass showed traits typical of a resource generalist, establishing on a wide variety of sites and being strongly influenced by competing vegetation; whereas Nuttall's alkaligrass appears to be more niche specific. Species that behave as resource generalists are more problematic than species linked to specific site characteristics because it is difficult to predict where they will establish. Therefore, a healthy crop cover on agriculturally productive sites is the best prevention against weeping alkaligrass establishment. For sodic sites, incapable of supporting a healthy crop, diligent weed control must be practiced to prevent the spread of either species of alkaligrass within agronomic systems.

## Introduction

To explain the factors affecting plant species distribution and abundance, studies commonly look for patterns at multiple scales (Carey et al. 1995, Martin and Chambers 2001, Dodd et al. 2002). At the regional or local scale, factors limiting the establishment of plant species are determined by a combination of biotic and abiotic site characteristics (Miller et al. 1995, Piernik 2003, Bekele and Hudnall 2006). As such, it is understood 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, Guo et al. 2005). 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.

Within northeastern Oregon, the local distribution of two species of alkaligrass, weeping alkaligrass (*Puccinellia distans* [Jacq.] Parl.) and Nuttall's alkaligrass (*Puccinellia nuttalliana* [Schult.] Hitch.), is important to regional land managers. However, these two species originated in different locales. 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 (Macke and Ungar 1971, Harivandi et al. 1983, Ashraf et al. 1986, Salo et al. 1996, Mintenko et al. 2002), with weeping alkaligrass perhaps more salt tolerant than Nuttall's alkaligrass (Salo et al. 1996, Moravcova and Frantik 2002). Observational records indicate a possible association between Nuttall's alkaligrass and saline depressions (Macke 1969, Brotherson 1987). Brotherson (1987) describes site characteristics along a transect, a portion of which is infested with Nuttall's alkaligrass. The

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Nuttall's alkaligrass section is recorded as having an average pH of 8.47, high levels of calcium, magnesium, sodium and potassium; and low levels of phosphorous, iron and zinc. Additionally, weeping alkaligrass also has been observed in saline depressions (Piernik 2003), as well as along heavily salted roadsides (Garlitz 1992, Davis and Goldman 1993) and ruderal areas (Moravcova and Frantik 2002). However, although these species have been casually documented occupying saline sites, in particular, saline depressions, no studies were found which quantitatively linked soil, environmental and vegetation characteristics with Nuttall's or weeping alkaligrass distribution and abundance. In addition, previous salt tolerance research on these two species has been under greenhouse and laboratory conditions (Macke and Ungar 1971, Harivandi et al. 1983, Ashraf et al. 1986, Salo et al. 1996, Mintenko et al. 2002), not representative of the complexities associated with plant survival and growth under field conditions. For farmers of the semi-arid, salt affected regions of eastern Oregon, the concern is whether either of these two species has the ability to move out of their 'typical' low productivity sites, and into valuable cropland.

To manage areas at risk of alkaligrass (both native and non-native) establishment, farmers operating within salt affected semi-arid ecosystems need to understand what factors are permitting the establishment of either species of alkaligrass through an understanding of the realized niche(s) that each of these alkaligrass species occupies. This paper investigates how the local scale distribution and abundance of weeping alkaligrass and Nuttall's alkaligrass may be related to the complex interactions of soil characteristics, microtopography and vegetation community dynamics.

## Methods

### Description of Study Area

Study sites were located throughout the semi-arid region of the Grande Ronde Valley of northeastern Oregon, US. Within the Blue Mountain Basin ecoregion, 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 natural vegetation on the terraces and loess hills consists of Idaho fescue (*Festuca idahoensis* Elmer), common snowberry (*Symphoricarpos albus* Blake), and Sandberg's bluegrass (*Poa sandbergii* J Presl.). On the floodplains, tufted hairgrass (*Deschampsia caespitosa* [L.] Beauv.), redtop (*Agrostis gigantea* Roth), and sedges (*Carex spp.*) are associated with wetter soils (Clark and Bryce 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* L.), peppermint (*Mentha piperit* L.) and peas (*Pisum sativum* L.). Precipitation ranges from 32 cm in the dry southern valley to 60 cm at the eastern end of the valley (Clark and Bryce 1997).

In the spring of 2004, we surveyed the area east of La Grande to Cove and north to Elgin, Oregon (Figure 1) for Nuttall's alkaligrass and/or weeping alkaligrass infestations. During the survey period, all roads in the survey area were driven; as well, farmers and agricultural consultants were contacted and questioned about incidences of alkaligrass on agricultural land. 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 total, 28 sites were found which matched the criteria.

From June 23 to July 9, 2005, all fields were sampled for soil chemistry, soil texture, environmental, as well as vegetation parameters. Most sites were within agriculturally productive fields growing peppermint, Kentucky bluegrass (*Poa pratensis* L.), wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), fescue (*Festuca spp.*), or pasture.

### Sampling Methods

Soil analyses were conducted on a bulked sample of 4 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; exchangeable (meq $L^{-1}$) cations of sodium, calcium, magnesium, potassium and phosphorous following the procedures outlined by the American Society of Agronomy (Thomas 1982), extractable (meq $L^{-1}$) boron, copper, manganese, zinc, iron, sulfur using DTPA extraction by ICP (Lindsay and

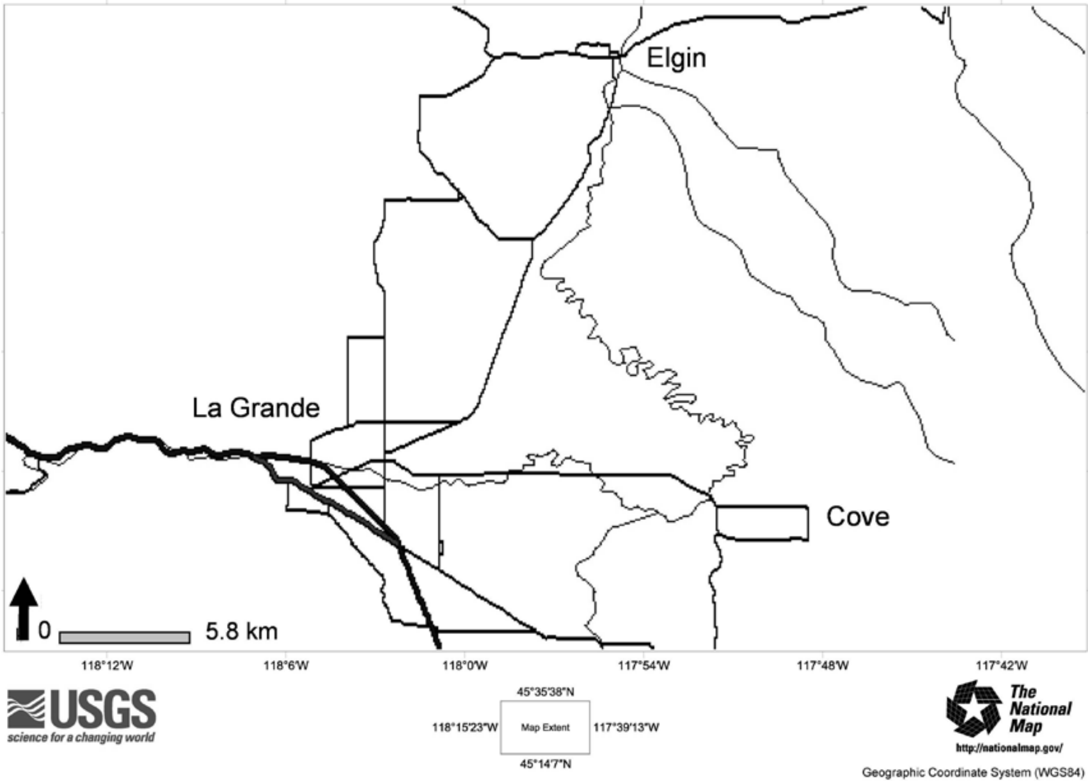


Figure 1. Alkaligrass survey zone encompassing the area north of La Grande to Elgin and east to Cove, Oregon. (Created from: http://nmviewogc.cr.usgs.gov/viewer.htm).

Norvell 1978); electrical conductivity (mmhos $cm^{-1}$) using the 1:2 dilution method (Gavlak et al. 2001); nitrate (kg $ha^{-1}$) and ammonium (kg $ha^{-1}$) via the chromotropic acid method (Gavlak et al. 2001). From the soil chemistry data, the sodium absorption ratio (SAR) was calculated for each site. Soils were classified to map unit based on the United States Department of Agriculture (USDA) soil classification descriptions. Sites were classified as normal, saline, saline-sodic or sodic soils by combining electrical conductivity ($EC_W$) measurements with SAR and pH (Brady and Weil 2002).

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 infestation 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 uninfested site, all the above information was collected as per the infested site.

### 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 (SAS ver 9.1). Principal components analysis selects several linear combinations that capture the majority of the variation of the multivariate responses (Ramsey and Schafer 2002).

Logistic regression was used to determine the soil and vegetation characteristics associated with the odds of a site being infested by Nuttall's alkaligrass and the odds of a site being infested by weeping alkaligrass (SAS ver 9.1). Logistic regression models a binary response variable (present versus absent) as a function of explanatory variables. To estimate the parameters of the logistic regression models for infestation, we used exact conditional likelihood because of the pairing of plots within fields and the small sample size. For all of the logistic regression models, we used the backwards model selection procedure.

Within the infested sites, multiple regression was used to determine the relationship between the abundance of weeping and Nuttall's alkaligrass and soil and vegetation characteristics. We used the Bayesian Information Criteria (BIC) as our model selection criteria.

## Results

### General Soil Types

Nuttall's alkaligrass infestations tended (73% of sites) to occur within the mildly to strongly alkaline Hot Lake silt loam soil. 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. Included within the Hot Lake silt loam series are small areas of Hot Lake soils which are even more poorly drained. Other soil series 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. Normal soil has a pH of less than 8.5 and an electrical conductivity of less than 4 mmhos $cm^{-1}$ (Brady and Weil 2002).

Weeping alkaligrass infestations 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.

### Factors Related to Infested Versus Uninfested Site Conditions

As described by PCA, Nuttall's alkaligrass exhibited a strong separation between the infested and uninfested sites (Figure 2A). 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. 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 2B) accounted for a cumulative variance of 55.7%.

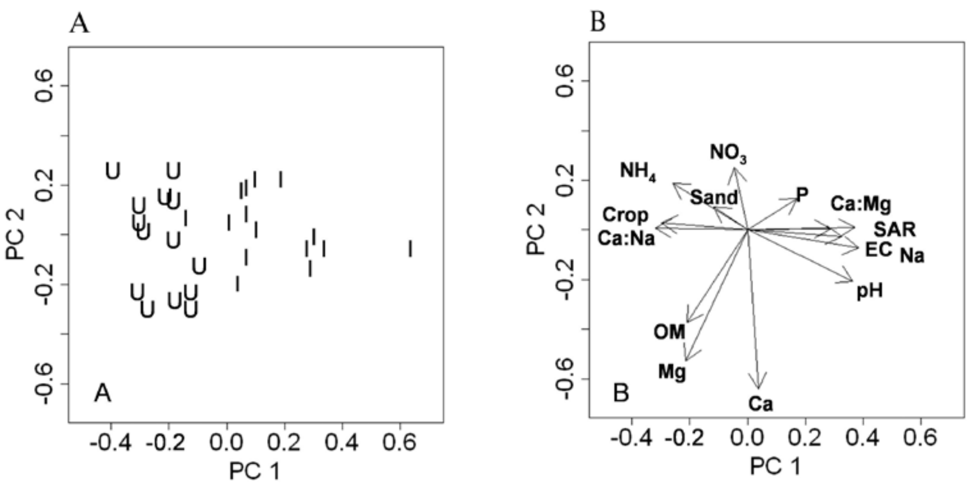


Figure 2. Nuttall's alkaligrass principal components analysis of (**A**) infested (I) versus uninfested (U) and the soil chemistry variables (**B**) dominating the separation.

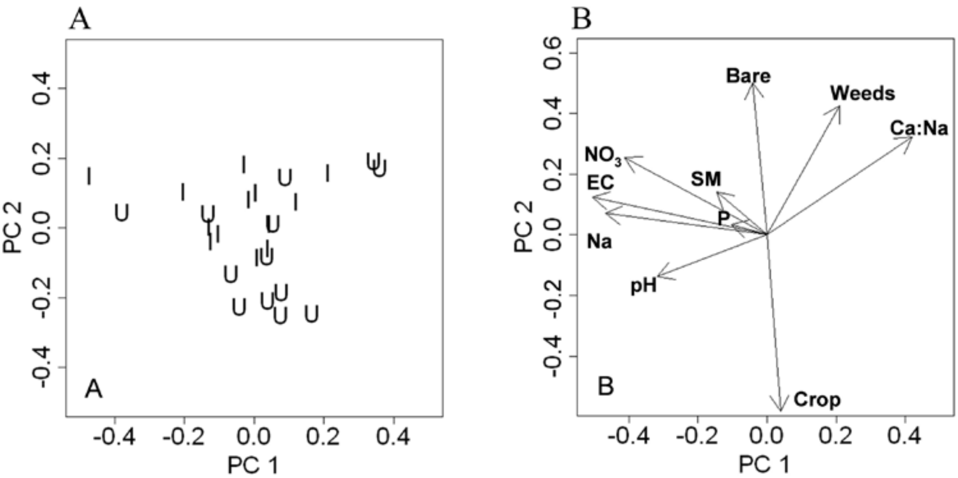


Figure 3. Weeping alkaligrass principal components analysis of (**A**) infested (I) versus uninfested (U) and the soil chemistry variables (**B**) dominating the separation.

Weeping alkaligrass exhibited a less clearly defined separation between the infested verus uninfested sites (Figure 3A). The first factor, a contrast between soil moisture (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 3B) accounted for a cumulative variance of 51.2%.

As for sites infested with Nuttall's alkaligrass versus weeping alkaligrass, a separation similar to that for sites infested with Nuttall's alkaligrass was witnessed (Figure 4A). 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 accounted for 36.8% of the variance within the data. The second factor, 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 accounted for 19.0% of the variability. A combination of factors 1 and 2 (Figure 4B) resulted in a cumulative variance of 51.2%.

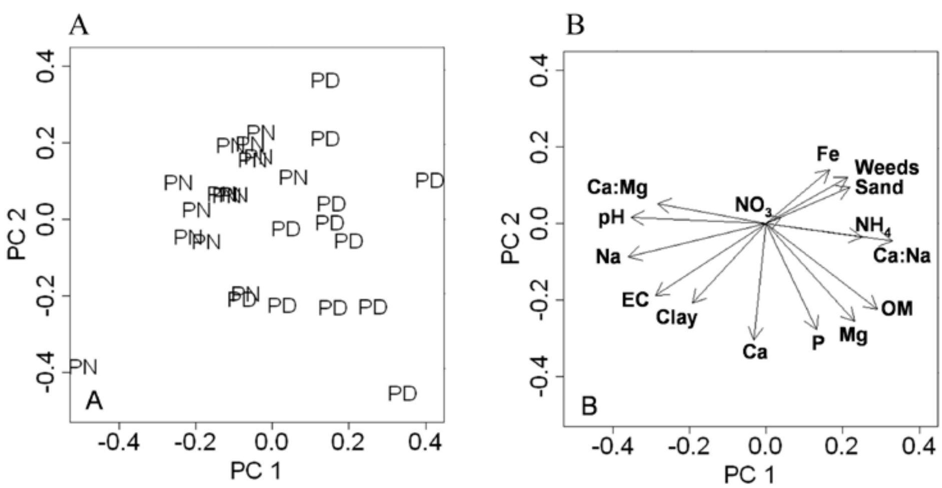


Figure 4. Principal components analysis of sites infested (**A**) with Nuttall's alkaligrass (PN) versus weeping alkaligrass (PD) and the soil chemistry variables (**B**) dominating the separation.

## Chance of Becoming Infested

Significant ($P \leq 0.05$) differences between Nuttall's alkaligrass sites included soil moisture, percent sand, percent organic matter, ammonium, pH, electrical conductivity, sodium and magnesium (Table 1), whereas the only factor related to weeping alkaligrass was percent crop cover (Table 1).

We used the results to verify logistic regression model selection (Table 1). For example, although percent crop cover on infested versus uninfested site was significantly different (Table 1), it was highly correlated with sodium ($r = -0.52$) and thus does not provide a further explanation to the odds of Nuttall's alkaligrass infestation. Therefore, the odds of Nuttall's alkaligrass infesting a site can by explained by the reduced model:

$$\text{Logit}(\pi_N) = 2.2 + 1.0X_{Na} - 1.2X_{MG} \qquad (1)$$

where Logit($\pi_N$) is the probability of Nuttall's alkaligrass establishment (or presence), $X_{Na}$ is exchangeable sodium (meq $L^{-1}$) ($P = <0.0001$) and $X_{MG}$ is exchangeable magnesium (meq $L^{-1}$) ($P = 0.0063$). Correlative effects were noted between magnesium and organic matter ($r = 0.35$) and thus the final model was chosen because magnesium provided the greatest explanation of the probability of infestation. There was no significant interaction between exchangeable sodium and exchangeable magnesium ($P = 0.85$). The final model suggests that a 1 meq $L^{-1}$ increase in sodium will result in a 2.7 fold increase (95% CI = 1.5 – 14.9 fold change) in the odds of Nuttall's alkaligrass establishment while holding exchangeable magnesium constant. Whereas a 1 meq $L^{-1}$ increase in exchangeable magnesium will result in a 3.3 fold decrease (95% CI = 1.3 – 42 fold change) in the odds of Nuttall's alkaligrass establishment, while holding exchangeable sodium constant.

Weeping alkaligrass exhibited a simpler separation between the infested verus uninfested sites driven solely by percent crop cover. The odds of weeping alkaligrass infesting a site can by explained by the model:

$$\text{Logit}(\pi_W) = 1.4_{(0.7)} - 0.05X_{cc\ (0.02)} \qquad (2)$$

where Logit($\pi_w$) is the log odds of weeping alkaligrass establishment (or presence) and $X_{cc}$ is the percent crop cover ($P = 0.001$). The final model suggests that a 10% decrease in percent crop cover will likely result in a 1.6 fold increase (95% CI = 1.2 - 2.5 fold change) in the odds of weeping alkaligrass establishment.

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. Variables that differed significantly include percent organic matter, pH, sodium and magnesium (Table 2). The odds of Nuttall's alkaligrass infesting a site versus weeping alkaligrass infesting a site can by explained by the reduced model:

$$\text{Logit}(\pi_{w/N}) = -1.2_{(1.1)} + 0.46X_{Na\ (0.1)} \qquad (3)$$

where Logit($\pi_{w/N}$) is the odds of Nuttall's alkaligrass establishment versus weeping alkaligrass establishment and $X_{Na}$ is exchangeable sodium (meq $L^{-1}$) ($P < 0.0001$). Once again, while Table

TABLE 1. The average difference between uninfested (UN) and infested (INF) sites. Paired by plot location (paired *t*-test), with *P* values and 95% confidence intervals

| Characteristic | Average Difference (UN vs. INF) | P value ($\alpha = 0.05$) | 95% CI |
|---|---|---|---|
| | Nuttall's alkaligrass | | |
| Soil moisture | 7.5 | 0.04 | 6.0 |
| Sand (%) | 6.4 | 0.01 | 4.6 |
| Organic matter (%) | 1.3 | 0.006 | 0.8 |
| $NH_4$ (kg/ha) | 8.5 | 0.007 | 5.1 |
| pH | -1.0 | <0.0001 | 0.3 |
| EC (mmhos/cm) | -0.5 | 0.01 | 0.4 |
| Mg (meq/L) | 2.5 | 0.0001 | 1.3 |
| Na (meq/L) | -9.4 | <0.0001 | 3.6 |
| | Weeping alkaligrass | | |
| Crop cover (%) | 56.5 | <0.0001 | 16.8 |

TABLE 2. Summary of significant soil chemical (*t*-test $\alpha$= 0.05) average measurements (95% confidence intervals in brackets) for sites infested with Nuttall's alkaligrass versus weeping alkaligrass.

| Characteristic | Infested: Weeping alkaligrass | versus | Nuttall's alkaligrass |
|---|---|---|---|
| Organic matter (%) | 3.53 (0.65) | | 2.03 (0.30) |
| pH | 8.31 (0.32) | | 9.26 (0.24) |
| Na (meq/L) | 3.26 (2.05) | | 12.02 (3.81) |
| Mg (meq/L) | 7.88 (1.46) | | 4.83 (0.74) |

2 would suggest a more complex model, the correlation between sodium, magnesium and organic matter restricted the model to the most significant variable, sodium. The final model suggests that of the infested sites a 1 meq $L^{-1}$ increase in sodium will result in 1.6 fold increase (95% CI = 1.2 – 2.2 fold change) in the odds of Nuttall's alkaligrass establishment versus weeping alkaligrass.

### Factors Affecting Plant Abundance Within Infested Sites

Results of the BIC model selection process revealed that within Nuttall's alkaligrass infested plots, the percent exposure of mineral soil accounted for 37% of the variability ($R^2$) in percent Nuttall's alkaligrass cover:

$$Y_N = 67.7_{(9.4)} - 0.65X_{MS\ (0.25)} \quad (4)$$

where $Y_N$ represents the percent cover of Nuttall's alkaligrass, $X_{MS}$ represents exposed mineral soil (%) ($P$ = 0.02). Under the range of conditions sampled, it can be expected that for a 10% increase in exposed mineral soil, the cover of Nuttall's alkaligrass will decline by 6.5% (SE = 2.5).

Within weeping alkaligrass infested plots, the percent cover of other species (crop and weeds combined) explained 57% of the variability ($R^2$) of percent cover of weeping alkaligrass as explained by:

$$Y_W = 61.9_{(7.7)} - 0.74X_{OS\ (0.19)} \quad (6)$$

where $Y_W$ represents the percent cover of weeping alkaligrass, $X_{OS}$ represents the percent cover of other plant species ($P$ = 0.003). Therefore, it can be expected that a 10% increase in percent cover of other plant species will result in a 7.4% (SE = 1.9) decrease in weeping alkaligrass cover.

Both weeping and Nuttall's alkaligrass appear to be positively associated with depressional areas. In particular, there appears to be a relationship between Nuttall's alkaligrass, sodium and depressional areas (Figure 5). However, it is difficult to conclude with certainty the change in odds of Nuttall's alkaligrass infestation due to the likely interplay of sodium and magnesium (Figure 5). Magnesium may play a role in offsetting the effects of sodium in depressional areas as is witnessed by the shift from infested to uninfested (Figure 5 – shift from a to b), possibly associated with increased magnesium.

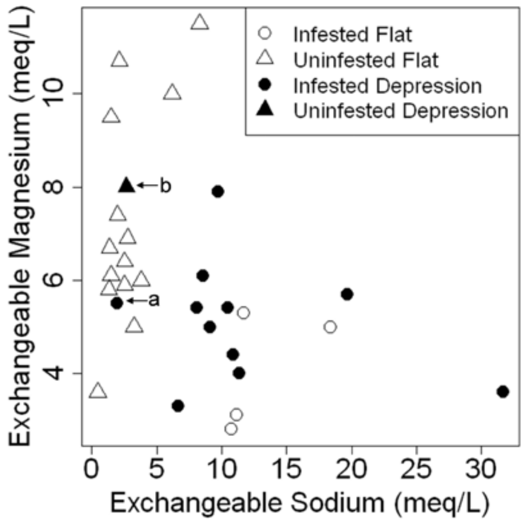


Figure 5. The relationship between exchangeable sodium (meq/L), magnesium (meq/L) and microtopography within Nuttall's alkaligrass infested sites. Note the shift from (a) infested depression to (b) uninfested depression at similar exchangeable sodium levels with greater exchangeable magnesium.

## Discussion

### Soil Chemistry

Within our study, we clearly found a negative relationship between alkaligrass abundance and competing vegetation. Agronomic species are typically sensitive to sodium and the soil conditions associated with salt.

Within saline soils, sodic soils are generally considered to be the most troublesome. In terms of soil structure, a high level of exchangeable sodium creates soil conditions that result 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 and the anion chloride, which compete with other beneficial cations, namely calcium and magnesium, on the cation exchange site (Marschner 2005). The nutrient imbalances of sodic soils affect the growth of plants, typically resulting in reduced abundance or quality (Grattan and Grieve 1999). However, the physiological role of nutrients in the development and growth of plants is complex (Gratten and Grief 1999). The interaction of soil chemistry on nutrient availability, differing nutritional requirements for plant species, physical plant adaptations to adverse growing conditions, the interplay of water and light availability, and attributes of the growing site itself, such as microtopography, also affect plant survival and growth.

At present, it is unknown if Nuttall's alkaligrass' sodium tolerance mechanism involves sodium exclusion at the root interface, intercellular adaptations, a sodium avoidance technique through dormancy, or a combination of all three. Schwarz and Redmann (1989) argue that the success of cool-season halophytes, like Nuttall's alkaligrass, may depend on their ability to complete their development before salt concentrations increase to inhibitory levels. Phenological development garden studies of Nuttall's alkaligrass, indicated that under sodic soil conditions, Nuttall's alkaligrass ceased tiller development as early as late-May under low precipitation conditions (Tarasoff et al. 2007). In the same study, Nuttall's alkaligrass did not appear to be affected cellularly by the high levels of sodium salts associated with the sodic soils. These results are consistent with laboratory studies which found that under increasing sodium concentrations, Nuttall's alkaligrass did not take up sodium ions (Harivandi et al. 1983), nor did this species flower at water potentials below -2.4 MPa (Guy et al. 1986).

## Site Topography

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 Nuttall's alkaligrass were sodic whereas depressions infested with weeping alkaligrass were not. In climates with a distinct dry season, like the Grande Ronde Valley, the spatial distribution of soil moisture is largely controlled by topography during the wet season, but not during the dry season (Grayson et al.1997). Typically, depressional areas act as water receiving sites, accumulating large volumes of water during the spring.

Most plants species not adapted to water logging will succumb to $O_2$ deficiency (anoxia) or toxicity of other gases within hours of soil saturation (Brady and Weil 2002) and may develop injury symptoms such as wilting, leaf senescence and epinasty over a period of several days (Drew 1990). For example, research by Martin and Chamber (2001) indicated that while Kentucky bluegrass could take advantage of relatively high soil-water availability, it could not tolerate saturated soil conditions, as witnessed by decreased shoot growth. More specifically, substantial yield reductions in soybean have been observed when excessive soil water occurs during the vegetative and reproductive stages of the plant (Reyna et al. 2003).

Flood-tolerant species typically elongate their stems above the water and develop arenchymatous tissue to allow the transport of oxygen down the shoots to the roots (Crawford 1978). Although it is currently unknown if weeping or Nuttall's alkaligrass contain a large percentage of arenchymatous tissue, extensive aerenchyma has been documented for another salt-tolerant member of the *Puccinellia* genus—*Puccinellia peisonis* (Stelzer and Läuchli 1980).

The other variable associated with topography is the movement of soluble salt ions through the soil profile. Of the three major ions – magnesium, calcium and sodium – magnesium is the most soluble, followed by calcium, and lastly sodium (Marschner 2005). As water collects in depressional areas; sodium will be the first salt to precipitate, followed by calcium, and lastly magnesium. The water content of the soil determines which salts remain in solution and move down the soil profile and which salts precipitate due to evaporative effects. Therefore, sodium is the most likely to accumulate in the upper soil layers where plant roots are found, calcium and magnesium may remain in the soil profile or be flushed out of the system, depending on the soil moisture.

It is unknown as to why weeping alkaligrass depressional areas were not sodic while those of Nuttall's alkaligrass were. A complete assessment of the landscape and associated soil profiles would be needed to understand the movement of soil salts.

## Competitive Exclusion

In isolation, most plant species are able to grow under a wide variety of conditions, but in natural communities their growth is often limited by a range of abiotic and biotic conditions. Previous work concluded that, when grown without competition, both species of alkaligrass were able to grow and produce seed in the widely divergent sodic versus normal soil type (Tarasoff et al. 2007). Further, weeping alkaligrass flourished under the normal soil type, producing nearly twice the biomass. The results of the current field study show a reduced realized niche due to competition from crop species and other weedy species.

For sites infested with weeping alkaligrass, the only factor related to abundance was competing vegetation, which included both crop cover and other weed species. Previous work documented that weeping alkaligrass' competitive attributes were greatly reduced when grown with Kentucky bluegrass; especially over time (Tarasoff et al. 2006, 2009). Hughs (1972) also commented that while weeping alkaligrass became the dominant species under saline conditions, it was not very competitive with Kentucky bluegrass under non-saline soil conditions. Therefore, as one might expect from an introduced species, weeping alkaligrass has followed the pattern of a resource generalist, capitalizing on available resources. A plant that behaves as a resource generalist can be troublesome as there is little predictability between plant-site associations.

In contrast, Nuttall's alkaligrass abundance on infested sites was not affected by competing vegetation ($P = 0.43$). It is more likely that intra-specific competition for soil nutrients and water are limiting the percent cover of Nuttall's alkaligrass. Therefore, Nuttall's alkaligrass abundance may be more affected by reduced matrix potentials, and the interplay of nutrient availability (i.e., cation exchange sites) associated with sodic soils than the toxic affects of sodium ions themselves.

### Management Implications

For farmers managing agriculturally productive sites within arid environments the primary management objectives should be maintaining a healthy crop cover to limit the establishment of resource generalist species like weeping alkaligrass, or unwanted niche specific species such as Nuttall's alkaligrass. However, in these ecosystems it is critical that land managers utilize irrigation carefully to prevent further salinization.

It is unlikely that soil remediation would be cost effective on sodic sites; therefore, on these sites, where Nuttall's alkaligrass is likely to be plentiful, and weeping alkaligrass may also be present, farmers should remove both species to prevent further distribution.

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