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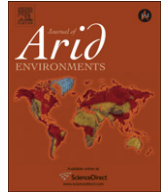
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Ecological effects of experimental drought and prescribed fire in a southern California coastal grassland

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ABSTRACT

How drought and fire disturbance influence different levels of biological organization is poorly understood but essential for robust predictions of the effects of environmental change. During a year of severe drought, we conducted a prescribed fire in a Mediterranean-type coastal grassland near Irvine, California. In the weeks following the fire we experimentally manipulated rainfall in burned and unburned portions of the grassland to determine how fire and drought interact to influence leaf physiological performance, community composition, aboveground net primary productivity (ANPP) and component fluxes of ecosystem CO₂ exchange and evapotranspiration (ET). Fire increased leaf photosynthesis (A_{net}) and transpiration (T) of the native perennial bunchgrass, *Nassella pulchra* and the non-native annual grass, *Bromus diandrus* but did not influence ANPP or net ecosystem CO₂ exchange (NEE). Surprisingly, drought only weakly influenced A_{net} and T of both species but strongly influenced ANPP and NEE. We conclude that despite increasing experimental drought severity, prescribed fire influenced leaf CO₂ and H₂O exchange but had little effect on the component fluxes of ecosystem CO₂ exchange. The differential effects of prescribed fire on leaf and ecosystem processes with increasingly severe drought highlight the challenge of predicting the responses of biological systems to disturbance and resource limitation.

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1. Introduction

Predicting biophysical phenomena across scales is a critical organizing theme in ecological research (Ehleringer and Field, 1993; Enquist et al., 2003; Jarvis and McNaughton, 1986; Lavorel and Garnier, 2002; Suding et al., 2008; Valentini et al., 1995). If larger scale phenomena are the collective dynamics of processes at smaller scales, it is essential to understand how patterns at one scale relate to patterns at other scales (Levin, 1992). For example, responses to resource availability and disturbance are theorized to scale across levels of ecological organization (Lavorel and Garnier, 2002). However, resource alteration and disturbance may drive species composition shifts and non-additive productivity responses related to resource mediated thresholds in recruitment and mortality (Smith et al., 2009). The existence of such thresholds may create scenarios in which the responses of individuals to resource availability and disturbance may not translate to ecosystem

responses without consideration of these modulating effects at the community level (Suding et al., 2008).

California's Mediterranean-type grasslands are characterized by year-to-year rainfall variability and frequent fire, providing a tractable system in which to examine the effects of resource availability and disturbance across scales of biological organization (Dukes et al., 2005). In southern California, future warming associated with anthropogenic atmospheric CO₂ increases may be accompanied by declines in winter season precipitation (Seager and Vecchi, 2010) and droughts of increasing severity (Bell et al., 2004; Cayan et al., 2010). Rainfall controls the productivity of California grasslands (Dukes et al., 2005; Harpole et al., 2007; Henry et al., 2006), with productivity varying widely between dry and wet years (Chou et al., 2008). In addition to influencing productivity, rainfall also influences community composition through shifts in the abundance of native and non-native grasses (Seabloom et al., 2003) due to differences in life history and functional rooting depths (Everard et al., 2010).

Against the backdrop of year-to-year rainfall variability, Mediterranean-type grasslands are strongly influenced by fire (Bartolome et al., 2004; George et al., 1992; Hatch et al., 1999;

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Henry et al., 2006; Noy-Meir, 1995). Episodic releases of soil nutrients associated with fire is likely to favor non-native annual grasses over native perennial bunchgrasses, due to the greater physiological responses (Ignace et al., 2007) and earlier plant phenology (Cleland et al., 2006) of the non-native grasses. While the functional impacts of water limitation on Mediterranean-type and other semi-arid grasslands are well studied (English et al., 2005; Harpole et al., 2007; Potts et al., 2006; St. Clair et al., 2009; Suttle et al., 2007), fire effects in these systems are less understood (Scheintaub et al., 2009).

The balance of CO₂ uptake by plants and release of CO₂ by plants and soil microbes is a critical variable in understanding ecosystem function (Baldocchi, 2008). Expressed as the difference between of CO₂ assimilation by photosynthesis (gross ecosystem exchange; GEE) and the release of CO₂ by plant and soil microbial respiration (ecosystem respiration; R_e), net ecosystem CO₂ exchange (NEE) integrates leaf and community processes (Flanagan et al., 2002; Jenerette et al., 2008; Potts et al., 2006). Likewise, by combining evaporation from soil and canopy surfaces with transpiration from stomata, evapotranspiration (ET) is critical in understanding the role of ecosystems in linking the movement of water between the land surface and the atmosphere. Used in a variety of experimental settings, chamber-based measurements have demonstrated the effects of seasonal rainfall (Harpole et al., 2007; Patrick et al., 2007), rainfall timing (Potts et al., 2006) and fire (Prater and DeLucia, 2006) on CO₂ exchange and ET.

The objectives of this research were to determine how fire disturbance and drought influence native and non-native grass physiological performance and, in turn, how these responses influence plant community composition and ecosystem CO₂ exchange and ET. To address this objective, we conducted a prescribed fire in a Mediterranean-type grassland in southern California during a growing season characterized by severe drought. In burned and unburned portions of the grassland, we constructed a rainfall manipulation experiment which had the effect of ameliorating drought conditions in plots which received supplemental rainfall while increasing drought severity in rainfall reduction plots. We predicted that prescribed fire and reduced drought severity would interact to influence the physiological performance and canopy cover of the non-native annual grass *Bromus diandrus*. Specifically, we predicted that the positive effects of prescribed fire on the physiological performance and canopy cover of *B. diandrus* would decline with increasing drought severity. In contrast, we predicted the physiological performance and abundance of the more extensively-rooted native perennial grass, *Nassella pulchra*, would be less responsive to prescribed fire and drought. At the canopy scale, we predicted that fire and drought-mediated shifts in physiological performance translated through changes in the canopy cover of *B. diandrus* and *N. pulchra*, would predict ecosystem CO₂ assimilation and evapotranspiration.

2. Methods

2.1. Site description

Field work was conducted on the Irvine Ranch Conservancy (IRC; 33° 44' N, 117° 42' W, elev. 365 m), 5 km north of Irvine, California on a northwest facing slope (<10%), having soils of fine-loamy, mixed, thermic Typic Palixeralfs sandy loam (California Soil Resource Lab, <http://casoilresource.lawr.ucdavis.edu>) during the 2006–2007 growing season. The IRC has a Mediterranean climate of warm, dry summers and cool, wet winters. Based on the nearest long-term weather station, mean annual temperature is 17 °C and mean annual precipitation is 325 mm (Tustin Irvine Ranch Station, Coop ID # 049087, 33° 43' N, 117° 47' W, elev. 36 m). The

2006–2007 growing season (November–May) was characterized by increasingly severe drought throughout southern California (National Climate Prediction Center, http://www.cpc.ncep.noaa.gov/products/monitoring_and_data/drought.shtml). A rain gauge at the research site recorded 79.4 mm of precipitation between November 2006 and May 2007 which was only ca. 26% of the historical average precipitation for the same monthly period.

Historically the site was grazed by cattle and sheep until ca. 10 years prior to the study. The vegetation is a mosaic of patches dominated by non-native annual grasses (e.g. *Bromus diandrus*, *Avena fatua*) or perennial, drought-deciduous shrubs (e.g. *Artemisia californica*, *Salvia melifera*). Larger, evergreen woody species such as *Rhus ovata*, *Malosma laurina* and *Quercus agrifolia* and succulent *Opuntia* spp. are widely distributed on the landscape as scattered individuals. We conducted this research in a 1 ha patch dominated by non-native annual grasses and scattered individuals of the native, perennial bunchgrass species *Nassella pulchra* (canopy cover of *N. pulchra* during the peak growing season < 5%).

2.2. Experimental design

Beginning October 2006, 24 6.1 × 12.2 m experimental plots containing similar, representative plant communities were identified. Plots were oriented with their long axis parallel to the hill slope and were assigned to one of four blocks based on their position relative to one another on the hill slope (6 plots per block). Within each block, plots were randomly assigned to one of three levels of rainfall manipulation (supplemental, ambient, and reduction; see section 2.3). Three weeks prior to establishing rainfall manipulations, half of the experimental area was burned in a prescribed fire on the morning of February 6, 2007. Ideally, burned and unburned controls would have been spatially interspersed across the hillside. However, because of safety and logistical constraints, the prescribed fire treatments were spatially segregated from unburned controls. In the weeks preceding the fire, a combination of unusually dry and cold conditions limited the germination and survival success of annual grasses and forbs. High humidity and calm winds during the burn resulted in a low intensity grass fire that consumed ca. 90% of the standing litter and live plant material, leaving the soil surface litter layer largely intact (Potts, personal obs.).

2.3. Rainfall collection and redistribution

To collect and redistribute rainfall, we built four 6.1 × 12.2 × 2.1 m shelters (Agra-Tech, Pittsburg, CA USA) over rainfall reduction plots in the burned and unburned portions of the grassland (total $n = 8$). This open-sided and open-ended shelter design was modified to include a manually retractable, clear, 6-mil polyethylene roof and gutters to collect and direct rainwater into storage tanks. Frames were constructed of eight, 12-gage steel tube arches mounted on similar steel posts driven into the soil. During construction, efforts were taken to minimize soil and vegetation disturbance in the underlying experimental plots.

To minimize direct shelter effects on plants and soils, plots were covered only when rainfall was forecast, and were uncovered as soon as rainfall ended and we could access the site (usually < 12 h after rainfall). In total, shelters were covered to collect rainfall 9 days from February–June 2007. To control for a possible shading effect of the gutters, we constructed simulated gutters of similar dimensions and orientation on ambient and supplemental rainfall plots using galvanized sheet-metal strips supported by metal fence posts.

Intercepted rainfall was directed into four, 5678 L polyethylene storage tanks (a capacity equivalent 51 mm of rainfall). Stored water was redistributed by pump and was applied to supplement

rainfall in plots in the burned and unburned portion of the grassland (eight plots in total) using drip-irrigation line fit with pressure-compensating emitters (Toro, Bloomington, MN USA), which eliminated the need to control for overspray or canopy shading associated with an overhead sprinkler system. Water was applied at an intensity of 50 mm h^{-1} , and did not cause overland redistribution of water within the plots. The cumulative amount of water delivered to each experimental plot was recorded with a residential-style water meter. In total, 41.4 mm of collected rainfall was distributed in 4 applications (March 14, March 18, April 7, May 1) to enhanced-water plots during the spring of 2007 (Fig. 1). During the 2006–2007 growing season (November–May), supplemented rainfall plots received 121 mm (39.5% of the November–May historic average total), ambient plots received 79.4 mm (26% of the November–May historic average total) and rainfall reduction plots received 61.5 mm (20% of the November–May historic average total).

2.4. Soil moisture and resin-available soil nitrogen

To assess pre-treatment spatial variability and to measure the effects of fire and rainfall on shallow soil moisture, we measured volumetric soil water content (θ) using time-domain reflectometry (TDR; Mini-Trase, Santa Barbara, CA USA). Measurements from three vertically-oriented, 15 cm TDR probes located in each plot were averaged to estimate plot mean θ on January 17, February 26, March 22 and April 23, 2007. Mean θ from the February, March and April sampling dates were pooled to estimate mean growing season θ for each experimental plot.

Plant-available soil nitrogen was assessed by extracting ammonium and nitrate ions from buried ion-exchange resin bags. In each experimental plot, 3 nylon cloth bags containing 5 g of mixed-bed ion exchange resin were buried to 10 cm depth in the soil on April 14 and were collected on May 10, 2007. Bags were stored on ice and returned to the lab where ammonium and nitrate ions were extracted with 100 ml of a 2.0 M KCl solution and analyzed using an automated plate reader following Weatherburn (1967) and Doane and Horwath (2003) respectively. Mean values of ammonium and nitrate in each plot were summed and are expressed as $\mu\text{g N g}^{-1} \text{ resin day}^{-1}$.

2.5. Leaf CO_2 and H_2O exchange

We measured midday net assimilation of CO_2 (A_{net}) and transpiration (T) on a native perennial bunchgrass, *Nassella pulchra* and

a non-native annual grass, *Bromus diandrus* growing nearby ($<1 \text{ m}$) in each plot. Individual *N. pulchra* were selected that appeared in a representative, healthy condition, were growing within a meter of the edge of the experimental plot (to minimize damage to the plot associated with trampling) and possessed a 15-cm basal diameter. Later in the growing season and particularly in rainfall reduction plots, *B. diandrus* mortality was high ($>90\%$). As much as possible, we selected *B. diandrus* representative of the live individuals in each plot.

Due to the large number of leaf gas exchange measurements, we sampled over two days in a stratified, random sequence to avoid confounding effects of any small day-to-day differences in environmental conditions. Sampling was conducted in advance of scheduled supplemental rainfall additions or forecast storms on April 1–2, April 15–16 and April 29–30. Measurements were made between 11:00 and 13:30 h on mature, representative leaves with a portable photosynthesis analyzer (LI-6400, Li-Cor, Lincoln, NE, USA). Within the LI-6400 leaf cuvette, the red/blue light source was set to $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and CO_2 concentration was maintained at $380 \mu\text{mol mol}^{-1}$. Cuvette vapor pressure deficit and air temperature were set to ambient conditions determined from an open, shaded cuvette. Gas exchange measurements were leaf-area corrected by measuring leaf width with a caliper and multiplying by the length of the cuvette. For the purpose of comparing treatments, the mean of physiological variables collected on the three sampling dates in each plot was used to represent mean growing season values for each plot.

2.6. Cover and ANPP

To assess the effects of fire and rainfall on grassland composition and litter cover, we used a canopy intercept approach with a $1 \text{ m} \times 1 \text{ m}$ frame divided into a $10 \text{ cm} \times 10 \text{ cm}$ grid positioned above the canopy on April 25, 2007. At each intersection point on the frame's grid (100 points), we noted plant canopy cover by functional type (annual grass, perennial grass or forb) and the presence/absence of litter on the soil surface. On May 17, 2007, aboveground plant material was clipped at the soil surface from two, $7.5 \text{ cm} \times 100 \text{ cm}$ strips and sorted into live and standing litter. Samples were dried for 48 h at 50°C and weighed to determine total live aboveground biomass as an estimate of annual net primary productivity (ANPP).

2.7. Ecosystem CO_2 exchange and evapotranspiration

We measured midday (11:00–14:00) ecosystem CO_2 exchange and evapotranspiration (ET) on April 6, April 19, May 4, 2007.

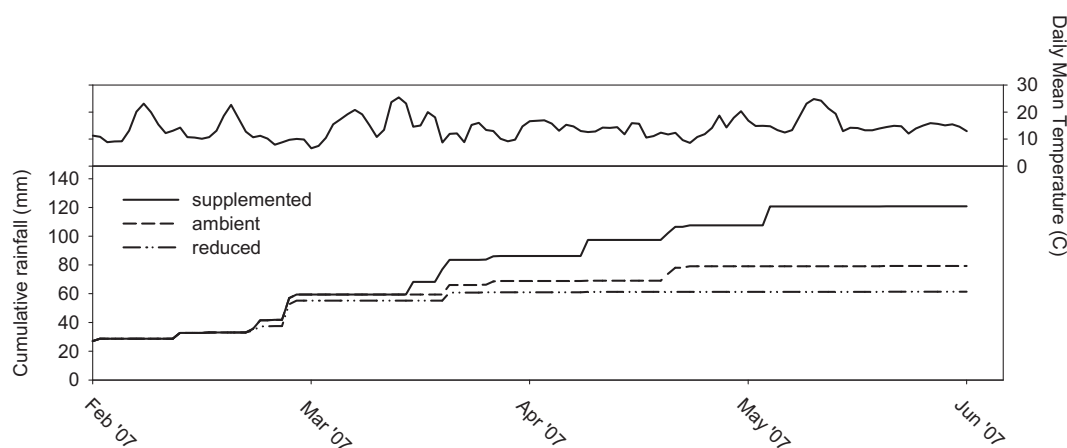


Fig. 1. 2007 Growing season mean daily temperature (upper panel) and cumulative rainfall and the effect of rainfall interception and redistribution (lower panel) in a coastal grassland fire and rainfall manipulation experiment near Irvine, California.

Logistical limitations meant that ecosystem gas exchange measurements were not conducted on the same days as leaf gas exchange measurements nor were the measurements scheduled in any specific relation to natural or supplemental rainfall. Sampling was conducted in a randomized sequence under sunny conditions (photosynthetically active radiation, PAR > 1400 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) with the exception of April 6 measurements which were conducted under partly sunny conditions (PAR = 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). Because of logistical constraints, our sampling was limited to a randomly selected subsample of three replicates of each fire and rainfall combination (total of 18 plots).

We measured net ecosystem CO₂ exchange (NEE), ecosystem respiration (R_e) and ET with a closed, static chamber (1.5 m long, 0.97 m wide, 1.44 m tall) following the chamber design, instrumentation and measurement protocols described by Harpole et al. (2007). Consistent, linear changes in CO₂ and water vapor concentrations during ca. 2 min measurement periods indicated that increasing water vapor concentration did not significantly influence stomatal conductance, canopy photosynthesis or soil CO₂ efflux (Huxman et al., 2004). During a typical measurement period air temperatures increased less than 2 °C. Because we focused on relative differences among experimental treatments, we did not assess the potential effects of leaks or wind on the estimate of ecosystem CO₂ exchange and ET (Saleska et al., 1999).

We analyzed CO₂ and water vapor concentration data according to Jasoni et al. (2005) to estimate ecosystem fluxes. We estimated midday gross ecosystem CO₂ exchange (GEE) as the difference between midday NEE and midday R_e . In addition, to better understand the influence of prescribed fire and drought on the relationship between ecosystem CO₂ exchange and water-use, we calculated ecosystem water-use efficiency (EWUE) as the ratio of NEE to ET (Baldocchi et al., 2001). Similar to leaf gas exchange measurements, the mean value of ecosystem gas exchange parameters collected on the three sampling dates in each plot was used to represent mean growing season values for the purpose of comparisons among treatments.

2.8. Statistical analyses

Data were examined to determine if they satisfied the assumptions of parametric statistics. In the case of ANPP, forb cover, perennial grass cover and plant-available soil nitrogen, data were normalized with a log₁₀ transformation. A three-way factorial ANOVA model was used to test the significance of rainfall treatment, species, prescribed fire and their interactions on mean growing season A_{net} , and T . We used a two-way factorial ANOVA to

test the significance of rainfall treatment, fire and their interactions on mean growing season ecosystem CO₂ exchange variables, ET and EWUE. Likewise, we used a two-way factorial ANOVA to test the significance of rainfall treatment, fire and their interactions on total cover, forb cover, annual grass cover, perennial grass cover, ANPP, middle growing season θ and plant-available soil nitrogen. In the case of significant rainfall effects, we compared rainfall treatments using post-hoc Tukey HSD tests.

To address the prediction that shifts in physiological performance translated through changes in canopy cover would drive response of ecosystem CO₂ assimilation, we calculated mean growing season cover-weighted A_{net} in each experimental plot as:

$$\text{cover-weighted } A_{\text{net}} = (\% \text{ cover} * A_{\text{net}})_{\text{annual grass}} + (\% \text{ cover} * A_{\text{net}})_{N. pulchra} \quad (1)$$

In this calculation, mean growing season A_{net} of *B. diandrus* was assumed to be representative of annual grasses. We compared cover-weighted A_{net} with mean growing season midday NEE, and GEE using linear regression. To address the same prediction with regards to water vapor fluxes, we analogously calculated mean growing season cover-weighted T and compared those values to mean growing season midday ET using linear regression.

Although we consider fire to be a main effect in our statistical analyses, prescribed fire was not a randomly assigned treatment in our experimental design because we conducted one large prescribed burn in order to more closely simulate a naturally-occurring fire. While this design is not unusual in studies involving fire (e.g. Killgore et al., 2009; O'Donnell et al., 2009), inferences regarding fire effects observed in this experiment should be considered cautiously (Hurlbert, 1984). All statistical analyses were conducted using JMP 7.0 (SAS Institute Inc., Cary NC USA).

3. Results

On January 17, prior to the prescribed fire and the initiation of the rainfall manipulation, volumetric soil moisture (θ) was not significantly different between plots slated for burned and unburned treatments (mean \pm SD = 8.48% \pm 0.99 and 9.08% \pm 0.73 respectively). Following the prescribed fire and the initiation of the rainfall manipulation, mean growing season θ did not differ between burned and unburned plots, but declined in response to increasing drought severity (Fig. 2A). Consistent with the removal of litter from the soil surface by fire, burned plots had lower percent litter cover than unburned plots (mean \pm SD = 88 \pm 7.8 and 98 \pm 2.0 respectively; $F_{2,18} = 19.55$; $P = 0.003$; not shown).

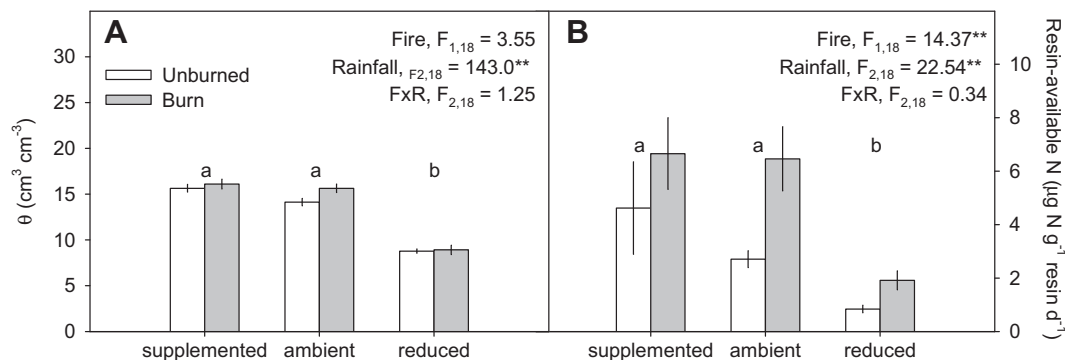


Fig. 2. Mean growing season soil moisture and resin-available nitrogen abundance in response to fire and rainfall manipulation in a coastal grassland near Irvine, California. (A) 15-cm integrated volumetric soil moisture (θ ; cm³ cm⁻³); (B) resin-available nitrogen ($\mu\text{g N g}^{-1} \text{resin d}^{-1}$). Error bars indicate SE; significant differences in means between rainfall treatments are illustrated with different lower case letters (Tukey HSD, $P < 0.05$). F -statistics with a single asterisk (*) indicate significance at $P < 0.05$; a double asterisk (**) indicates $P < 0.01$.

Similarly, resin-available N declined with increasingly severe drought. In contrast to θ , resin-available N responded positively to prescribed fire (Fig. 2B).

Across levels of drought, the native perennial bunchgrass *N. pulchra* had consistently higher rates of midday net assimilation of CO₂ (A_{net}) than the non-native annual grass *B. diandrus* (Fig. 3A, significant species effect). In both species, fire significantly increased A_{net} , but particularly for *N. pulchra*, giving rise to a significant species-by-fire interaction (Fig. 3A). Consistent with prevailing dry conditions during the 2007 growing season, added rainfall significantly increased A_{net} , although these effects were small in comparison with the positive effect of prescribed fire (Fig. 3A). Similar to A_{net} , mean mid-season transpiration (T) of *N. pulchra* was greater than *B. diandrus* and in both species, T was positively influenced by prescribed fire (Fig. 3B).

Total canopy cover increased in response prescribed fire while declining in response to increasing drought severity (Fig. 4A). The positive response of canopy cover to prescribed fire was driven by a positive response of forbs to prescribed fire. Burned plots had greater forb cover than unburned plots (mean \pm SD = 16.1 ± 3.9 and 2.2 ± 0.7 respectively; $F_{2,18} = 15.21$; $P = 0.0011$; not shown). Estimates of non-native annual grass and native perennial *N. pulchra* canopy cover reveal contrasting drought effects. Annual grass cover declined with increasingly severe drought (Fig. 4A) while the cover of *N. pulchra* significantly increased with increasingly severe drought (Fig. 4B). Moreover, while prescribed fire did not influence annual grass cover, the cover of *N. pulchra* was significantly lower in burned plots than in unburned plots (Fig. 4B). Similar to annual

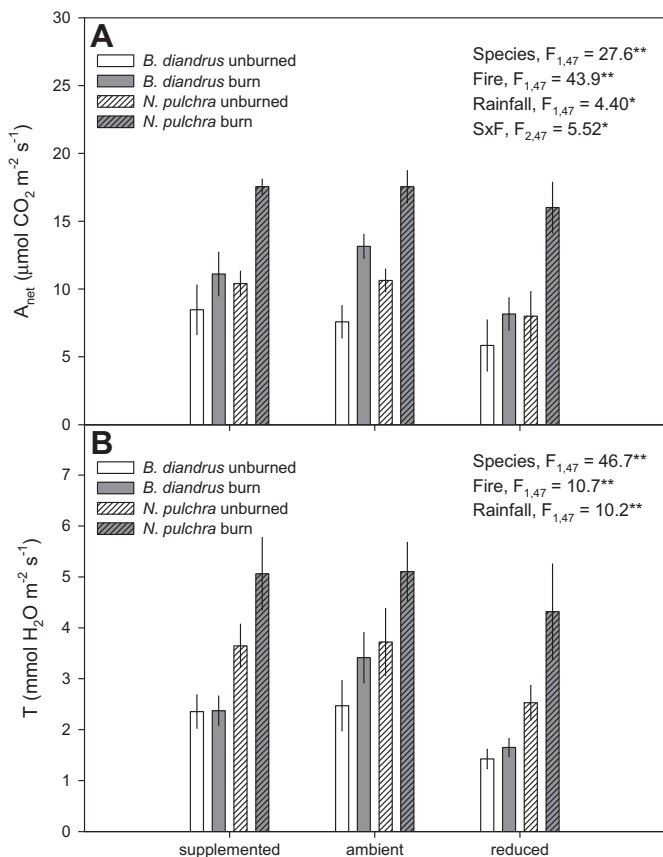


Fig. 3. Mean growing season midday leaf gas exchange parameters of a non-native annual grass *Bromus diandrus* (open bars) and a native, perennial bunchgrass, *Nassella pulchra* (hatched bars) in response to fire and rainfall manipulation in a coastal grassland near Irvine, California. (A) Leaf net CO₂ assimilation (A_{net} ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); (B) leaf transpiration (T ; $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). F -statistic notation follows Fig. 2.

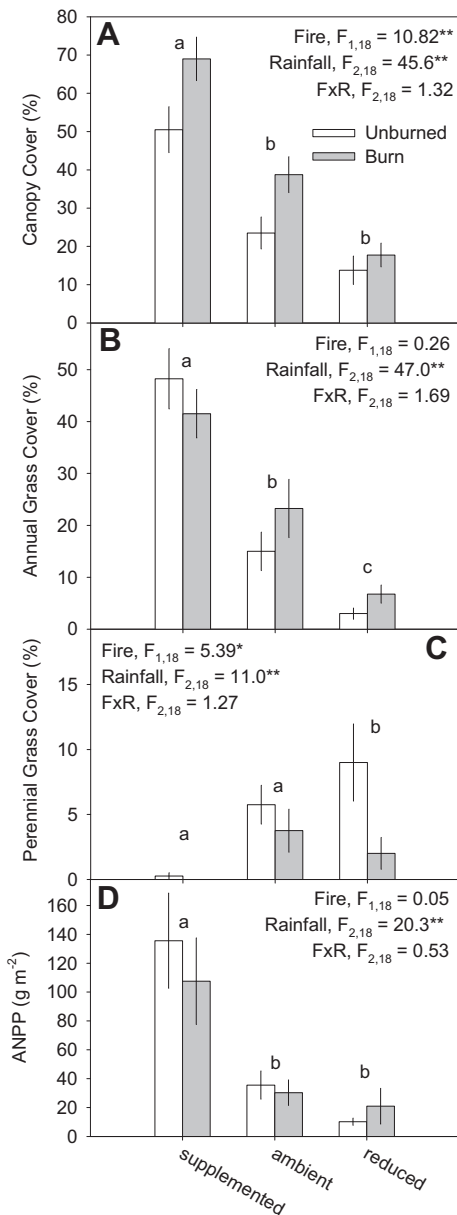


Fig. 4. Mid-growing season plant community canopy cover of (A) non-native, annual grass, the native perennial bunchgrass, *Nassella pulchra*, and forbs; (B) non-native, annual grass; (C) the native, perennial bunchgrass, *Nassella pulchra*. (D) Annual net primary productivity (aboveground live biomass; g m^{-2}). Symbols and F -statistic notation follow Fig. 2.

grass cover, aboveground net primary productivity (ANPP) declined with increasingly severe drought and was not influenced by fire (Fig. 4C).

Increasingly severe drought constrained midday net ecosystem CO₂ exchange (NEE) as illustrated by decreasing negative values indicating decreasing ecosystem C-assimilation (Fig. 5A). This NEE decrease was the result of proportional declines in gross ecosystem CO₂ exchange (GEE; Fig. 5B) and ecosystem respiration (R_e ; Fig. 5C). Unlike the effect of drought, ecosystem CO₂ exchange variables did not respond to fire. Evapotranspiration (ET) decreased as drought severity increased while in contrast with ecosystem CO₂ exchange variables, prescribed fire increased ET in experimental plots with the least severe drought, but not in others (Fig. 5D). Supported by the pattern of ET response, ecosystem water-use efficiency (EWUE) declined in response to fire (Fig. 5E; $P = 0.058$).

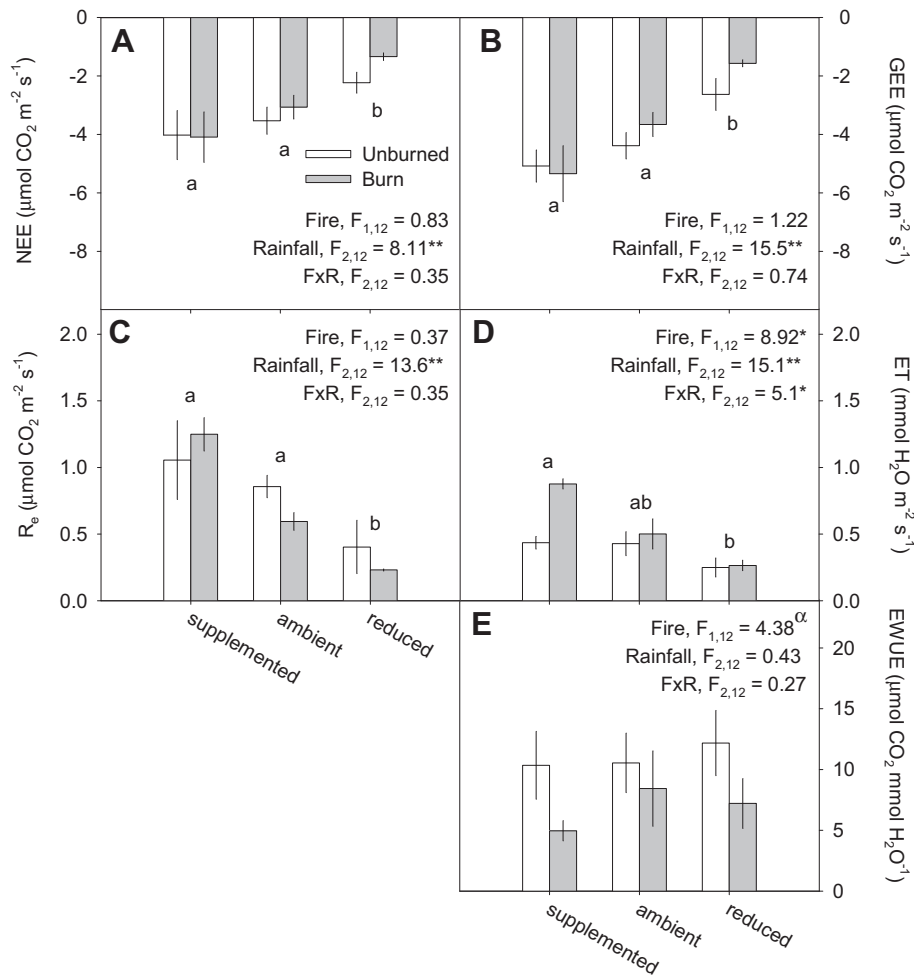


Fig. 5. Mean growing season ecosystem CO₂ and H₂O fluxes during the 2007 growing season in response to fire and rainfall manipulation in a coastal grassland near Irvine, California. (A) Net ecosystem CO₂ exchange (NEE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); negative values indicate increasing ecosystem CO₂ assimilation. (B) Gross ecosystem CO₂ exchange (GEE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); negative values indicate increasing ecosystem CO₂ assimilation. (C) Ecosystem respiration (R_g; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); positive values indicate increase ecosystem CO₂ loss. (D) Evapotranspiration (ET; $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$); positive values indicate ecosystem H₂O loss. (E) Ecosystem water use efficiency (EWUE; $\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$) estimated from mean growing season measurements of NEE and ET. Increasing efficiency (greater CO₂ uptake per H₂O loss) is expressed as larger positive values of EWUE. Symbols and *F*-statistic notation follow Fig. 2; the *F*-statistic noted with (α) indicates $P = 0.058$.

To better understand how shifts in physiological performance combine with changes in canopy cover to influence ecosystem function, we compared mean growing season cover-weighted leaf gas exchange parameters with mean growing season ecosystem CO₂ fluxes and ET using linear regression. Across levels of drought and regardless of prescribed fire, cover-weighted A_{net} was negatively correlated with NEE (Fig. 6A). Likewise, cover-weighted A_{net} was negatively correlated with GEE (Fig. 6B). In contrast, cover-weighted T was not significantly correlated with ET (data not shown).

4. Discussion

In contrast with our first prediction, we found little evidence to show that drought severity interacts with low intensity, prescribed fire to affect leaf physiological performance or ecosystem CO₂ exchange in a California Mediterranean-type grassland. This result was surprising given the general expectation that disturbance and resource alteration would interact to influence biological processes across scales. For example, Smith et al. (2009) recently proposed a hierarchical response framework (HRF) describing ecosystem dynamics in response to disturbance in the face of sustained shifts

in resource availability. By linking metabolism with demography to describe ecosystem dynamics, the HRF predicts that chronic resource increases, such as those associated with increasing atmospheric CO₂ concentration or N deposition, will interact with disturbance to influence ecosystem function (Smith et al., 2009). In the present study, we examined ecological responses to chronic resource limitation (drought) and disturbance (prescribed fire) and observed a generally straightforward pattern of biological responses. These results suggest the potential to extend the HRF described by Smith et al. (2009) to address the effects of chronic resource limitation and disturbance across broader scales of space and time.

Leaf photosynthesis (A_{net}) and transpiration (T) of both *B. diandrus* and *N. pulchra* increased in response to fire and decreased in response to increasingly severe drought (Fig. 3A–B). Similar, positive physiological responses of grasses to fire have been observed in a Chihuahuan desert grassland (Allred and Snyder, 2008) and tall grass prairie (Knapp, 1985). Surprisingly, this positive A_{net} response to fire was more pronounced among *N. pulchra* than among *B. diandrus* (Species \times Fire; Fig. 3A). This enhanced responsiveness of A_{net} to fire may have been associated with the ability of deeply-rooted *N. pulchra* to access sufficient

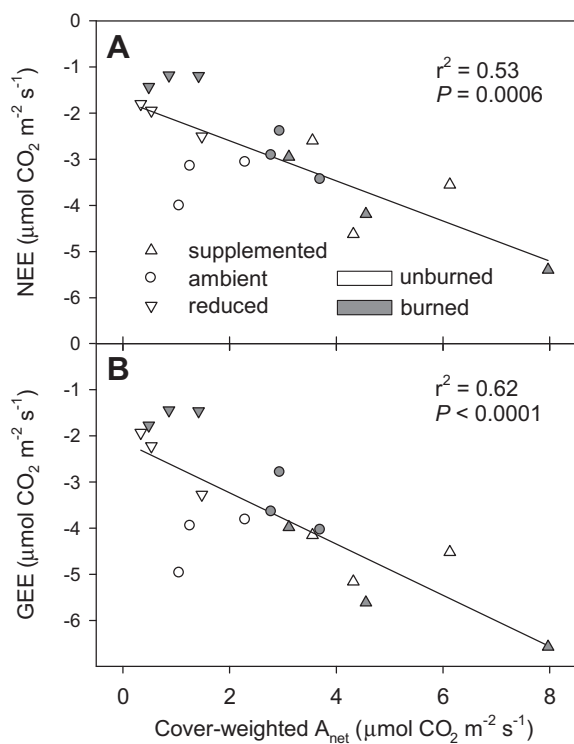


Fig. 6. (A–B) Cover-weighted mean growing season midday leaf net CO_2 assimilation (A_{net} ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) versus mean growing season midday ecosystem CO_2 assimilation parameters in response to fire and rainfall manipulation in a coastal grassland near Irvine, California; negative Y-axis values indicate increasing ecosystem CO_2 uptake. (A) Net ecosystem CO_2 exchange (NEE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). (B) Gross ecosystem CO_2 exchange (GEE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

water across a range of drought conditions than the more shallowly-rooted *B. diandrus* and is consistent with species contrasts in *T* (Fig. 3B) as well as the observations of others (Holmes and Rice, 1996).

In contrast with our prediction that fire-mediated increases in physiological performance would translate to increases in cover, annual grass cover did not respond to fire (Fig. 4B) while fire induced a decline in *N. pulchra* cover (Fig. 4C). Any explanation of how prescribed fire influenced a decline in *N. pulchra* cover should account for the observed positive effect of prescribed fire on A_{net} . For example, the negative effects of prescribed fire on *N. pulchra* cover may have been associated with herbivory on surviving individuals growing in burned plots where their resprouting, green tillers were particularly conspicuous. The activity of native herbivores has been linked to the growth and survival of *N. pulchra* in California grasslands although this effect is not necessarily influenced by prescribed fire (Dyer and Rice, 1997; Watts, 2010).

The lack of a fire effect on annual grass cover was consistent with the lack of a fire effect on ANPP (Fig. 4D). Although prescribed fire increased resin-available N (Fig. 2B), water limitation across the experimental drought treatments appears to have limited canopy development and productivity. Our observation of the neutral effect of fire on productivity is consistent with findings of other investigations on the productivity effects of fire on Mediterranean-type grasslands in California (Hervey, 1949; Henry et al., 2006) and are in broad agreement with the findings of a recent synthesis of fire effects in semi-arid shortgrass steppe (Scheintaub et al., 2009). Moreover, the non-linear response of ANPP to increasing drought severity suggests the potential of a threshold-type response of productivity to

chronic resource limitation (Fig. 4D). A threshold response of ANPP to increasing drought severity may be explained by the characteristics and timing of individual rainfall events interacting with the physiology and life-history strategies of the plant functional types present in a community (Ogle and Reynolds, 2004).

We found partial support for the hypothesis that fire and drought-mediated shifts in physiological performance translated through changes in canopy cover of *B. diandrus* and *N. pulchra* would predict ecosystem CO_2 assimilation and ET (Fig. 6A–C). For example, increasing drought severity caused a small decline in A_{net} in both *B. diandrus* and *N. pulchra* (Fig. 3A) while influencing a shift in the relative abundance of annual and perennial grasses (Fig. 4B–C) and reducing GEE (indicated by less negative values; Fig. 5B). In the case of both NEE and GEE comparisons with cover-weighted A_{net} , treatment-specific regressions do not explain additional variance suggesting a common scaling relationship links cover-weighted A_{net} and ecosystem CO_2 assimilation in response to experimental drought and prescribed fire (Fig. 6A–B).

A possible consequence of the positive effects of prescribed fire and reduced drought severity on annual grass physiological performance would be an increase in leaf transpiration relative to soil evaporation resulting in an increase in ecosystem water use efficiency (EWUE). In fact, EWUE declined in response to prescribed fire, though this effect was only marginally significant (Fig. 5E). As the ratio of NEE to ET (Baldocchi et al., 2001), EWUE is influenced by canopy structure and leaf area, autotrophic and heterotrophic respiration, and evaporation from the soil surface (Emmerich, 2007). The removal of standing litter by fire could explain the slight decline in EWUE. By increasing light penetration to the soil surface and thereby increasing soil surface temperatures (Henry et al., 2006), fire may have increased soil surface evaporation relative to leaf transpiration in burned plots. Moreover, the shallow rooting depth of annual grasses may have limited the contribution of leaf transpiration to ET (Baldocchi et al., 2004). Indeed, when fires of greater intensity influence a shift in plant functional types leading to shifts in phenology and functional rooting depth, more dramatic shifts in the timing and magnitude of ET fluxes have been observed (Prater and DeLucia, 2006).

Experimental drought and prescribed fire have a range of effects on biophysical and ecological processes in an ecosystem dominated by non-native annual grasses. Our findings reinforce the idea that interpreting the significance of organism level responses to ecosystem function requires the context of changes at the community level (Suding et al., 2008). Moreover, we observed a general lack of interactive effects of experimental drought and prescribed fire which suggests the need to extend current theory to include predictions of the effects of chronic resource limitation and disturbance on biological systems across levels of organization.

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