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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 CO_2 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 CO_2 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 CO_2 and H_2O exchange but had little effect on the component fluxes of ecosystem CO_2 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.

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 CO_2 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 CO_2 uptake by plants and release of CO_2 by plants and soil microbes is a critical variable in understanding ecosystem function (Baldocchi, 2008). Expressed as the difference between of CO_2 assimilation by photosynthesis (gross ecosystem exchange; GEE) and the release of CO_2 by plant and soil microbial respiration (ecosystem respiration; R_e), net ecosystem CO_2 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 CO_2 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 CO_2 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 CO_2 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 Palexeralfs 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