RESEARCH ARTICLE

Do Tree Canopies Enhance Perennial Grass Restoration in California Oak Savannas?

Karen A. Stahlheber[1,2] and Carla M. D'Antonio[1]

Abstract

Scattered trees in grass-dominated ecosystems often act as islands of fertility with important influences on community structure. Despite the potential for these islands to be useful in restoring degraded rangelands, they can also serve as sites for the establishment of fast growing non-native species. In California oak savannas, native perennial grasses are rare beneath isolated oaks and non-native annual grasses dominate. To understand the mechanisms generating this pattern, and the potential for restoration of native grasses under oaks, we asked: what are the effects of the tree understory environment, the abundance of a dominant non-native annual grass (*Bromus diandrus*), and soils beneath the trees on survival, growth, and reproduction of native perennial grass seedlings? We found oak canopies had a strong positive effect on survival of *Stipa pulchra* and *Poa secunda*. Growth and reproduction was enhanced by the canopy for *Poa* but negatively impacted for *Stipa*. We also found that *Bromus* suppressed growth and reproduction in *Stipa* and *Poa*, although less so for *Stipa*. These results suggest the oak understory may enhance survival of restored native perennial grass seedlings. The presence of exotic grasses can also suppress growth of native grasses, although only weakly for *Stipa*. The current limitation of native grasses to outside the canopy edge is potentially the result of interference from annual grasses under oaks, especially for short-statured grasses like *Poa*. Therefore, control of non-native annual grasses under tree canopies will enhance the establishment of *S. pulchra* and *P. secunda* when planted in California oak savannas.

Key words: *Bromus diandrus*, California grassland, canopy effect, facilitation, interference, oak savanna restoration, *Poa secunda*, *Quercus*, *Stipa pulchra*.

Introduction

Recent restoration efforts in degraded rangelands, pastures, and savannas have utilized trees or shrubs as nuclei for restoration efforts (Zhao et al. 2007; King & Stanton 2008; Pueyo et al. 2009) because of the increased resources associated with their surroundings (Belsky et al. 1989; Scholes & Archer 1997). This may be particularly important in arid or semi-arid regions where the inter-tree environment can be harsh (Call & Roundy 1991). Providing less stressful microclimates for establishment of desired seedlings can enhance restoration success in habitats where plant survival is low or unpredictable (Padilla & Pugnaire 2006; Gómez-Aparicio 2009). The association between high resource patches with non-native species (Maron & Connors 1996) or the attraction of animal dispersers of non-native species to trees (Milton et al. 2007), however, can create "islands of invasion." Preferential restoration of tree understories may therefore offer several benefits, including increased survival of target native plants and reduction of non-natives in otherwise highly invaded patches. Despite this, the mechanisms that control distributions of herbaceous plants relative to trees are rarely tested experimentally.

Oak savannas are broadly distributed across California as part of a gradient from open grassland to oak woodland habitat and contain both evergreen and deciduous trees (Allen-Diaz et al. 2007). Oaks within these savannas enhance nutrients (Frost & Edinger 1991; Dahlgren et al. 1997), alter water availability via hydraulic redistribution (Ishikawa & Bledsoe 2000), and provide essential habitat for many wildlife species (Avery & Vanriper 1989). Across the region, evergreen and deciduous oak canopies have similar, strong influences on understory composition despite differences in their environmental effects (Parker & Muller 1982; McClaran & Bartolome 1989; Marañón & Bartolome 1994). Comparable effects of many species of oak trees on the environment and surrounding composition have been documented in numerous Mediterranean climates (Marañón et al. 2009). In California, oak savannas have been invaded by winter annual grasses from the Mediterranean Basin, which now make up the dominant portion of the vegetation (Bartolome et al. 2007). The oak understory environment in particular is highly favorable for the non-native grass *Bromus diandrus* (Marañón & Bartolome 1989; Marañón & Bartolome 1993; Rice & Nagy 2000).

[1]Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106, U.S.A.
[2]Address correspondence to K. A. Stahlheber, email stahlheber@lifesci.ucsb.edu

Where historical disturbances have occurred, native perennial grasses are rare beneath isolated savanna oaks, even when they occur in adjacent open grassland (Stromberg & Griffin 1996; Stahlheber 2013). Despite likely variation in their former importance (Bartolome & Gemmill 1981; Hamilton 1997; Bartolome et al. 2007), today perennial grasses are an important component of restoration efforts throughout California (Stromberg et al. 2007). Understanding how to best enhance their persistence in highly invaded communities is important for guiding restoration success. Additionally, given the general paucity of native species in the understory of most isolated trees, the target community for a 'restored savanna understory' is unclear. In particular, little is known about the mechanisms responsible for the current limitation of native perennial grasses to open habitats within many savannas, or about which native perennial grasses might be viable restoration options for the oak understory. Likewise the role the current abundance of exotic grasses plays in limiting establishment of perennial grasses under oaks needs further clarification. This study therefore addresses questions of applied interest as well as the broader question of how savanna trees influence coexistence of species within a savanna matrix, which will be relevant in many Mediterranean-climate and semi-arid savannas.

In this article, we describe the performance of experimentally planted native perennial grass seedlings under canopies of the deciduous oak *Quercus lobata* and in adjacent open grassland with and without competition from the aggressive, non-native annual grass, *B. diandrus*. We ask: How do trees influence the survival, growth, and reproduction of native perennial grasses? In particular, we tested the individual and interactive effects of (1) oak canopy presence, (2) levels of competition with a non-native annual grass, and (3) soil origin (oak nutrient enrichment vs. not) on the survival, growth, and reproduction of two planted, native, perennial grass species: *Stipa pulchra* and *Poa secunda*. The two species were chosen because they are both assumed to have been more abundant in California prior to the last century of intensive land use, both are widely distributed and of interest to restoration practitioners, yet they differ from each other in phenology and allocation in ways that we would expect to influence their performance. Although with only two species we cannot determine which exact characteristics are responsible for potential performance differences, this study can provide guidance on whether or not these trait differences do affect responses to trees and annual grasses.

We hypothesized that increased moisture beneath savanna trees during the dry season (Parker & Muller 1982; Ishikawa & Bledsoe 2000) would enhance native grass seedling survival in shade, although growth and reproduction responses would depend on the degree of shading (Holmgren et al. 2012). We also hypothesized that high density exotic annual grasses would be detrimental for both natives. Lastly, resource-rich soils derived from beneath oaks may increase growth and reproduction. The net effect of interactions with annuals may also vary among canopy and soil treatments. For example, high nutrients in oak soils may increase growth of the non-native annual grass more so than the perennial grasses.

Methods

Study Site

This study was conducted at Sedgwick Ranch (34°41′N, 120°2′W), a 2,388 ha. ecological reserve located near Santa Ynez, California. The site's Mediterranean climate is characterized by hot, dry summers and cool, wet winters with a mean annual precipitation of 380 mm. Inter-annual variation in rainfall is considerable: Precipitation for the water years 2008–2009, 2009–2010, and 2010–2011 (from September 1 to August 31) was 332, 540, and 669 mm, respectively. This site is on the drier end of the distribution for the deciduous oaks, although evergreen oaks occur further south (Allen-Diaz et al. 2007).

Experimental plots were established at two sites with oak savanna plant communities, consisting of isolated *Quercus lobata* Nee, *Quercus agrifolia* Nee and *Quercus douglasii* Hook. & Arn. within a matrix of annual grassland dominated by *Bromus diandrus* Roth. and *Avena barbata* Link. The first site, "Figueroa," is a wide, gently sloping canyon with deep, well-drained alluvial soils in the Salinas series (fine-loamy, mixed, superactive, thermic Pachic Haploxerolls) (Shipman 1972). Prior land uses included livestock grazing and cultivation for hay. The second site, "Mesa," is a level uplifted Pleistocene terrace with sandy loam soils in the Positas series (fine, smectitic, thermic Mollic Palexeralfs) (Shipman 1972). Livestock grazing has been the predominant land use for at least the past century, with no evidence of plowing or cultivation (Tyler et al. 2008).

Study Species

The two native perennial grasses that were the focus of this study were *Stipa pulchra* Hitchc. (*Nassella pulchra* [Hitchc.] Barkworth) and *P. secunda* J. Presl. The former is a caespitose, non-rhizomatous perennial grass sometimes cited as the former dominant in coastal California grasslands, (but see Bartolome & Gemmill 1981; Bartolome et al. 1986; Hamilton 1997). *Poa secunda* is also an extremely widespread, native, densely caespitose, non-rhizomatous perennial grass (Soreng 2007) commercially available to restoration practitioners. It may have been a very common component of more arid regions of the California grassland prior to disturbance and invasion (Bartolome et al. 2007).

In addition to differing in persistence of aboveground tissue (*Poa* aboveground tissue dies completely in the summer), these taxa differ in their size at maturity with *Poa* typically smaller-statured (culms 15–120 cm; Soreng 2007) than *Stipa* at Sedgwick Reserve (culms 35–100 cm; Jackson and Roy 1986; Barkworth 2007). They also differ in reproductive timing: at Sedgwick Reserve *Poa* completes its seed production before the annual grasses have fully set seed (early April) while *Stipa* can maintain seed production into the summer, particularly if rain occurs in April or May. As a result, we anticipated that *Poa* and *Stipa* would respond differently to interactions with the non-native, winter annual grass *B. diandrus* Roth.

Transplant Experiment Methods

Within each site, we selected five ungrazed replicate locations and established paired *Q. lobata* understory and open grassland 2.5×2.5 m plots. Homogenized soils that had been removed from each site were used in planting grass seedlings within holes 15 cm wide and 30 cm in depth (Appendix S1, Supporting Information). Half of the planting holes in each plot were filled with homogenized oak soil, and the other half with homogenized open grassland soils. Within each soil type, half were planted with *Poa* or *Stipa*, using two individuals in each hole. Either no *Bromus* seeds, 6 seeds (low density) or 30 seeds (high density) were added to each hole. These treatments were assigned randomly to each hole within a plot. All non-*Bromus* weeds were removed, and low density and no *Bromus* holes were weeded of *Bromus* periodically. Low density plots were maintained at approximately 20% cover in both habitats to represent a less labor-intensive management effort than total removal of *B. diandrus*. High density plots were left unweeded, and seeding densities were representative of seed rain in nearby open grasslands (Molinari, unpublished data).

Plants were monitored bimonthly from March 2009 until July 2011. We measured diameter at the base of each plant using calipers, along with the presence or absence of flowering stalks. In 2009 and 2010, when seeds on a plant were ripe, flowering stalks were cut and the number of glumes counted for each plant. In 2011, at peak flowering season (May for *Poa* and July for *Stipa*) we harvested all above ground biomass for each plant and weighed them, separating vegetative and reproductive parts, after drying at approximately 50°C for 1 week.

Environmental Characterization

We collected soil samples from the two sites for characterization in the lab. Figueroa soil samples came directly from the soils used in planting treatments but for the Mesa site we used data from another study that included the same locations (Stahlheber 2013). Soil moisture and light availability (photosynthetically active radiation [PAR]) data were collected in March of 2011 (Appendix S1).

Data Analysis

We compared soil properties and ambient light between habitats using *t* tests. Soil moisture, percent of ambient PAR, and plant biomass were compared between treatments using fully factorial standard least square (SLS) linear models in JMP 9.0 (©2010 SAS Institute Inc., Cary, NC, U.S.A.); Appendix S1). In addition to the treatments and interactions, we also added a term to each SLS model for the number of surviving plants (of the original two) within each hole to account for any effects of intraspecific competition. Post-hoc Tukey honest significant difference (HSD) tests were used to differentiate between treatment levels where necessary.

To analyze the effects of the treatments on transplanted perennial grass seedling survival, we used regression tree analysis to recursively partition proportional survival into homogenous groups (De'ath & Fabricius 2000). Survival was calculated at the plot level as the proportion of original transplants remaining alive within each treatment combination in November 2009 and 2010, and at final harvest in 2011. Best models were selected by 10-fold cross-validation using the *rpart* package for R (Therneau et al. 2012).

Results

Environmental Conditions

Soils differed between the sites and habitats (Table 1). At both sites, soil carbon and nitrogen were higher in soils collected beneath oaks, although the C:N ratio only differed between habitats at Mesa. Electroconductivity and water holding capacity were also consistently higher under the trees. Soil moisture values (March 2011) were typically higher under oaks (21.2%) compared with open grassland (17.6%) ($F_{[1,210]} = 95.43$, $p < 0.01$). This was mostly driven by the large difference between understory and open grassland habitats at Figueroa (23.0 and 16.6%) rather than the Mesa where mean soil moisture was not significantly different between habitats (19.6 and 18.6%) ($F_{[1,210]} = 54.71$, $p < 0.01$). Other treatments did not affect soil moisture.

Table 1. Differences between soil properties under trees and in open grassland at each site, compared using *t*-tests allowing unequal variances between groups.

Site	Soil Property	Oak Mean ± SE	Open Mean ± SE	t	p
Figueroa	pH	6.29 ± 0.20	6.51 ± 0.09	1.02	0.39
	Electroconductivity (μs/cm)	124.3 ± 5.5	62.0 ± 2.9	-10.1	<0.01
	Total % carbon	1.810 ± 0.039	1.420 ± 0.026	-8.279	<0.001
	Total % nitrogen	0.181 ± 0.002	0.148 ± 0.005	-5.442	0.006
	C:N ratio	10.007 ± 0.290	9.600 ± 0.187	-1.170	0.293
	Water holding capacity (%)	56	50		
Mesa	pH	5.36 ± 0.16	4.38 ± 0.10	5.30	<0.01
	Electroconductivity (μs/cm)	388.7 ± 50.4	125.1 ± 26.9	4.6	<0.01
	Total % carbon	3.483 ± 0.270	1.833 ± 0.104	5.694	<0.001
	Total % nitrogen	0.374 ± 0.025	0.234 ± 0.009	5.416	<0.001
	C:N ratio	9.234 ± 0.295	7.811 ± 0.239	3.749	<0.001
	Water holding capacity (%)	58	43		

Sample size for water holding capacity ($n = 2$) prevented statistical analysis.

Ambient light was highly variable from one sampling day to the next, especially in open grassland. Nonetheless, plots under oaks at both sites averaged significantly lower ambient PAR ($437 \pm 23 \, \mu mol/m^2 s$) than those in open grassland ($1078 \pm 47 \, \mu mol/m^2 s$; $t = -12.16$, $p < 0.01$). Light availability under oaks (PAR_{under}/PAR_{open}), however, was higher at Figueroa (50%) compared with Mesa (35%; $t = -4.30$, $p < 0.01$). Increasing density of *Bromus* also strongly reduced light availability at the soil surface ($F_{[2,208]} = 27.29$, $p < 0.01$). High density of *Bromus* reduced PAR by approximately 40%.

Importance of the Oak Canopy

Regression trees of *Stipa* and *Poa* survival highlighted the importance of habitat, especially as it interacted with planting site (Fig. 1). We found that by the end of the experiment in
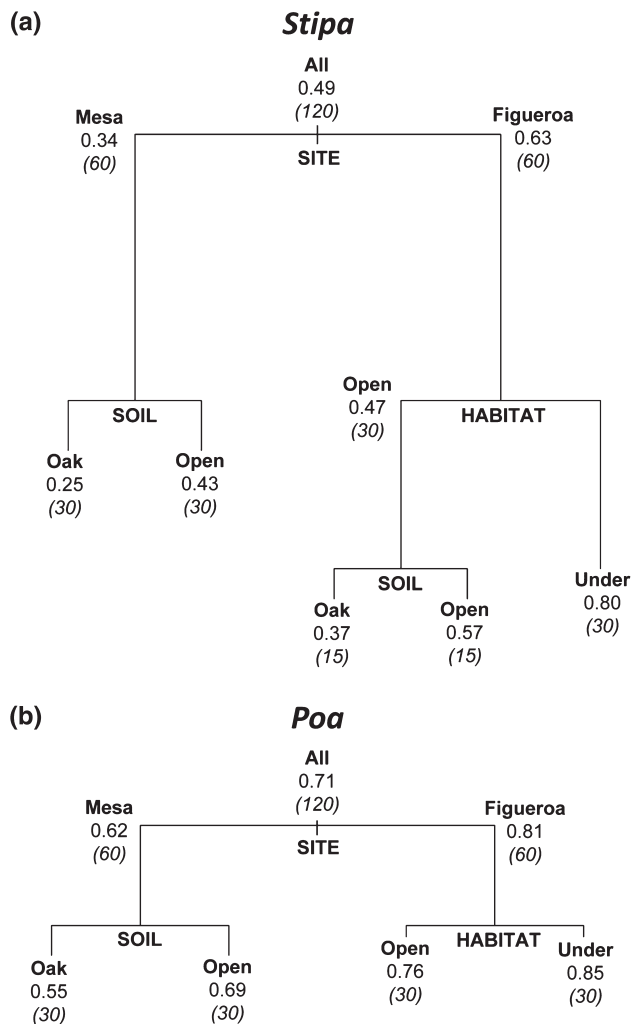
(a) *Stipa*

(b) *Poa*

Figure 1. Regression trees partitioning survival (proportion of original planted seedlings with green leaves) to final biomass collection in 2011 for (a) *Stipa pulchra* and (b) *Poa secunda*. The relative length of vertical lines is proportional to the deviance explained by that particular split. At each node are given the mean survival and number of observations (in parentheses).

2011, site determined the first major regression trees split for both species. *Stipa* survival was higher in Figueroa compared with Mesa (63 vs. 34%). At Mesa, the overall *Stipa* survival of 34% did not split on habitat (oak canopy vs. open) as it did at Figueroa where survival in open habitats was 47% compared with 80% under oak canopies. Overall *Poa* survival was higher at Figueroa compared with Mesa (81 to 64%). Habitat influenced *Poa* survival at Figueroa but not at Mesa, similar to *Stipa* (Fig. 1). Regression trees for the initial 2 years revealed similar patterns for both species (Appendix S2).

At final harvest in 2011, vegetative biomass of *Stipa* and *Poa* differed strongly between habitats but in opposite ways (Fig. 2). Mean *Stipa* biomass was strongly suppressed under the oak canopy compared with the open (1.61 vs. 4.20 g; $p < 0.01$) whereas *Poa* biomass was significantly greater under trees compared with the open (1.09 vs. 0.48 g; $p < 0.01$). As with survival for both species, the difference between habitats was greater at the Figueroa site. Hence, as might be expected, we found a significant interaction effect between site and habitat factors for vegetation biomass responses of *Stipa* and *Poa* (see first table in Appendix S3). These effects mirrored patterns in basal diameter growth rate as measured throughout the experiment (Appendix S3).

Reproductive biomass also differed strongly between habitats (oak canopy vs. open) for both species, again in opposite ways (Fig. 3). At Figueroa, *Stipa* plants in the open grassland
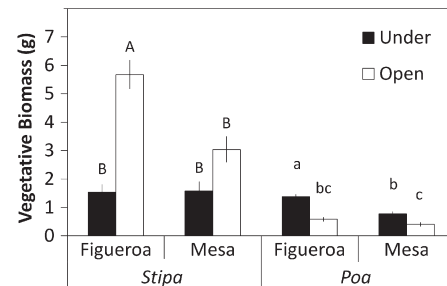

Figure 2. Mean vegetative biomass for plots in open and under habitats at both sites. Error bars indicate one standard error above and below the mean. Letters indicate significant differences within a species with a post-hoc Tukey's HSD test.
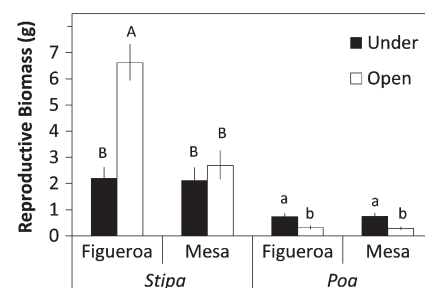

Figure 3. Mean reproductive biomass for plots in open and under habitats at both sites. Error bars indicate one standard error above and below the mean. Letters indicate significant differences within a species with a post-hoc Tukey's HSD test.

produced significantly more reproductive biomass than those under trees (4.34 vs. 2.12 g; $p < 0.01$) whereas *Poa* plants produced less reproductive biomass in the open than under canopies (0.54 vs. 0.87 g; $p < 0.01$). Differences in reproductive biomass for *Stipa* were less distinctive at Mesa, but for *Poa* the two sites were similar. We also examined the ratio of reproductive biomass to vegetative biomass and found no differences between habitats for either species (see first table in Appendix S3). Patterns of seed production (number of glumes) in 2009 and 2010 were similar to those found for reproductive biomass (e.g. *Poa* produced more glumes under oak canopies; Appendix S4).

Density of Annual Grasses

Our high density treatment attained an average of 40% *Bromus diandrus* cover by the second year (2010), representative of observed natural densities in open grassland plots. High density treatments in the understory became more dense over time (up to 60% on average by 2011), whereas cover in the open grassland remained closer to 30%.

The density of *Bromus* influenced performance of both *Poa* and *Stipa*, although to a lesser extent than habitat. *Stipa* reproductive biomass was significantly higher in fully weeded treatments than at any density of *Bromus* (Fig. 4). This effect differed between sites and soil origins (see first table in Appendix S3). At Mesa, *Stipa* in oak soil produced more reproductive biomass when weeded than with high density *Bromus*. In open soil there was no difference between densities. At Figueroa, this difference between soil types was reversed, as well as less pronounced. Increasing *Bromus* density had more of an effect
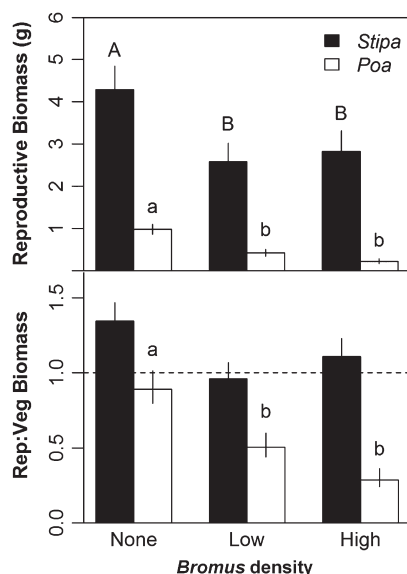

Figure 4. Mean reproductive biomass and ratio of reproductive to vegetative biomass for both perennial grass species growing at different densities of *Bromus diandrus*. Error bars indicate one standard error above and below the mean. Letters indicate significant differences within a species with a post-hoc Tukey's HSD test. Dotted line in the bottom panel represents a 1:1 relationship where reproductive and vegetative biomass are equivalent.

in open soil. There was no corresponding effect of *Bromus* on *Stipa* vegetative biomass (see first table in Appendix S3) or on the percent of seedlings surviving in any year of the experiment (Fig. 1; and Appendix S2). Although there was a trend for *Stipa* plants to allocate more biomass to reproduction when *Bromus* was absent (Fig. 4), this was affected by habitat. *Stipa* plants under oaks allocated significantly more biomass to reproduction when *Bromus* was absent (see second figure in Appendix S3).

Poa produced significantly more reproductive biomass with no neighboring *Bromus* than with low or high densities (Fig. 4). This effect was stronger under the oak canopy compared with the open grassland (see first table in Appendix S3). Increasing *Bromus* density also had a strong negative effect on *Poa* vegetative biomass (see first table in Appendix S3). This mirrors the strong impact of *Bromus* density on the growth rate of *Poa* throughout the experiment, compared with the more mild effects of *Bromus* on *Stipa* growth (Appendix S3). Allocation to reproduction was reduced 3-fold by *Bromus* for *Poa* (Fig. 4), and unlike results for *Stipa* this did not differ across habitats.

Soil Source

Although soil occasionally influenced survival, growth, or reproduction of native grasses, its effect was relatively minor and inconsistent compared with the influences of habitat and *Bromus* density. Soil had the largest impact on *Stipa* survival at Mesa and in the open grassland sites at Figueroa (Fig. 1). In all cases, *Stipa* survived at higher rates in open-derived soils. *Stipa* plants also produced more vegetative and reproductive biomass where soil origin and habitat were matched (see first table in Appendix S3). Soil source did not affect the ratio of reproductive to vegetative biomass.

Poa survival was only affected by soil origin at Mesa where, like *Stipa*, survival was slightly higher in open-derived soils (Fig. 1). In contrast to *Stipa*, however, *Poa* in oak soil always produced more vegetative biomass compared with those in soil from open grassland (0.91 vs. 0.67 g; $p < 0.01$). We found a similar pattern for reproductive biomass (see first table in Appendix S3) and seed production in 2010 (Appendix S4). Soil source did not affect allocation to reproduction in *Poa*.

Discussion

Planted *Poa secunda* and *Stipa pulchra* seedlings differed in their sensitivity to the oak canopy as well as to annual grass density. The oak understory environment promoted higher survival for both species. Despite this, *Stipa* grew better outside the canopy and did not obviously benefit from being planted in oak soils. By contrast, *Poa* had enhanced growth and reproduction under the oak canopy relative to open grassland and always benefited from growing in oak soil. High density, unweeded *Bromus* treatments also attained higher *Bromus* cover under the oaks, indicating a positive, direct effect of oaks on annual grass cover. *Poa* was equally sensitive to *Bromus* cover in the open grassland and oak understory; however, *Stipa* was only affected by *Bromus* in the latter habitat. Thus, indirect negative effects

of the tree via facilitation of *Bromus* may limit colonization beneath isolated trees, particularly *Stipa*. In restoration efforts, control of neighboring annuals may be more important beneath the canopy relative to open grassland.

Although both *Stipa* and *Poa* have lower growth rates than annual grasses (Jackson & Roy 1986; Hamilton 1997), they differ from each other in many ways. *Stipa* is a larger grass with a later, more flexible flowering phenology compared with the small, early-flowering *Poa*. Similar to Jackson and Roy (1986), in a separate greenhouse trial we found higher root:shoot ratios for *Poa* seedlings compared with *Stipa* (Appendix S5). Slowly developing shoots could cause *Poa* seedlings to undergo more competition for light. *Stipa*, on the other hand, appears be a robust competitor with winter annual grasses in open grassland, as found in previous studies (Seabloom et al. 2003; Corbin & D'Antonio 2004; Fehmi et al. 2004). These differences and others may contribute to the variation in responses of *Stipa* and *Poa* to annual grasses, although without a broader suite of native species we cannot isolate which characteristics are most important in creating this response.

Colonization of native grasses may also be limited by interference from annual grasses immediately after germination. As we used transplants of young seedlings in this experiment rather than starting the individual grasses from seeds, we did not observe if interactions among germinating grasses could also contribute to the absence of perennial grasses in the understory. *Vulpia myuros*, another European annual grass, is known to reduce establishment of *S. pulchra* from seed (Brown & Rice 2000). Bartolome and Gemmill (1981) also found that germination of *S. pulchra* was suppressed by annual grasses. Less is known about *Poa* germination. The combination of intense competition following germination, faster growth of annuals beneath the trees, and lower ambient light may effectively prevent perennial grasses such as *S. pulchra* and *P. secunda* from gaining a foothold in the understory.

Both grasses responded strongly to the presence of the canopy compared with the other treatments, such as soil origin. Therefore altered microclimate in the understory may be more influential than resource enrichment. The major environmental differences between these two habitats were light availability and soil moisture. Shading can ameliorate the effects of drought, especially at intermediate light levels (Holmgren et al. 2012). Grasslands in California are frequently considered to be water-limited (Harpole et al. 2007), and soil moisture was increased beneath the canopy in our early spring measurements. Nevertheless, the density of *Bromus* and the number of surviving perennials did not affect soil moisture, indicating the competition for water among the grasses is likely not occurring at this time. Earlier and later in the growing season, however, competition with the tree for water may be significant, especially under trees with extensive shallow roots (Callaway et al. 1991).

Oaks across the California savanna differ in their leaf habit (deciduous vs. evergreen) as well as rooting strategies (Callaway 1990; Mahall et al. 2009), which will alter their effects on native grasses. Evergreen trees tend to rely more on surface moisture in many seasonally dry settings, including California, the Mediterranean *macchia* (Valentini et al. 1992), and

Brazilian *cerrado* (Jackson et al. 1999). In our experiment, the deeply rooted, deciduous *Quercus lobata* facilitated the development of high density *Bromus diandrus* treatments, which had strongly negative effects on *Poa* and weaker negative effects on *Stipa*. This is in contrast to the effect of *Q. lobata* on the environment, which was overall positive for *Poa* and negative for *Stipa*. California savanna oaks with other combinations of characteristics such as shallow rooted evergreens may have different effects on establishing native grasses.

Trees play central roles in restoration of degraded pasture in other arid and semi-arid savannas which share many non-native winter annuals with California, such as Australia (Ludwig & Tongway 1996) and the *espinales* of central Chile (Ovalle et al. 1999). In California, isolated oaks tend to harbor dense associations of non-native species, yet they are of high conservation value for birds and wildlife. Thus they may be a high priority target for restoration, despite the lack of information about their understory prior to invasion. The high survival of *Stipa* and *Poa* under the *Q. lobata* canopies and the enhanced growth of *Poa* when the density of the annual grass *B. diandrus* is low suggests that oak understories are suitable restoration sites for planting these two perennial native grasses if annual grass density is controlled.

Implications for Practice

- Both *Stipa pulchra* and *Poa secunda* could be used to restore native perennial grasses in California oak savannas, as they both grew and produced seeds successfully under *Quercus lobata* canopies and in the open. *Stipa*, however, performed better in open grassland whereas *Poa* grew best in under *Q. lobata*.
- To establish *P. secunda* and *S. pulchra* under oak canopies, we recommend controlling the density of non-native annual grasses such as *Bromus diandrus* to very low numbers. This will be less important in open grassland for *S. pulchra*.
- The direction of the effect of oaks on *Stipa* and *Poa* was consistent across valley bottom and upland terrace sites, indicating that these results apply to a variety of settings.

LITERATURE CITED

Allen-Diaz, B., R. Standiford, and R. D. Jackson. 2007. Oak woodlands and forests. Pages 313–338 in R. C. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial vegetation of California. 3rd edition. University of California Press, Berkeley.

Avery, M. L., and C. Vanriper. 1989. Seasonal changes in bird communities of the chaparral and blue oak woodlands in central California. Condor **91:**288–295.

Barkworth, M. E. 2007. *Nassella*, in M. E. Barkworth, K. M. Capels, S. Long, L. K. Anderton, and M. B. Piep, editors. Flora of North America vol. 24 (available from http://herbarium.usu.edu/webmanual).

Bartolome, J. W., and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. Madrono **28:**172–184.

Bartolome, J. W., S. E. Klukkert, and W. J. Barry. 1986. Opal phytoliths as evidence for displacement of native Californian grassland. Madrono **33:**217–222.

Bartolome, J. W., W. J. Barry, T. Griggs, and P. Hopkinson. 2007. Valley grassland. Pages 367–393 in M. G. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial vegetation of California. 3rd edition. University of California Press, Berkeley.

Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology **26:**1005–1024.

Brown, C. S., and K. J. Rice. 2000. The mark of Zorro: effects of the exotic annual grass *Vulpia myuros* on California native perennial grasses. Restoration Ecology **8:**10–17.

Call, C., and B. Roundy. 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. Journal of Range Management **44:**543–549.

Callaway, R. M. 1990. Effects of soil water distribution on the lateral root development of three species of California oaks. American Journal of Botany **77:**1469–1474.

Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. Ecology **72:**1484–1499.

Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology **85:**1273–1283.

Dahlgren, R. A., M. J. Singer, and X. Huang. 1997. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. Biogeochemistry **39:**45–64.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology **81:**3178–3192.

Fehmi, J. S., K. J. Rice, and E. A. Laca. 2004. Radial dispersion of neighbors and the small-scale competitive impact of two annual grasses on a native perennial grass. Restoration Ecology **12:**63–69.

Frost, W. E., and S. B. Edinger. 1991. Effects of tree canopies on soil characteristics of annual rangeland. Journal of Range Management **44:**286–288.

Gómez-Aparicio, L. 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology **97:**1202–1214.

Hamilton, J. G. 1997. Environmental and biotic factors affecting the occurrence of the native bunchgrass *Nassella pulchra* in California grasslands. Ph.D. dissertation. University of California, Santa Barbara.

Harpole, W. S., L. Goldstein, and R. J. Aicher. 2007. Resource limitation. Pages 119–127 in M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, editors. California grasslands ecology and management. University of California Press, Berkeley.

Holmgren, M., L. Gómez-Aparicio, J. Quero, and F. Valladares. 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. Oecologia **169:**293–305.

Ishikawa, C. M., and C. S. Bledsoe. 2000. Seasonal and diurnal patterns of soil water potential in the rhizosphere of blue oaks: evidence for hydraulic lift. Oecologia **125:**459–465.

Jackson, L. E., and J. Roy. 1986. Growth patterns of Mediterranean annual and perennial grasses under simulated rainfall regimes of southern France and California. Acta Oecologica Oecologia Plantarum **7:** 191–212.

Jackson, P. C., F. C. Meinzer, M. Bustamante, G. Goldstein, A. Franco, P. W. Rundel, L. Caldas, E. Igler, and F. Causin. 1999. Partitioning of soil water among tree species in a Brazilian cerrado ecosystem. Tree Physiology **19:**717–724.

King, E. G., and M. L. Stanton. 2008. Facilitative effects of aloe shrubs on grass establishment, growth, and reproduction in degraded Kenyan rangelands: implications for restoration. Restoration Ecology **16:**464–474.

Ludwig, J. A., and D. J. Tongway. 1996. Rehabilitation of semiarid landscapes in Australia. II. Restoring vegetation patches. Restoration Ecology **4:**398–406.

Mahall, B. E., C. M. Tyler, E. S. Cole, and C. Mata. 2009. A comparative study of oak (*Quercus*, Fagaceae) seedling physiology during summer drought in southern California. American Journal of Botany **96:**751–761.

Marañón, T., and J. Bartolome. 1989. Seed and seedling populations in two contrasted communities: open grassland and oak (*Quercus agrifolia*) understory in California. Acta Oecologica Oecologia Plantarum **10:**147–158.

Marañón, T., and J. W. Bartolome. 1993. Reciprocal transplants of herbaceous communities between *Quercus agrifolia* woodland and adjacent grassland. The Journal of Ecology **81:**673–682.

Marañón, T., and J. W. Bartolome. 1994. Coast live oak (*Quercus agrifolia*) effects on grassland biomass and diversity. Madrono **41:**39–52.

Marañón, T., F. I. Pugnaire, and R. M. Callaway. 2009. Mediterranean-climate oak savannas: the interplay between abiotic environment and species interactions. Web Ecology **9:**30–43.

Maron, J. L., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. Oecologia **105:**302–312.

Mcclaran, M. P., and J. W. Bartolome. 1989. Effect of *Quercus douglasii* (Fagaceae) on herbaceous understory along a rainfall gradient. Madrono **36:**141–153.

Milton, S. J., J. R. U. Wilson, D. M. Richardson, C. L. Seymour, W. R. J. Dean, D. M. Iponga, and Ş. Procheş. 2007. Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. Journal of Ecology **95:**648–661.

Ovalle, C., J. Aronson, A. Del Pozo, and J. Avendan. 1999. Restoration and rehabilitation of mixed espinales in central Chile: 10-year report and appraisal. Arid Soil Research and Rehabilitation **13:** 369–381.

Padilla, F. M., and F. I. Pugnaire. 2006. The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment **4:**196–202.

Parker, V. T., and C. H. Muller. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. American Midland Naturalist **107:**69–81.

Pueyo, Y., C. L. Alados, B. García-Ávila, S. Kéfi, M. Maestro, and M. Rietkerk. 2009. Comparing direct abiotic amelioration and facilitation as tools for restoration of semiarid grasslands. Restoration Ecology **17:**908–916.

Rice, K. J., and E. S. Nagy. 2000. Oak canopy effects on the distribution patterns of two annual grasses: the role of competition and soil nutrients. American Journal of Botany **87:**1699–1706.

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics **28:**517–544.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences **100:**13384–13389.

Shipman, G. E. 1972. Soil survey of northern Santa Barbara area, California. United States Department of Agriculture Soil Conservation Service, Washington, D.C.

Soreng, R. J. 2007. Poa, in M. E. Barkworth, K. M. Capels, S. Long, L. K. Anderton, and M. B. Piep, editors. Flora of North America vol. 24 (available from http://herbarium.usu.edu/webmanual).

Stahlheber, K. A. 2013. The influence of savanna oaks on California grassland plant composition. Ph.D. dissertation. University of California, Santa Barbara.

Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. Ecological Applications **6:**1189–1211.

Stromberg, M. R., C. M. D'Antonio, T. P. Young, J. Wirka, and P. R. Kephart. 2007. California grassland restoration. Pages 254–280 in M.

R. Stromberg, J. D. Corbin and C. M. D'Antonio, editors. Ecology and management of California grasslands. University of California Press, Berkeley.

Therneau, T., B. Atkinson, and B. Ripley 2012. *rpart*: Recursive Partitioning. R package version 3.1-55. (available from http://CRAN.R-project.org/package=rpart).

Tyler, C. M., F. W. Davis, and B. E. Mahall. 2008. The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. Forest Ecology and Management **255:**3063–3074.

Valentini, R., G. E. S. Mugnozza, and J. R. Ehleringer. 1992. Hydrogen and carbon isotope ratios of selected species of a Mediterranean macchia ecosystem. Functional Ecology **6:**627–631.

Zhao, H.-L., R.-L. Zhou, Y.-Z. Su, H. Zhang, L.-Y. Zhao, and S. Drake. 2007. Shrub facilitation of desert land restoration in the Horqin Sand Land of inner Mongolia. Ecological Engineering **31:**1–8.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional methodological details.
Appendix S2. Survival regression trees.
Appendix S3. Additional biomass and growth results.
Appendix S4. Seed production.
Appendix S5. Germination and root–shoot ratios.