The effect of small gaps in California annual grassland on above-ground biomass production

J. S. Fehmi, E. A. Laca and K. J. Rice
Department of Agronomy and Range Science, University of California, One Shields Avenue, Davis, CA 95616-8515, USA

Abstract
Small gaps and clumped species distributions are common in grasslands. In California annual grasslands, patches of *Lolium multiflorum* Lam. and *Bromus hordeaceus* L. are often separated by gaps. These gaps potentially limit the productivity and associated resource use of these grasslands. The effect that differences in spatial aggregation, gap distribution and species mixing on 20-cm-diameter plots has on overall forage production by these two grasses was tested. There were three levels of aggregation: whole plots planted; half planted/half empty; two opposing quarters planted/two empty. Each species was planted in each distribution, and they were combined as mixed, half *L. multiflorum*/half *B. hordeaceus* and two quarters *L. multiflorum*/two quarters *B. hordeaceus* (nine treatments). Plant aggregation had no significant effect on above-ground production of whole plots, but individual tillers near gaps were significantly larger than others. Plasticity in the growth of individual annual grasses effectively buffered against variation in average productivity resulting from variations in plant distribution. There were significant (*P* < 0.001) differences in forage production as a result of the species the plots contained. Plots containing only *L. multiflorum* produced 4053 kg of dry matter (DM) ha⁻¹, *B. hordeaceus* plots produced 2448 kg of DM ha⁻¹, and plots containing both species produced 4712 kg of DM ha⁻¹. At small scales, spatial distribution was less important than species composition in determining annual grassland productivity.

Keywords: spatial pattern, additive design, plant distribution, small-scale gaps, competitive effects

Introduction
Small gaps and patchy species distributions have been commonly observed throughout many grasslands and rangelands. Heady (1958) reported the occurrence of numerous 6·5 cm² bare patches in California grasslands. Pitt and Heady (1978) and Bartolome *et al.* (1980) reported foliar cover of 0·20–0·70 on grasslands distributed across California. Gaps and patchy spatial distributions of plants common in the annual grasslands of California may be related to resource limitation, as Bartolome *et al.* (1980) found that total foliar cover was well correlated with total precipitation on plots spanning California. However, aggregation of plants into monospecific clumps appears to be an inefficient strategy for resource capture by these grasses. Despite high root densities and effective exploitation of below-ground space (McConnaughay and Bazzaz, 1991), resources captured by plants should be maximized when individuals are well distributed (Sutherland and Benjamin, 1993; Benjamin, 1996). Grassland gaps appear to have the potential to limit the productivity of such grasslands.

Among others, two introduced grasses, *Lolium multiflorum* Lam. (Italian ryegrass; all nomenclature per Hickman, 1993) and *Bromus hordeaceus* L. (Blando brome; previously *B. mollis* per Munz and Keck, 1968), often dominate portions of the California grassland (Wu and Jain, 1979; Heady *et al.*, 1992) and are commonly found together (e.g. Gulmon, 1979; Fehmi, 1998). Both these grasses are preferred species and represent a significant forage component of California annual grasslands (Jain *et al.*, 1970; Young *et al.*, 1996). We observed that patches of bare soil or plant litter often occurred between nearly monospecific small patches of these species in addition to other grasses. Studies are lacking that have considered the effect of gaps and spatial distribution on the production of *L. multiflorum* and *B. hordeaceus*. 

Correspondence to: Dr J. S. Fehmi, ERDC-CERL, 2902 Newmark Drive, Champaign, IL 61826, USA. E-mail: j-fehmi@eccer.army.mil

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This work was carried out to evaluate the plant-level relationship of inter- and intra-specific competition of *L. multiflorum* and *B. hordeaceus*, the reaction of plants to gaps and the relationship between species aggregation and interaction. It was expected that, as aggregation increased (decreasing evenness in spatial distribution), above-ground biomass production would decrease for both *B. hordeaceus* and *L. multiflorum* and that the effects would not be significantly different between the two species. In some of our other work (unpublished), we found that competition for water within the California annual grassland took place at scales of <10 cm. From that work, we hypothesized that small-scale differences in spatial distribution, plant species composition and disturbance of the order of 300 cm² (i.e. pattern at scales of a 10-cm radius) could be important determinants of overall community productivity. We also expected that species grown alone would have about the same production as when the species were grown together and hypothesized that there would be no interaction effects.

**Materials and methods**

Research was conducted at the University of California’s Davis Experimental Farm (38°33’N, 121°47’W) on Yolo silty loam soils (fine-silty, mixed, non-acid, thermic typic xerorthents).

**Initial experiment**

In December 1997, 36 4·5 × 6·0 m plots separated by 1·5 m were designated. Subplots containing only *L. multiflorum* or *B. hordeaceus* were established from seed at a constant rate of two seeds cm⁻² and alternated within the larger plots. Subplot sizes were 1·50 × 1·50 m, 0·75 × 0·75 m or 0·15 × 0·60 m. Subplot size stayed the same within each plot and was randomly assigned to whole plots as part of a randomized complete block design with four blocks and three replications per block. For each plot, two *L. multiflorum* and two *B. hordeaceus* tillers were selected randomly and harvested from the edge near bare ground (gap), from the centre of a monospecific plot of each species and from the edge where the two species were adjacent (12 tillers per plot). Harvesting took place on 20 April 1998. All tillers were harvested at ground level, dried at 65°C for 48 h and weighed.

The two tillers per sampling location were averaged, and **ANOVA** analysis of the tiller weights included the explanatory variables: species (*L. multiflorum*, *B. hordeaceus*), adjacent planting (bare ground, *L. multiflorum*, *B. hordeaceus*) and subplot size (1·50 m, 0·75 m, 0·15 m). The tiller weights were log transformed to stabilize the variance.

**Main experiment**

In a standard additive design (Snaydon, 1991) with nine treatments (Figure 1), two grasses, *L. multiflorum* and *B. hordeaceus*, were established from seed in 20-cm-diameter plots at a constant rate of one seed cm⁻². The plots were divided to allow for three degrees of aggregation: no divisions (whole plots planted); one division (half planted, half empty); and two divisions (two opposing quarters planted, two empty). Each species was planted alone in each distribution and also as a combined treatment with both species present in each of the three distributions: completely mixed; half *L. multiflorum*/half *B. hordeaceus*; and two quarters *L. multiflorum*/two quarters *B. hordeaceus*. Ten replications of each treatment were established in randomized complete blocks. During planting, the individual plots were surrounded with an equal mix of *L. multiflorum* and *B. hordeaceus* to constrain gap size to within the plot size. Within blocks, the plots were separated by 30 cm, and the blocks themselves were 2–4 m apart. Daily watering during the first week after planting minimized seed dislocation by wind and other factors. Otherwise, natural rainfall of 220 mm provided the only water between planting in January and the harvest of all above-ground material within plots in May. Exact harvest dates for each block were determined by the phenological stage of plants in the matrix surrounding the plots. The single-species plots for each block were harvested when the majority of that species in the adjacent matrix was at the hard-dough stage and before seeds began to disarticulate. As determined by treatment assignment, half the combined plots were harvested based on *B. hordeaceus* phenology and the other half based on *L. multiflorum*. Before any plots were harvested, leaf area index was estimated with an Accupar Ceptometer (Decagon Devices, Pullman, WA, USA) based on a 10 × 1 cm sampling area above and below the vegetation (within the gaps if present) on each side of each plot. During planting, single seeds were planted and marked in the centre of the half planted and the monospecific whole planted plots. The resulting tillers were handled separately during harvesting for comparison with the data from the initial experiment. All samples harvested were dried at 65°C for 48 h before being weighed.

Tiller weights were analysed by the same procedure as in the initial experiment. Above-ground biomass produced within the 20-cm-diameter plots was analysed using **ANOVA** with composition (*B. hordeaceus*, *L. multiflorum*, combined) and degree of aggregation of competitors (whole plots, halves, quarters) as main effects. A covariate to represent the harvest date was added to the model to account for differences caused by
harvesting combined plots based on plant phenological stage. The dependent variable was log transformed to stabilize the variance.

Above-ground biomass was chosen as the response variable in this part of the experiment for three reasons. First, above-ground biomass was readily related to measures of forage production. Secondly, it measured the group effects of individual tiller weight. Thirdly, biomass accumulation has often been a better estimate of plant performance than other measures such as height (McConnaughay and Bazzaz, 1990) and, in annual grasses, it is reliably correlated with fitness measures such as seed production (Gulmon, 1979). Both species are known for having plastic growth (senescing at heights of 5–10 cm and producing a single seed, or at heights of 65–80 cm and producing 150–300 seeds; Gulmon, 1979), and individual plants survive at densities above two plants cm$^{-2}$ (Gulmon, 1979; Wu and Jain, 1979).

**Results**

**Initial experiment**

There were significant differences ($P < 0.001$) between species tiller weights, in adjacent planting effects and in the interaction between them (Table 1). Both species were substantially larger when adjacent to gaps. The interaction shown by the analysis occurred when the two species were adjacent to one another. *B. hordeaceus* tiller weights adjacent to *L. multiflorum* were not different from those obtained when it grew in competition with its own species but, in the same comparison for *L. multiflorum*, its tiller weights were significantly more when grown next to *B. hordeaceus*. The subplot size treatment had no effect ($P = 0.740$) and, similarly, no other interaction was significant.

![Figure 1](https://example.com/fig1.png)

**Figure 1** Schematic representation of the treatment combinations as applied to the plots. *Bromus hordeaceus* and *Lolium multiflorum* are abbreviated Brho and Lomu respectively.
Table 1 Mean tiller weights (mg) for the initial experiment in 1998.

<table>
<thead>
<tr>
<th>Adjacent planting</th>
<th>Same species</th>
<th>Other species</th>
<th>Gap</th>
<th>Species effects*** (0.08)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adjacency effects*** (0.10)</td>
<td>31.86 [3.46]</td>
<td>44.34 [3.79]</td>
<td>113.14 [4.73]</td>
<td>Interaction*** (0.14)</td>
</tr>
</tbody>
</table>

Log-transformed values used for analysis are in curled brackets. Standard error for differences of means between the log-transformed data are in parentheses. The table represents 216 data points in a balanced design. ***P < 0.001.

Main experiment

The tiller weights from the main experiment had the same relative response as the initial experiment despite the species effects not being significant (P = 0.21; Table 2). The adjacent planting and the interaction were again significant with P-values of 0.015 and 0.038 respectively. Of the plants, one L. multiflorum (adjacent to a gap) produced more than one tiller. Otherwise, tillers are synonymous with plants.

No significant (P = 0.589) differences in above-ground biomass were associated with the aggregation treatment (Table 3, dividing the plots into halves, quarters or whole plots) regardless of composition treatment (B. hordeaceus, L. multiflorum or combined). Mean above-ground biomass of B. hordeaceus and L. multiflorum (Table 3) was not significantly different (P = 0.554) between the different gap distributions in the single-species plots, although there was a trend towards reduced production with increased aggregation. Within the combined plots (those plots with both species grown together), there were also no differences attributable to the aggregation treatment (P = 0.592; Table 4). However, plots containing both species produced significantly more above-ground biomass (4712 kg of DM ha⁻¹; P < 0.001) than the single-species plots, and L. multiflorum produced more (4053 kg of DM ha⁻¹) than B. hordeaceus (2448 kg of DM ha⁻¹; Table 3). Individual species above-ground biomass, in combined plots was less than in single-species plots. L. multiflorum production was reduced by 19%, and B. hordeaceus was reduced by 42% (Table 4). No significant (P = 0.732) aggregation by composition interactions were detected.

There were no significant differences in the estimated leaf area index from differences in planting (B. hordeaceus, L. multiflorum or gap; P = 0.627) or the adjacent planting (P = 0.171). Interactions between planting and adjacent planting were similarly not significant (P = 0.193). Data from the half- and whole-plot treatments (Table 5) compare directly with the tiller weight data and were the most likely to show differences; however, no trends are apparent. The data show that the estimated leaf area index of vegetation at ground level within the gaps was indistinguishable from planted areas.

Discussion

The lack of difference in above-ground biomass with changing plant and gap aggregation shows that groups of plants buffered average productivity caused by spatial processes. Within-species size hierarchies (e.g. Bonan, 1988) created by plastic growth may explain the lack of differences found between plots with gaps and those without them. Plastic growth of grasses has been shown to result in similar resource depletion rates and production at both high and low densities (Gordon et al., 1989; Gordon and Rice, 1993). In this study, plants that were adjacent to gaps were significantly larger than

Table 2 Mean tiller weights (mg) for the main experiment in 1999.

<table>
<thead>
<tr>
<th>Adjacent planting</th>
<th>Same species</th>
<th>Other species</th>
<th>Gap</th>
<th>Species effects (0.26)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adjacency effects* (0.32)</td>
<td>28.82 [3.36]</td>
<td>22.51 [3.11]</td>
<td>57.45 [4.05]</td>
<td>Interaction* (0.45)</td>
</tr>
</tbody>
</table>

Log-transformed values used for analysis are in curled brackets. Standard error for differences of means between the log-transformed data are in parentheses. The table represents 60 data points in a balanced design. *P < 0.05.
those in patch interiors (Tables 1 and 2), expressing growth plasticity. These larger plants may have translated their unimpeded access to gap resources into disproportionate resource use and a similar production at plot level to plots without gaps. This is similar to the reduction in the spatial effects projected by Hara and Wyszomirski (1994) as a result of competitive asymmetries between plants. In our case, plants on the edges of patches were substantially more important, in terms of biomass, than those in the interior of the patch. This would make sense, because plants are immobile and respond only to individual plants or available resources in their neighbourhood rather than responding to the population of competing plants as a whole (Harper, 1977). Although some studies have found equal effects despite differences in radial distribution of competitors (Weiner, 1985), more evidence seems to point to the aggregation or spatial pattern of competitors, regardless of species, as being important in determining the fitness of individual plants (Bergelson, 1993). Our data suggest that these individual plant effects, when scaled up to a 20-cm-diameter plot, buffer the effects of differences in plant distribution resulting in relatively constant above-ground biomass.

Analysis of the leaf area index data also demonstrates plastic growth of these annual grasses. The grassland canopy was able to close the 10-cm-wide gaps effectively. Plot segments occupied by grasses were indistinguishable from gaps, providing additional evidence that resources in gaps were fully used by the adjacent plants. The data for *B. hordeaceus* and *L. multiflorum* exhibited a trend towards decreased above-ground biomass, with increasing gap size. Projecting this trend beyond the experimental plot size suggests that gaps may represent

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Mean above-ground biomass (kg DM ha⁻¹) for the main experiment.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Plot division treatments</strong></td>
<td>Bromus hordeaceus</td>
</tr>
<tr>
<td>Whole</td>
<td>2690 (292)</td>
</tr>
<tr>
<td>Quarters</td>
<td>2436 (101)</td>
</tr>
<tr>
<td>Halves</td>
<td>2220 (265)</td>
</tr>
<tr>
<td>Species effects***</td>
<td>2448 (136)</td>
</tr>
<tr>
<td>Division effects</td>
<td>3982 (285)</td>
</tr>
</tbody>
</table>

Standard error of the mean is in parentheses. ***P < 0.001.

<table>
<thead>
<tr>
<th>Table 4</th>
<th>Mean above-ground biomass (kg DM ha⁻¹) of the separated individual species from the combined species plots in the main experiment.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Plot division treatments</strong></td>
<td>Bromus hordeaceus</td>
</tr>
<tr>
<td>Whole</td>
<td>1348</td>
</tr>
<tr>
<td>Quarters</td>
<td>1494</td>
</tr>
<tr>
<td>Halves</td>
<td>1444</td>
</tr>
<tr>
<td>Species effects*** (196)</td>
<td>1429</td>
</tr>
<tr>
<td>Division effects (239)</td>
<td>4536</td>
</tr>
<tr>
<td>Interaction (340)</td>
<td>4606</td>
</tr>
</tbody>
</table>

Standard errors for differences of means are in parentheses. ***P < 0.001.

<table>
<thead>
<tr>
<th>Table 5</th>
<th>Estimated leaf area index (m² m⁻²) for the main experiment.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Adjacent planting</strong></td>
<td>Bromus hordeaceus</td>
</tr>
<tr>
<td>Planting</td>
<td>3.06 (0.35)</td>
</tr>
<tr>
<td>Lolium multiflorum</td>
<td>2.91 (0.42)</td>
</tr>
<tr>
<td>Gap</td>
<td>3.73 (0.74)</td>
</tr>
<tr>
<td>Adjacency effects</td>
<td>3.12 (0.26)</td>
</tr>
</tbody>
</table>

Standard error of the mean is in parentheses.
available resources, but a lower limit to effective size may exist. This hypothesis fits with existing knowledge about grassland gaps. Gaps in grasslands are known to be important for the regeneration of some grassland species (e.g. McConnaughay and Bazzaz, 1990), may be critical for plant species co-existence (Lavorel et al., 1994) and have the potential to structure the plant communities for many years after their formation (e.g. Hobbs and Mooney, 1995). However, 75–150 cm² gaps did not limit the realized productivity of our simple system, which suggests that the under-utilized resources are few and that gaps are of limited importance in the California annual grassland.

Average production was greater from the plots containing both species than from plots with either species grown alone. This finding of more above-ground biomass, in mixtures is consistent with other work showing that the mixture of two plant species should produce more biomass, than monocultures (e.g. Tilman et al., 1996). The increased above-ground biomass, in the combined plots suggests the potential for spatial partitioning of resources between these grasses. This type of partitioning is well known for other, less similar species, such as grasses and woody plants (e.g. Dodd et al., 1998), and logically leads to recommendations for combining plants that differ in phenology or rooting depth to maximize plant community resource use and forage production. Our data show that combinations of grasses or other similar plants may also exhibit significant resource partitioning and increased total resource uptake.

The Californian annual grassland dominated by L. multiflorum and B. hordeaceus is normally used for low-intensity livestock rearing with the use of half or less of the annual DM production as the usual land management goal. Small gaps (<200 cm²) and cover above 0.50 in these grasslands (e.g. Pitt and Heady, 1978) appear not to be limiting forage production in this system. Similarly, the normal mixed distribution of grasses (e.g. Gulmon, 1979; Fehmi, 1998) also does not appear to limit productivity. Both larger gaps and large monospecific patches, if common, may merit management activity such as seeding to increase forage production.

The significant interaction between L. multiflorum and B. hordeaceus in terms of the response in tiller weight to the other species as a neighbour (Tables 1 and 2) was surprising. Gulmon (1979) had found that L. multiflorum and B. hordeaceus were effectively equal in competitive ability in mixtures. However, our data support earlier research by McKell et al. (1969), who found that L. multiflorum was a better competitor than B. hordeaceus and that the biomass production of B. hordeaceus was greater in monospecifics than in mixtures. This effect scales up to the plot level in the trend towards increased production in the combined plots with the species in opposing quarters (Table 4). Interestingly, this treatment corresponds most closely to our observation of the distribution of these two species in natural settings. B. hordeaceus benefits from the conspecific refuge of its own species, whereas L. multiflorum benefits from being bordered by the patch of the other species. This plant interaction requires further experimentation for resolution of the mechanisms involved.

Although at the whole-plot level, differences in small-scale plant aggregation did not have a significant impact on above-ground biomass production, differences in spatial location at the individual tiller level made a significant and substantial difference in plant size. This supports the concept that the spatial distribution of plants is as important as the number of plants per unit area. In more applied terms, the local density of plants needs to be taken into account to reflect community dynamics. In earlier modelling work (Fehmi and Laca, 1998), we assumed that individual plant response was similar across a wide range of spatial arrangements. Our results bore almost no relationship to the outcome of field experiments, and we now attribute the inaccurate responses of the model to the erroneous assumptions about spatial behaviour. Although this type of assumption is rarely tested (Molofsky, 1999), a productive direction for future research might concentrate on the dominant individuals, such as those at the boundaries of patches, rather than treating all individuals equally. This simple change in perspective will require a substantial increase in sampling requirements, because the location and characteristics of each plant becomes important.

Determining the factors that structure grassland patterns, especially for annual grasslands, is another area with much research potential. In some sense, communities dominated by annual plants, such as the annual grasslands of California, are reinvaded every year. Although there has been some work demonstrating a seed bank, the vast majority of the annual grass seeds germinate when exposed to conditions suitable for germination (Bartolome, 1979). This implies that seed rain is critical for the occupation of any particular area by plants. Other work (Fehmi and Laca, 1999) has shown that the seed rain for these two species is not random and that the majority of seeds were dispersed in one area away from the parent plant. The fact that this seed rain does not cover the entire surface evenly and that the resulting seed distribution is clumped seems unremarkable. However, this pattern leads us to speculate that many gaps in the Californian annual grassland could result from patchy seed distribution rather than from other causes. Gaps in grasslands have been commonly attributed to disturbance effects such as grazing, humans, frost heave or soil movement, but they may also be caused by soil microsite differences,
plant litter distribution and seed predation among others. The determination of the origins and impact of observed spatial patterns is critical to the perception of grassland function.

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