

Responses of a California annual grassland to litter manipulation

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Abstract

Question: What are the physical and chemical effects of plant litter on annual grassland community composition, above-ground net primary production (ANPP), and density?

Location: California annual grassland.

Methods: We manipulated litter and light levels independently and in concert. Litter removal and litter addition treatments tested both the physical and chemical impacts of litter's presence. We additionally simulated the effect of litter physical shading by using shade cloth, and added powdered litter to test for the chemical impacts of decomposing litter.

Results: Increased whole litter and shading decreased grass germination and establishment, but not that of forbs or legumes. Species shifts occurred within all groups across treatments, including a transition from small-seeded to large-seeded grass and legume species with increased shading. ANPP was highest in control plots (473 ± 59 g/m²), and species richness was highest in litter removal plots. While the physical effects of litter via shading were significant, the chemical effects of adding powdered litter were negligible.

Conclusions: This work suggests that over one growing season, the physical impacts of litter are more important than chemical impacts in shaping community structure and ANPP in annual grasslands. Changes in light availability with altered litter inputs drive shifts in species and functional group composition. Litter feedbacks to ANPP and species composition of local patches may help maintain diversity and stabilize ANPP in this grassland.

Keywords: Annual forb; Annual grass; *Avena fatua*; Community composition; Legume; Patch dynamics; Seed size; Shading.

Nomenclature: Hickman (1993).

Abbreviations: ANPP = Above-ground net primary production; PAR = Photosynthetically active radiation.

Introduction

Plant litter affects community composition and ecosystem properties in many systems, including grass-dominated communities (Facelli & Pickett 1991a; Xiong & Nilsson 1999). However, research on litter impacts in grasslands has largely focused on prairies and old-fields, systems dominated by perennials. Annual grasslands are common, particularly in California, where non-native European annual grasses have largely replaced native perennial bunchgrasses. Litter dynamics in these systems are not well documented, but may become important if global changes alter the quality and quantity of litter production (Zavaleta et al. 2003; Henry et al. 2005).

Plant litter alters both the physical and chemical growth environments, and as a result affects germination, establishment, and plant growth. Shading by litter changes the soil microclimate by reducing the quantity and quality of light, increasing soil moisture, and reducing temperatures and temperature extremes (Knapp & Seastedt 1986; Facelli & Pickett 1991a; Jensen & Gutkunst 2003). Because seedling germination occurs as a result of temperature, light, and moisture cues, litter shading can have a significant effect on germination success and timing (Chiariello 1981; Lenz et al. 2003; Stinchcombe & Schmitt 2006). In California grasslands, light and temperature are the primary limiting factors to plant growth and establishment (Chiariello 1981). Chemically, litter decomposition can be a source of nutrients but also toxic chemicals, which can reduce germination rates (Dejong & Klinkhamer 1985). Though many studies manipulate and measure the physical effects of litter on the plant environment (Reynolds et al. 2001; Lenz et al. 2003), none study chemical impacts of natural levels of decomposing litter on grassland communities.

Litter impacts on germination and establishment result in shifts in community composition. Previous research on these effects in grass-dominated systems has revealed few consistent patterns (Heady 1956; Tilman 1993; Foster & Gross 1998; Xiong & Nilsson 1999; Boeken & Orenstein 2001; Lenz et al. 2003; Fynn et al. 2004). Often, species richness, germination, and establishment decline with the presence of litter (but see

Suding & Goldberg 1999; Boeken & Orenstein 2001), as litter can negatively affect germination of both forbs and grasses (Xiong & Nilsson 1999). As a result, significant but inconsistent shifts in community composition between grasses and forbs are often seen. Since few seeds survive more than one year in grassland seed banks (Young & Evans 1989), litter can affect seed longevity (Rotundo & Aguiar 2005), and plants growing from seed are more affected by litter than perennials growing from tillers or bulbs (Jensen & Gutekunst 2003), we expect litter impacts on community composition in a California annual grassland to be particularly significant.

Grassland above-ground net primary production (ANPP) is highly variable in response to litter manipulation. Medium levels of litter addition tend to have no or a slightly positive effect on total ANPP (Facelli & Pickett 1991a; Xiong & Nilsson 1999). Litter addition up to 3.5 × natural levels in an annual grassland increased plant ANPP (Heady 1956), although Carson & Peterson (1990) speculate that litter in such high amounts generally has the opposite effect. An ongoing global change experiment in a nearby California grassland found interannual year-to-year oscillations in litter biomass (Zavaleta et al. 2003), which potentially led to important community and ecosystem changes. Litter-induced oscillations have been postulated in perennial grasslands with and without annual weeds (Tilman & Wedin 1991; Bascompte & Rodriguez 2000; Haddad et al. 2002). Such cycles may be more likely in annual-dominated, nutrient-rich systems (Silvertown 1991).

We designed this study to evaluate how varying levels of litter alter community composition and ANPP in an annual grassland, and investigated seed size as a trait correlated with those alterations. By manipulating light availability and litter levels independently, we were able to determine the relative importance of physical and chemical effects of litter in this system. We also investigated the potential for oscillations in this annual grassland.

Methods

This study was conducted in San Mateo County, California at the Jasper Ridge Biological Preserve of Stanford University (37°24' N, 122°14' W, 150 m a.s.l.). The climate type is mediterranean, with hot, dry summers and cool, wet winters. The site is located on an east-facing hill in an annual climax grassland that is dominated by European annual grasses – *Avena fatua*, *Bromus hordeaceus*, *Lolium multiflorum* – which comprise ca. 80% of the total ANPP. Dominant forbs include *Geranium dissectum*, *Vicia sativa*, *Crepis vesicaria*, and *Erodium botrys* (all non-native) and *Hemizonia congesta* (native). We designated four functional groups based on

phylogenetic history (grasses), life history (annual forbs, biennial forbs (*Crepis vesicaria*)), and nitrogen (N)-fixing potential, as this site is demonstrably N-limited (legumes *Vicia sativa*, *Medicago polymorpha*) (Shaw et al. 2002). The site is unmanaged, though lightly grazed by deer and occasionally disturbed by gophers.

Experimental design

In mid-October 2002, before the start of winter rains, we established 35 square 0.25 m² plots in six parallel rows with a 0.5 m buffer between each plot. Five separate treatments were applied randomly to the plots: control, litter removal, whole litter addition, powdered litter addition, and shade cloth. The powdered litter addition treatment was designed to test the effect of an increase in the chemical impacts of litter on an annual grassland without added physical effects. The shade cloth treatment was designed to increase the most significant physical effect of litter (shading) without adding additional nutrients.

The control plots were left unaltered. In the litter removal plots, all plant material and litter was clipped to the soil surface and removed, exposing bare ground. The average mass of senescent material taken from the removal plots was 398 g/m². We added 100 g of that material, supplemented with additional unmodified litter collected nearby, to each of the whole litter addition treatment plots in a manner simulating natural litter patterns. We additionally ground litter in a Cyclotec 1093 Sample Mill, weighed out 100 g for each powdered litter addition plot, and applied it evenly on the soil surface under existing litter. In the shade cloth treatments, two layers of 75% shade cloth were suspended above each plot so that flaps hung down to the litter layer. Small slits were cut in both layers of shade cloth to prevent water obstruction. The top layer of shade cloth was removed in mid-January 2003 in order to roughly mimic the natural decomposition of litter.

Environmental measurements

To determine light penetration, we measured percent photosynthetically active radiation (PAR) above the canopy and at ground level with a Sunfleck Ceptometer (Decagon Devices) in temporary treatment replicates which were created in the area surrounding the experimental plots.

To evaluate the relative effect of treatments on soil temperature, measurements were taken with a soil probe thermometer on a day mid-growing season. Three measurements were taken at 10 cm depth in each plot.

Vegetation harvests

The first harvest was collected in mid-December, 2002, two weeks after initial germination. Two 6 cm × 6 cm subplots were chosen randomly from the treated plots. Both subplots were harvested to the soil surface and any plant rooted in the harvest square was taken. As it was impossible to identify species identity, plants were sorted to functional group and counted. Removed biomass was returned to the subplot to minimize disturbance.

A second similar harvest was conducted in early May 2003, close to peak biomass. One 12 cm × 12 cm subplot was located in a community-representative, previously un-harvested area of the treated plots. Litter, perennial plants, and plants with vine-like growth tendencies (*Vicia sativa*, *Crepis vesicaria*) were clipped so that only biomass within the subplot was taken, regardless of where the individual was rooted. We separated litter from the new ANPP that had accumulated during the study period, and then sorted the harvested shoots by species and counted numbers of individuals (forbs) or tillers (grasses). Samples were dried at 70 °C and weighed.

Average seed masses for the most common grass and forb species in our plots were calculated by weighing sets of ten seeds from a previous common garden experiment (*Avena fatua*, *Avena barbata*, *Bromus hordeaceus*, *Lolium multiflorum*, *Vulpia myuros*), control plots in this experiment (*Bromus diandrus*), or from a common collection site near treatment plots (*Erodium botrys*, *Medicago polymorpha*, *Vicia sativa*, *Geranium dissectum*, *Hemizonia congesta*). Further analyses were performed on *Avena fatua*, the dominant grass species. We removed all *Avena fatua* seeds from litter removal, control, and shade cloth treatments and weighed sets of ten seeds. Shoot material was ground on a Wiley Mill (size 40 mesh). Total carbon and nitrogen content were determined on an elemental analyser (Carlo Erba model NA 1500, Carlo Erba, Milan, Italy).

We defined establishment as the proportion of individuals or tillers surviving from the December to May harvests on an individuals/area basis. Each grass tiller was counted as an individual, as we could not determine if treatments affected tiller production (which is often low). Tiller mass in a treatment was calculated as species biomass divided by the number of plant tillers.

Data analysis

All analyses were done with the statistical software package JMP 4.0 (SAS Inc.). Species richness (S) and Simpson's indices of diversity (D) and evenness (E) were calculated for each plot. Diversity (D) = $1/(\sum p_i^2)$, where p_i is the proportion of the i th species. Evenness (E) = D/S . Tukey's Honestly Significant Difference Test was used for multiple comparisons and Student's t -test for paired comparisons. Statistics were performed on log-transformed data (biomass, number) or arcsine-square root transformed data (proportions).

Results

Pre-treatment standing dead biomass reduced PAR by $90.7 \pm 1.6\%$ (Table 1); litter addition and shade cloth light reduction were significantly different from each other and from the control. Soil temperature was significantly reduced by the presence of litter and shade cloth (Table 1). Added powdered litter had disappeared by December harvest, and at the beginning of May, control, powdered litter addition, and shade cloth treatments did not differ significantly in the amount of whole litter left on the plots (ca. 200 g/m²). Litter addition plots (400 g/m²) had significantly higher litter levels (Table 1). Half of the senescent material initially on the plots, regardless of treatment, had decomposed by the May harvest.

Powdered litter addition did not significantly affect germination, survival, or any community measure at the end of the growing season. Because the chemical effects of litter were not significant, physical (shading) effects became our primary interest; litter manipulation and shade cloth treatments thus affected community and ecosystem dynamics through the same mechanism.

Germination and establishment

Total germination peaked at $9.3 \pm 1.0 \times 10^3$ individuals/m² in control plots, and was minimal at $3.8 \pm 0.4 \times 10^3$ individuals/m² in shade cloth plots (Table 2). Germination was highest in all control plots for all four functional groups. Litter removal did not significantly affect germination, but shading above control levels decreased total germination and grass germination significantly. Annual forb and legume germination also

Table 1. Effects of treatments on photosynthetically active radiation (PAR), soil temperature mid-May, and final litter biomass (mean ± SE). Different letters indicate significant differences at $\alpha = 0.05$.

	Litter removal	Control	Powdered litter addition	Litter addition	Shade cloth
% Reduced PAR	0	90.7 ± 1.6 ^a	90.7 ± 1.6 ^a	97.2 ± 0.7 ^b	99.5 ± 0.1 ^c
Soil Temp (°C)	13.9 ± 0.05 ^a	13.2 ± 0.08 ^b	13.1 ± 0.06 ^b	12.8 ± 0.09 ^c	12.3 ± 0.02 ^d
May litter (g/m ²)	0	205.7 ± 20.6 ^a	187.1 ± 20.1 ^a	411.2 ± 55.4 ^b	219.2 ± 17.7 ^a

Table 2. Effects of treatments on total, grass, annual forb, biennial forb, and legume ANPP and density at first (Germination - December) and second (May) harvests (mean \pm S.E.). Different letters indicate significant differences between treatments at $\alpha = 0.05$.

	Litter removal	Control	Litter addition	Shade cloth
Germination (no./m²)				
Total	8,690 \pm 1,026 ^{ab}	9,256 \pm 897 ^a	6,062 \pm 409 ^b	3,819 \pm 449 ^c
Grass	7,827 \pm 976 ^a	8,115 \pm 675 ^a	5,605 \pm 396 ^a	3,304 \pm 450 ^b
Annual Forb	685 \pm 85 ^a	734 \pm 192 ^a	337 \pm 61 ^a	377 \pm 56 ^a
Legume	179 \pm 66 ^a	376 \pm 170 ^a	119 \pm 47 ^a	119 \pm 45 ^a
May Density (no./m²)				
Total	13,294 \pm 1,597 ^a	11,885 \pm 1,750 ^a	4,931 \pm 439 ^b	1,944 \pm 238 ^b
Grass	11,925 \pm 1,509 ^a	11,091 \pm 1,781 ^a	4,444 \pm 1,163 ^b	1,478 \pm 207 ^c
Annual Forb	804 \pm 195 ^a	764 \pm 80 ^a	486 \pm 119 ^a	466 \pm 88 ^a
May ANPP (g/m²)				
Total	338 \pm 24 ^{ab}	474 \pm 59 ^a	392 \pm 43 ^{ab}	257 \pm 35 ^b
Grass	250 \pm 26 ^a	369 \pm 51 ^a	294 \pm 35 ^a	148 \pm 39 ^b
Annual forb	36 \pm 8 ^a	32 \pm 7 ^a	28 \pm 9 ^a	21 \pm 4 ^a
Biennial forb	6 \pm 2 ^{ab}	12 \pm 4 ^a	3 \pm 2 ^b	40 \pm 15 ^{ab}
Legume	19 \pm 8 ^a	20 \pm 6 ^a	27 \pm 6 ^a	27 \pm 6 ^a

showed a tendency, though non-significant, to decrease with increased shade.

Across all treatments, 26.6 \pm 2.9% of grass plants established on average, compared to 44.0 \pm 5.6% of annual forbs ($P < 0.01$). The proportion of grass individuals surviving from December to May decreased with increased shade from 41.0 \pm 6.3% in the bare plots to 13.4 \pm 3.7% in the shade cloth plots ($P < 0.05$) (Fig. 1), while forb establishment was unaffected by treatment. Forb establishment was significantly greater than grass establishment in litter addition and shade cloth plots ($P < 0.05$).

Density and ANPP

Total (grass + forb) density in May peaked at 13.3 \pm 1.610³ individuals/m² in bare plots and was lowest at 1.9 \pm 0.210³ individuals/m² in shaded plots (Table 2). ANPP had a unimodal shape, with peak ANPP in control plots, a trend toward a decline at lower shade levels, and a significant decline at higher shade levels (Table 2, Fig. 5).

Peak grass density occurred in bare plots and peak

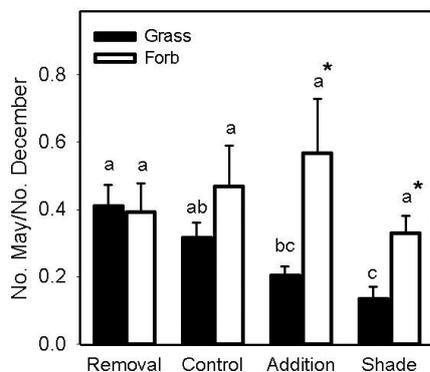


Fig. 1. Effects of treatments on grass and forb establishment (mean \pm SE) in response to treatments. Letters indicate significant differences between treatments at $\alpha = 0.05$; * indicates significant differences between functional groups at $\alpha = 0.05$.

ANPP in control plots. The average mass of grass tillers increased significantly with shading ($P < 0.02$, not shown). Six dominant grass species in the plots range in average seed mass from 0.92 mg (*Vulpia myuros*) to 22.3 mg (*Avena fatua*). Based on seed size, the dominant grass species fell into two distinct categories, which we used in further analyses: large-seeded species (*Avena fatua*, *Avena barbata*, *Bromus diandrus*) with seed mass averaging 16.5 \pm 3.1 mg, and small-seeded species (*Bromus hordeaceus*, *Lolium multiflorum*, *Vulpia myuros*) with seeds averaging 1.8 \pm 0.6 mg. Large and small-seeded species also differed in tiller mass (170.1 \pm 42.4 mg vs. 14.2 \pm 4.3 mg, respectively). Large-seeded grass species had peak absolute ANPP in litter addition plots, whereas small-seeded grass species dominated litter removal plots. With increased shade, large-seeded grass species increased in their proportion of grass ANPP from a low of 29.6 \pm 7.2% (litter removal) to a high of 93.0 \pm 2.6% (shade cloth) (Fig. 2).

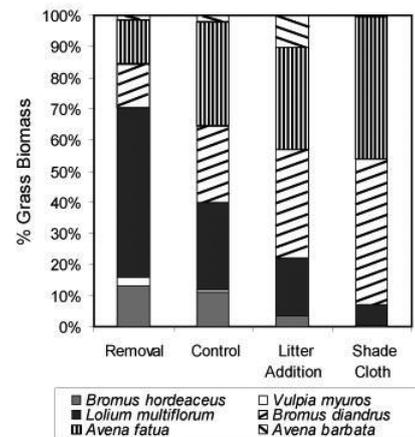


Fig. 2. Treatment effects on grass ANPP species composition for six dominant species at peak biomass. Line-fills are 'large-seeded' species; solid fills are 'small-seeded' species.

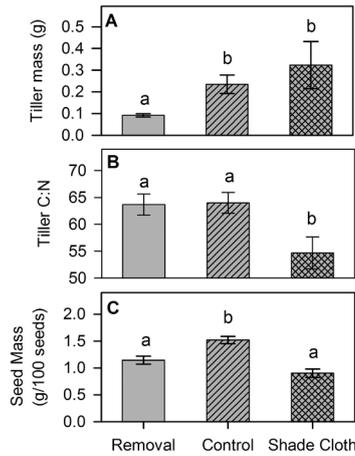


Fig. 3. *Avena fatua* tiller and seed responses to three treatments, mean \pm SE. **A.** Tiller mass (g) **B.** Tiller carbon:nitrogen ratio; **C.** Seed mass (g/100 seeds)

Average mass of *Avena fatua* tillers was significantly lower in litter removal plots (Fig. 3A). Under shade cloth, non-reproductive plant parts appeared flimsy, and contained significantly lower % C and higher % N in shade cloth plots as compared to controls. As a result, *A. fatua* grown under shade cloth had a carbon:nitrogen (C:N) ratio of 54.7 ± 3.0 whereas control C:N was 64.0 ± 2.0 (Fig. 3B). Additionally, *A. fatua* grown under control conditions had significantly heavier seeds (1.5 ± 0.1 g/100 seeds) than *A. fatua* grown in litter removal (1.1 ± 0.1) or shade cloth (0.9 ± 0.1) treatments (Fig. 3C).

Annual forb ANPP did not change significantly across treatments (Table 2), although there was a trend towards a decrease in annual forb density with shading. *Geranium dissectum* ANPP dominated, and its proportion of annual forb ANPP increased from $46.0 \pm 0.1\%$ in litter removal plots to $100 \pm 0\%$ in shade cloth plots (Fig. 4). Neither *G. dissectum* ANPP or density responded to treatment, although tiller mass trended toward an increase with shading ($P < 0.10$). *Hemizonia congesta* seeds were significantly smaller than those of *G. dissectum* ($P < 0.01$) and both were smaller than those of *Erodium botrys* ($P < 0.0001$). Biennial forb (*Crepis vesicaria*) ANPP was significantly higher ($P < 0.0001$) in shade cloth plots when compared to other treatments (Table 2).

Total legume ANPP did not significantly change with treatments (Table 2) but the proportion of legume ANPP that was *Medicago polymorpha* declined significantly with the presence of litter on the plots ($P < 0.02$, Fig. 4). No *M. polymorpha* was sampled in litter addition or shade cloth treatments. *Vicia sativa* seeds were significantly larger than those of *M. polymorpha* ($P < 0.0001$).

Species richness declined with increased shading ($P < 0.001$). However, Simpson species diversity increased linearly with shading ($P < 0.05$), as did species evenness

($P < 0.05$). Functional group diversity as calculated by Simpson's Index was lowest at control litter levels and highest in shade cloth plots ($P < 0.05$), where functional group evenness was also highest. Overall, grasses decreased in relative proportion of ANPP with increased shade, and legumes and forbs increased (Fig. 5).

Discussion

Powdered litter addition

The addition of powdered litter had no significant effects on community ANPP or composition. The influx of extra nutrients entering the system from accumulated litter may have been too small to cause increased growth in the first year. Over 80% of the litter was grass biomass, which is nutrient-poor in comparison to dicots (Cornelissen & Thompson 1997), after the retranslocation of nutrients into seeds leads to high C:N ratios (Franck et al. 1997). This experiment added only about 2 g/m^2 of N in litter whereas a previous experiment in this grassland found significant effects of 7 g/m^2 added inorganic N (Dukes et al. 2005). Net mineralization during decomposition may have been delayed until too late in the growing season to have had a measurable effect. Xiong et al. (2001) postulated a similar time-lapse mechanism for the non-significant effects of their low-level powdered litter treatment on riparian vegetation.

Shifts in community composition

Shifts in grass species composition likely started at germination. Small-seeded species germinate earliest in high-light environments, allowing resource (nutrients, water, and light) pre-emption and perhaps competitive exclusion of large-seeded grass species (Fowler 1984, 1988; Dyer et al. 2000). As a result, the small-seeded *Lolium multiflorum*, *Bromus hordeaceus* and *Vulpia myuros* were robust and

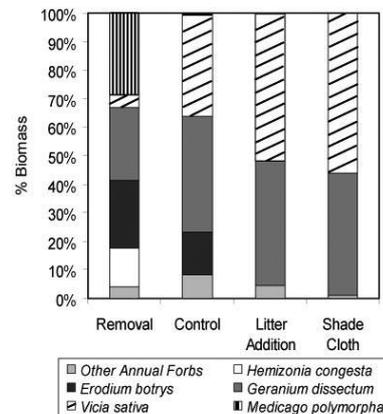


Fig. 4. Treatment effects on legume and forb ANPP species composition at peak biomass. Line-fills are legume species; solid-fills are annual forbs.

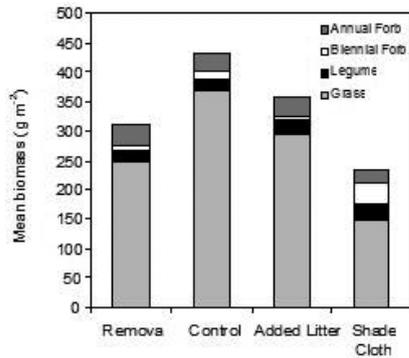


Fig. 5. Treatment effects on average ANPP (total and that of four functional groups) at peak biomass.

common in litter removal plots, whereas the large-seeded *Avena fatua* was small with smaller seeds. Even in the absence of competition from small-seeded grasses, *Avena fatua* and other large grasses may have performed poorly in litter removal plots due to increased heat and decreased water availability in that environment.

Since small-seeded species have a higher light requirement for germination, their emergence was negatively affected by reductions in light quantity under higher shade treatments, as seen in previous work (Gross 1984; Jensen & Gutekunst 2003; Eckstein & Donath 2005; Kostel-Hughes et al. 2005). In plots with heavier shade, large-seeded grasses likely germinated more successfully and had greater initial resources for growth, allowing establishment and resource pre-emption (Carson & Peterson 1990; Facelli & Pickett 1991a). Grasses were both larger and taller under heavier litter treatments in another California annual grassland (Heady 1956). However, large tiller mass under heavy shade might also be a result of plants bolting to reach light. The flimsy appearance of *A. fatua* in concert with a reduction in C:N under shade cloth implies less carbon invested in structural carbon compounds. The smaller seed mass of *A. fatua* under shade may have been due to a lack of available nutrient resources as plants attempted to outgrow their heavily shaded environments. Previous work in tallgrass prairie has shown decreases in specific leaf mass, leaf thickness, and structural tissue in shaded plants (Knapp & Gilliam 1985).

The decline in overall species richness with increased shading was due in large part to the reduced presence of small-seeded grass species. In addition, many forb species were found only in litter removal and control plots. *Hemizonia congesta* only germinated in high-light plots, consistent with previous research (Chiariello 1981), and with its small seed size compared to other resident forbs. The loss of other forb species from the community with increased shade (e.g. *H. congesta*, *Erodium botrys*, *Anagallis arvensis*) resulted in *Geranium dissectum* increasing in dominance. In a similar annual grassland all forb species except the most common (*E. botrys*) exhibited significant reductions in ANPP with

increasing litter, resulting in an increase of dominance of that species (Heady 1956).

Although legume ANPP was constant across treatments, species replacement did occur. Variation in the environmental tolerances of *Medicago polymorpha* and *Vicia sativa* resulted in a shift in dominance from *M. polymorpha* in litter removal plots to *V. sativa* in control plots, and the loss of *M. polymorpha* from plots with added litter and shade cloth. *Medicago polymorpha* is a weedy, mat-forming clover which is often found in disturbed, sunny areas, whereas *Vicia sativa* may germinate but fails to establish in high temperature, low water potential environments (Wagner & Spira 1994; Saoub 2003). *Vicia sativa* seeds are significantly larger than those of *M. polymorpha*; therefore, mechanisms similar to those that drive changes in grass species composition with increased shade may be driving that of legumes. Despite constant ANPP, shifts in nitrogen-fixing species can be important in an ecosystem context if they result in changes in nitrogen-fixation potential. Agricultural research investigating crop yield with rotations of *M. polymorpha* and *V. sativa* demonstrated that *M. polymorpha* rotations resulted in higher crop yields, perhaps mediated through higher inputs of nitrogen into the ecosystem (Fischer et al. 2002).

In contrast to species richness, species- and functional diversity increased with increased shading; with increased shading, the density that remained was more evenly distributed across the surviving species and functional groups. Although legume and annual forb ANPP were not significantly affected by shade, the relative contribution of these groups to overall ANPP increased. Sydes & Grime (1981b) found a similar trend in the understory of a forest, where litter released the community from grass dominance and increased overall diversity. In addition, the ANPP of the biennial forb species *Crepis vesicaria* was significantly higher in shade cloth plots. Potentially, *C. vesicaria* was an exceptional competitor where light levels were reduced by 99.5%; however, the shade cloth may also have protected the forb from herbivory by deer.

ANPP and density dynamics

A decrease in plant ANPP with the removal of all litter is consistent with previous work in many systems (Heady 1956; Xiong & Nilsson 1999; Boeken & Orenstein 2001; Lenz et al. 2003). However, most studies do not show such a strong decrease in overall ANPP at high (above control) litter levels – possibly because annual grasses are more significantly impacted by litter than the perennial grasses which dominate other investigated systems (Monk & Gabrielson 1985). Perennials have different patterns of allocation and response directions than annual grasses (Jackson & Roy 1986), which could change the magnitude and direction of results relative to annual forbs. The unimodal trend in ANPP seen in our results differs from the monotonic increase in ANPP observed at up to 1380 g/m² of litter in another

California annual grassland (Heady 1956). Grass made up less than 40% of the ANPP in that location, whereas Jasper Ridge grasslands are over 80% grass – and litter impacts on overall ANPP were driven primarily by grasses. Annual grasses appear to be more susceptible to litter than forbs – here negatively, but in another experiment, annual grasses responded positively to litter where the community as a whole did not (Lenz et al. 2003).

Shade cloth does not mimic the natural patchiness of senescent material in grasslands. Reductions in spatial variability potentially led to heteroskedasticity of the data; variance under shade cloth treatments was often lower than that of control and litter addition treatments. Spatial variability caused by litter is an important characteristic of grasslands, as it provides for increased diversity through microsite variation (Sydes & Grime 1981a; Monk & Gabrielson 1985; Fowler 1988; Bascompte & Rodriguez 2000). Boeken and Orenstein (2001) investigated between-generation responses in an annual grassland system in patches of similar size to this study; they found that spatial patterning of senescent grass from one year was critical for species distributions and survival in the next. In our system, areas of low-litter input are particularly important for persistence of species in most functional groups. Although the litter-ANPP relationship in this annual grassland is not strong enough to support large (ecosystem-scale) ANPP oscillations postulated by some workers, small-scale (patch level) oscillations likely occur and stabilize grassland ANPP. Many of the external disturbances that occur in this grassland which affect the plant growth environment (such as insect and mammal disturbances) occur at small scales on the order of our 0.25-m² plots and 100-cm² sampling areas. Past research has demonstrated that the natural variability in grassland ANPP can lead to localized patches of grassland with high levels of plant material (up to 1900 g/m² ANPP, unpublished data). Intense shade provided by the resulting high litter levels will reduce subsequent above-ground production, increase average litter quality through shifts in species composition, and potentially decrease structural carbon and lower C:N ratios. As a result, smaller amounts of more decomposable litter will be produced, moving the patch back towards control levels of standing ANPP. Although not addressed here, litter-induced mechanical barriers to seed dispersal and plant growth could also significantly contribute to patch-level multigenerational oscillations in ANPP.

Conclusions

Over one growing season in an annual grassland, we found that physical impacts of litter shaped community structure and ANPP, but chemical impacts of litter did not. Changes in light availability associated with litter inputs drove shifts in species and functional group composition. Annual grasses may be particularly sensitive to the effects of plant litter. Our results suggest that spatial

variability in the plant growth environment, caused by disturbance-produced bare ground and natural variation in the litter layer, is critical for the maintenance of diversity and overall stability of ANPP in this grassland. Shifts in the amount of litter present in an ecosystem have the potential to feed back to future years' community composition and ecosystem structure and function.

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