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Competitive Effects of Nuttall's and Weeping Alkaligrass in Kentucky Bluegrass

Abstract

Mechanisms of interspecific and intraspecific competition and survival between the agronomic species Kentucky bluegrass (*Poa pratensis* L. 'Midnight'), with the native grass Nuttall's alkaligrass (*Puccinellia nuttalliana* (Schult.) Hitchc.) and the introduced grass weeping alkaligrass (*Puccinellia distans* (Jacq.) Parl) 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 pair-wise combinations. Response surfaces and substitution analysis of the three species were generated within the matrix to study competition dynamics between the species. Plants were grown under natural conditions, on a pH neutral (6.9) silt loam site, with no added irrigation or fertilizer. In general, in year 1, weeping alkaligrass was more competitive than Nuttall's alkaligrass and both species were far more competitive than Kentucky bluegrass. Both weeping and Nuttall's alkaligrass exhibited low survival (40% and 60%, respectively) following harvesting. There was also a shift in competitive effects in Year 2, such that weeping alkaligrass was equally competitive with Kentucky bluegrass, and both were far more competitive than Nuttall's alkaligrass. Even though weeping alkaligrass had very low survival rates its affect on Kentucky bluegrass into year 2 was equal to that of year 1. Thus, the legacy effect of weeping alkaligrass will likely have long-term implications to a rotation of Kentucky bluegrass plants, even if removed in the first year. However, the notion of a legacy effect of competition should not be limited to an agricultural setting. It is highly likely that similar interactions are exhibited across plant communities and that long term competition studies are required to adequately address this issue.

Introduction

Kentucky bluegrass (*Poa pratensis* L.) is a perennial seed crop of primary importance in eastern Oregon (Union County). In 2003, in Union County, there were 4795 certified hectares of Kentucky bluegrass, representing approximately 43% of the certified grass seed production for that area (Oregon State University 2003). In sodic areas of Kentucky bluegrass fields, alkaligrass (*Puccinellia* spp.) is a dominant perennial weedy species. The common name 'alkaligrass' refers to either one of two species of alkaligrass: Nuttall's alkaligrass, a native grass to the region or weeping alkaligrass, an introduced species from Eurasia. Often undistinguishable 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 (Walenta, Oregon State University, personal communication). Due to their similar seed size to Kentucky bluegrass, it is very difficult to eliminate either Nuttall's or weeping alkaligrass during the seed cleaning process.

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). Nuttall's alkaligrass has been documented on saline (Macke 1969) and sodic (Tarasoff 2006) depressions, 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 (Garlitz 1992, Davis and Goldman 1993) and ruderal areas (Moracova and Frantik 2002, Tarasoff 2006). Both Nuttall's and weeping alkaligrass could be considered facultative halophytes (Macke and Ungar 1971, Beyschlag et al. 1996, Moracova and Frantik 2002), as neither species requires salt to complete its lifecycle. Moreover, studies on phenological development, biomass accumulation and seed production of the two species indicate that under sodic versus normal soil type conditions, weeping alkaligrass had a greater biomass accumulation in

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normal soils; whereas, Nuttall's alkaligrass had no significant difference in biomass accumulation or seed production under the opposing conditions (Tarasoff et al. 2007). In eastern Oregon, it has been observed that the native species Nuttall's alkaligrass tends to behave like a niche specific species, dominating areas of high pH and sodicity; whereas weeping alkaligrass exhibits resource generalist characteristics, dominating areas low in competition (Tarasoff 2006)

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* (Ryel et al. 1996). However, to date, 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, researchers (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 are analyzed, thus allowing for the study of inter- and intraspecific competition.

Typically, however, plant competition is studied under a short time frame. 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 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.

We studied the competitive interactions and survival rates among three species: Kentucky bluegrass, Nuttall's alkaligrass, and weeping alkaligrass in pair-wise matrices over a two year period to evaluate the potential for either alkaligrass species to affect Kentucky bluegrass production in eastern Oregon.

Methods

We grew seedlings of each of the three species, weeping alkaligrass, Nuttall's alkaligrass, and Kentucky bluegrass 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. A preplant comparison of seedling size was conducted. Ten seedlings of each species were harvested from the greenhouse and dried for 48 hrs at 65 C to ensure that there were no significant differences between the initial sizes of the three species ($P > 0.05$).

One month old seedlings were transplanted from September 22-24, 2004. Pair-wise combinations were 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, productive soils described as coarse-silty mixed, superactive, mesic Typic Haploxerolls (Walla Walla silt loam - cultivated) (Dyksterhuis and High 1985). More specifically, the site is a silt loam with a pH of 6.9 and 1.8% organic matter. The average precipitation for the region is 429 mm.

We planted monocultures of each species 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 2 m alley between plots. Alleys were bare and were maintained bare throughout the study. 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.

Throughout the course of the study, broadleaf and grass weed control was maintained to ensure there were no competing plants. 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, all 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. In addition, the number of inflorescences per plant and plant height were recorded

Statistical Analysis

Several linear and non-linear models were fit to the biomass, inflorescence production, and height data for both species in each of the pair-wise matrices. The adequacy of each model was evaluated using an assessment of the residuals (normally distributed), the R^2 value, and, by incorporating the law of parsimony, as the ability to biologically interpret model parameters was of primary importance. Plant height was not significantly affected by planting density of any species (P>0.05); therefore, no further analysis was conducted. Inflorescence production models closely mimicked the biomass models; therefore, for relevance and brevity, only the inflorescence models will be presented and discussed.

For all three pair-wise experiments, inflorescence production per plot was 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 inflorescence production of species Y with respect to the density of species X and species Y and the interaction of the densities of species X and Y.

Results

Visual representation of the inflorescence production data was modeled using 3-dimensional response surface graphs (Figure 1). Best fit models with their respective R^2 results are presented in Table 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 was influenced by total density. As well, because the data was log transformed for analysis and then back transformed for discussion, the confidence intervals around the mean were 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.

Year 1

The interaction term of $\beta_5(X_i Y_i)$ was significant, thus the effect of the two plant densities on yield cannot 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 1A–1F visually represent the best-fit models for each pair-wise comparison as outlined in Table 1.

It is apparent from Figures 1A and 1B that weeping alkaligrass and Nuttall's alkaligrass had a strong, negative impact on Kentucky bluegrass inflorescence production. Interspecific competitive effects on Nuttall's alkaligrass inflorescence production were less pronounced when grown with Kentucky bluegrass (Figure 1C) than weeping alkaligrass (Figure 1D). At low densities of weeping alkaligrass, the interspecific effect of competition was less pronounced when grown in combination with Kentucky bluegrass (Figure 1E) than Nuttall's alkaligrass (Figure 1F). Intraspecific competition will be described below.

Changes in Inflorescence Production 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 changes in inflorescence production were affected at various densities. There are an abundance of possible 'slices' through the response surface which can be presented. The comparisons

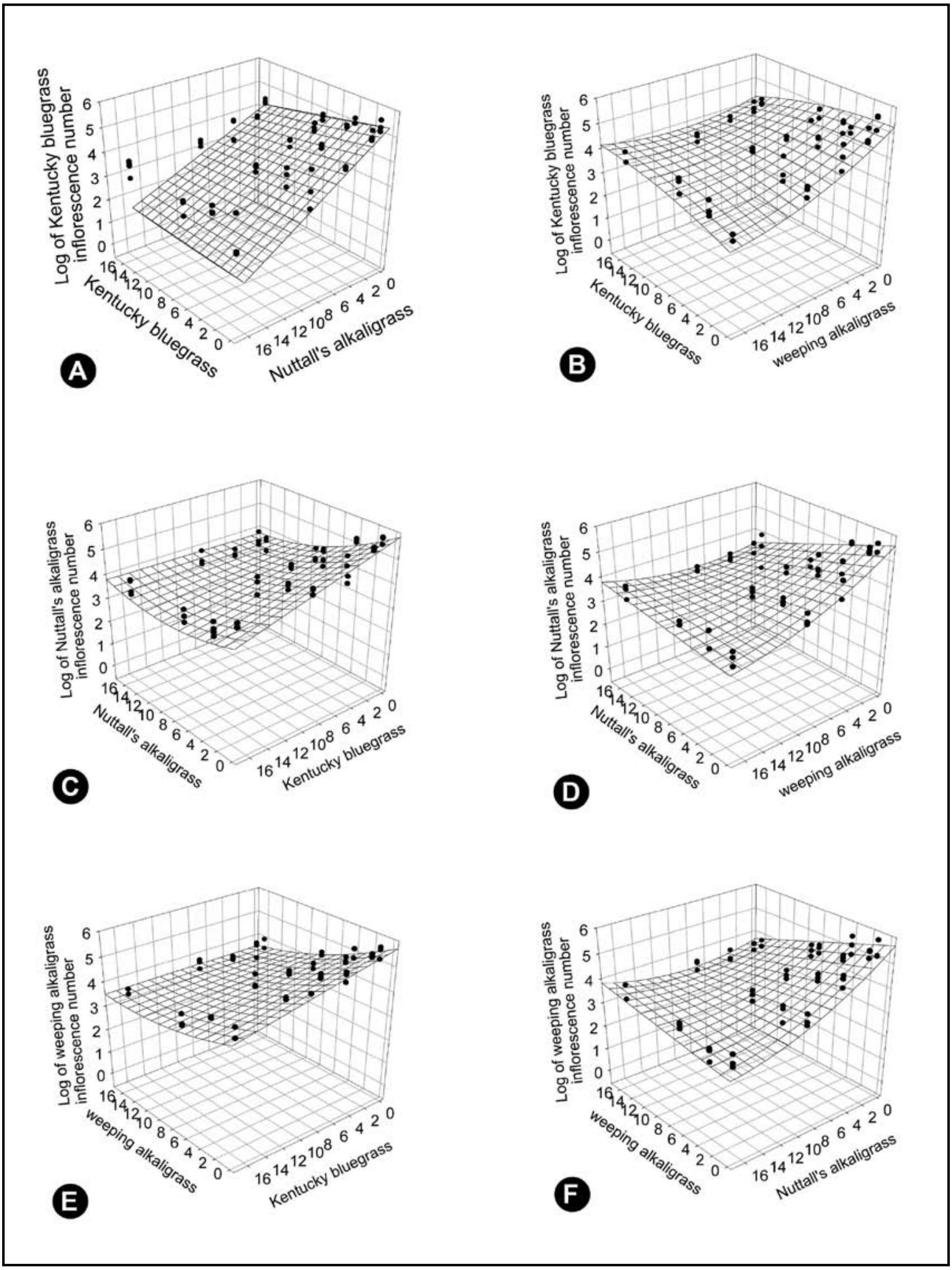

Figure 1. Year 1 comparison of competition on the log of inflorescence production of weeping alkaligrass, Nuttall's alkaligrass and Kentucky bluegrass. The X and Z axes indicate the planting density per $0.25m^2$ of each species, respectively.

TABLE 1. Year 1 best-fit models for average inflorescence production (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	Model	R^2
Kentucky bluegrass X weeping alkaligrass			
Kentucky	Inflor.	$LogY_k = 5.12 – 0.21D_w – 0.004D_k + 0.005D_w^2 - 0.005D_k^2 + 0.007D_wD_k$	0.82
Weeping	Inflor.	$LogY_w = 5.58 – 0.19D_w – 0.07D_k + 0.004D_w^2 + 0.004D_wD_k$	0.87
Kentucky bluegrass X Nuttall's alkaligrass			
Kentucky	Inflor.	$LogY_k = 5.36 – 0.24D_n – 0.08D_k + 0.006D_n^2 + 0.005D_nD_k$	0.80
Nuttall's	Inflor.	$LogY_n = 5.69 – 0.22D_n – 0.10D_k + 0.006D_n^2 + 0.006D_nD_k$	0.94
Nuttall's alkaligrass X weeping alkaligrass			
Weeping	Inflor.	$LogY_w = 5.51 – 0.11D_w – 0.25D_n + 0.006D_n^2 + 0.009D_wD_n$	0.89
Nuttall's	Inflor.	$LogY_n = 5.44 – 0.22D_w – 0.12D_n + + 0.005D_n^2 + 0.009D_wD_n$	0.81

presented in this paper are the effects on inflorescence production (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 2). Substitution rates clearly indicate the percent change in inflorescence production of a species when subjected to a one plant increase in intraspecific versus interspecific competition.

Not surprisingly, the graphs in Figure 2 indicate that the effect of each additional unit increase diminished with higher original densities regardless of species. Kentucky bluegrass was more affected by an additional weeping alkaligrass or Nuttall's alkaligrass than an additional Kentucky bluegrass regardless of the initial Kentucky bluegrass density (Figure 2A). For example, with an initial density of 6 Kentucky bluegrass per 0.25 m^2, the addition of one Nuttall's alkaligrass resulted in an average inflorescence reduction of 18% ($\pm$ 4%), versus 17% (+ 3, - 4%) with the addition of one weeping alkaligrass, yet only 3% (+ 2, -3%) with one Kentucky bluegrass.

Nuttall's alkaligrass was more affected by an additional weeping alkaligrass than a Nuttall's alkaligrass or a Kentucky bluegrass. For example, at the same initial density of 6 Nuttall's alkaligrass plants per 0.25 m^2, the addition of 1 weeping alkaligrass resulted in a reduction of inflorescence production by 15% (+ 4, -5%), versus 6.5% ($\pm$ 1%) with one Nuttall's alkaligrass, and 5% (+ 1%) with one Kentucky bluegrass (Figure 2B).

Similarly, at an initial density of 6 weeping alkaligrass plants per 0.25 m^2, the addition of 1 Nuttall's alkaligrass resulted in an overall reduction of the average inflorescence production by 17% (+3, -4%), versus 15% (+ 4, -5%) with one weeping alkaligrass, and only 4% ($\pm$1%) with one Kentucky bluegrass plant (Figure 2C).

Therefore, across many densities, an additional Nuttall's or weeping alkaligrass was more likely to reduce biomass production of Kentucky bluegrass than Kentucky bluegrass itself; however, weeping alkaligrass was consistently equal to or a stronger competitor than Nuttall's alkaligrass when grown together or in combination with Kentucky bluegrass. The results can be summarized by the following equations:

For KBG ~ PN=PD>KBG

For PN ~ PD>PN=KBG

For PD ~ PD=PN> KBG

Where PD represent weeping alkaligrass, PN represents Nuttall's alkaligrass and KBG is Kentucky bluegrass.

Species Survival

In the beginning of Year 2 (June), all species were assessed for new growth. Of the three species, weeping alkaligrass had the lowest survival rates at 40% $\pm$ 12, followed by Nuttall's alkaligrass at 60% $\pm$ 11, and lastly Kentucky bluegrass at 98% $\pm$ 2.

Year 2

The low survival of weeping alkaligrass and Nuttall's made it impossible to accurately measure the effect of competition on these two species.

Note: There were 2 captions supplied for Fig. 3. The second was ——————> Not sure what to do with it.

Figure 3. Year 2 comparison of competition on the log of inflorescence production of Kentucky bluegrass in year 2. The X and Z axes indicate the planting density per $0.25m^2$ of each species, respectively.

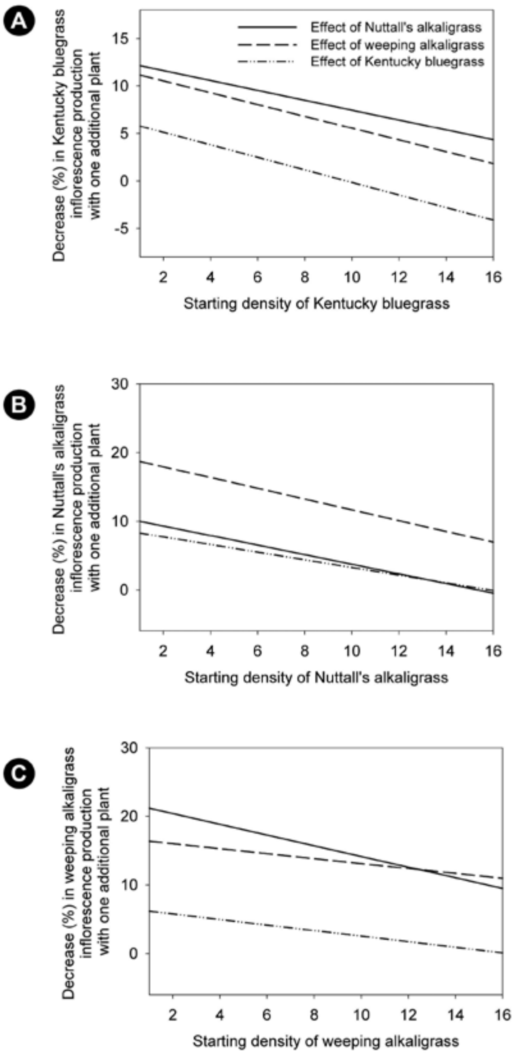

Figure 2. Year 1 change (%) in average inflorescence production of Kentucky bluegrass (A), Nuttall's alkaligrass (B) and weeping alkaligrass (C) at differing initial densities with the addition of one Kentucky bluegrass versus an additional weeping or Nuttall's alkaligrass.

However, even with the mortality of the two alkaligrass species it was still possible to measure the effect of the initial planting densities of the two species on year 2 inflorescence production of Kentucky bluegrass.

Model selection followed the same procedures as outlined in Year 1. Response surfaces of the modeled inflorescence data are displayed in Figure 3.

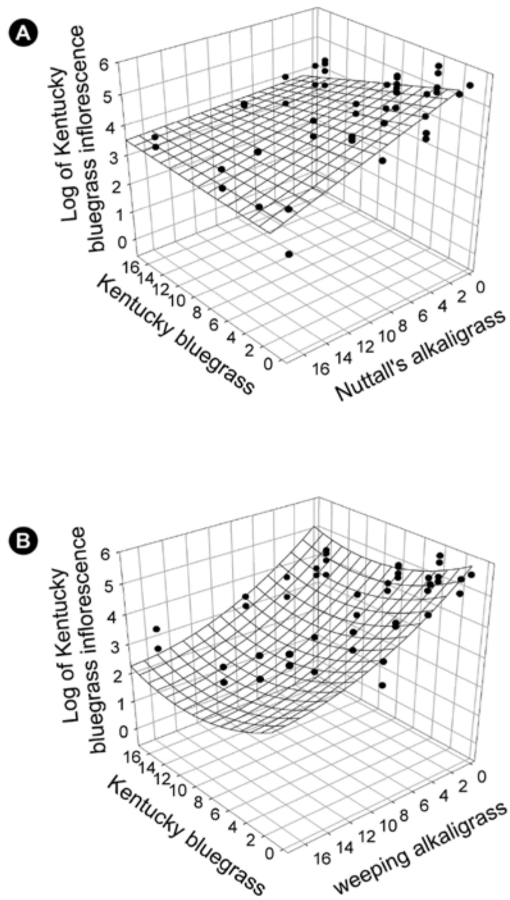

Figure 3. Average percent survival (± 95% confidence intervals) of Nuttall's alkaligrass (A), weeping alkaligrass (B) and Kentucky bluegrass June of year 2 (post harvest) when grown in two-way combinations.

In year 2, the effect of Nuttall's alkaligrass or weeping alkaligrass on Kentucky bluegrass inflorescence production continued to be density dependant (Figure 3) as explained by the models:

$$\mathrm{Log}Y_k = 6.01 - 0.30D_w - 0.23D_k + 0.01D_w^2 + 0.008D_k^2 \quad [2]$$

$$\mathrm{Log}Y_k = 5.73 - 0.14D_n - 0.11D_k + 0.007D_nD_k \quad [3]$$

where $\log Y_k$ is the log of inflorescence production of Kentucky bluegrass with respect to the density (D) of species w (weeping alkaligrass), species n (Nuttall's alkaligrass, and/or species k (Kentucky bluegrass). The R^2 values for equations 2 and 3 were 0.77 and 0.68, respectively.

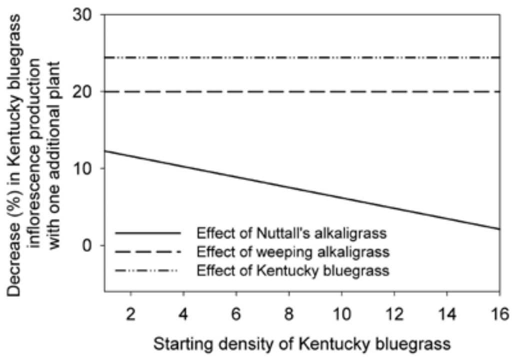

Figure 4. Year 2 change (%) in average inflorescence production of Kentucky bluegrass at differing initial densities with the addition of one Kentucky bluegrass versus an additional weeping or Nuttall's alkaligrass at the time of planting.

Changes in Inflorescence Production with the Addition of One Plant

In year 2, Kentucky bluegrass inflorescence production was more affected by an additional weeping alkaligrass or Kentucky bluegrass at the time of planting than an additional Nuttall's alkaligrass plant (Figure 4). For example, with an initial density of 6 Kentucky bluegrass plants per 0.25 m^2, the addition of one Nuttall's alkaligrass resulted in an overall reduction of the average inflorescence production by 8.0% (+ 2.3, - 2.4%), versus 20.3% (+ 6.7, - 7.5%) with one weeping alkaligrass, and 25.9% (+ 7.7, - 8.6%) with one Kentucky bluegrass plant.

Discussion

Year 1—Competiton

The poor competitive abilities of Kentucky bluegrass in Year 1 could be partially a result of the differing growth rates of the three species. Kentucky bluegrass is generally considered to be a slow establishing plant (Brown and Munsell 1945) whereas Nuttall's alkaligrass and particularly weeping alkaligrass exhibit rapid growth rates (Tarasoff et al. 2007). The rapid growth of the alkaligrass species may inhibit Kentucky bluegrass growth in year 1 via shading and water utilization. Kentucky bluegrass prefers full sun conditions, does not perform well under a shaded canopy (Christians 2003), and readily enters dormancy under excessive drought conditions (Wang and Huang 2004).

The competitive abilities of weeping alkaligrass and Nuttall's alkaligrass may be linked to their differing, yet advantageous, growth habits. Nuttall's alkaligrass is a tall (80 – 100 cm) erect plant, with an open plant architecture whereas weeping alkaligrass is a shorter (usually 40-60 cm), decumbent plant with a dense plant architecture. The height of Nuttall's alkaligrass may allow the plant to grow above the canopy of the other two species while the decumbent, dense nature of weeping alkaligrass might allow it to smother competing vegetation. From this study, it appears that the decumbent nature of weeping alkaligrass gave it a competitive advantage when grown with Kentucky bluegrass or Nuttall's alkaligrass.

Species Survival

The low survival rates and compensatory growth of weeping alkaligrass may be the 'Achilles heel' of this plant. It was observed (C. Tarasoff, personal observation) that both alkaligrass species, in particular weeping alkaligrass, exhibited compensatory plant growth following harvest. The continuation of plant growth, and inflorescence production, into the dry summer months may have resulted in a depletion of the plant's carbohydrate reserves, which may have contributed to the mortality of both species; in particular weeping alkaligrass.

Although unaccountable, the effect of late-season mowing (i.e., harvest in year 1) may have contributed substantially to survival. Ryel et al. (2006) reported that weeping alkaligrass' competitive effects may have been negatively affected by an intolerance to mowing. Nuttall's alkaligrass has also been documented to be intolerant of 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. Thus, the Kentucky bluegrass seed harvesting method may have inadvertently reduced weeping and Nuttall's alkaligrass survival.

Year 2—Competition

Although Kentucky bluegrass was slow to establish in the first year, its rhizomonous growth form and tolerance to mowing allowed it to achieve site dominance by year 2. Kentucky bluegrass 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). In particular, the cultivar 'Midnight' is noted for its exceptional tolerance to close mowing, drought tolerance and high tiller density (http://www.bluegrasses.com/info/midnight.html). These characteristics likely enabled the plant to survive the harvesting procedures and flourish under no irrigation. Additionally, Midnight's high tiller density may have also contributed to its strong competitive nature.

While alkaligrass had a difficult time surviving the Kentucky bluegrass harvesting procedures, the legacy effect of year 1 alkaligrass plants may reduce Kentucky bluegrass yields the following year. These results were witnessed in our study; only 40% of the original weeping alkaligrass plants survived into year 2, yet the species continued to reduce Kentucky bluegrass production by approximately 20%. The reduction in Kentucky bluegrass was basically unchanged from year 1 to year 2 despite the significant mortality of weeping alkaligrass. Therefore, it is possible that there is a legacy effect of competition which continues to affect plant growth long after the competing vegetation is removed.

Management Implications

Although weeping alkaligrass is likely to be a greater threat to Kentucky bluegrass seed production in eastern Oregon than Nuttall's alkaligrass, these results should not diminish the significant effect of Nuttall's alkaligrass. Even in plots where Nuttall's and weeping alkaligrass died, the effect of competition from the first year carried over to the second, reducing Kentucky bluegrass production in year 2. Thus, diligent weed control of both species early in the growing season will reduce direct competition, the legacy effect of competition, seed bank development and weed spread through Kentucky bluegrass seed contamination.

Had our study followed a typical competition study time line of one year we would have drawn erroneous conclusions. General conclusions derived from year 1 would lead managers to believe that both species of alkaligrass are equally more competitive than Kentucky bluegrass and that Kentucky bluegrass is a very weak competitor. However, in year 2, the growth strategy of all three species played a large role in survival and growth. Our results pose an interesting avenue for future research. At what stage of development/competition interaction does a competitor have a lasting effect on plant growth? How long will it take a species to recover from the legacy effect of competition? Can managers predict, and thus manage for, the potential legacy effect of competition? Additionally, how might the legacy effect of competition limit or inhibit our efforts to restore complex ecosystems? To effectively answer these questions, researchers must develop long-term competition studies.

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