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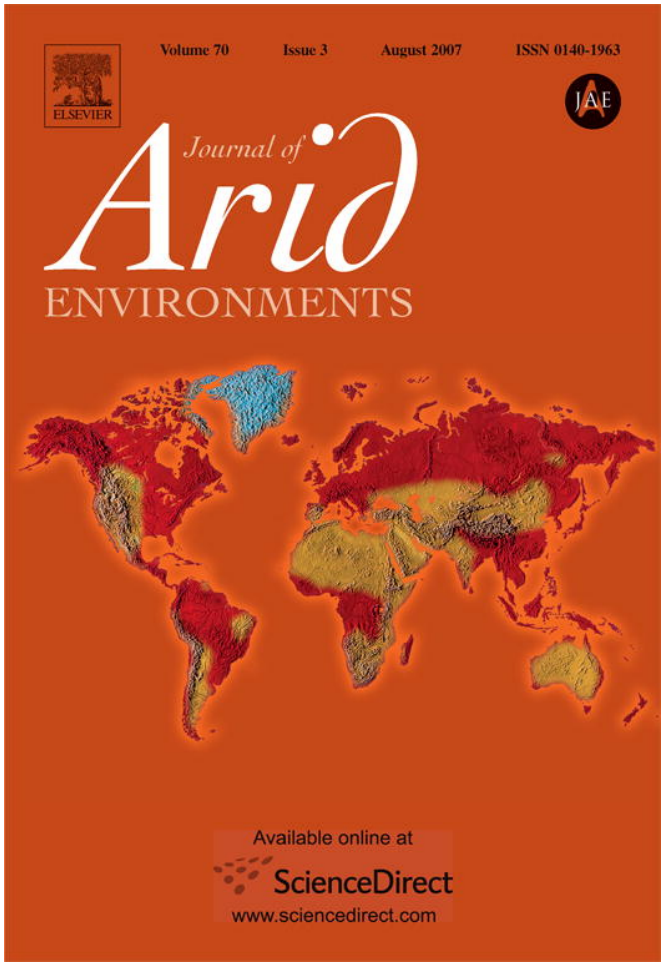

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Comparative plant responses of *Puccinellia distans* and *Puccinellia nuttalliana* to sodic versus normal soil types

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Abstract

In the Grande Ronde Valley of eastern Oregon, two perennial grass species within the genus *Puccinellia*; *Puccinellia distans* (L.) Parl. (weeping alkaligrass) and *Puccinellia nuttalliana* Hitchc. (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, *P. distans* grew larger and produced up to 4 times the number of viable seed than did *P. nuttalliana*. Growth rates and seed production of *P. nuttalliana* were not affected by soil type; yet, *P. distans* 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; *P. distans* was able to continue tiller production through out the growing season whereas *P. nuttalliana* ceased tiller development soon after onset of reproduction.

Pucinellia distans adjusted osmotically to a much lower solute potential (−3.6 MPa) than *P. nuttalliana* (−2.3 MPa) under sodic soils. Under normal soil conditions, *P. distans* maintained a higher relative water content (80%) than *P. nuttalliana* (60%) at the same osmotic potential (−2.3 MPa).
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Keywords: Alkaligrass; *Puccinellia distans*; *Puccinellia nuttalliana*: Phenology; Salt tolerance

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1. Introduction

Puccinellia distans (weeping alkaligrass) and *Puccinellia nuttalliana* (Nuttall's alkaligrass) typically occupy high pH soils throughout North America (Brotherson, 1987; Hughes, 1972; Macke and Ungar, 1971). *P. distans*, an introduced species from Eurasia, is widespread across arid and saline environments of North America (Hitchcock, 1971). Whereas *P. nuttalliana*, 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., 1983; 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).

Kentucky bluegrass (*Poa pratensis*) seed is a 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 (Walenta, pers. comm., 2000). In 2003, in Union County, there were 4795 certified acres 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. Undistinguished to 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, pers comm., 2000). 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, resulting in lowered market values for the Kentucky bluegrass seed crop.

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, 1979). Grime felt that the external

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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 concludes that all plants have evolved a distinct strategy enabling them to prevail in a given habitat. A plant that flourishes under low stress and low disturbance would have a competitive strategy; one that 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 naturally 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, an experiment was designed which studied plant characteristics such as life-history characteristics, phenological development, and plant–water relations of the two species when grown on sodic versus normal soil types.

2. Materials and methods

2.1. 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 as described by Brady and Weil (2002). To remove any potential soil contaminants such as pathogens and parasites, each soil type was steam autoclaved for 4 h at 150 C. Soil characteristics for the two soil types are presented in Table 1.

2.2. Life-history characteristics

2.2.1. Germination

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 *P. distans* or ten *P. nuttalliana* adequately afterripened (18 months at 21 C) seeds. Seeds used in this experiment were collected from multiple distinct sites within a large acreage in the Grande Ronde valley (45°29′15.9″N, 117°56′4″W). 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.

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Table 1
Soil characteristics for the sodic versus normal soil used in the experiment

Soil characteristics	Sodic	Normal
pH	9.1	6.0
Ca (meq/100 g)	20.0	3.6
Mg (meq/100 g)	8.5	0.9
Na (meq/100 g)	9.7	0.2
EC (meq/100 g)	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

Germination counts started following the first sign of emergence and followed on days 4, 7, 14, and 21 after emergence. To prevent severe desiccation 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.

2.2.2. 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 Feekes scale 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), where $\mathrm{GDD} = [(T_{max} + T_{min})/2] - T_b$, 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 ($T_b = 0\,\mathrm{C}$).

2.2.3. 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).

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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.

2.2.4. 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 *P. distans* averaged 5 seeds per spikelet and *P. nuttalliana* averaged 4.5 seeds per spikelet (Hitchcock, 1971). Average seed production was calculated using the formula $SP = F_S S_I I_P S_V$, 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.

2.3. Plant–water relations

In 2005, at 5 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 $-\pi = -RT\mathrm{Cs}$, where $-\pi$ is the osmotic potential measured in MPa, R is the ideal gas constant ($8.31\,\mathrm{J\,K^{-1}\,mol^{-1}}$), T is the absolute temperature (K) and Cs is the measured osmolality (mOsm per L). Relative water content was calculated using the equation

$$\mathrm{RWC}(\%) = [(\mathrm{FW} - \mathrm{DW})/(\mathrm{TW} - \mathrm{DW})] \times 100,$$

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.

2.3.1. 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 (SAS v.9.1). Number of tillers (y) was characterized using the sigmoidal regression equation $y = a/(1 + e^{-(x-x_o)/b})$ (SigmaPlot v.9.0), where x is the number of growing degree days.

3. Results

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

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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 as determined by ANOVA.

3.1. Life-history characteristics

3.1.1. Germination

In both years, both species exhibited relatively high rates of germination on both soil types under non-limiting soil moisture conditions. More *P. nuttalliana* seeds were likely to emerge in sodic than normal soils ($P = 0.03$, df_{79}) at 4 d after first emergence (AFE). However, the rate of germination was mitigated over time as there was no difference between soil types by 7 d AFE (Fig. 1). While *P. distans* had a slightly greater germination under normal soil than sodic soil, the differences were not significant ($P = 0.85$, df_{79}). 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 *P. distans* than *P. nuttalliana*, there was no difference by 21 d AFE ($P = 0.70$, $df_{3,\ 156}$).

3.1.2. Phenological development

Both species initiated each stage of phenological development after approximately the same accumulation of growing degree day regardless of soil type or year (Figs. 5 and 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, *P. distans* consistently accumulated more tillers throughout the growing season than did *P. nuttalliana* (Figs. 5 and 6). In year 1, on normal soils tiller development was not different between the two species. However, on sodic soils while

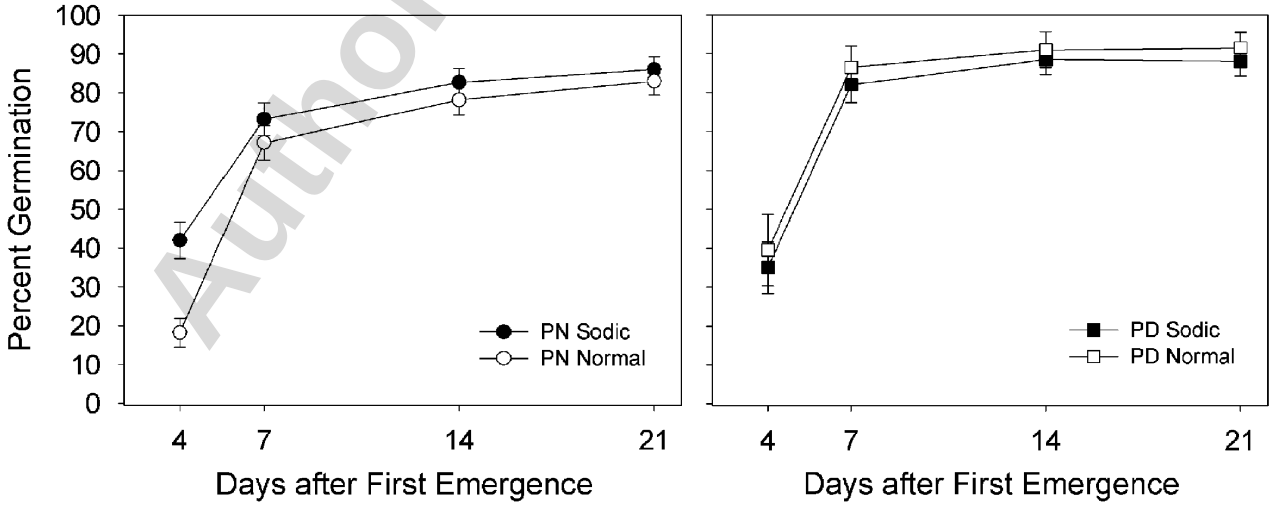

Fig. 1. Comparison of *Puccinellia nuttalliana* (PN) and *Puccinellia distans* (PD) germination with 95% confidence intervals when grown on sodic versus normal soil types for combined years.

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tillering of both species slowed after the flowering stage, tiller production of *P. distans* on sodic soils ($R^2 = 0.95$, $df_{3,86}$) slowed less than *P. nuttalliana* ($R^2 = 0.96$, $df_{3,86}$). In year 2, under normal soil conditions *P. distans* ($R^2 = 0.82$, $df_{3,141}$) tiller development was greater than *P. nuttalliana* ($R^2 = 0.80$, $df_{3,141}$). Under sodic soil conditions, tillering of *P. nuttalliana* ($R^2 = 0.70$, $df_{3,141}$) appeared to stop once the species initiated the boot stage of development (800 GDD); while tillering slowed in normal soils ($R^2 = 0.80$, $df_{3,141}$) after flowering was initiated (1100 GDD). In both sodic ($R^2 = 0.88$, $df_{3,141}$) and normal ($R^2 = 0.82$, $df_{3,141}$) soil conditions, the tillering rate of *P. distans* slowed marginally after flowering (1100 GDD) but never appeared to stop (Fig. 6).

3.1.3. 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 ($P = 0.03$, $df_{1,65}$). In year 2, a species by soil interaction was significant for the number of tillers ($P = 0.002$, $df_{1,109}$), and the number of inflorescence ($P = 0.003$, $df_{1,109}$). 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.

3.1.3.1. P. nuttalliana by soil type. Differences in biomass accumulation by soil type within each year for *P. nuttalliana* were variable and generally not significant by the mature seed harvest (Figs. 2 and 3). Between years, *P. nuttalliana* grew taller, produced more tillers, and greater biomass regardless of soil type in year 1 than year 2 ($P<0.05$) (Figs. 2 and 3).

3.1.3.2. P. distans by soil type. Under sodic soil conditions, *P. distans* exhibited more vigorous growth in year 1 than year 2 with greater biomass and tiller accumulation (Figs. 2 and 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, *P. distans* 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 ($P = 0.03$, $df = 14$) 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 ± 0.8 g/plant) than those grown in normal soils (8.39 ± 2.8 g/plant) (Fig. 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.

3.1.3.3. P. nuttalliana versus P. distans. After the tillering stage, *P. nuttalliana* was taller than *P. distans* ($P<0.05$) throughout the growing season (Figs. 2 and 3). The difference between the heights of the two species can be seen in the field, where *P. distans* is prostrate and *P. nuttalliana* is upright.

In year 1, the species were different in their biomass accumulation across both soil types ($P = 0.004$, $df_{1,65}$); however, there did not exist a species by soil type interaction ($P = 0.93$, $df_{1,65}$) (Fig. 2). The significant difference between the species may be attributed to the rapid growth rate of *P. nuttalliana* on sodic soils at the emergence stage.

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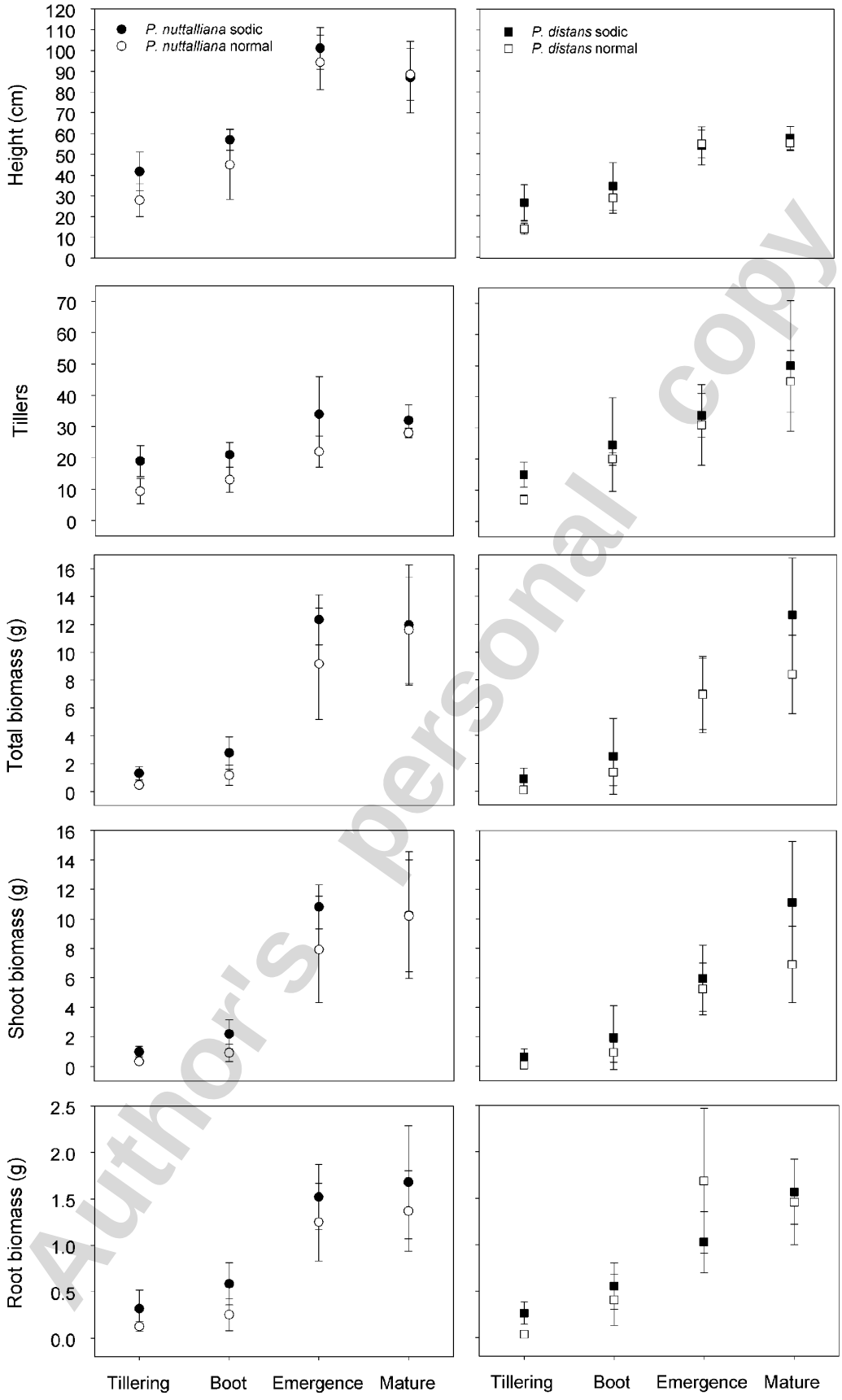

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Fig. 2. Year 1 comparison of biomass accumulation and partitioning for *Puccinellia nuttalliana* and *Puccinellia distans* with 95% confidence intervals when grown in sodic versus normal soil types.

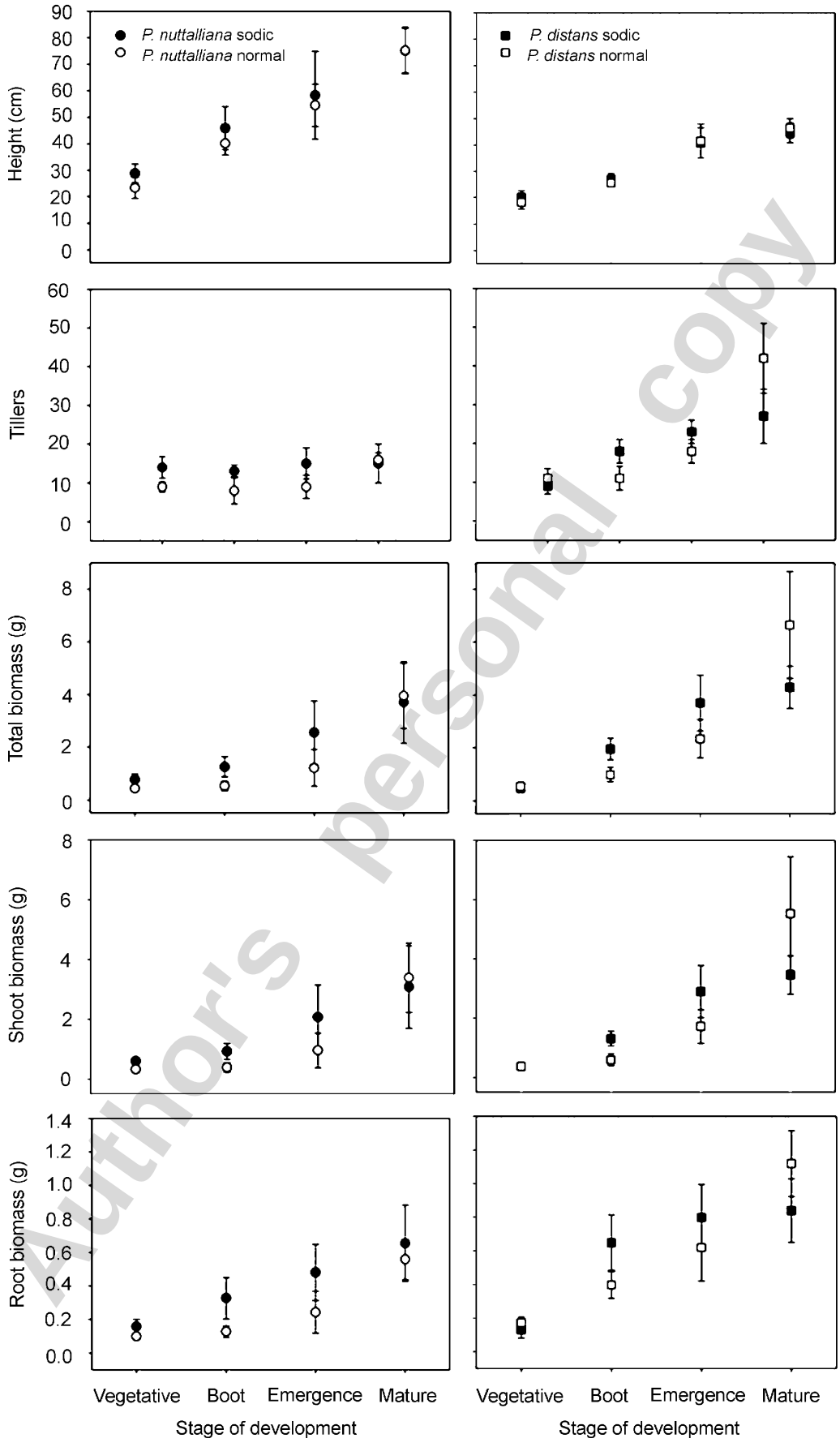

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Fig. 3. Year 2 comparison of biomass accumulation and partitioning for *Puccinellia nuttalliana* and *Puccinellia distans* with 95% confidence intervals when grown in sodic versus normal soil types.

In year 2, the species were different in their biomass accumulation across both soil types ($P<0.0001$, $df_{1,106}$); however, once again, there did not exist a species by soil-type interaction ($P = 0.13$, $df_{1,106}$) (Fig. 3). At the mature harvest, when grown in normal soils, total biomass of *P. distans* was no different (6.64 ± 2.0 g/plant) than *P. nuttalliana* (4.0 ± 1.2 g/plant) at the mature harvest date (Fig. 3).

3.1.4. Fitness (seed production)

3.1.4.1. P. nuttalliana by soil type. Inflorescence production by *P. nuttalliana* at the mature harvest was unaffected by the different soil types in year 1 ($P = 0.6$, df = 8) or year 2 ($P = 0.8$, df = 14). Yet, from year 2 versus year 1, there was a decrease in the average inflorescence per plant on sodic soils ($P = 0.02$, df = 11), as well as on normal soils ($P<0.0001$, df = 11) (Table 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, $75\% \pm 6.0$ versus $73\% \pm 6.2$ 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 2).

3.1.4.2. P. distans by soil type. Inflorescence production by *P. distans* at the mature harvest was unaffected by the different soil types in year 1 ($P = 0.50$, df = 9), yet was

Table 2
Comparison of average inflorescence, spikelet and maximum potential seed production per plant after 1 year of growth for *Puccinellia nuttalliana* and *Puccinellia distans* when grown in sodic versus normal soil types

	Inflorescence/plant			
	Sodic		Normal	
	Year 1	Year 2	Year 1	Year 2
P. distans	22 (10)	19 (3)	19 (9)	12 (3)
P. nuttalliana	21 (9)	12 (4)	23 (2)	11 (4)
	Spikelets/inflorescence			
	Sodic		Normal	
	Year 1	Year 2	Year 1	Year 2
P. distans	404 (44)	233 (53)	369 (9)	355 (113)
P. nuttalliana	175 (55)	138 (49)	176 (78)	140 (48)
	Average seed yield/plant			
	Sodic		Normal	
	Year 1	Year 2	Year 1	Year 2
P. distans	33 774	16 823	31 550	19 170
P. nuttalliana	12 403	5589	13 298	5059

Average values followed by 95% confidence interval where applicable.
Note: average seed yield calculated in 2005 using Eq. (1) ($SP = F_S S_I I_P S_V$).

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significantly higher on sodic soils in year 2 ($P = 0.001$, df = 12). From year 1 to year 2, there was a decrease in the average inflorescence per plant on sodic soils ($P = 0.01$, df = 12), yet not on normal soils ($P = 0.10$, df = 9).

Within each year, soil type did not affect the average number of spikelets per inflorescence. Yet, in year 2, *P. distans* 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 2).

3.1.4.3. P. nuttalliana versus P. distans. There were no differences in inflorescence number at the mature harvest between the two species in year 1 when grown on normal soil ($P = 0.32$, df = 8) or sodic soil ($P = 0.76$, df = 9) as well as in year 2 (Table 2). However, *P. distans* consistently produced more spikelets per inflorescence than *P. nuttalliana* under all conditions ($P < 0.05$). Therefore, depending on the conditions, *P. distans* produced 2–4 times the average seed yield than *P. nuttalliana*.

3.2. 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).

3.2.1. P. nuttalliana

P. nuttalliana 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 (Fig. 4). The cessation of osmotic adjustments of *P. nuttalliana* corresponded to relative water contents of approximately 85% (Fig. 4).

3.2.2. P. distans

Under both soils conditions, *P. distans* exhibited a linear relationship between osmotic potential and relative water content. Under sodic soil conditions, *P. distans* was able to osmotically adjust to values of at least −3.5 MPa at relative water contents of less than 60% (Fig. 4). At relative water contents $\leqslant 87\%$, *P. distans* had significantly lower osmotic values for the same relative water contents when grown in sodic versus normal soils, indicating osmotic adjustment. In this experiment, *P. distans* did not reach a condition where osmotic adjustment ceased (Figs. 5 and 6).

4. Discussion

Some plants that naturally occur in harsh environments are contained by competitive exclusion and would otherwise flourish under productive agricultural habitats if given the opportunity.

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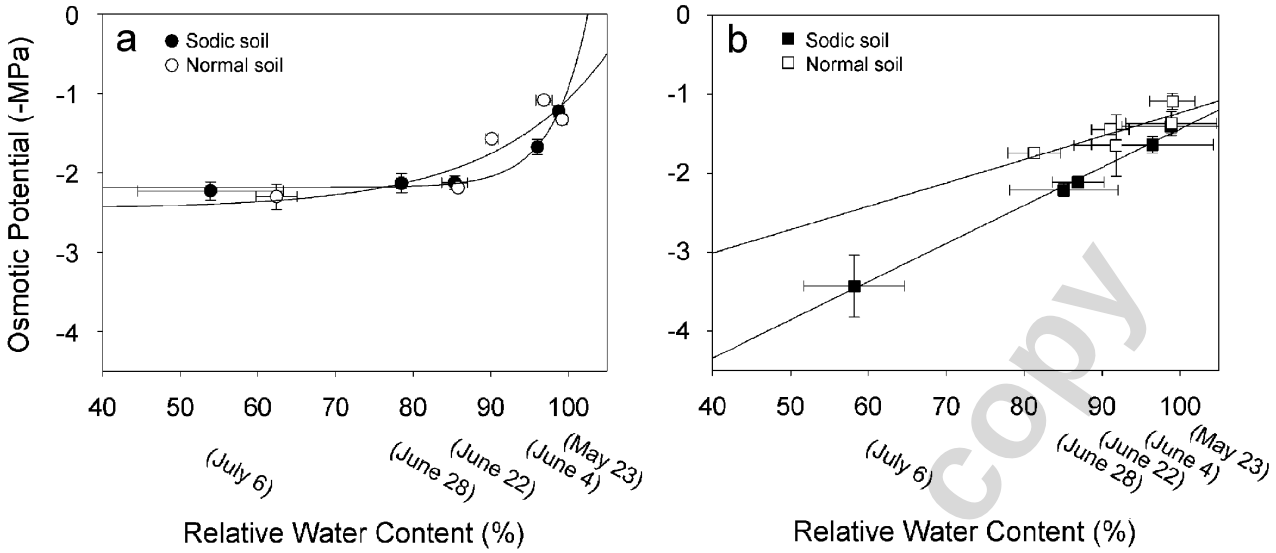

Fig. 4. Year 2 comparison of changes in osmotic potential versus relative water content for (a) *Puccinellia nuttalliana* and (b) *Puccinellia distans* with 95% confidence intervals when grown in sodic versus normal soil types. Dates given correspond to sample date and are associated with the sodic soil value for that date.

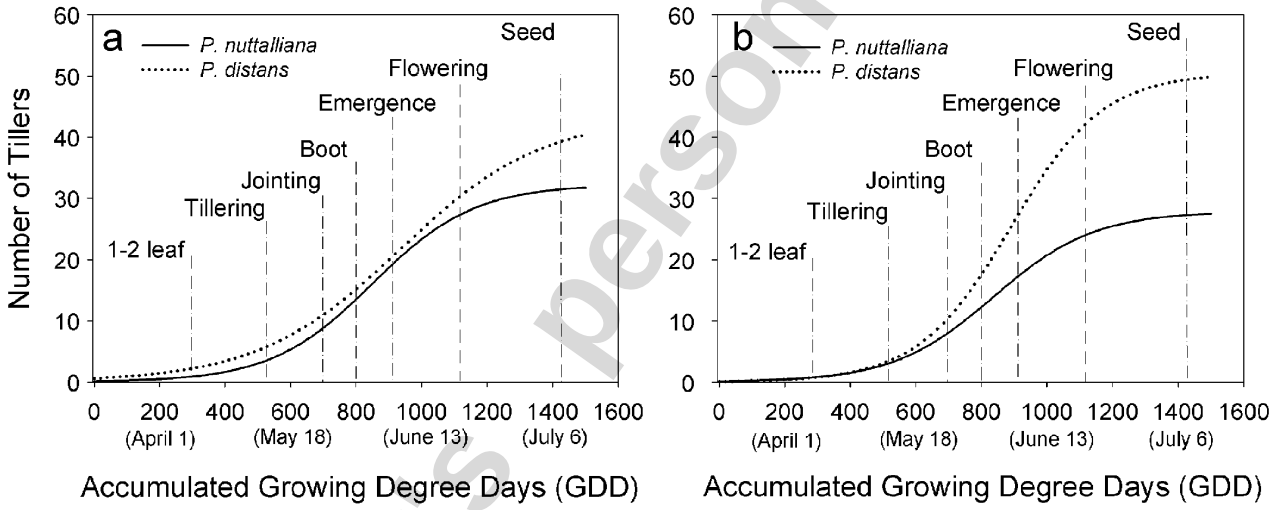

Fig. 5. Year 1 comparison of *Puccinellia nuttalliana* and *Puccinellia distans* phenological development rates and tiller development based on accumulated growing degree days under (a) normal versus (b) sodic soil types.

P. nuttalliana 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, *P. distans* 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 *P. distans* 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 *P. nuttalliana* would be outcompeted by more competitive plant species.

In terms of salt tolerance, *P. nuttalliana* did not appear to be affected cellularly by the high levels of sodium salts associated with the sodic soils. However, this result is not surprising since it had previously been reported that under increasing sodium

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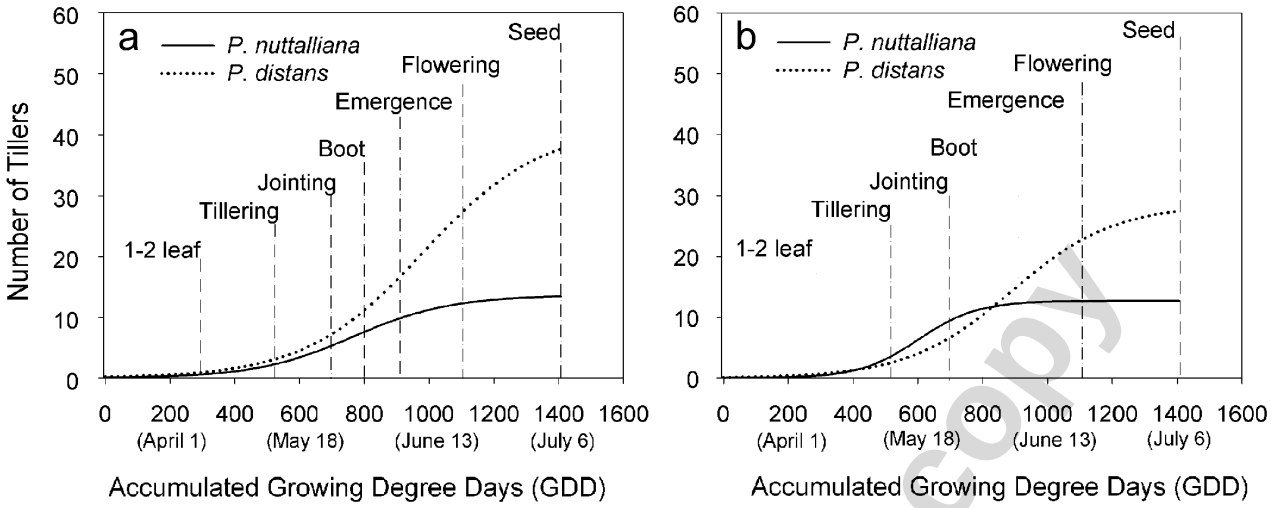

Fig. 6. Year 2 comparison of *Puccinellia nuttalliana* and *Puccinellia distans* phenological development rates and tiller development based on accumulated growing degree days under (a) normal versus (b) sodic soil types.

concentrations, *P. nuttalliana* did not take up sodium ions (Harivandi et al., 1982, 1983). Osmotic adjustments allow the potential for maintaining photosynthesis and growth as the water deficit increases (Turner and Jones, 1980 in Gusta and Chen, 1987), and therefore, tolerance of water stress often involves low osmotic potentials (Morgan, 1984) as observed in *P. distans*. The ability of *P. distans* to osmotically adjust to maintain a higher level of vegetative growth throughout the summer is clearly a competitive advantage. However, it is unknown whether the species was adjusting via sodium salts or soluble carbohydrates.

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 *P. nuttalliana* 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 *P. distans* between years indicated that sodium salts rather than water may be the factor limiting growth on normal soils. Higher relative water contents at the same osmotic potential under normal soil conditions, suggest a greater drought tolerance for *P. distans* than *P. nuttalliana*.

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

5. Conclusion

Historically, most land managers of eastern Oregon have not distinguished between *P. distans* and *P. nuttalliana*, 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 *P. distans* exhibited competitive characteristics versus the stress-tolerator *P. nuttalliana*. In conclusion, for farmers of eastern Oregon, *P. distans* may pose a greater threat in terms of expansion into crop land with normal soil conditions if there is no competition.

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References

Ashraf, M., McNeilly, T., Bradshaw, A.D., 1986. The potential for evolution of salt (NaCl) tolerance in seven grass species. New Phytologist 103, 299–309.

Ball, D., Frost, S., Gitelman, A., 2004. Predicting timing of downy brome (*Bromus tectorum*) seed production using growing degree days. Weed Science 52 (4), 518–524.

Beyschlag, W., Ryel, R.J., Ullmann, I., Eckstein, J., 1996. Experimental studies on the competitive balance between two Central European roadside grasses with different growth forms 2. Controlled experiments on the influence of soil depth, salinity and allelopathy. Botanica Acta 109, 449–455.

Brady, N., Weil, R., 2002. The Nature and Properties of Soils. Prentice-Hall, Upper Saddle River.

Brotherson, J.D., 1987. Plant community zonation in response to soil gradients in a saline meadow near Utah Lake, Utah County, Utah. Great Basin Naturalist 47 (2), 322–333.

Craine, J., 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of Ecology 93, 1041–1052.

Davis, J.I., Goldman, D.H., 1993. Isozyme variation and species delimitation among diploid populations of the *Puccinellia nuttalliana* complex (*Poaceae*): character fixation and the discovery of phylogenetic species. Taxon 42, 585–599.

Garlitz, R., 1992. The spread of *Puccinellia distans* (reflexed saltmarsh grass) in Michigan. The Michigan Botanist 31, 69–74.

Grime, J., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111 (982), 1169–1194.

Grime, J., 1979. Plant Strategies and Vegetation Processes. Wiley, London.

Gusta, L., Chen, T., 1987. The Physiology of Water and Temperature. ASA-CSSA-SSSA, Madison.

Harivandi, M.A., Butler, J.D., Soltanpour, P.N., 1982. Effects of sea water concentrations on germination and ion accumulation in alkaligrass (*Puccinellia* spp.). Communications in Soil Science and Plant Analysis 13 (7), 507–517.

Harivandi, M.A., Butler, J.D., Soltanpour, P.N., 1983. Effects of soluble salts on ion accumulation in *Puccinellia* spp. Journal of Plant Nutrition 6 (3), 255–266.

Haun, J., 1973. Visual quantification of wheat development. Agronomy Journal 65, 116–119.

Hitchcock, A.S., 1971. Manual of the Grasses of the United States. Dover Publications Inc., New York.

Hughes, T.D., 1972. *Puccinellia distans*—a salt-tolerant grass. In: Hughes, T.D. (Ed.), Illinois Turfgrass Conference. Illinois Cooperative Extension Service, Champaign, IL, p. 76.

ISTA, 1996. International rules for seed testing rules 1996. Seed Science and Technology 24 (Suppl.).

Jones, M.M., Turner, N.C., 1978. Osmotic adjustments in leaves of sorghum in response to water deficits. Plant Physiology 61, 122–126.

Klepper, B., Rickman, R., Zuzel, J., Waldman, S., 1988. Use of growing degree-days to project sample dates for cereal crops. Agronomy Journal 80, 850–852.

Macke, A.J., 1969. The effects of salinity upon the germination and seedling growth of *Puccinellia nuttalliana* (Hitchc.). Masters of Science, Ohio University.

Macke, A.J., Ungar, I.A., 1971. The effects of salinity on germination and early growth of *Puccinellia nuttalliana*. Canadian Journal of Botany 49, 515–520.

Mintenko, A.S., Smith, S.R., Cattani, D.J., 2002. Turfgrass evaluation of native grasses for the Northern Great Plains region. Crop Science 42, 2018–2024.

Moravcova, L., Frantik, T., 2002. Germination ecology of *Puccinellia distans* and P. limosa. Biologia, Bratislava 57 (4), 441–448.

Morgan, J., 1984. Osmoregulation and water stress in higher plants. Annual Review Plant Physiology 35, 299–319.

Mueller, R., Richards, J., 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. Annals of Botany 58 (6), 911–921.

Piernik, A., 2003. Inland halophilous vegetation as indicator of soil salinity. Basic Applied Ecology 4, 525–536.

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Rejmanek, M., Richardson, D., 1996. What attributes make some plant species more invasive? Ecology 77 (6), 1655–1661.

Salo, L.F., Artiola, J.F., Goodrich-Mahoney, J.W., 1996. Plant species for revegetation of a saline flue gas desulfurization sludge pone. Journal of Environmental Quality 25, 802–808.

Schuster, J., De Leon Garcia, R., 1973. Phenology and forage production of cool season grasses in the southern plains. Journal of Range Management 26 (5), 336–339.

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