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ORIGINAL PAPER

Mechanisms of influence of invasive grass litter on germination and growth of coexisting species in California

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Abstract In grasslands, litter has been recognized as an important factor promoting grass persistence and the suppression of forbs. The invasive European annual grass *Bromus diandrus* (ripgut brome) is widespread throughout California, where it produces a persistent and thick litter layer. The native grass, *Stipa pulchra*, is also common in some grassland settings and can also produce persistent litter, yet it is typically associated with more forbs. Very little is known about the mechanisms through which these two common grass species influence seedling establishment of both exotic invasive and native herbs. Here, we evaluated the effect of *B. diandrus* and *S. pulchra* litter on seedling establishment of two invasive (the grass *B. diandrus* and the forb *Centaurea melitensis*) and two native (the grass *S. pulchra*, and the forb *Clarkia purpurea*) herbaceous plants in a greenhouse setting. Our results showed that *B. diandrus* litter cover hindered seedling establishment of the four species tested, but that the degree and mechanism of inhibition was dependent on which species was tested, life form (e.g. monocot/dicot) and seed size. Seedling emergence of the two forb species was more vulnerable to litter cover than either grass species and both forbs had smaller seed size. After germination, only seedling biomass of *B. diandrus* itself was reduced by litter (both *B. diandrus* and *S. pulchra*). We found no significant effects of leachate of either grass species on seedling emergence of any species, while a high concentration of *B. diandrus* leachates inhibited root growth of all species including *B. diandrus* seedlings. *Stipa pulchra* litter leachates did not affect *S. pulchra* or *C. melitensis* seedlings although it did suppress *B. diandrus* and *C. purpurea* seedling growth. Our findings provide direct experimental evidence for the mechanism of effect of litter on these coexisting invasive and native species. Such evidence helps advance our understanding of role of *B. diandrus* and *S. pulchra* litter in California grassland.

Keywords Allelopathy · *Bromus diandrus* · Bunch grass · Ripgut brome · Soil nitrogen · Thatch

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Introduction

The accumulation and decomposition of plant litter has long been identified as an important factor influencing both vegetation structure (Facelli and Pickett 1991; Xiong and Nilsson 1997, 1999) and ecosystem functioning (Wardle et al. 1997; Handa et al. 2014; Barbe et al. 2017). Accumulations of recalcitrant plant litter can reduce seed germination and alter species composition and productivity (Hamrick and Lee 1987; Amatangelo et al. 2008; Wolkovich et al. 2009). In harsh environments, litter can facilitate the establishment and growth of plants and enhance species diversity by improving moisture conditions (Fowler 1986; Willms et al. 1986). Plant litter also plays a critical role in nutrient cycling, organic matter turnover and community structure and dynamics (Gessner et al. 2010; van der Putten et al. 2016). Interestingly, both the effects of grass-litter (in contrast to other litter types) and the effects of litter in grasslands (in contrast to other ecosystem types) could be positive or negative depending on the setting (Xiong and Nilsson 1999). In fact, a meta-analysis by Loydi et al. (2013) found an overall neutral effect of litter presence on seedling emergence and survival and a positive effect on seedling biomass, and they pointed out that litter effects depend on many variables including litter amount, study condition, grassland type and the seed size of species influenced by the litter. In addition, different litter types had differential effects of on woodland and grassland species, and the different effects were probably related to litter structure (Donath and Eckstein 2008).

The mechanisms through which litter influences plant species and ecosystems are both direct and indirect (Facelli and Pickett 1991; Xiong and Nilsson 1997; Bonanomi et al. 2011). The presence of litter affects the exchange of water between the soil and the atmosphere, an effect frequently observed in grasslands (Weaver and Rowland 1952; Fowler 1986) where litter increases water availability through shading of the soil surface. Litter also constitutes a physical barrier for seedling establishment because it may keep seeds from reaching the soil, as well as physically inhibit the emergence of seedlings (Bosy and Reader 1995; Olson and Wallander 2002). Moreover, litter may have negative effects on seed germination, and plant growth through chemical inhibition, termed allelopathy (Foster and Gross 1998; Bonanomi et al. 2011; Cummings et al. 2012).

Exotic invasive species have the potential to influence plant composition and nutrient cycling of the invaded ecosystem via their living and dead (litter) plant matter (Ehrenfeld 2003, 2010; Chen et al. 2013; Eppinga and Molofsky 2013; Jo et al. 2016, 2017). In grasslands, the abundance of recalcitrant grass litter can be enhanced following invasion (Evans et al. 2001; Molinari and D'Antonio 2014). Litter has been recognized as an important factor promoting exotic grass persistence (Lenz et al. 2003; Cox and Allen 2008; Molinari 2014; Molinari and D'Antonio in review), suggesting that it may function as a positive feedback mechanism (Molinari and D'Antonio, in review). In the last few decades, it has been documented that litter of invasive plants has the potential to influence species composition by modifying nutrient availability, reducing light levels, creating a physical barrier and releasing allelochemicals (Bergelson 1990; Hierro and Callaway 2003; Callaway and Ridenour 2004; Amatangelo et al. 2008; Yelenik and Levine 2011; Kaproth et al. 2013; Loydi et al. 2015). Bergelson (1990) found that the dead grass blades of invasive grass *Poa annua* decreased seedling emergence and survival of the two studied annual weeds and changed the population dynamics of annual plants. Litter accumulation of an exotic perennial species (*Holcus lanatus*) was found to inhibit seed germination of itself, with no significant effects on seed germination of the native perennial species *Stipa pulchra* (formerly *Nassella pulchra*) (Reynolds et al. 2001). Dead material of the invasive plant black mustard has potential to depress seedling emergence and growth of other native and exotic species through allelopathy (Bell and Muller 1973). While several studies evaluate these physical, chemical and biological effects of litter (e.g.) in isolation, the mechanisms have rarely been studied simultaneously.

In California, exotic annual grasses have widely invaded grassland and shrubland habitats. The Eurasian annual grass *Bromus diandrus* (ripgut brome), is widespread throughout California (D'Antonio and Vitousek 1992; Malmstrom et al. 2005), New Zealand (Tozer et al. 2007) and Australia (Kleemann and Gill 2009), and forms dense stands that when not grazed by livestock develop a persistent and thick leaf litter layer (Molinari and D'Antonio 2014). Although seed germination and seedling establishment are two key stages of a plant's lifecycle that seem to be particularly sensitive to the presence of litter, the chemical and physical mechanisms through which *B. diandrus* litter influences seedling establishment of exotic invasive and native herbs has not been studied. In addition, native grassland species, like the widespread perennial bunchgrass *Stipa pulchra* can also create a persistent litter layer. However, in contrast to *B. diandrus*, *S. pulchra* provides habitat conditions that support a broad spectrum of native grassland organisms (Stromberg et al. 2007), including a diversity of native herbs (Molinari and D'Antonio 2014). Allelopathic potential of aqueous leachates of *S. pulchra* leaf litter was demonstrated on a common exotic grass *Avena fatua* in California (Hull and Muller 1977), yet we know nothing about how *S. pulchra* and *B. diandrus* leachates compare or whether allelopathic potential will be realized against a wider range of target species.

Here, we selected two common exotic annual species and two native herbaceous species to study the influence of *B. diandrus* and *S. pulchra* litter on seedling establishment within a controlled greenhouse setting. These species were chosen for study because of their commonness and their ecological importance (see Materials and methods). Additionally, patches dominated by the two different species can be found nearby to one another with *S. pulchra* patches supporting diverse native forb assemblages, while *B. diandrus* patches generally have poor native forb expression (Molinari and D'Antonio 2014). The specific questions we evaluate are: (i) What are the effects of different amounts of *B. diandrus* litter cover on emergence, and growth of its own seeds and those of three potentially coexisting species? (ii) How do litter effects compare between *B. diandrus* and *S. pulchra*? And (iii) what is the differences in allelopathic potential between *B. diandrus* and *S. pulchra* litter in terms of effects on seedling emergence and growth of the four common grassland species? Question 1 focuses solely on *B. diandrus* because we know this species is associated with very dense litter and almost monospecific stands (Molinari and D'Antonio 2014). Yet we do not know what amount of litter actually inhibits seed germination or growth. We predicted that *B. diandrus* litter may facilitate its own seedling emergence and growth but inhibit coexisting species. Because *S. pulchra* coexists with other species, we predicted that its litter would have less of an effect than *B. diandrus* litter. Likewise, we predicted that the effects of litter leachates might be stronger for *B. diandrus* litter because of its low association with forbs in the field.

Materials and methods

Study sites and species

The study site is Sedgwick Reserve (34°42′04.38″N, 120°02′50.81″W), a 2358 ha reserve that is part of the University of California Natural Reserve System (UCNRS) and located in the Santa Ynez Valley. The reserve is 29 km from the coast, receives approximately 400 mm per year of precipitation and is transitional between wetter coastal prairies and the drier grasslands of the Central and San Joaquin Valleys (Bartolome et al. 2007). The climate in this region is Mediterranean, with hot dry summers and cool wet winters. In this reserve, both the exotic species *Bromus diandrus* and native dominated grassland patches of *Stipa pulchra* (purple needle grass) are scattered (Molinari 2014), which spurred interest in comparing the effect of grass litter of two dominant species in neighboring grassland habitats on common exotic and native species in this region (details in Table 1). The species chosen to test against these litter types included a common noxious weed (*Centaurea melitensis*), a common native forb (*Clarckia purpurea*) and the most common exotic (*B. diandrus*) and native (*S. pulchra*) grasses in this region. *Centaurea melitensis* has been demonstrated to benefit from disturbance in California grassland (Gerlach and Rice 2003) so we predicted it would be suppressed by grass litter. By contrast, *C. purpurea* has been shown to maintain high biomass with exotic grasses in ungrazed grasslands (HilleRisLambers et al. 2010). Hence, we predicted it would be less affected by grass litter.

Soil, seed and litter collection

Soils were collected from a region of Sedgwick that is in the Salinas soil series (Soil Survey Staff 2003) in August 2011. These are clay loam soils that are typical in alluvial valley bottoms of Sedgwick Reserve. The soil was collected from five different locations within a 0.2 km^2 area of the Figueroa region of the Reserve and includes soils from 0–30 cm deep. The vegetation was similar at all five locations, open grassland

Table 1 The basic information of the four selected species. Values are the means ± 1 SE

Origin	Species	Family	Life form			Seed size without cover and awn (g/1000 seeds)	Seed germination percentage (%)
Invasive	*Bromus diandrus*	Poaceae	Monocot	Annual	Grass	7.28 ± 0.91	100 ± 0.00
Invasive	*Centaurea melitensis*	Asteraceae	Dicot	Annual	Forb	1.65 ± 0.10	100 ± 0.00
Native	*Stipa pulchra*	Poaceae	Monocot	Perennial	Grass	4.11 ± 0.53	82 ± 7.58
Native	*Clarkia purpurea*	Onagraceae	Dicot	Annual	Forb	0.48 ± 0.04	100 ± 0.00

consisting mostly of the exotic annual grasses *B. diandrus*, *A fatua*, and *B. hordeaceous*. Soils from all five sites were homogenized with a cement mixer and then was sieved through 4 mm mesh to remove large rock and coarse root material. The resulting soil was then mixed in a 2:1 ratio with 2 parts of field soil to one part of a standard commercial soil mix (Sunshine Mix 4, Canada). This was done to improve drainage and texture in the greenhouse pots.

Seeds of the four species were collected from more than 30 individuals at multiple sites along a 5 km stretch in Figueroa Valley. Seed collection occurred in the spring of 2009 and 2011 and seeds belonging to a single species were pooled across individuals and sites. Germination percentage and seed size were measured for each species prior to the start of the greenhouse experiment. Seed size was measured within three group of 1000 seeds, and seed germination percentage were measured using five groups of 10 seeds. Seed germination percentage was evaluated by counting the number of seeds that germinated on moist filter paper over a one week period (Table 1). *Bromus diandrus* and *S. pulchra* litter was also collected at the end of the 2011 growing season. It was harvested from multiple individuals along the same stretch of Figueroa Valley where seed collection occurred. Litter was cut with shears as close to the ground surface as possible on plants that had senesced within the last two months and litter was air dried in the lab.

Greenhouse experiment

The study was conducted in the Schuyler greenhouse, on the campus of the University of California, Santa Barbara, USA. All pots were watered every 2 days. They were initially watered with overhead sprinklers and thereafter the soil water content was adjusted to 30% (about half of the soil water holding capacity) by weighing each pot during irrigation. No nutrient supplement was added. Air temperature during the experiment ranged between 10.0 and 22.2 °C with a relative humidity of 35%. To maintain the uniformity of the growth conditions, the pots were rotated among table positions at the time of each irrigation.

Experiment I: effects of *B. diandrus* litter cover on seedling emergence and seedling growth

Sixteen seeds of a single species were sown onto the surface of the soil in each pot (13 × 13 × 13 cm) prior to applying litter. Each treatment was replicated five times. The quantities of dried *B. diandrus* litter initially applied on top of the seeds was 2 g (1 cm thick in height), 4 g (2 cm) or 8 g (4 cm), henceforth denoted as low, medium and high litter cover, respectively. The medium quantity of *B. diandrus* litter equaled the annual litter production of the year 2010 measured in field plots invaded by *B. diandrus* at Sedgwick Reserve (Molinari and D'Antonio 2014). No litter was added to the control pots.

Experiment II: effects of *B. diandrus* versus *S. pulchra* litter on seedling emergence and seedling growth

We determined the effect of litter on seed emergence and seedling growth by sowing 16 seeds of each species into pots (13 × 13 × 13 cm) covered with different litter types. The litter types were invasive grass (*B. diandrus*) and native bunchgrass (*S. pulchra*). No litter was placed on the control pots. The quantity of litter of all the types was 4 g (the same as the medium quantity, above). Each treatment was replicated five times.

Experiment III: chemical effect of litter on seedling emergence and seedling growth

To determine the chemical effect of litter on germination and root development, we prepared high and low concentration litter leachates. The high concentration leachate was 0.04 g ml^{-1} by shaking (60 RPM with a shaker) 100 g litter with 2.5 L water for 4 h. We then filtered the solution, and diluted part of the *B. diandrus* solution with distilled water to create a low concentration leachate (0.01 g ml^{-1}). We did not have a low concentration *S. pulchra* solution. Distilled water was used as a control. Sixteen seeds of each species were sown in each pot (13 × 13 × 13 cm) with the same soil mixed soil as above experiment I and II, and then irrigated with the litter leachates twice a week. Each treatment was replicated five times. Auto-irrigation system was not used in this experiment in order to add the litter leachates. The soil water content was set to 30% by weight.

Experiment IV: effects of litter on soil moisture and soil inorganic N pools

In the above three experiments, we focused on the effects of litter on the growth of the four plant species. In this experiment, in order to determine the effects of litter alone on soil moisture and inorganic N, we prepared 45 pots with the same mixed soil as above three experiments (I, II and III). But in these 45 pots, no seeds were sown in order to exclude the effects of plant uptake on soil moisture and inorganic N. The 45 pots were treated with the same litter cover (*B. diandrus* litter quantity [low, medium and high] and litter types (*B. diandrus* litter and *S. pulchra* litter) and litter leachates (Low and high concentration of *B. diandrus* litter, high concentration of *S. pulchra* litter) described above. Each treatment was replicated five times.

Soil samples were collected from the 45 pots after 12 weeks to coincide with the harvesting of plant materials in the above three experiments (I, II and III). Moist samples were sieved through a 2-mm mesh. Exchangeable NO_3^- and NH_4^+ were determined for all fresh soil samples by extracting 5 g collected soil (wet weight) with 50 mL 2.0 M KCl shaken for 1 h, and then vacuum filtered through a glass fiber filter (Pall Gelmann Type A/E 1.0 µm). Extracts were frozen until analysis. Inorganic N concentrations were analyzed using a Lachat auto-analyzer (Lachat 1989); NO_3^- was reduced by Cd followed by Griesse-Ilovsay reaction, and analyzed colorimetrically (Lachat method #12-107-04-1-B, Milwaukee, WI), and NH_4^+ was analyzed using the diffusion method (Lachat method #31-107-06-5-A, Milwaukee, WI). Simultaneously, soil water content was gravimetrically measured after oven-drying at 105°C for 24 h and extracted soil weights were corrected for moisture content. The concentrations of NH_4^+ and NO_3^- in soil are expressed on a soil dry weight basis.

Measurements of seedling emergence and growth

Seeds were sowed on 29th October and germination started on 3rd November 2011. Seedlings that emerged above the litter were recorded daily and ceased after 14 days when no new seedlings emerged. Only seedlings that penetrated the litter layer were considered as successfully emerged. Therefore, we assume that the percentage of emerged seedlings at the end of the experiment represents cumulative emergence. Seedling emergence percentage (%) = germinated seeds/total seeds × 100.

After 12 weeks of seedling growth, all plant materials were harvested, and the aboveground biomass, and root biomass per pot were measured after drying for 72 h at 60 °C. The total biomass and root to shoot ratio were calculated.

Statistical analyses

In order to test the effects of litter treatments on seedling emergence and seedling growth of the four plant species, three separate two-way ANOVA models corresponding with the three types of litter treatments (i.e. litter quantity, litter type or litter leachate) were run using litter treatment and plant species as the factors. In order to further illustrate the interaction between plant species and litter treatments, we conducted Turkey HSD post hoc tests for those significant interactions between species and litter treatment. For each species, we tested whether the effects of litter quantity, litter type and litter leachates on seedling emergence and seedling biomass differed significantly with one-way ANOVA at $P < 0.05$. In addition, we tested whether the effects of litter treatments on soil inorganic N pools and soil moisture differed significantly with one-way ANOVA at $P < 0.05$ respectively. All analyses were performed using SPSS 20.0 for Windows (SPSS, Chicago, Illinois, USA).

Results

Effects of *B. diandrus* litter cover on seedling emergence and growth

Bromus diandrus litter cover significantly reduced seedling emergence percentage (SEP) and seedling growth of the four species but the effect varied by species (Table 2, significant litter quantity × species interaction, Fig. 1a). Among the four species, SEP of the two dicot forbs appeared to be strongly affected by the "high" litter treatment (Fig. 1a) and no seedlings of *C. melitensis* emerged in that treatment. Generally, *B. diandrus* had the highest SEP of the four species but neither grass was reduced by the higher two litter treatments. Seedling emergence of *S. pulchra* was only significantly reduced by the lowest quantity of *B. diandrus* litter (Fig. 1a), an unusual finding.

Biomass and root to shoot (R/S) ratios were influenced by *B. diandrus* litter cover (biomass only) and species independently (Table 2; Fig. 1b, c). There were no significant interaction effects on biomass and R/S ratio between *B. diandrus* litter cover and plant species, yet *B. diandrus* and *C. purpurea* achieved greater biomass than the other two species, and the biomass of the three studied annual species (*S. pulchra* = perennial) appeared to be strongly reduced by the high litter treatment (Fig. 1b). The two invasive species, *B. diandrus* and *C. melitensis,* had much higher R/S ratio than the two native ones but no species R/S ratios were affected by litter quantity (Fig. 1c).

Fig. 1 Effects of *B. diandrus* litter quantity on seedling ▸ emergence (**a**), biomass (**b**) and R/S ratio (**c**) of the four species. Values are the means ± 1 SE, and values followed by the same lowercase letter within each species do not differ significantly at the $P < 0.05$. Horizontal line and capital letter correspond to species level differences. Sixteen seeds were sown in each pot for measuring seedling emergence, while two seedlings were left in each pot for seedling growth after counting emergence. The treatments are: no litter cover, low quantity (Low-BD), medium quantity (Med-BD) and high quantity of *B. diandrus* litter (High-BD), with 5 replicates

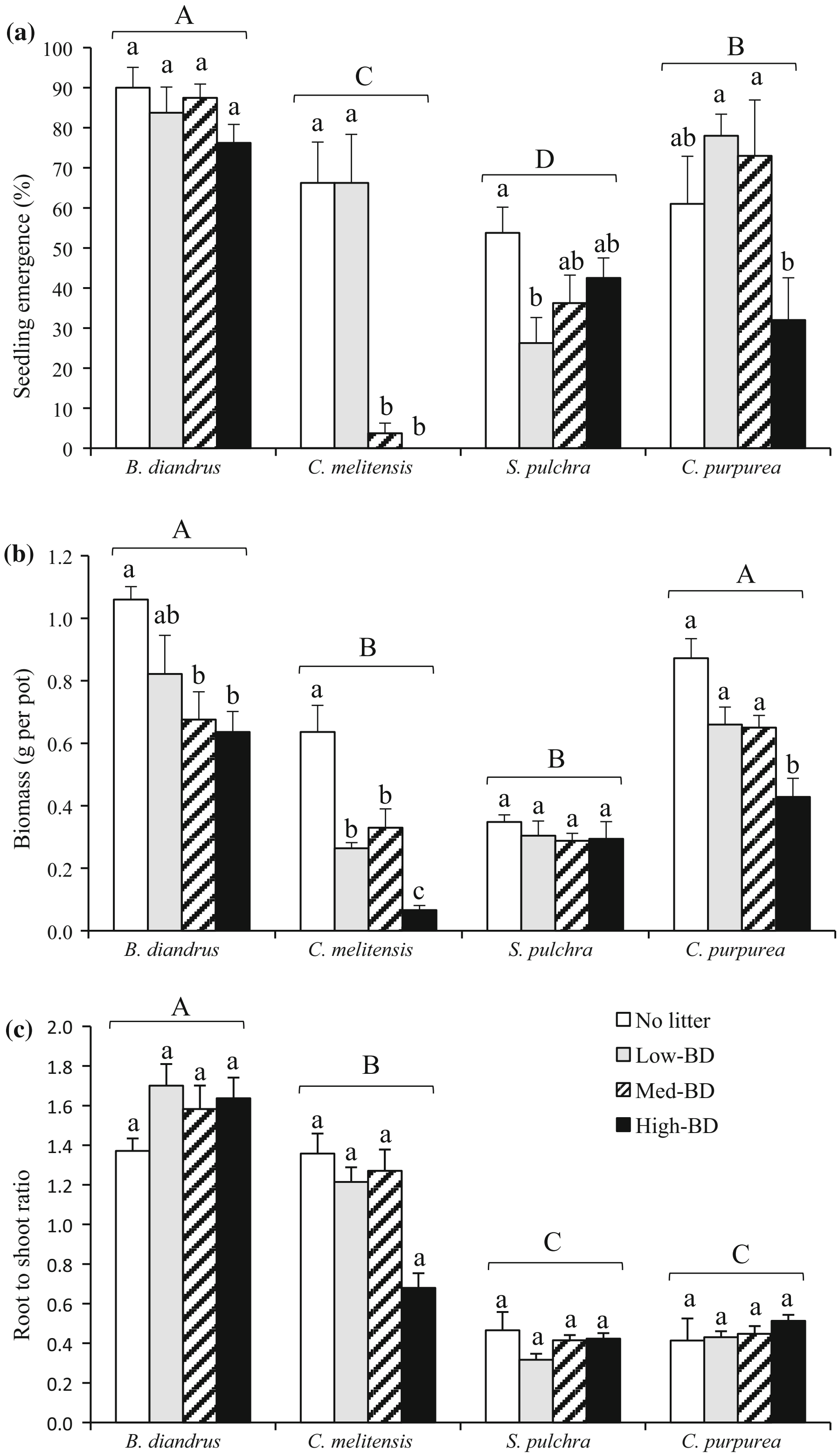
Effects of litter type (*B. diandrus* vs. *S. pulchra*) on seedling emergence and growth

Litter type significantly affected SEP and seedling growth of the four species (Table 2) and the effects again varied by plant species (Table 2; Fig. 2). Litter type affected SEP for *Centaurea melitensis* and *S. pulchra* but not the other two species. In *C. melitensis*, SEP was reduced by both *B. diandrus* and *S. pulchra* litter cover. For *S. pulchra*, *B. diandrus* litter cover did not significantly reduce SEP but *S. pulchra* litter cover reduced its own SEP (Fig. 2a). *Bromus diandrus* responded to litter type in terms of biomass production with lower biomass in both *B. diandrus* and *S. pulchra* litter addition (Fig. 2b). The biomass of *C. melitensis* and *S. pulchra* showed significantly different responses to *B. diandrus* litter versus *S. pulchra* litter, namely *B. diandrus* litter significantly reduced the biomass of *C. melitensis* and *S. pulchra* while *S. pulchra* litter did not (Fig. 2b). The two invasive species *B. diandrus* and *C. melitensis,* had much higher R/S ratio than the two native species, but there

Table 2 The effects of *B. diandrus* litter quantity, litter types (no litter, *B. diandrus* litter and *S. pulchra* litter) and litter leachates of *B. diandrus* and *S. pulchra* on the seedling emergence and plant growth of the invasive species and native species

Variable Source	*df*	Seedling emergence		Total biomass		Root to shoot ratio	
		F	*P*	F	*P*	F	*P*
BD litter quantity	3	12.047	**<0.0001**	12.660	**<0.0001**	0.143	0.934
Species	3	33.934	**<0.0001**	31.100	**<0.0001**	63.209	**<0.0001**
BD Litter quantity × Species	9	6.647	**<0.0001**	1.324	0.243	0.720	0.688
Litter type	2	7.042	**0.002**	15.385	**<0.0001**	1.334	0.273
Species	3	42.045	**<0.0001**	25.454	**<0.0001**	91.916	**<0.0001**
Litter type × Species	6	5.656	**<0.0001**	5.375	**<0.0001**	3.285	**0.009**
Litter leachate	3	1.568	0.206	16.804	**<0.0001**	5.745	**0.002**
Species	3	12.591	**<0.0001**	33.776	**<0.0001**	131.652	**<0.0001**
Litter leachate × Species	9	0.560	0.824	1.352	0.229	2.985	**0.005**

Species refers to the identity of the species being planted. Statistically significant values (P <0.01) are presented in bold type


(a)
Seedling emergence (%)
0
10
20
30
40
50
60
70
80
90
100
A
C
D
B
a a a a
a a b b
a b ab ab
ab a a b
B. diandrus
C. melitensis
S. pulchra
C. purpurea
(b)
Biomass (g per pot)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
A
B
B
A
a ab b b
a b b c
a a a a
a a a b
B. diandrus
C. melitensis
S. pulchra
C. purpurea
(c)
Root to shoot ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
A
B
C
C
a a a a
a a a a
a a a a
a a a a
No litter
Low-BD
Med-BD
High-BD
B. diandrus
C. melitensis
S. pulchra
C. purpurea

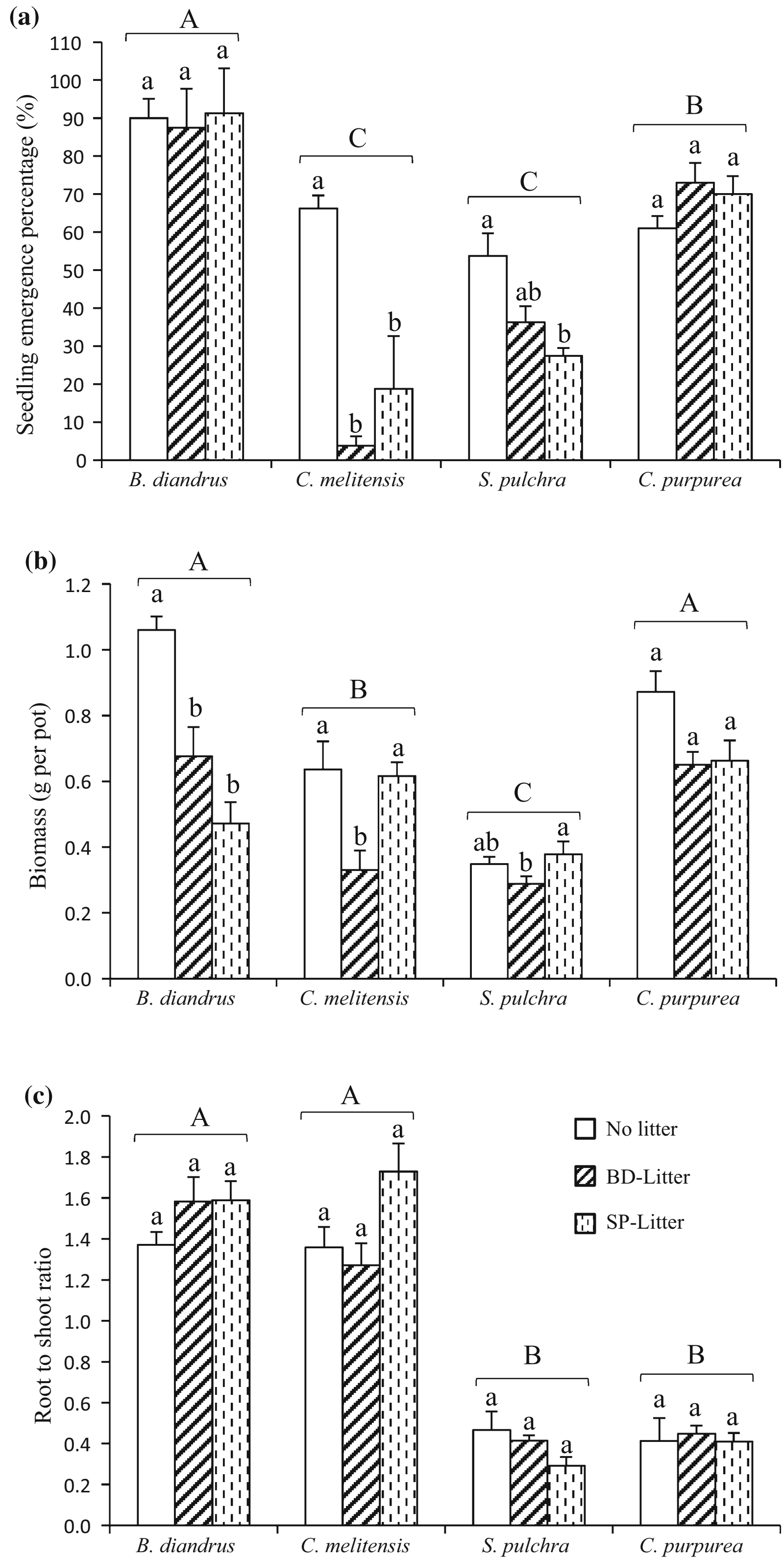


Fig. 2 Effects of litter types on seedling emergence (**a**), biomass (**b**) and R/S ratio (**c**) of the four species. Values are the means ± 1 SE, and values followed by the same lowercase letter within each species do not differ significantly at the $P < 0.05$. Horizontal line and capital letter correspond to species level differences. Sixteen seeds were sown in each pot for measuring seedling emergence, while two seedlings were left in each pot for seedling growth after counting seedling emergence. The treatments are: no litter cover, medium quantity of either *B. diandrus* litter (BD-litter) or *S. pulchra* litter (SP-litter), with 5 replicates

were no significant effects of litter type on R/S ratio (Fig. 2c, Table 2).

Chemical effects of litter on seedling emergence and growth

Litter leachates had no significant effects on SEP of any species (Table 2, Fig. 3a), while they had significant effects on seedling biomass and R/S ratios of the four species and effects varied by species (Table 2, Fig. 3b, c). Litter leachates decreased seedling biomass of the four species relative to the control, but the leachate strengths or species did not vary in their effects on biomass of any species (Table 2, Fig. 3b). Only the R/S ratio of *C. melitensis* responded to the different leachate treatments, namely *B. diandrus* litter leachates significantly reduced the R/S ratio of *C. melitensis* while *S. pulchra* litter did not (Fig. 3c). In general, among the four species, the biomass of *S. pulchra* was reduced the most (average − 47.95%) by litter leachates, while that of *C. melitensis* was reduced the least (average − 38.78%), and the biomass of *S. pulchra* and *C. melitensis,* was not reduced by *S. pulchra* leachate relative to control (Fig. 3b). As in the other experiments, the two invasive species *B. diandrus* and *C. melitensis* had much higher R/S ratio than the two native ones across all leachate treatments (Fig. 3c).

Effects of litter on soil moisture and soil inorganic N pools

Litter cover significantly increased soil moisture but there were no significant differences in soil moisture among the various *B. diandrus* litter cover treatments (Fig. 4). Within the litter treatments, the medium quantity of *S. pulchra* litter had higher soil moisture than low quantity *B. diandrus* litter (Fig. 4). Soil NO_3^- was much higher than soil NH_4^+ in all treatments (Fig. 5). Litter cover led to significantly decreased soil nitrate compared to controls (Fig. 5a) but had no effect on soil NH_4^+ relative to the control (no litter cover) (Fig. 5b). Litter leachates had no significant effects on soil NO_3^- relative to the control (water) (Fig. 6a), although the high concentration of *B. diandrus* leachate increased soil NH_4^+ (Fig. 6b).

Discussion

Studies of invasive plants have stressed the potential for litter feedbacks to facilitate invasion (Ehrenfeld 2003; Liao et al. 2008; Farrer and Goldberg 2009; Loydi et al. 2015). Yet, in the present study, *B. diandrus* litter cover did not facilitate its own seedling emergence or promote its own biomass so a positive feedback was not supported by this greenhouse study. *Bromus diandrus* litter did however, hinder the seedling growth of the other species tested (Fig. 1) and as predicted, it inhibited *C. melitensis* more than *C. purpurea*. Overall, it inhibited the two forb species more than the grasses, which are both larger seeded. This study also shows that grass species litter is not all equivalent. *Bromus diandrus* and *S. pulchra* litter had significantly different effects on seedling emergence and seedling growth (Table 2, Fig. 2). Despite the fact that both species can be common or co-dominate Carlifornia grassland (Molinari and D'Antonio 2014), *B. diandrus* litter generally had stronger effects than *S. pulchra* litter. This is consistent with the higher diversity of forbs that co-exist within *S. pulchra* patches compared to adjacent low diversity stands of *B. dianndrus* (Molinari and D'Antonio 2014). This study thus highlights the role that both litter quantity and different litter types may play in influencing seedling establishment in an annual dominated ecosystem.

Possible mechanisms responsible for species specific effect of litter cover

The impact of litter is complicated by many factors (Facelli and Pickett 1991; Xiong and Nilsson 1999). Litter cover usually enhances soil moisture which facilitates seed germination and seedling performance, but at the same time litter may present a physical barrier for seedling emergence and shoot extension thereby reducing a seedling's ability to capture sunlight (Bosy and Reader 1995; Olson and Wallander 2002). Our results showed that *B. diandrus* litter reduced the seedling emergence or growth of all the plants tested. The highest quantity of *B. diandrus* litter had the strongest effects on the dicot species, *C. melitensis* and *C. purpurea* (Fig. 1). If moisture is the most important limiting factor to plant growth in this system, then the three annual species studied should

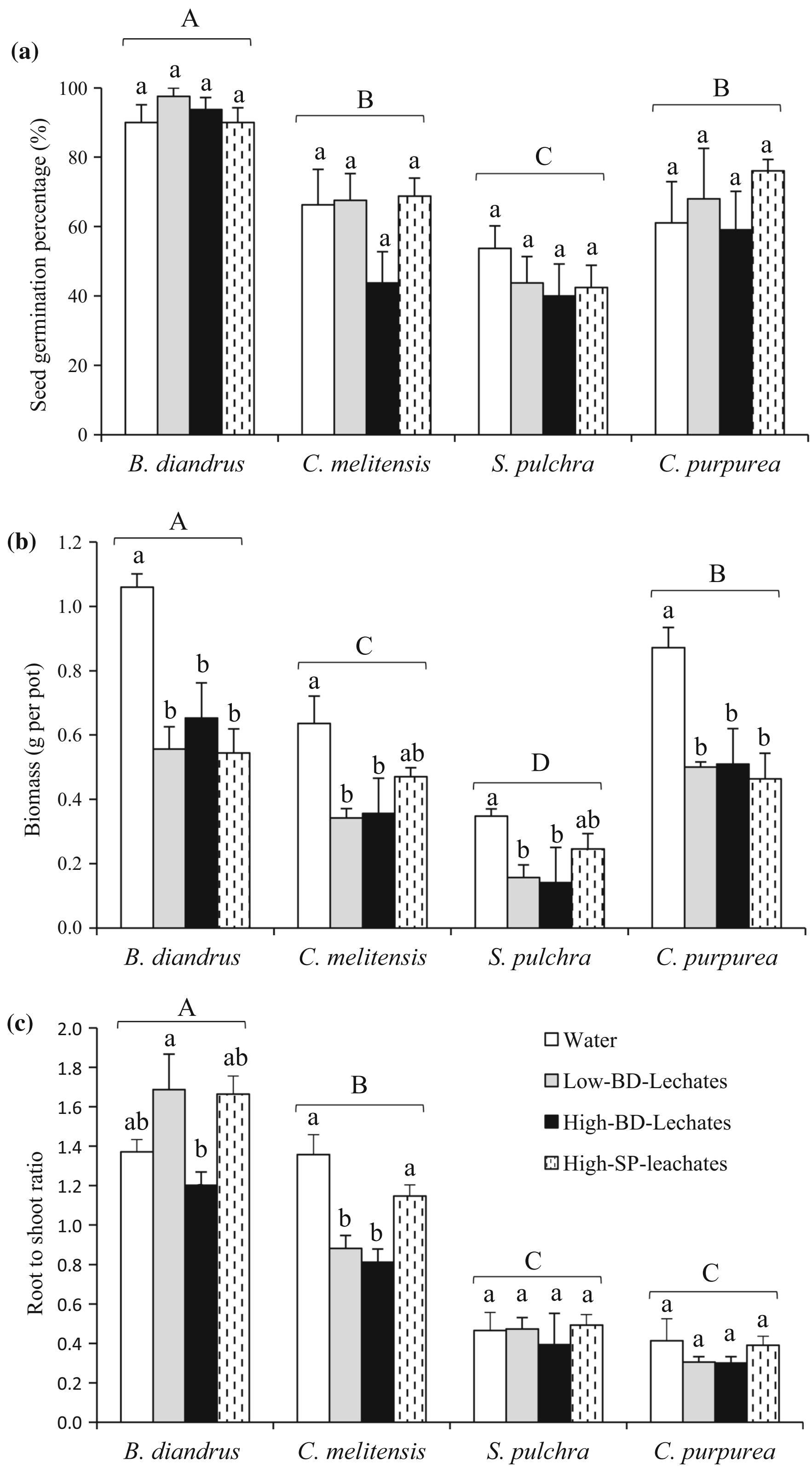


Fig. 3 Effects of litter leachates on seed germination (**a**), biomass (**b**) and R/S ratio (**c**) of the four species. Values are the means ± 1 SE, and values followed by the same lowercase letter within each species do not differ significantly at the $P < 0.05$. Horizontal line and capital letter correspond to species level differences. Sixteen seeds were sown in each pot for measuring seed germination, while two seedlings were left in each pot for seedling growth after counting seed germination. The treatments are: water, low and high concentration of *B. diandrus* litter (L and H-BD-Leachates), and high concentration of *S. pulchra* leachates (H-SP-Leachates), with 5 replicates

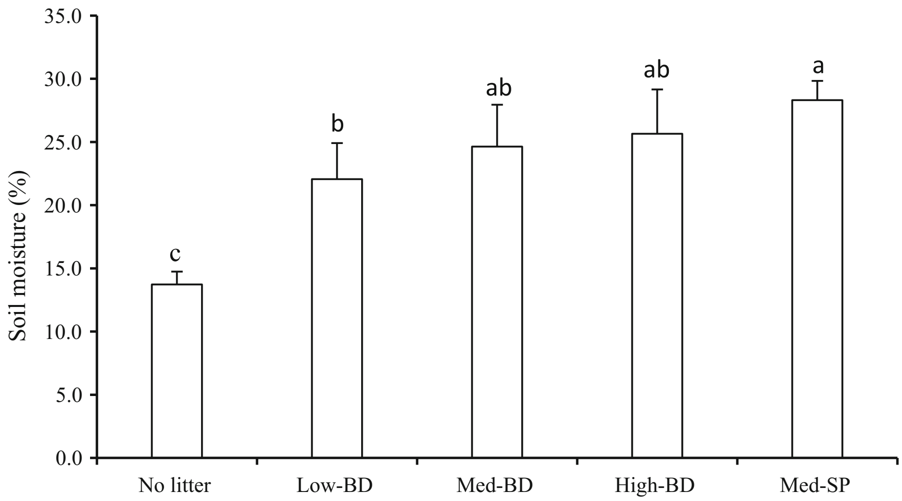


Fig. 4 Effects of litter treatments on soil moisture. Values are the means ± 1 SE, and values followed by the same letter do not differ significantly at the $P < 0.05$. The treatments are: no litter cover; low quantity of *B. diandrus* litter (Low-BD), medium quantity of *B. diandrus* litter (Med-BD), high quantity of *B. diandrus* litter (High-BD) and medium quantity of *S. pulchra* litter (Med-SP), with 5 replicates

have done better with *B. diandrus* litter treatments since they increased soil moisture relative to control. However, from a biomass perspective, they performed no better than the control and performed worst with high quantities of *B. diandrus* litter despite the increases in soil moisture. These results suggest that, positive effects of litter on soil moisture are outweighed by negative effects possibly on light interception.

The influence of litter on light and seedling emergence may be more pronounced in small seeded species (Foster and Gross 1998; Eckstein and Donath 2005; Amatangelo et al. 2008; Ruprecht et al. 2010; Loydi et al. 2013; Molinari and D'Antonio 2014) which tend to have a higher light requirement for germination than large seeded ones (Milberg et al. 2000; Koutsovoulou et al. 2013). Several studies and a meta-analysis have demonstrated a stronger negative effect of litter on emergence of species with smaller seeds (Jensen and Gutekunst 2003, Eckstein and Donath 2005; Loydi et al. 2013). Our results are consistent with these observations since *C. melitensis* and *C. purpurea* were smaller seeded species (Table 1) and show a greater reduction in emergence with litter than the two larger-seeded species. In addition, among the four species tested there are also differences in seedling morphology that may also affect seedling emergence (Gross 1984). The two small-seeded species *C. melitensis* and *C. purpurea* are dicots (Table 1), and have elliptical cotyledons and they form flat, rosettes with a horizontal habit at the early seedling stage. In contrast the two larger-seeded species are grasses (monocots Table 1), with long, narrow cotyledons. These emerge vertically and initial seedlings form an erect to semi-erect plant. Seedlings with an upright or vertical growth form can emerge through deep litter or vegetation better than those with a horizontal growth form (Grimes 1979). Bergelson (1990) for example concluded that *Poa annua* L. (Poaceae) suffered relatively less mortality than annual dicot invaders in the presence of litter because the shape of grass blades of *Poa* appears to allow easy penetration up through the litter. Of all the species including in our study, *C. melitensis* has the broadest leaves and its rosette has much broader leaves than *C. purpurea* and it was the most reduced by litter. In contrast, monocots, like *S. pulchra*, and thin linear leaved dicots like *C. purpurea* may be better suited for emergence through litter than species with broad leaves or basal rosettes, like *C. melitensis*. Thus *C. melitensis*'s growth form is likely a constraint to its emergence through moderate and high quantities of leaf litter (Gross 1984). Field observations suggest spatial separation of *B. diandrus* and *C. melitensis*, such that more productive areas (e.g. under oak trees or pastures with rich soil) with high exotic grass

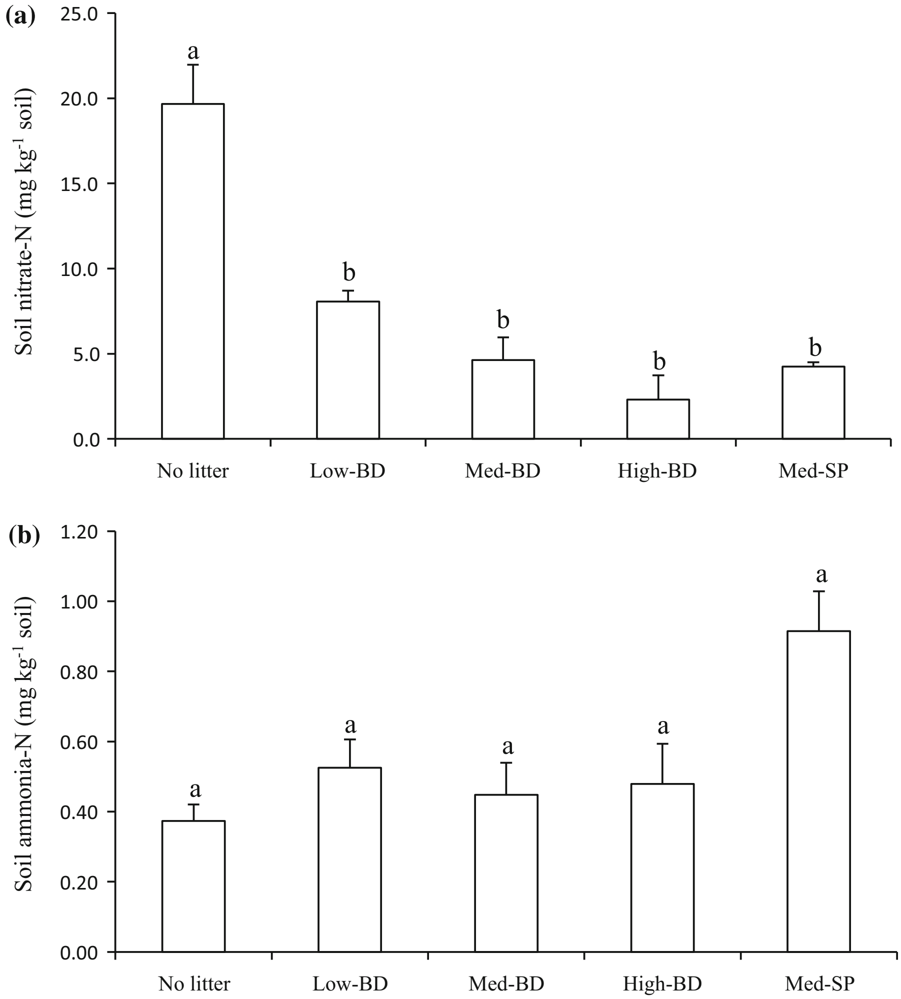


Fig. 5 Effects of litter treatments on soil nitrate and ammonia. Values are the means ± 1 SE, and values followed by the same letter do not differ significantly at the $P < 0.05$. The treatments are: no litter cover; low quantity of *B. diandrus* litter (Low-BD), medium quantity of *B. diandrus* litter (Med-BD), High quantity of *B. diandrus* litter (High-BD) and medium quantity of *S. pulchra* litter (Med-SP), with 5 replicates

production are generally devoid of *C. melitensis*, which is often found in lower productivity areas or disturbed areas within grassland with little litter accumulation (Gerlach and Rice 2003). As we predicted, *C. purpurea* was less affected by litter except at the highest cover (Fig. 1).

Effects of litter type and leachates

Litter effects have been shown to differ by litter type (Xiong and Nilsson 1999; Donath and Eckstein 2008). Our results however, showed that when litter amount is held constant (medium level), both grass litters had similar effects on germination and growth of seedlings (Fig. 2). This may be because both are grasses: had we used litter from a wider variety of life forms we may have seen more similar results to those of other studies. The two grasses did differ in their impacts more when the litter was leached with greater effects from *B. diandrus* compared to *S. pulchra* litter.

Many studies suggest that allelopathy may contribute to the capability of exotic species becoming dominants in invaded plant communities (Callaway and Aschehoug 2000; Ridenour and Callaway 2001; Murrell et al. 2011). In the present study, litter

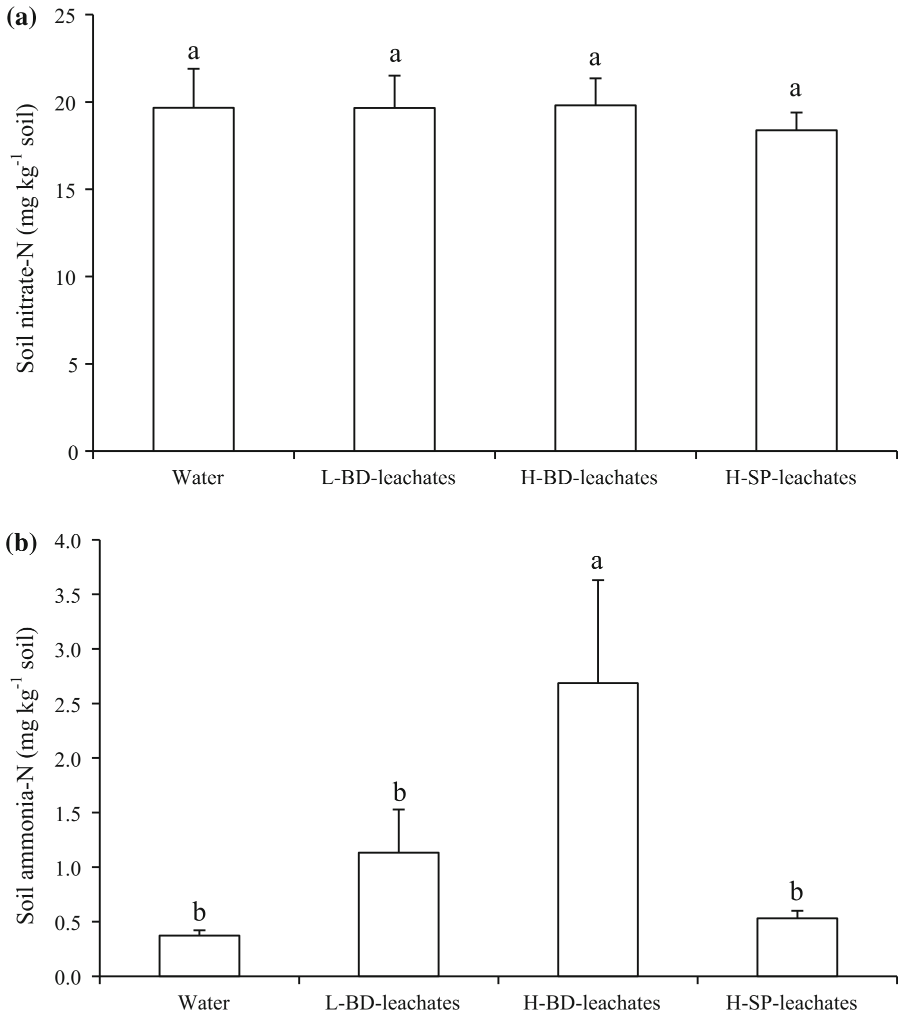


Fig. 6 Effects of litter leachates on soil nitrate and ammonia. Values are the means ± 1 SE, and values followed by the same letter do not differ significantly at the $P < 0.05$. The treatments are: water, low and high concentration of *B. diandrus* litter (L and H-BD-Leachates), and high concentration of *S. pulchra* leachates (H-SP-Leachates), with 5 replicates

leachates had no significant effects on seed germination but they did significantly reduce seedling biomass of all four species tested (Fig. 3). However, Loydi et al. (2015) found that while litter leachates of non-native species delayed and reduced seed germination of native species, they increased biomass per seedling of those seedlings that emerged. The negative effects of allelochemicals on seed germination seem to cease shortly after germination, suggesting other mechanisms such as competition for nutrients or light may be more important in influencing the germination and the early stages of seedling recruitment of those native species (Loydi et al. 2015). In our study, because there were no consistent differences between the effect of leachates of the invader *B. diandrus* compared to the native grass *S. pulchra*, it seems unlikely that allelopathy of *B. diandrus* alone is contributing to its successful invasion. In addition, our results show that seedling emergence of the invasive *C. melitensis* was significantly reduced by both *B. diandrus* and *S. pulchra* litter but not litter leachate (Fig. 2a) suggesting that this species is inhibited by the physical barrier created by litter rather than chemical qualities of the litter.

Litter effects on nutrient availability

Soil nutrient availability can influence plant invasions (Davis et al. 2000; Miki and Kondoh 2002; Chen et al. 2013). Litter from invasive plants has the potential to change nutrient cycling and to facilitate invasion (Ehrenfeld 2003; Farrer and Goldberg 2009). N immobilization during litter decomposition could contribute to the suppressant effect of litter quantity on seedling emergence and growth. Litter N immobilization presumably occurs during early stages of decomposition (e.g. the present study lasted 3–4 months), when litter N cannot meet the N requirements of microbial decomposers. The effect of litter cover on N immobilization should be much stronger with larger amounts of litter, as high moisture availability and low UV intensity under large amounts of litter favor microbial activity (Xiang et al. 2008; Lin et al. 2015). This is supported by our data showing soil NO_3^- decreased with increased litter quantity while litter quantity had no significant effects on soil NH_4^+ content, which was generally low (Fig. 5). Immobilization of NH_4^+ by microbes in litter treatments, should reduce the overall substrate available for nitrification thus the total mineral N measured goes down in with greater litter cover.

Species-specific N preferences may contribute to *B. diandrus* dominance and distribution in California oak woodlands (Aanderud and Bledsoe 2009). In the present study, the change of soil inorganic N pools caused by litter cover may influence seedling growth. The decreased available N resulting from litter cover (Fig. 5) may have negative effects on the growth of co-occurring species particularly those that prefer NO_3^- over NH_4^+. *Bromus diandrus* itself has been shown to prefer NH_4^+ over NO_3^- (Aanderud and Bledsoe 2009). The increased NH_4^+ we found in the *B. diandrus* litter leachates (Fig. 6b) may thus have positive effects on the growth of *B. diandrus*. These changes to soil inorganic N pools may alleviate some of the negative effects of litter on seedling growth of *B. diandrus*.

Litter and plant community dynamics

Ehrenfeld (2003) and others (Liao et al. 2008; Farrer and Goldberg 2009; Loydi et al. 2013; Molinari and D'Antonio 2014) have suggested that litter of invasive species can lead to positive feedbacks and ultimately the rise to dominance invaders and decline in native species in field settings. Alternatively, litter of an invader could facilitate other invaders and in that way lead to accelerated impacts of several invaders on native ecosystems (Simberloff and Von Holle 1999). However, our results showed that *B. diandrus* litter reduced its own biomass as well as the biomass of the other invasive species, *C. melitensis* (Fig. 2a and 2b), which does not support either a synergism among invaders, or a positive feedback by *B. diandrus* on itself. The lack of a positive litter-plant feedback was in contrast to a study by Molinari (2014) who found evidence for a positive feedback between *B. diandrus* and its litter in studies conducted in the field at Sedgwick Reserve. Her field study showed that moderate levels of *B. diandrus* litter facilitated its establishment and enhanced its seed production, a result also found by Mariotte et al. (2017) who studied another invasive annual grass, *Elymus caput-medusae*, invading grasslands in northern California. Both studies found that litter of these invaders reduced the diversity of native species and Molinari (2014) demonstrated that it was this litter and not direct competition, that was the primary cause for low native species presence in grasslands invaded by this species.

It is possible that the greenhouse conditions of the present study (stable temperature, humidity and constant irrigation) and pot structure (edges) may block air flow and reduce differences in soil moisture or N availability that may occur in the field. This interpretation is supported by our results that although litter cover increased soil moisture, there were no differences among the different levels of cover (e.g. *B. diandrus* litter quantity) in their influence on soil moisture (Fig. 4). In the field, the increase in soil moisture caused by litter cover may be more pronounced and thus important than in greenhouse. Furthermore, the greater wind movement, higher temperature and drier air in the field may cause plants to be subjected to more drought stress than those plants in greenhouse where soil moisture was rather high compared to typical values seen in California grasslands. Thus, favorable environmental conditions in the greenhouse could mask a positive feedback of *B. diandrus* litter. Loydi et al. (2013) found that the effects of litter differed between some field versus greenhouse studies.

The negative effect of *B. diandrus* litter on both *S. pulchra* and *C. melitensis* is consistent with the lower diversity associated with *B. diandrus* in the field. In contrast to *B. diandrus* litter, *S. pulchra* litter, while it reduced *C. melitensis* SEP similarly to *B. diandrus* litter, it did not affect growth of its seedlings. Thus, if *C. melitensis* seedlings get started near *S. pulchra* plants, their growth will not be impeded by its litter so *C. melitensis* may be more likely to invade *S. pulchra* grassland than *B. diandrus* grassland in the absence of soil disturbance. *Stipa pulchra* is the most commonly used native grass in California grassland restoration (Stromberg et al. 2007). Yet here it had the lowest germination (SEP) of all species and its growth was suppressed by *B. diandrus* litter and leachates. Seabloom (2011) demonstrated dramatic variation in *S. pulchra* emergence among years and sites in field settings in California and overall germination was low. If *B. diandrus* litter is present where *S. pulchra* is seeded or where seedlings are growing, our results suggest it has the potential to contribute to the poor performance of seedlings of this important grassland species. In addition, litter of *B. diandrus* decays slowly likely because of its high C to N ratio (85.97) and lignin to N ratio (6.66) (Lin and King 2014). This high persistence and legacy of thick litter offers a long time period for impacts and feedbacks to plant community development in California grasslands.

Conclusions

One of the many effects of non-native annual grass invasion into grasslands is the build-up of litter. The effects of litter on four common grassland species depended on growth form, monocot/dicot and seed size, and was less influenced by plant origin (invasive vs. native). In addition, physical effects of litter were greater to both seedling emergence and seedling growth, while chemical effects primarily affected root/shoot allocation. Poor *S. pulchra* recruitment and low presence in grasslands invaded by *B. diandrus* may be the result of low seedling emergence (limited viable seed) and reduced growth rather than the physical barrier created by *B. diandrus* litter. Our results can inform restoration by evaluating the response of native species and invasive species (e.g. based on growth form, monocot/dicot and seed size) to the thatch/litter of the non-native species *B. diandrus* and the native one *S. pulchra*.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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