Aboveground growth responses of the annual grasses, *Bromus diandrus* and *Bromus hordeaceus*, to clipping and simulated trampling.

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Abstract The community composition of California grasslands and oak woodlands has been transformed from native perennial to annual grasslands through competitive exclusion. Biomass allocation and growth traits of annual grasses such as *Bromus diandrus* (rip gut brome) and *Bromus hordeaceus* (soft brome) are two reasons that they are successful competitors. Livestock grazing may facilitate spread, but the growth responses of exotic annual grasses are unclear. Looking at the aboveground growth response of *B. diandrus* and *B. hordeaceus* to clipping and simulated trampling, I predicted that production of biomass would be greatest under no treatment and lowest under a combined clipping and trampling treatment. This study occurred over a five-month period, during which I collected aboveground biomass and other growth indicator data from February to April 2009. I found that the clipping and combined treatments reduced aboveground biomass, but not inflorescence production, while trampling neither inhibited nor promoted growth. The trampling response may have been indicative of trampling-tolerance by *B. diandrus* and *B. hordeaceus*; along with the neutral reproduction response, these traits potentially aid in their dominance over perennials in California grasslands.

Introduction

Exotic annual grasses of California possess traits for fast growth that facilitate both their competitive exclusion and replacement of native plants in California grasslands and oak woodlands (D'Antonio and Vitousek 1992, Bartolome and Klukkert 1986). Exotic annual grasses accelerate their aboveground growth through emerging leaves and culm (a hollow or pithy stem) production, with limited leaf senescence during the growing season (Jackson and Roy 1986). This leaf development reduces soil surface light availability, and therefore photosynthetic capability, of slow-growing seedling competitors (Jackson and Roy 1986, Tang *et al.* 1988, Thompson and Harper 1988, D'Antonio and Vitousek 1992). When competing with perennial seedlings, invasive annuals' belowground biomass, composed of rapidly-produced dense and shallow root systems, allows them to more effectively take up water and nutrients, reducing soil moisture and depleting nutrient resources (Da Silva and Bartolome 1984, Elliot and White 1989, D'Antonio and Vitousek 1992). Overall, annual grasses have a faster growth rate than perennial seedlings (Garnier and Laurent 1994). It is thought that competitive exclusion by exotic annual grasses has significantly impacted oak seedling regeneration in California's oak woodlands (Gordon *et al.* 1989, Danielson and Halvorson 1990) and diminished the abundance of native perennial grasslands (Bartolome and Klukkert 1986). Understanding the growth patterns of exotic annual grasses is therefore an important key to comprehending community composition of California grasslands.

Bromus diandrus Roth. (rip gut brome) and *Bromus hordeaceus* L. (soft brome) are two common exotic annual grasses that have come to dominate California valley grasslands (D'Antonio and Vitousek 1992). Holmes and Rice (1996) found that *B. diandrus* aboveground and belowground biomass production was nearly four times that of the native perennial bunchgrass, *Nasella pulchra*. These two annuals also have been linked to limited resource availability for native plants (Dyer and Rice 1999). There is evidence, therefore, that *B. diandrus* and *B. hordeaceus* suppress the growth of native plants as well as deter the invasion of native species into exotic annual grasslands (Robinson *et al.* 1995, Dyer and Rice 1999).

In addition to inherently faster growth rates, interactions with disturbance may facilitate the spread of non-native grasses. For example, disturbance by grazing livestock has been observed to influence the growth of grasses and is of historical and current relevance in California's grasslands (Heady 1975). Intensive livestock grazing on coastal grasslands began in California in 1773 following Spanish colonization, spreading inland in 1824 as land grants provided for cattle ranches (Bartolome *et al.* 2007, Jackson and Bartolome 2007). The exact floristic composition of California grasslands prior to European arrival is unknown, but the current theory proposes that complex bunchgrass communities occurred in some of the Coast Ranges and the northern Central Valley, transitioning into annual grasslands and forb-dominated areas in the southern Central Valley (Hamilton 1997). Regardless, livestock grazing in the late 19th century is considered to have been a major factor in shifting grasslands from to exotic annual-dominated vegetation (Burcham 1975, Jackson and Bartolome 2007).

There are multiple means by which livestock may disturb a landscape. One well-documented mechanism is grazing, or aboveground biomass removal (Heitschmidt and Stuth 1991, Heady and Child 1994, Jackson and Bartolome 2007). A selective defoliation by large mammals can immediately lead to both a lower level of carbon uptake and a lower photosynthetic rate for a plant, inhibiting its production of biomass (Del-Val and Crawley 2005, Jackson and Bartolome 2007). Within days or weeks of defoliation, a plant will typically react with some form of compensatory growth. Responses range from undercompensation, a partial replacement of total biomass, to overcompensation, a production of greater biomass than that which was originally lost (Belsky 1986). One plant may respond negatively to defoliation, undercompensating with especially stunted root yields (Branson 1956); other plant individuals may overcompensate by increasing allocation to photosynthetic leaves, uptake of nutrients, and water use efficiency (Hobbs 1996). If defoliation occurs close to the soil surface and at regular intervals, aboveground and belowground biomass production is reduced over time for medium and tall-statured grasses (Heady 1975). In an experiment by Savelle and Heady (1970), shorter-statured species (*Festuca megalura*, *Bromus rubens*, *Erodium botrys*) grew more rapidly following defoliation than the larger *B. diandrus*. All grasses in the study developed minimally during the winter, with most growth occurring in April and May (Savelle and Heady 1970). The response of an individual plant to defoliation, even within a single species, is highly variable and sensitive to timing, nutrient availability, and plant associations (Maschinski and Whitham 1989). Annual grass growth responses to grazing vary depending on the species and season (Savelle and Heady 1970).

Growth responses of grasses due to defoliation or grazing are often examined with clipping experiments. Clipping treatments vary in conditions and methods, but in greenhouse-based experiments, the treatment will usually include aboveground biomass of a potted plant being trimmed to stubble height (Savelle and Heady 1970, Heady 1975, Kimball and Schiffman 2003). The amount of re-growth vegetation will indicate how the plant responds to regular defoliation (Heady 1975). Potted plant clipping treatments are valuable tools for studying defoliation as they may remove the stress of competition for water, light and nutrient resources that may limit plant growth in a natural environment (Kimball and Schiffman 2003); however, they also oversimplify the complexity of grazing disturbances (Heady 1975). Defoliation does not address all of the grazing pressures, specifically the impacts of animal trampling on plant growth.

Trampling is typically defined as when an animal’s mass is distributed over a relatively small area, physically altering the soil (Pietola *et al.* 2005, Jackson and Bartolome 2007). Trampling may damage the plant by cutting, bruising or breaking the plant, and can reduce vegetative cover (Packer 1963, Heady 1975) but these response are not as well-studied as defoliation. Previous studies have focused on soil properties such as bulk density (Daniel et al. 2002), water infiltration rates (Larsen *et al.* 1998, George *et al.* 2002), or surface runoff (Jackson and Bartolome 2007), or on plant composition responses such as species richness (Kotanen 1995, Hayes and Holl 2003). Kotanen (1995) observed an increase in native species richness in California grasslands following trampling by feral pigs, but also predicted such disturbance to support an increase in exotic grasses. Hayes and Holl (2003) attempted to control for soil disruption by grazers in a mesic grassland community, but found that burrowing by small mammals had skewed the results. Due to independent factors, trampling effects on growth have been difficult to quantify.

Incorporating a trampling mechanism into a potted clipping treatment may be a valuable tool to understand plant growth responses to multiple disturbance mechanisms from cattle grazing. Abdel-Magid *et al.* (1987) used a similar method to determine the re-growth response of perennial sod grasses to simulated trampling under a continuous grazing system. They found that trampling caused both a reduction in aboveground biomass production and an increase in the detachment of aboveground biomass (Abdel-Magid *et al.* 1987). This particular study, however, did not include a clipping treatment. In addition, this study observed growth response only in perennial grasses. There have been no such studies of clipping responses in exotic annual grasses. It would be invaluable to understand how these annuals respond under both a simulated animal trampling and clipping treatment because of the importance of their allocation and growth traits in determining their dominance in the California grassland ecosystems.

My question, therefore, is what are the aboveground growth responses of *B. diandrus* and *B. hordeaceus* to clipping and simulated trampling? I will test my question by conducting an experimental growth study, examining the effect of a simulated trampling mechanism and clipping treatment to plant growth, measured by culm height, leaf length, number of leaves, and number of inflorescence. Based on the responses of exotic annuals from previous studies, I predict that total aboveground biomass will be greatest under no treatment, and lowest under a combined clipping and trampling treatment. I will test for both the effects of simulated trampling and clipping individually, as well.

Methods

Methods and Objectives I conducted an observational lab study to identify the plant growth response of *Bromus diandrus* Roth. and *Bromus hordeaceus* L. under a simulated trampling and clipping treatment. I measured the plants' aboveground biomass production over time under all treatment combinations.

The two test species of interest for this study were *B. hordeaceus* and *B. diandrus*. *B. diandrus* is an annual grass native to Europe now found throughout the United States and South America, with a flowering time from April to June (Jepson 1993). *B. hordeaceus* is also an annual grass native to Eurasia and found throughout North America and South America, with a flowering time from April to July (Jepson 1993). The study was conducted in a latthouse at the Oxford Field Tract facilities (Berkeley, CA, USA). The seeds for the study were planted on December 9, 2008 and the study was completed on April 15, 2009. The seeds were collected from the Hillside Natural Area in El Cerrito, California by Professor James Bartolome (Environmental Science, Policy, and Management). The largest seeds were selected assuming seed size has a positive correlation with viability (Stanton 1985). The plastic pots were 15.0 cm in diameter and depth. Each pot was filled with approximately 0.28 kg of potting mix (Supersoil, Scotts Company LLC, Marysville, OH, USA). This mix is pH balanced, composed of forest product compost, compost, sphagnum peat, and a wetting agent, and contains 0.14% Nitrogen, 0.02% potassium, 0.09% phosphorous, and 0.25% iron. The potting mix was selected for its suitability and availability.

A total of eighty pots were used for the study (n=10 for each treatment and species), and were distributed randomly in a grid system. To reduce sampling bias, each pot was randomly assigned a treatment and a species. Within each pot, eight seeds of either species were planted in a 2 cm diameter circle. Based on their different germination strategies, *B. diandrus* seeds were submerged immediately below the soil surface (approx. 1.5 cm) and *B. hordeaceus* seeds were placed on the soil surface. The plants were grown under ambient light and temperature conditions, with daily watering to maintain a moist soil surface.

Sampling Procedures There were four treatment types: a control, clipping only, trampling only, and clipping and trampling combined. Each treatment began when all plants reached a minimum height of 8 cm (Savelle and Heady 1970), and there after was applied once every two weeks for the remainder of the study. Production of aboveground biomass was estimated by measuring the longest leaf length, total number of leaves, tallest culm length, and total number of inflorescences per pot once a week (with one exception). After taking these measurements, the vegetation was trimmed and collected for pots that require clipping. The clipping method consisted of all aboveground biomass being trimmed from the mature samples to an even 3 cm stubble height (Savelle and Heady 1970). Clipped material was saved, oven dried (65° C) and weighed as an estimate of aboveground biomass production. After clipping, the pots that require trampling were trampled. The trampling simulator I used is based on the original design from Abdel-Magid *et al.* (1987) with modifications to the “hoof” size, weight, and dimensions (Fig. 1), to produce the average estimated pressure of a cow (1.2 kg/cm^2) (Abdel-Magid *et al.* 1987). This pressure was applied for approximately 1 to 2 seconds, assuming all major damage to the plant would occur within this time period. At the end of the study, the aboveground biomass for all the pots was clipped to the soil surface, dried (65° C), and weighed.

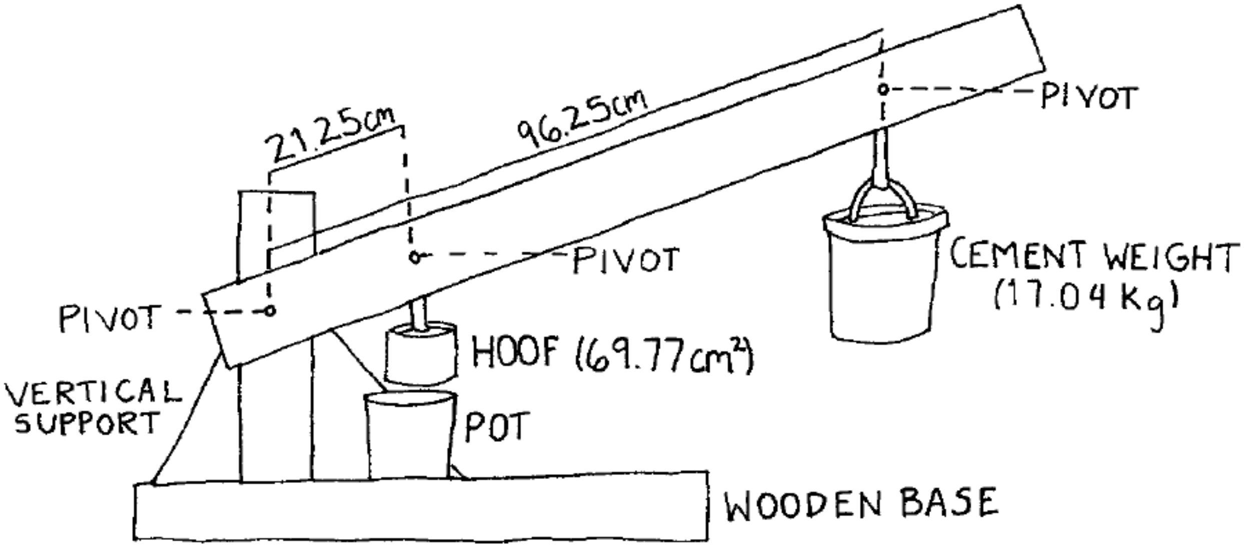

Figure 1. Dimensions and design of trampling simulator.

Techniques of analysis A repeated-measure analysis of variance (ANOVA) was used to test whether clipping and simulated trampling influenced longest leaf lengths, tallest culm heights, number of leaves, and number of inflorescence ($P < 0.05$). If there was a significant time by treatment effect, a single-factor ANOVA and Tukey's HSD test was applied to test treatment significance at each measurement time. The significance of total aboveground biomass was tested with a single-factor ANOVA. These approaches were selected because there where more than two levels of treatment and the data is parametric. I used the statistical program JMP (version 8, SAS Institute, Cary, NC) for all analysis.

Precision of Measurements On April 1, all growth indicators (culm height, leaf length, number of leaves, and number of inflorescence) were re-assessed in the first five pots to reduce the effect of measurement error. If the variation was greater than five percent between the repeated measures, the particular data set was removed from the study.

Results

Precision of Measurements The variation between my measurements of number of leaves was greater than five percent, and so no further analysis was made of this data set.

Aboveground growth There was a significant treatment effect on aboveground growth for both *Bromus diandrus* and *Bromus hordeaceus* as measured in culm height, leaf length, and number of inflorescence (Table 1). Time also significantly influenced the treatment impact on these three growth factors, however, and so single-factor ANOVAs were used to assess the treatments at each time of measurement.

Table 1. Significance of treatment (repeated-measure ANOVA), time, and treatment by time (Greenhouse-Geisser correction) on aboveground growth of *B. diandrus* and *B. hordeaceus*.

Bromus diandrus	Treatment			Time			Treatment × Time		
	F	df	P	F	df	P	F	df	P
Culm Height	52.25	3	<.001	339.59	1.8	<.001	51.19	5.5	<.001
Leaf Length	02.33	3	<.001	069.14	3.2	<.001	11.39	9.7	<.001
No. of Inflorescence	08.67	3	0.001	186.19	3.1	<.001	04.28	9.4	<.001

Bromus hordeaceus	Treatment			Time			Treatment × Time		
	F	df	P	F	df	P	F	df	P
Culm Height	27.19	3	<.001	68.50	2.1	<.001	18.52	6.4	<.001
Leaf Length	29.54	3	<.001	29.15	3.4	<.001	8.583	10.3	<.001
No. of Inflorescence	6.551	3	0.001	95.57	2.9	<.001	2.774	7.5	0.010

Culm Height Prior to March 13, the different treatments did not cause significant variation in culm heights of *B. diandrus*. After March 13, the plants under the clipping and combined treatments consistently had lower culm heights than the control and trampling treatments (Table 2 and Fig. 2). There were no significant differences between the averages of the clipping and combined treatments and between those of the control and trampling treatments. This pattern repeated with *B. hordeaceus* (Table 2 and Fig. 3). Prior to March 13, the trampling treatment *B. hordeaceus* plants had the greatest culm heights of all four treatments, but afterwards there was no significant difference between the trampling and control treatment (Table 2).

Leaf Length A similar pattern in treatment effects was observed with leaf length. From February 27 to the end of the study, the control and trampled plants for both species had significantly greater average leaf lengths than did the clipped and combined treatment plants (Table 2, Fig. 2 and 3). There was one measurement date that the data contradicted this pattern. On March 6, the trampled and control *B. hordeaceus* plants had greater leaf length than the clipping and combined treatment plants, respectively, but did not have an equal treatment effect (Table 2).

Number of Inflorescence Although there was a significant difference among the treatments overall in number of inflorescence, there were no consistent trends for either species. April 1 and 8 were the only two sampling dates where the clipping and combined treatments significantly reduced number of inflorescence on *B. diandrus* as compared to the trampling and control treatments (Table 2). There were no inflorescence produced by any of the plants before March 18 (Fig. 2). Similarly, there were no significant differences among the treatments in number of inflorescence on *B. hordeaceus* on four sampling dates throughout the study (Table 2).

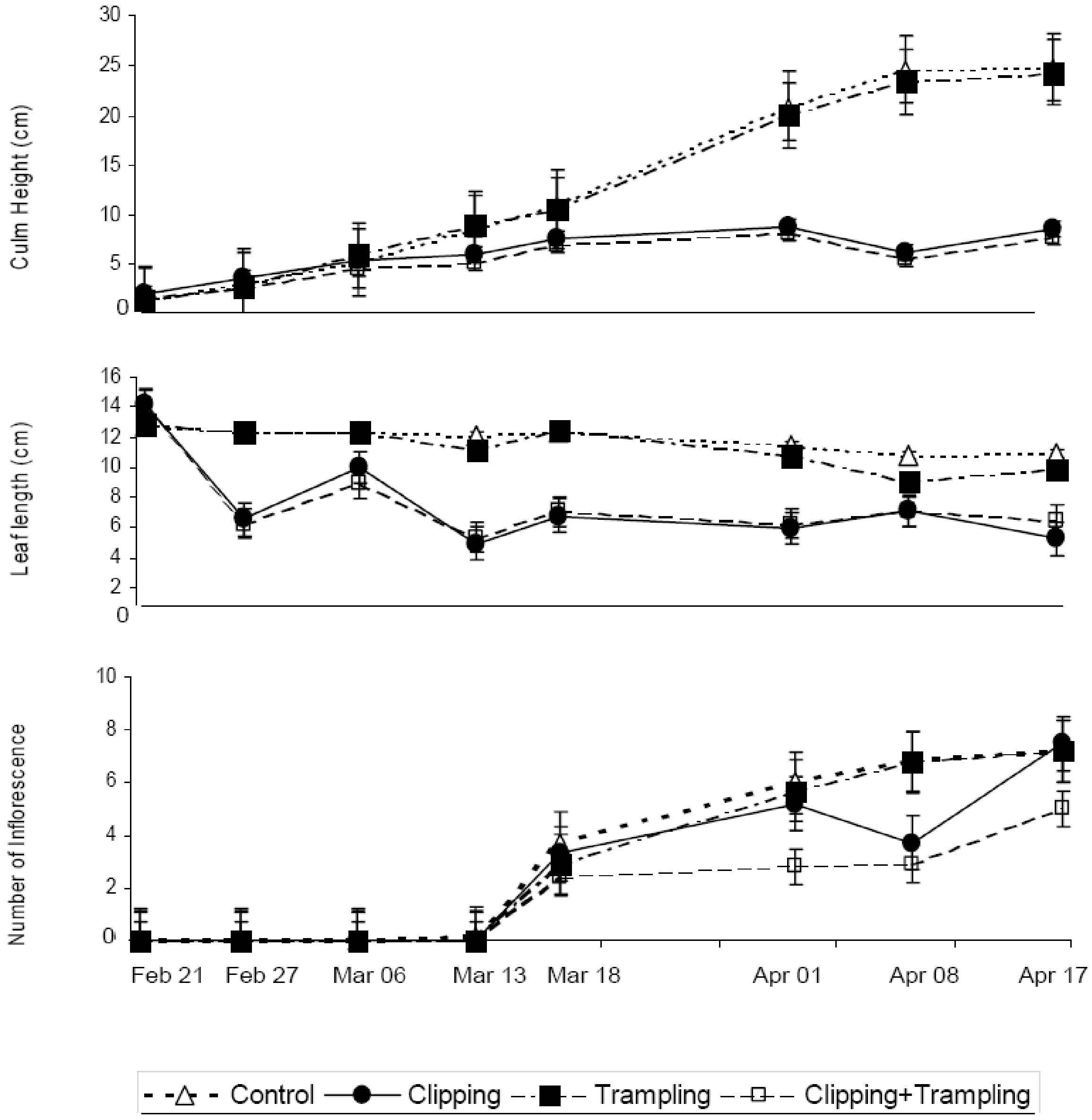

Figure 2. Average culm height, leaf length, and number of inflorescence produced for all treatments of *B. diandrus* over time.

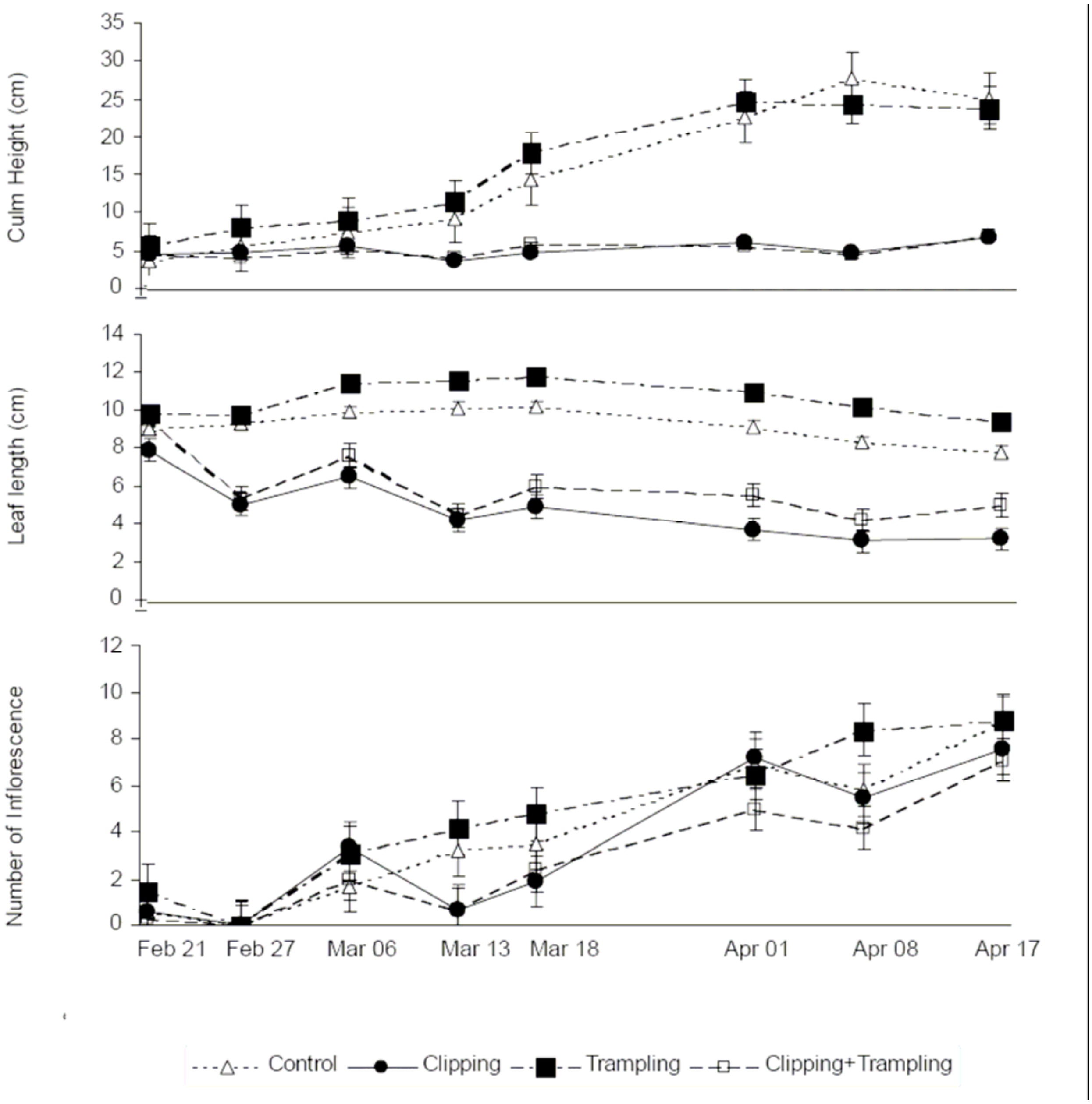

Figure 2. Average culm height, leaf length, and number of inflorescence produced for all treatments of *B. diandrus* over time.

Table 2. Significant differences between treatment types (Tukey HSD's test) at each sampling time on average culm height, leaf length, and number of inflorescence of *B. diandrus* and *B. hordeaceus*. BRDI=*Bromus diandrus* and BRHO=*Bromus hordeaceus*. A=Control, B=Clipping, C=Trampling, D=Clipping+Trampling.

BRDI	Sampling Time							
	Feb 21	Feb 27	Mar 06	Mar 13	Mar 18	Apr 01	Apr 08	Apr 17
Culm Height	A,C=B,D	A,C=B,D	A,C=B,D	A,C>>B,D	A,C>>B,D	A,C>>B,D	A,C>>B,D	A,C>>B,D
Leaf Length	A,C=B,D	A,C>>B,D	A,C>>D<B	A,C>>B,D	A,C>>B,D	A,C>>B,D	A,C>>B,D	A,C>>B,D
No. of Inflorescence	A,C=B,D	A,C=B,D	A,C=B,D	A,C=B,D	A,C=B,D	A,C>>B<D	A,C>>B,D	A,C=B,D

BRHO	Sampling Time							
	Feb 21	Feb 27	Mar 06	Mar 13	Mar 18	Apr 01	Apr 08	Apr 17
Culm Height	B,C,D>>A	C>>A,B,D	C>>B,D<A	A,C>> B,D	A,C>> B,D	A,C>> B,D	A,C>> B,D	A,C>> B,D
Leaf Length	A,C=B,D	A,C>>B,D	C>>B,D A>>B	A,C>> B,D	A,C>> B,D	A,C>> B,D	A,C>> B,D	A,C>> B,D
No. of Inflorescence	A,C=B,D	C>>D<A,B	A,C=B,D	A,C>>B<D	C>>B,D<A	A,C=B,D	A,C>>D<B	A,C=B,D

Biomass Total aboveground biomass was significantly greater under the control and the trampling treatment than under the clipping and combined treatment for both *B. diandrus* (One-factor ANOVA and Tukey's HSD test, F=10.17, df=3, P<.001) and *B. hordeaceus* (One-factor ANOVA and Tukey's HSD test, F=9.17, df=3, P<.001). There were no significant variations in biomass for either species between the control and trampling treatment, and the clipping and combined treatment.

Discussion

Over the full length of the study, the four treatments caused significant variation in the culm height, leaf length, and number of inflorescence of both *Bromus diandrus* and *Bromus hordeaceus* (Table 1). The clipping and the combined treatments consistently resulted in shorter leaf length, shorter culm height, and lower total biomass than produced by the control and the trampling treatments (Fig. 2 and 3). There was no significant variation between the clipping and combined treatments, nor between the control and trampling treatments, for these three measurements. Both species' number of inflorescence produced was not clearly influenced by any of the four treatments.

This reduction in aboveground growth over time with regular clippings has previously been documented by other defoliation studies (Savelle and Heady 1970, Heady 1975). Under a 3 cm stubble height defoliation intensity and two-week treatment frequency, an incredibly high growth rate for both species would be necessary to compensate for the biomass lost by defoliation. The negative response to clipping observed in *B. diandrus* and *B. hordeaceus,* therefore, may have been related to the intensity as well as the frequency of defoliation. Different clipping intensities also can produce different growth responses, where a moderate intensity (6 cm stubble height) may increase biomass production and a severe intensity (ground level) reduces it (Georgiadis *et al.* 1989). Savelle and Heady (1970) found that as frequency of clipping *B. diandrus* increased from every five weeks to every week, aboveground biomass decreased. In this study, however, *B. diandrus* growth reduced with all frequency levels, and under no frequency used did *B. diandrus* demonstrate an equal or overcompensation to biomass loss. The frequency and intensity of clipping likely significantly reduced growth by both grasses.

Reproductive biomass (inflorescence) was not severely reduced following clipping. Other studies have observed significantly decreased inflorescence production following regular defoliation (Georgiadis *et al.* 1989, Noy-Meir and Briske 1996, Gutman *et al.* 2002). The reproductive growth of *B. diandrus* and *B. hordeaceus* varies in this study from patterns previously observed, and may indicate changed biomass allocation in response to environmental pressures. According to Cohen's (1971) model, annual grasses will switch biomass allocation from vegetative to reproductive parts at a precise time during their growing season. The decrease in culm height and leaf length, and the relatively constant number of inflorescence, may suggest the two grasses' seasonal response to invest only in reproductive biomass. But annual grasses may also allocate the majority of new biomass to reproductive parts if they are under high stress conditions, such as severe defoliation (Bazzaz 1987). Stress and seasonality, therefore, may explain why inflorescence production was maintained under the clipping and combined treatment.

In comparison, the predicted reduction of biomass due to trampling did not occur (Packer 1963, Heady 1975), suggesting that *B. diandrus* and *B. hordeaceus* may be trampling-tolerant species. These species can both withstand the initial disturbance of trampling and successfully recover from it (Cole 1995). Cole (1995) found that plants with grass morphological features, like long and thin leaves, are most resistant to trampling on aboveground growth (Cole 1988). However, Cole (1995) was primarily referring to matted and low growing grasses; in previous studies, taller grass species like *B. diandrus* and *B. hordeaceus* have often reduced in height and in leaf length following trampling (Kuss 1986, Sun and Liddle 1993). Their conflicting responses across this range of studies, including mine, indicates that *B. diandrus* and *B. hordeaceus* may in fact not be trampling-tolerant species: other factors may have determined their neutral response. The trampling intensity might have been too low to notably affect growth. Under light trampling regimens, ranging from four to ten footfalls, other grasses have shown no response or only a minor (5%) decrease in aboveground growth (Abdel-Magid *et al.* 1987, Sun and Liddle 1993); the one footfall applied in trampling was not intense enough to negatively impact aboveground growth. Alternatively, the trampling mechanism may have been over-simplified, without the factors that typically damage biomass. More accurate and expensive tools have been used to replicate animal trampling, incorporating vertical pivot movement to mimic walking and variation in hoof pressure (Di *et al.* 2000). Using these mechanisms, reductions in grasses' biomass production have been observed (Ferrero 1991, Di *et al.* 2001). *B. diandrus* and *B. hordeaceus* may be trampling-tolerant species, but their neutral responses may also be due to lack of stimuli.

The dominance of *B. diandrus* and *B. hordeaceus* in California grasslands may be explained by their responses to simulated grazing. When defoliated, both species were unable to compensate for aboveground biomass loss. This disadvantage may open up the canopy, shifting resource dominance from the annuals to competitive seedlings. A change in the resource balance can cause a further shift in the species composition of a grassland (Noy-Meir *et al.* 1989). However, both species were able to produce inflorescence even under high intensity clipping. Thus while perennials seedlings may out-compete on a seasonal timescale, the annual grasses' fitness has not reduced; it produces the same number of viable offspring to compete in the next generation. And if B. *diandrus* and *B. hordeaceus* are indeed trampling-tolerant, they may better withstand grazing disturbance than their perennial competitors.

To better determine how grazing influences exotic annual grass growth, future research should expand on a more complex study design. Simulated trampling should be further developed, beginning with a stronger understanding of cows' hoof movements to produce a better trampling mechanism. This study design would possibly highlight some variables of simulated trampling, utilizing a more extensive array of exotic annual grasses, different frequencies of trampling, and seasonal variation. Two major limitations of my own study were the plants' limited environmental resources and the exclusion of belowground biomass when analyzing plant growth. Withholding nutrients to the plants after seeding and restricting root growth through pot size may have resulted in less biomass than if the plants had been in an uncontrolled environment. It is also impossible to holistically understand plant growth without belowground biomass data. Multiple studies have found that aboveground grazing reduces belowground biomass growth (Verkaar 1986, Detling 1988, Fitter 1989). Annual exotic grasses succeed thanks to their rapid allocation to both aboveground *and* belowground biomass, and so both components are integral to grazing studies (Da Silva and Bartolome 1984, Jackson and Roy 1986, Tang *et al.* 1988, Thompson and Harper 1988 Elliot and White 1989, D'Antonio and Vitousek 1992). Belowground biomass was not analyzed in my study due to time constraints.

Considering both the historical and current state of California grasslands, better understanding grazing impacts is essential for predicting the future composition of exotic annual grasslands. Identifying what aspects of grazing inhibit or promote exotic annual grass growth—as in the case of *B. diandrus* and *B. hordeaceus*, which reduce growth after defoliation and maintain it under trampling—can lead to a more successful management of grasslands and aid in the transition from exotic- to native-dominated landscapes.

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