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Importance of soil moisture and its interaction with competition and clipping for two montane meadow grasses

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Abstract

Meadow classification studies have demonstrated the importance of water table fluctuation patterns in determining plant community composition in the western United States. However, a mechanism causing an overall increase in *Poa pratensis* ssp. *pratensis* populations and local declines in *Deschampsia cespitosa* populations in western montane meadows over the past century has not been defined. In order to better understand plant species interactions in these often highly grazed systems, we observed aboveground responses of *Poa* and *Deschampsia* to changes in species composition, soil moisture gradients, and clipping in the field. As well, we conducted a factorial greenhouse experiment, varying plant density, water availability, and clipping. While *Poa* is adapted to dry meadows and *Deschampsia* to wet meadows, their ranges overlap in wet conditions where soil moisture averages 50% in the early growing season. *Deschampsia* appears to be excluded from dry meadows where *Poa* is prevalent and soil moisture is closer to 30% water content in the early growing season. Our greenhouse experiment revealed that *Deschampsia*'s competitive ability decreases, while *Poa*'s increases, at soil moistures of 19%. However in more mesic conditions (50% soil moisture), each species aboveground biomass, tillering, and inflorescence weight was adherent to soil moisture conditions, and species interactions were less important. Our early growing season clipping treatments significantly reduced biomass of both grasses, but did not appear to favor one species over the other. This work points to the importance of soil water content in determining the performance of each plant species and the level of species interactions in montane meadows.

Introduction

Montane meadow classification studies suggest that local hydrology is the most important factor determining plant species associations and distributions in meadow communities (Halpern 1986; Allen-Diaz 1991; Castelli et al. 2000). Water table fluctuations affect vegetation growth by altering soil development and soil chemical properties (Chambers 1999), inducing periods of drought stress (Grevilliot et al. 1998), creating anaerobic conditions (Castelli et al. 2000), and modifying temperatures that catalyze biotic processes (Ratliff and Harding 1993). Within these montane systems, co-dominant grasses *Deschampsia cespitosa* and *Poa pratensis* are indicators of distinct wet and dry meadow types (Ratliff 1982; Volland 1985). *Deschampsia cespitosa* often grows where water tables remain higher throughout much of the summer growing season compared with drier areas where *Poa pratensis* is found (Allen-Diaz 1991). In spite of the split classification between these grasses, they often grow in association with each other.

Besides water table differences, other plausible factors, such as competition and grazing, may influence the growth, abundance, and distribution of these meadow species. The importance of competition in montane meadows and alpine grasslands has been demonstrated (del Moral 1983; Theodose and Bowman 1997; Martin and Chambers 2001a). Yet, the exact mechanism forming plant species associations in these systems is not well understood. Water is a likely limiting resource for which meadow species must compete. Available water can be patchily distributed throughout meadows and decrease as water tables drop over the growing season (Allen-Diaz 1991). Grazing may further alter biotic interactions. Grazing may reduce biomass enough to cause competitive release (Briske 1991; Damhoureyeh and Hartnett 1997) or maintain competition by favoring growth of disturbance-adapted species (Chesson and Huntly 1997).

One of the most historically persistent disturbance regimes in montane meadows is domestic grazing. Though grazing is an important component of grassland ecosystems, domestic grazing has been criticized for a number of potentially detrimental impacts that it has had on ecological communities in western United States mountain ranges over the past century (Kauffman and Krueger 1984; Kattelmann and Embury 1996; Belsky et al. 1999). Shifting intensities and durations of grazing can alter species composition, distribution, and productivity (Crawley 1987). Besides direct impacts of livestock foraging, other effects of former grazing management are also prevalent throughout the system. For instance, it was common practice to channelize and drain meadows in order to increase forage (Gibbens and Heady 1964; Heady and Zinke 1978). The most notable effects of heavy grazing and poor management on meadow ecosystems include alterations in species composition (Kauffman et al. 1983a; Ratliff 1985; Dull 1999), vegetation loss (Kauffman et al. 1983a), erosion (Kauffman et al. 1983b), redistribution of nutrients (Woodmansee 1978), and lowered water tables (Odion et al. 1988; Knapp and Mathews 1996). Disturbances resulting from domestic grazing are often responsible for altering community processes enough to facilitate the introduction and spread of invasive species (Hobbs and Huenneke 1992; D'Antonio et al. 1999). Thus, understanding current species interactions in the wake of past managements is important for deciding future management.

Two widespread grass species of montane meadows are *Poa pratensis* and *Deschampsia cespitosa*. *Poa pratensis* ssp. *pratensis* is a naturalized rhizomatous grass that has been indirectly introduced and directly seeded in western meadows (Stewart 1939), while *Deschampsia cespitosa* is a native bunch grass. Though evidence of *Poa pratensis* ssp. *pratensis* introduction and invasion into the eastern United States is well documented (Schery 1965), there is still some question as to what extent the entire north-western complex of *Poa pratensis* is of Eurasian decent (Cronquist et al. 1977). Thus, we were unable to distinguish between possible native versus non-native ecotypes during our study. *Poa pratensis*, hereafter, called *Poa* is a co-dominant meadow species with *Deschampsia cespitosa* Beuv., studied herein and simply called *Deschampsia*. The range of *Poa* has been increasing in western montane meadows (Menke et al. 1996; Weaver et al. 2001), and whether this is a result of grazing, decreased water tables, or competitive effects is unknown. Though there are no records of a trend in *Deschampsia* decline in western montane meadows overall, local conversions from *Deschampsia*-dominated communities to *Poa*-dominated communities have occurred (Volland 1978).

Both *Poa* and *Deschampsia* are highly valued for their forage, yet noted to respond differently to grazing, and have been categorized accordingly (USDA 1994). *Poa* is considered an "increaser" following grazing (Weaver 1954; Ratliff 1982), whereas *Deschampsia* is a "decreaser" (Ratliff 1982; Volland 1985) under heavy grazing, yet tolerant of moderate grazing levels (Sampson et al. 1951). Conversely, removing grazing does not necessarily favor *Deschampsia* over *Poa* (Volland 1978). Defining the outcome of grazing management on these two species is still highly speculative and may be aided by better understanding the interaction of abiotic and biotic factors affecting their abundance and distribution.

Through field and greenhouse studies, we ask whether there is evidence of competition between *Poa* and *Deschampsia*, and if water relations and simulated grazing (i.e., clipping) interact to affect the performance of these two species, as measured by aboveground biomass, tiller number, and inflorescence weight. We hypothesize that there will be a gradient of soil moistures along which these plants grow in the field, and that *Deschampsia* and *Poa* performance will have an inverse relationship with soil moisture, with *Deschampsia* adapted to wetter conditions and *Poa* adapted to drier conditions. In all but the wettest conditions, we predict that *Poa* will have the competitive ability to reduce *Deschampsia* performance, and that this effect will be more pronounced after clipping.

Methods

Field study site

Our study was conducted at Sagehen Creek Field Station (39°N 25′ 57″, 120°W 14′ 13″), located on the eastern side of the Sierra Nevada mountain range at 1920 meters in elevation, 13 km north of Truckee, California. The study site was dispersed across two adjacent meadow systems, Sagehen and Kiln, encompassing 8 hectares within the Sagehen Creek watershed. These meadow soils are Aquolls and Borolls laden with volcanic rock outcrops and fragments (Hanes 1994). Mineral-rich springs are abundant throughout the Sagehen Creek basin, increasing the hydrologic complexity of the meadows (Johnson and Needham 1964). Precipitation is highly variable year to year and mostly occurs as winter snow falling from November to April and averaging 90 cm per year (McCurdy 2000). Typical meadow vegetation is a mix of grasses, forbs, and sedges surrounded by upland areas consisting of sagebrush (*Artemesia* spp.) and forests of lodgepole pine (*Pinus contorta* ssp. *murrayana*) and Jeffrey pine (*Pinus jeffreyii*). Logging and livestock grazing were once much more pronounced in these meadow basins than today. In 1955 grazing ceased altogether at Sagehen, while Kiln meadows continued to be grazed by sheep, though not in the six years prior to this study. We conducted this study over the 2000 growing season at sites where *Poa* and *Deschampsia* grow both together and apart.

Field data collection and analysis

Across Sagehen and Kiln meadows, we delineated thirty sites with one the following three vegetation types: *Deschampsia*-dominated, *Poa*-dominated, and mixtures of the two species. These sites were no less than 4 × 3 m and no greater than 11 × 10 m in size and were scattered throughout the entire meadow system. One pair of 1-m^2 plots were randomly placed at each site, totaling ten paired plots for each vegetation type. A one-time clipping treatment was applied randomly to one plot of each pair on 27 June 2000, cutting vegetation to the ground with a weed whip and leaving 1-4 cm of stubble depending on ground micro-topography.

Aerial cover of *Deschampsia* and *Poa* was measured in every plot prior to clipping in order to test equality between paired plots within the same site, using a point-hit method with a 0.5 m wide, 10-point frame (Cook and Stubbendieck 1986). A total of fifty hits per plot were obtained by systematically moving the frame across the plot, recording target species only. As plants began to senesce, each target species was randomly sampled for the following performance measures: total aboveground biomass, number of tillers, and biomass of inflorescences. Plants were clipped at the base of the leaf sheath and this aboveground biomass was oven-dried at 65 °C for 48 hours before weighing.

Within respective plots, we randomly harvested five *Deschampsia* plants per plot. Due to the rhizomatous growth form of *Poa*, we were unable to distinguish individual plants and sampled an area of 10 × 10 cm of *Poa* instead. This area allowed a sufficient count of tillers, but was small enough to exclude much of the biomass of neighboring species. We selected several of these areas in a plot by using a grid with ten randomly marked 10 × 10 cm cells. For each marked cell, presence or absence of *Poa* was recorded. If present, we harvested up to ten samples of *Poa* per plot. Relative performance of each species was analyzed at the plot scale between vegetation types (plots where each species grew alone or in mixture) and clipping treatments (clipped and unclipped plots). Species measures were averaged by plot before being tested across treatments and conditions.

We collected gravimetric soil moistures at each site on three consecutive dates, 16 June, 13 July, and 27 July. Cores were 2 cm in diameter and taken at soil depths of 0-10 cm and 10-20 cm. Three cores per site at each depth were extracted in maximally spaced, random locations nearby the paired plots to capture variability while minimizing disturbance. Each set of three cores were pooled in a sealable plastic bag and weighed before and after oven drying for 24 hours at 100 °C. In order to detect any differences in soil moistures across vegetation types, we used non-parametric Kruskal-Wallis tests, followed by post-hoc multiple comparisons (Zar 1999).

A split-plot, multi-factorial analysis of variance (ANOVA) was used to test hypotheses regarding plant performance under different vegetation types and clipping treatments, using the following model:

$$X_{ijkl} = \mu + A_i + B(A)_{j(i)} + C_k + AC_{ik} + CB(A)_{kj(l)} + e_{l(ijk)}$$

Where X = plant response variable, A = vegetation type, B = site of each paired plot, and C = clipping treatment. We assumed that $CB(A)_{kj(l)}$ is equal to zero, meaning that there is no interaction between treatments and plots (Underwood 1997). Though this assumption could not be directly tested, we tested a related assumption that paired plots were alike by performing a paired t-test on the pre-treatment cover data. Vegetation type and clipping were considered fixed effects, whereas site was considered a random effect. The F-test for effects of vegetation type used mean square error (MSE) of site nested within vegetation type, whereas other effects used the model MSE. Significance was tested at the level of $\alpha = 0.05$.

Response variables for both focal species included aboveground biomass, tiller number, and inflorescence weight as an indicator of reproductive output. Data were log-transformed, except *Poa* tiller numbers, which were not transformed, to meet assumptions of normality (Zar 1999). Large deviations from ANOVA assumptions, as was the case with inflorescence weight for both species, required non-parametric tests; *Deschampsia* data were ranked and standardized while *Poa* data were only tested in unclipped plots using Wilcoxon rank-sum (Zar 1999). Significant effects of site were further tested to account for environmental variability using an analysis of covariance (ANCOVA) with soil moisture as a covariate. Model fitness was tested using Goodness of Fit F-test (Selvin 1995). Data were analyzed using SAS version 8 (SAS 1985).

Greenhouse experimental conditions

In order to directly examine the effects of competition across a controlled soil moisture gradient, we conducted a greenhouse experiment in an ambient temperature room at the University of California, Berkeley simultaneous with the field season. Greenhouse soils were composed of UC Davis Mix (96% peat moss, 2% redwood soil conditioner, and 2% Monterey sand). Each planted pot was initially watered evenly and given an equal proportion of fertilizer, Plantex 20-20-20® recommended for 2 weeks of growth, after which no additional fertilizer was applied.

Eighteen-day-old seedlings of *Poa* and *Deschampsia*, from seed collected at the field site a year prior, were transplanted from flats into 8 cm diameter by 8 cm deep clay pots following an additive series design (Silvertown and Lovett-Doust 1993) on 9 June 2000. At this time, ten seedlings of each species were collected with roots intact for measurements of initial dry weight. *Poa* and *Deschampsia* were grown separately and together in clay pots in arrangements that allowed maximal, but equivalent spacing between plants and a buffer from the pot edges. Total plant density in each pot ranged from one to four, and every possible species combination was grown at each density. We chose the above plant densities after observing and measuring the growth of a single *Deschampsia* plant in a large pot for 10 weeks. The foliar diameter of the trial plant was approximately the same as the clay pots used in the experiment, thus 4 plants per pot was expected to be above the pot's carrying capacity.

In order to reduce mortality due to transplanting, all plants were watered equally for ten days, thereafter water treatments began. Pots were randomly placed along the greenhouse bench in blocked water treatments: wet, moderate, and dry. There were five replicate pots of each planting combination per watering treatment. Also, two plant-less pots were randomly placed in each watering treatment for soil moisture measures. Depending on evaporation rates, pots in wet treatments were placed in trays to reduce desiccation and watered once or twice a day, while moderate treatments were watered once a day to once every other day, and dry treatments, which received the least water, were watered once every third day. One week following the initiation of water treatments, a clipping treatment was applied. Two of the five replicates in all water treatments were clipped once to a stubble height of approximately 1 cm, mimicking field clipping treatments.

Greenhouse data collection and analysis

Soil gravimetric water measurements were taken throughout the study at three random times to measure the gradient of watering treatments. Soil moistures were analyzed using repeated measures ANOVA.

After 10 weeks of growth, all individual plants were clipped at the base and aboveground biomass was dried at 65 °C for 48 hours and weighed on an analytical balance to one-hundredths of a gram. Final aboveground biomass per plant was averaged by species within a pot. Thus, for data analysis, a pot was the sample unit. We chose an analysis that required a sub-set of our data and included the following ratios of *Deschampsia* to *Poa* in a pot: 1:0, 2:0, 3:0, 4:0, 1:1, 1:2, 1:3, 0:1, 0:2, 0:3, 0:4, 2:1, and 3:1. Due to one plant mortality and seedling misidentification six pots were discarded. Nonetheless, we accounted for unequal sample size in our analysis, and there resulted in at least two samples for each possible treatment combination, and often more. We analyzed these data using an asymmetrical ANOVA outlined by Underwood (Underwood 1986, 1997), which has been used for competitive studies of invertebrates in aquatic systems (e.g., Creese and Underwood 1982; Schmitt 1985; Cross and Stiven 1999).

Each target species was analyzed separately in a two part series of asymmetrical control analysis of variance (ANOVA) (Winer et al. 1991; Underwood 1997) at $\alpha = 0.05$ level of significance. Controls represented a single plant in one pot and were compared against same species and mixed species pots. The initial asymmetrical control, multi-factorial ANOVA tested for differences in aboveground biomass between the controls versus all other treatments. These results precluded further analysis of intra- and interspecific competition if treatments were not significant. Competition was tested with a second, similar ANOVA procedure where the response was again final aboveground biomass of the target species, *Poa* or *Deschampsia*. In these tests, pots were compared to each other and tested for effects of increased plant density and identity of species added on target species biomass. Thus, model factors included plant densities, species added, water, clipping, and their respective interactions. A significant interaction of species added and density reflects competitive effects (Underwood 1997). Thus, if the non-target species decreases the biomass of the target with each successive density at a faster rate than the target species on itself, the non-target species is competitively dominant.

Results

Soil moisture

There was a gradient of soil moistures found in both the field and greenhouse. The surface (0-10 cm depth) of field soils ranged from more than 70% soil moisture in wet meadows at the start of the growing season to less than 15% soil moisture in dry meadows by the end of the growing season. Field soil moistures within each vegetation type for all dates and at both depths were highly, significantly correlated and thus soil moisture analyses included only the first date of surface depth cores. The soil moisture at surface depths early in the growing season were significantly correlated to surface soil moistures later in the season ($r = 0.85$, $p < 0.0001$, $n = 30$; $r = 0.84$, $p < 0.0001$ $n = 30$, chronologically) and soil moistures at lower depths early and later in the growing season ($r = 0.91$, $p < 0.0001$, $n = 30$; $r = 0.84$, $p < 0.0001$, $n = 30$; $r = 0.87$, $p < 0.0001$, $n = 30$, respectively). *Deschampsia*-dominated and mixed-species plots were no different from each other, but *Poa*-dominated plots were significantly drier from the other vegetation types ($X^2 = 10.49$, $p < 0.005$, d.f. = 2). Greenhouse soil moistures were within range of those occurring under natural field conditions (Figure 1). The gradient of wet to dry soil moisture treatments was maintained throughout the greenhouse experiment (treatment: $F = 417.87$, $p < 0.0002$, d.f. = 2, 6; time: $F = 0.05$, $p < 0.95$, d.f. = 2, 6; treatment × time: $F = 2.91$, $p < 0.12$, d.f. = 4, 6). Soil moisture increased as treatments went from dry to moderate to wet and each treatment was separated by approximately a 10% difference in soil moisture. The wet treatment in the greenhouse was most similar to the *Deschampsia*-dominated and mixed-species field sites in the early growing season. The moderate water treatment was most similar to the *Poa*-dominated sites in the early growing season. The dry treatment in the greenhouse was drier than the *Poa*-dominated sites measured in the early growing season, but more similar to these sites as the soil water decreased through the season.

Plant performance in clipping treatments

Prior to applying the clipping treatment, cover of each focal species was similar between the paired plots at each site (for *Poa*-dominated plots: $t = 0.9251$, $p < 0.38$ d.f. = 8; for *Deschampsia*-dominated plots: $t = 0.4135$, $p < 0.67$, d.f. = 8; and for mixed-species plots: $t = 1.4767$, $p < 0.17$, d.f. = 8 for *Poa* and $t = 0.2677$, $p < 0.79$, d.f. = 8 for *Deschampsia*). Thus, clipped and un-clipped plots had no significant pre-treatment differences within each vegetation type.

After clipping, *Poa* and *Deschampsia* were unable to recover fully by the end of the growing season and aboveground biomass, tillering, and inflorescence weight were all highly, significantly reduced in clipped versus unclipped plots (see Table 1). Average aboveground biomass of *Poa* was reduced by 78% in

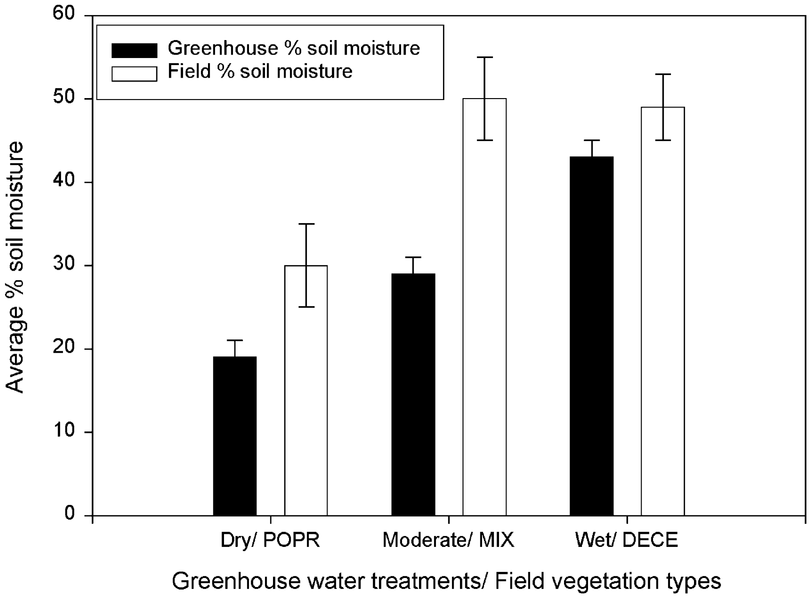

Figure 1. Soil moisture in greenhouse water treatments and field vegetation types (DECE: *Deschampsia*-dominated; POPR: *Poa*-dominated; MIX: mixture of species). Greenhouse and field data were analyzed separately (mean ± 1 SE).

Table 1. ANOVA tables for field aboveground biomass, tiller number, and inflorescence weight of Deschampsia cespitosa and Poa pratensis, testing for effects of vegetation type (veg) and clipping treatments (clip), and site.

source	d.f.	MS	F	significance	MS	F	significance	MS	F	significance
Deschampsia										
	Aboverground biomass/plant				*Tiller number/plant*			*Inflorescence weight/plant*		
Veg[1]	1	0.001	0.00	P < 0.96	0.34	0.60	P < 0.45	0.51	1.33	P < 0.26
Clip	1	14.59	78.54	P < 0.0001*	1.17	4.09	P < 0.06	27.42	137.59	P < 0.0001*
Site	18	0.62	3.33	P < 0.01*	0.57	2.00	P < 0.08	0.38	1.90	P < 0.09
Veg*Clip	1	0.26	1.38	P < 0.26	0.66	2.30	P < 0.15	0.65	3.27	P < 0.09
Error	18	0.19			0.29			0.20		
Poa										
	Aboveground biomass/10x10cm area				*Tiller number/10x10cm area*			*Inflorescence weight/10x10cm area*		
Veg[1]	1	0.39	12.14	P < 0.003*	396.90	16.53	P < 0.0007*			
Clip	1	2.24	115.19	P < 0.0001*	176.40	14.46	P < 0.001*			
Site	18	0.03	1.65	P < 0.15	24.01	1.97	P < 0.08			
Veg*Clip	1	0.26	13.48	P < 0.002*	160.0	13.11	P < 0.002*			
Error	18	0.02			12.20					

[1] Error used is site (vegetation type).

clipped treatments, whereas average aboveground biomass of *Deschampsia* was reduced by 76%. While clipping only marginally reduced tillering of *Deschampsia*, clipping significantly reduced tiller numbers of *Poa* and completely eliminated the current year's reproductive growth. *Deschampsia* plants in clipped plots were able to produce some reproductive tillers, but overall inflorescence weight was significantly reduced. After clipping, *Poa* biomass and tillering decreased significantly more in the *Poa*-dominated plots than the mixed plots (Figure 2B). However, *Deschampsia* responded similarly to clipping when growing with versus without *Poa* for all variables tested (Table 1, Figure 2A).

In the greenhouse, clipping seedlings and reducing water stunted growth of each species (see Table 2).

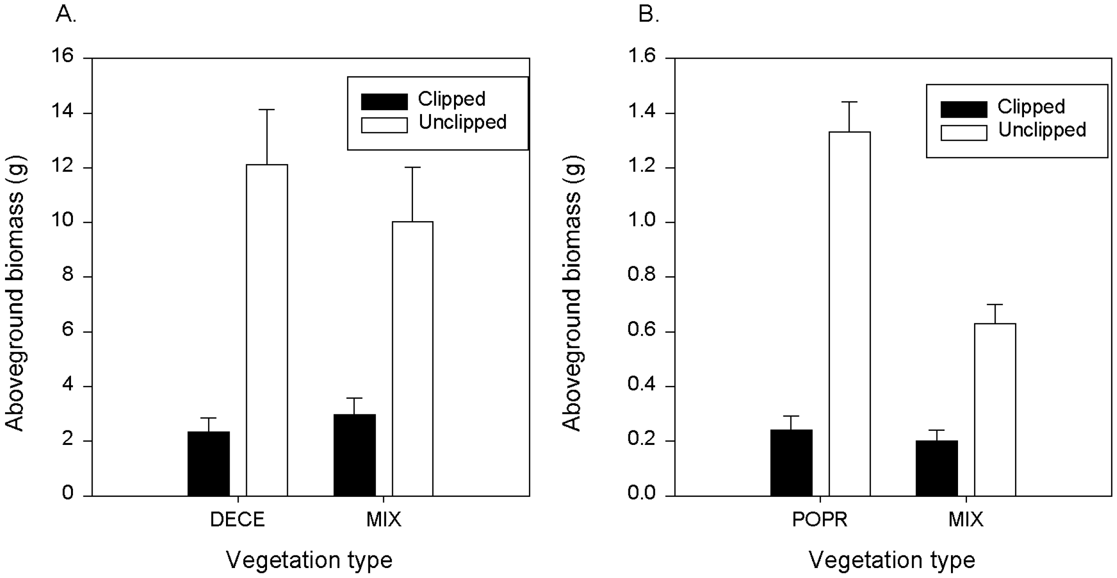

Figure 2. Deschampsia cespitosa and *Poa pratensis* aboveground biomass in field vegetation types (DECE: *Deschampsia*-dominated; POPR: *Poa*-dominated; MIX: mixture of species) and clipping treatments. Data for each species were analyzed separately (mean ± 1 SE).

Clipping alone reduced the growth of each species to approximately half its potential. This decrease was most dramatic in the wet treatments and least dramatic in the dry treatments, leading to a significant clipping × water interaction for both grass species. Competitive effects were not apparent in clipping treatments.

Plant performance in mixed and unmixed plots

Poa grew similarly between sites, yet differently between vegetation types (Table 1). *Poa* aboveground biomass was half the weight in mixed-species plots as compared to *Poa*-dominated plots (Figure 2B). *Poa* tillering was also significantly reduced where it grew in a mixture with *Deschampsia*. Sexual reproductive potential of *Poa*, assessed by the weight of inflorescences, was no different between mixed and unmixed stands in all unclipped treatments ($Z = -0.62$, $p < 0.54$, d.f. = 1) and very low overall. Under natural conditions, *Poa* was observed to flower and set seed earlier than *Deschampsia*; most *Poa* set seed around mid-July while most *Deschampsia* plants set seed in early to mid-August. Thus, *Poa* was observed senescing before *Deschampsia* had begun to bolt.

Deschampsia performance was not significantly different between plots with *Poa* versus without *Poa* (Table 1, Figure 2A). However, due to significant site-to-site differences in *Deschampsia* aboveground biomass, we performed an ANCOVA test with soil moisture as a covariate. The best-fit model excluded the interaction term and showed soil moisture to explain a large amount of the variation among sites ($R^2 = 0.11$; $F = 3.47$, $p < 0.04$, d.f. = 2, 37). Across all sites, soil moisture was positively correlated to *Deschampsia* biomass ($t = 2.63$, $p < 0.01$, d.f. = 1). A non-significant interaction between soil moisture and vegetation type indicated that *Deschampsia* biomass increases similarly in both *Deschampsia*-dominated and mixed-species plots in response to soil moisture.

Competitive interactions in the greenhouse

When examining species and density interactions across all water and clipping treatments, we found indirect evidence for competitive relations. Initial seedling sizes averaged 0.0017 g/ plant and were no different between species ($F = 0.30$, $p < 0.59$, d.f. = 1,18). After ten weeks of growth in the greenhouse, *Deschampsia* controls growing alone had smaller aboveground biomass than *Poa* controls ($t = 2.25$, $p < 0.03$, d.f. = 28). The aboveground biomass of both species' control plants were greater than their counterparts in the competition treatments ($F = 66.28$, $p < 0.0001$, d.f. = 1, 59 for *Poa* controls and $F = 86.75$, $p < 0.0001$, d.f. = 1, 61 for *Deschampsia* controls) and prompted further analysis for potential competitive effects (see Table 2). Increasing plant

Table 2. ANOVA tables for greenhouse aboveground biomass of *Deschampsia cespitosa* and *Poa pratensis*, testing for effects of density, identity of species added, clipping, and water treatment.

Source	d.f.	MS	F	significance
Deschampsia				
Density	2	1.25	18.86	$P < 0.0001$*
Species added	1	1.61	24.29	$P < 0.0001$*
Clip	1	10.01	151.39	$P < 0.0001$*
Water	2	6.53	98.77	$P < 0.0001$*
Den.*sp.add	2	0.02	0.23	$P < 0.80$
Den.*clip	2	0.01	0.16	$P < 0.85$
Den*water	4	0.06	0.91	$P < 0.46$
Sp.add*water	2	0.25	3.79	$P < 0.03$*
Clip*water	2	0.69	10.39	$P < 0.0001$*
Sp.add*Clip	1	0.02	0.26	$P < 0.61$
Den.*sp.add*clip	2	0.05	0.72	$P < 0.50$
Den.*clip*water	4	0.03	0.45	$P < 0.77$
Den.*sp.add*water	4	0.01	0.17	$P < 0.95$
Sp.add*clip*water	2	0.06	0.98	$P < 0.38$
Den*sp.add*clip*water	4	0.26	4.01	$P < 0.01$*
Error	61	0.07		
Poa				
Density	2	1.21	14.04	$P < 0.0001$*
Species added	1	0.28	3.25	$P < 0.08$
Clip	1	11.79	136.80	$P < 0.0001$*
Water	2	7.41	85.91	$P < 0.0001$*
Den.*sp.add	2	0.08	0.96	$P < 0.39$
Den.*clip	2	0.03	0.37	$P < 0.69$
Den*water	4	0.02	0.23	$P < 0.92$
Sp.add*water	2	0.08	0.91	$P < 0.41$
Clip*water	2	0.28	3.28	$P < 0.04$*
Sp.add*Clip	1	0.00	0.00	$P < 0.96$
Den.*sp.add*clip	2	0.12	1.44	$P < 0.25$
Den.*clip*water	4	0.09	1.09	$P < 0.37$
Den.*sp.add*water	4	0.02	0.25	$P < 0.91$
Sp.add*clip*water	2	0.03	0.34	$P < 0.71$
Den*sp.add*clip*water	4	0.02	0.25	$P < 0.91$
Error	59	0.09		

density in a pot significantly reduced the aboveground biomass of *Poa* and *Deschampsia*. Overall, *Poa* grew marginally worse with neighbors of its own species than with *Deschampsia* (Table 2, Figure 3). For *Deschampsia*, biomass was reduced more when growing with *Poa* compared to growing with conspecifics (Table 2, Figure 4). However, there was no significant interaction between species added and density across all treatments. Thus, across all water and clipping treatments, both *Poa* and *Deschampsia* additions reduced the growth of *Deschampsia* at a similar rate, but growing with *Poa* led to lower overall biomass.

Yet, when looking at the interaction between species added, density, water, and clipping, competitive effects became apparent (Table 2). A significant interaction between species added and water treatment demonstrated that *Poa* reduces the biomass of *Deschampsia* more dramatically than conspecifics as soil moisture declines. Also, a significant four-way interaction between all factors suggests a competitive interaction between *Poa* and *Deschampsia*. In dry treatments, *Deschampsia* biomass was reduced at a higher rate with increases in *Poa* densities compared to increases in *Deschampsia* density within unclipped plots, indicating that *Poa* is competitively dominate over *Deschampsia* (Figure 4).

Discussion

Importance of soil moisture

Similar to previous studies of meadow vegetation and water tables (e.g., Ratliff 1982; Allen-Diaz 1991; Castelli et al. 2000), we found that the distributions of *Poa* and *Deschampsia* are strongly linked to soil moistures. Though we expected to find a linear relationship between soil moisture and species abundances and distributions in the field, we found that there is a large shift in soil moistures between *Poa*-dominated sites versus *Deschampsia*-dominated and mixed-species sites. Mixed-species sites are similar in soil moisture to *Deschampsia*-dominated sites. *Deschampsia* grows where surface soil moistures average 50% water content early in the growing season, and tends to grow larger with increasing amounts of water. In these conditions, *Poa* aboveground biomass and abundance, but not necessarily vigor, is reduced and *Deschampsia* performance appears unaffected by its presence. Conversely, *Poa*'s reduced performance in mixed-species stands appears to result from high soil water content, not interactions with *Deschampsia*. In drier conditions (30% surface soil moisture in the early growing season) where *Poa* is most abundant and grows largest aboveground, *Deschampsia* is not found. Though there is no evidence of competition between these grasses in mixed-species sites where the soil moisture averages 50% in the early growing season, our greenhouse study indicates that aboveground biomass of *Deschampsia* may decrease via competition with *Poa* when soil moisture content is below 20%.

In the greenhouse, *Deschampsia* was able to survive under soil moistures where it appears to be excluded in the field. It is within these dry conditions, where soil moistures averaged 19%, that there were

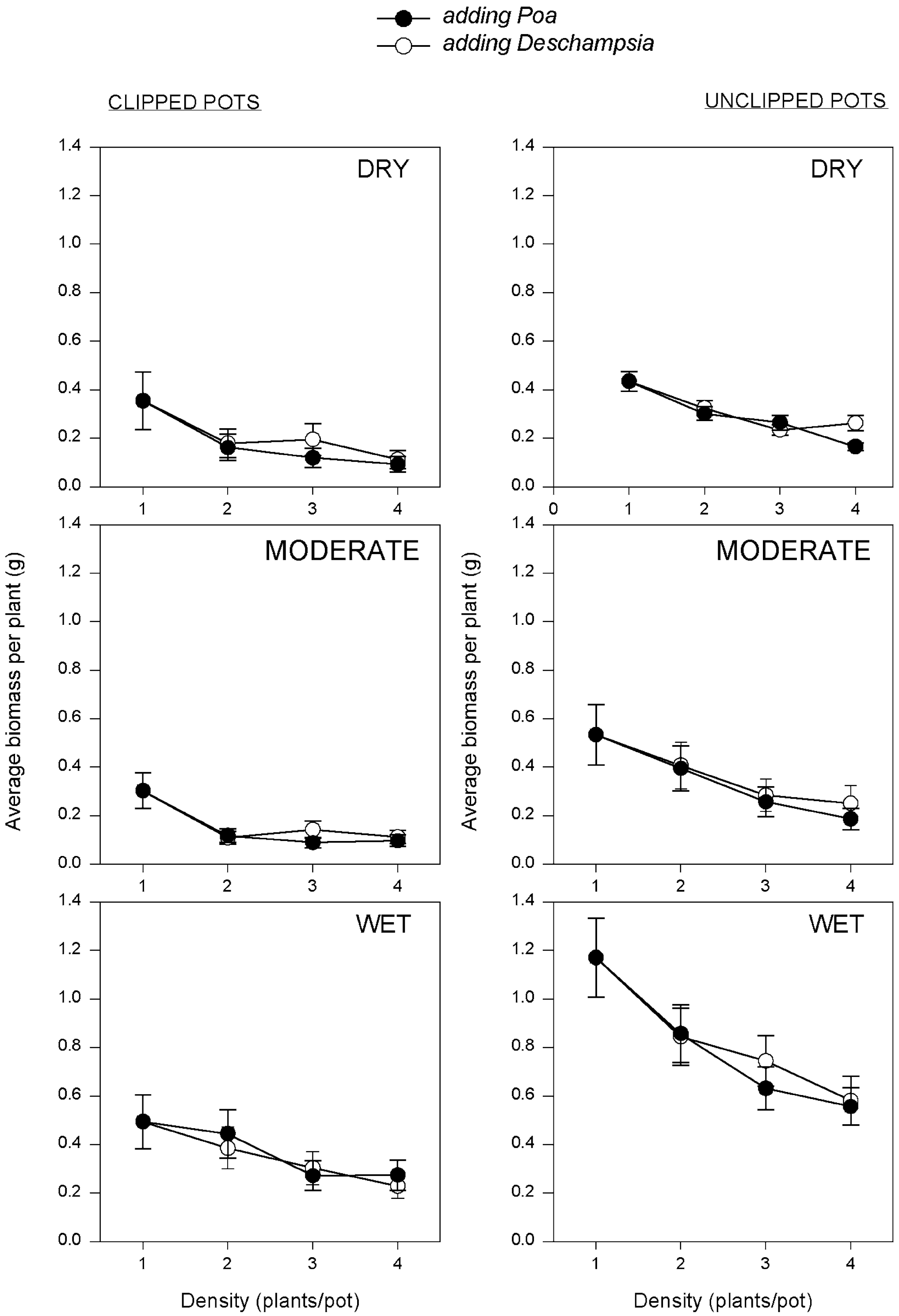

Figure 3. Poa pratensis aboveground biomass after ten weeks of growth in greenhouse competition trials under different watering and clipping treatments (mean ± 1 SE).

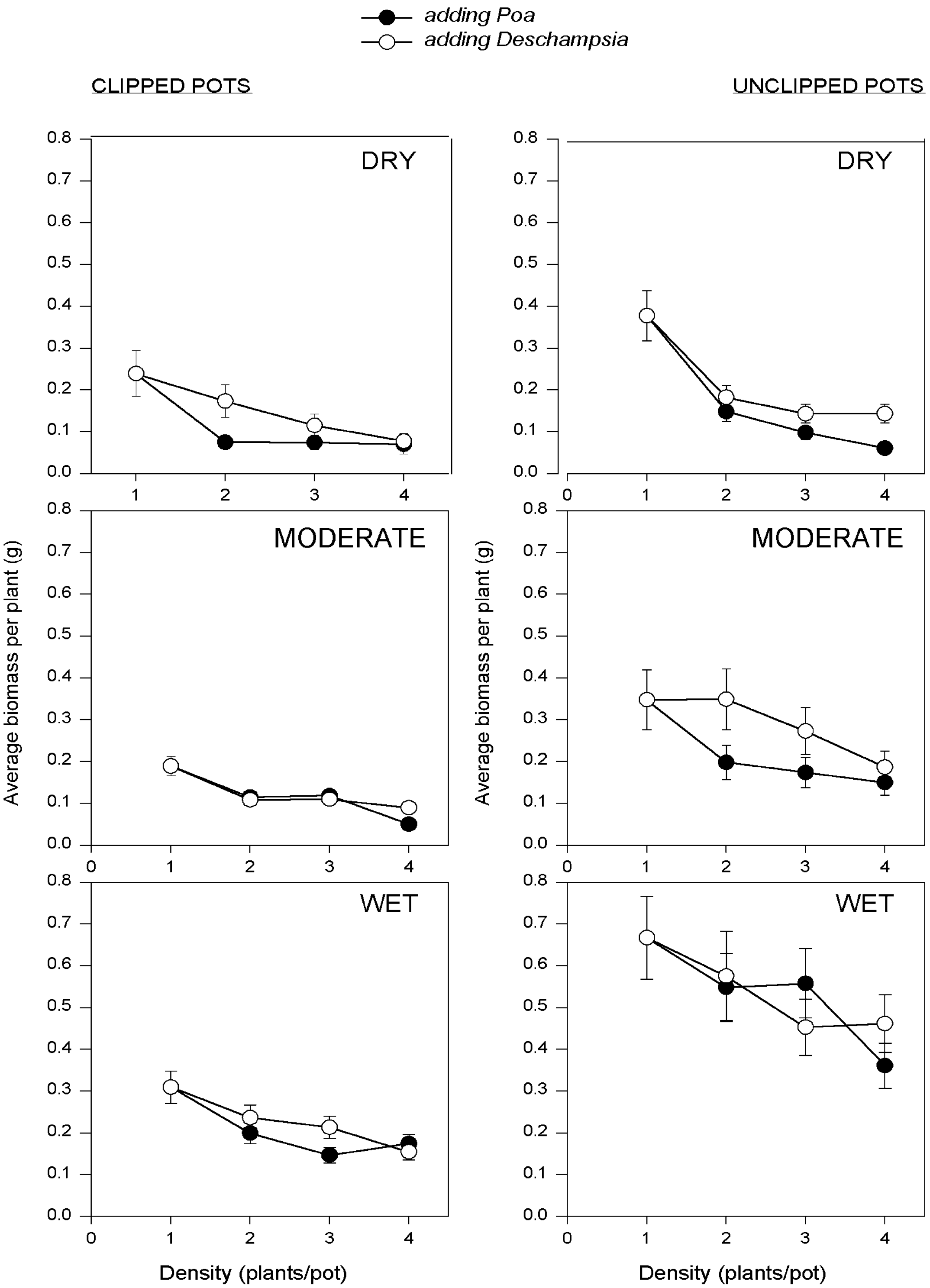

Figure 4. Deschampsia cespitosa aboveground biomass after ten weeks of growth in greenhouse competition trials under different watering and clipping treatments (mean ± 1 SE).

signs of competitive suppression from *Poa*. It is likely that the water resource was drawn-down by *Poa* at the cost of availability to *Deschampsia* (Tilman 1988). In the dry meadows, *Poa* may similarly operate to competitively exclude *Deschampsia*. Though grass distributions are primarily controlled by soil moisture, water availability may also mediate competitive interactions between *Poa* and *Deschampsia* when and where soils are relatively dry. We conclude that *Deschampsia*'s competitive ability decreases at low soil moistures. Under moderate (29% soil moisture) and wet (43% soil moisture) greenhouse treatments, there was no indication of competition between *Poa* and *Deschampsia*. *Poa* is intolerant of anaerobic conditions (Wasser 1982; Chambers 1999; Castelli et al. 2000) and its growth may be limited in wet conditions where water tables are high throughout much of the growing season. *Deschampsia* has demonstrated tolerance to anaerobic conditions (Rahman and Rutter 1980) and appears adapted to wet soil conditions. Thus, in wet conditions, abiotic factors alone appear to drive species distributions rather than biotic interactions.

Role of grazing

The observed increase in *Poa* abundance in montane meadows of the Sierra Nevada mountains over the last century is likely a response to large-scale restructuring of the ecosystem. Some grazing practices have been directly responsible for altering water tables through stream incision, thus causing a shift in edaphic conditions, often towards drier conditions (Menke et al. 1996). These are large-scale effects of poor grazing practices, but we were interested in the direct effects of clipping upon these grasses at the level of species interactions. Though grazing can manipulate community composition and is implied as facilitating the spread of *Poa* and population decline of *Deschampsia* (e.g., Pond 1961; Volland 1978; Stohlgren et al. 1989), we did not find a clear role of grazing in the relationship of *Poa* and *Deschampsia* in this short-term study.

In both the greenhouse and field studies, clipping did not appear to alter the interaction between species. Both species were severely reduced by early season clipping yet similarly resilient to it, and there did not appear to be a competitive advantage of *Poa* over *Deschampsia* after grazing, as has been suggested by models of range condition (Dyksterhuis 1949). Instead, clipping may have temporarily ameliorated any effects of competition by reducing biomass of both species (Briske 1991). For example, competitive suppression of *Deschampsia* by *Poa* in dry greenhouse conditions was only apparent in the un-clipped plots, and did not appear in clipped plots at the end of 10 weeks. Here clipping may have been severe enough to ameliorate interactions. In a similar study, which tested late-season clipping, there was also little evidence of grazing interacting with competition of *Poa* and a common meadow sedge, *Carex nebrascensis* (Martin and Chambers 2001a, b). Though these authors suggest that early-season clipping may have resulted in an effect, we found this was not so. However, we concur with their findings that temporal and spatial processes in meadows are complex and that longer studies directed in interstitial spaces may yield interesting results (Martin and Chambers 2002).

There are many potential effects of grazing, and clipping may not be as influential upon established plants, but may be more important in creating gaps for species establishment. Having different phenologies, *Poa* and *Deschampsia* vary in their strategies for reproduction and dispersal. There is very little regeneration in meadows (del Moral 1983; Chambers 1995), making it difficult to observe this life history stage. However, *Deschampsia* must establish by seed, while *Poa* can establish either by seed or rhizomatously. The low reproductive tillering in *Poa* we found, especially following clipping, indicates that this species expands its range primarily via vegetative growth. We found *Poa* to senesce earlier in the field and gain seedling biomass more rapidly in the greenhouse than *Deschampsia*, demonstrating *Poa*'s potential for early, rapid growth in favorable conditions (Etter 1951; Weaver 1954; Atkin et al. 1996; Martin and Chambers 2001a). Thus, following a meadow disturbance such as grazing, *Poa* may be able to colonize gaps more effectively than other species, depending on soil moisture conditions (Martin and Chambers 2001a).

Our data point to the primary importance of edaphic conditions driving plant distributions. Both short-term field and greenhouse results indicate that *Poa* distributions are unlikely to spread into wet meadows. While *Deschampsia* appears adapted to wet meadows, its competitive ability rapidly declines in dry meadows where *Poa* grows abundantly. *Poa*'s rapid vegetative growth and competitive strength in drier conditions may inhibit growth of less competitive species in dry meadows. One early season clipping of *Deschampsia* and *Poa* does not appear to alter their interactions, however the complete spectrum of grazing effects upon these grasses is less clear and prompts further investigation of spatio-temporal dynamics. Maintaining sufficient hydrologic flow in these meadows to perpetuate areas of wet soil appears integral to sustaining a mosaic of meadow vegetation.

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