

Controls on gross production by a semiarid forest growing near its warm and dry ecotonal limit

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ABSTRACT

Climate change is expected to move the spatial patterns of temperature and water availability poleward and upslope, with concomitant shifts in vegetation distribution. Vegetation growing near its southern or low-elevation range limit may prove especially susceptible to mortality and displacement. We investigated the controls on Gross Primary Production (GPP) by an oak and pine stand located just above the lower forest limit in Southern California's San Jacinto Mountains. The local climate was montane Mediterranean, and the stand experienced extensive mortality in the early 1990s and from 2002 to 2004 coincident with extended droughts. The maintenance of high rates of CO₂ uptake in winter, and access to water deep in the soil column in summer, allowed for a year-round growing season. The evergreens at the site remained photosynthetically active year-round despite frequent freezing nights. High rates of CO₂ uptake were observed at air temperatures below 8 °C, which is colder than has been reported for other ecosystems. Winter cold exerted a minor limitation on GPP, and winter warming would have a small effect on GPP. Vegetation withdrew water from the soil, saprolite, and fractured granitic bedrock to support transpiration and CO₂ uptake during the dry summer, which further expanded the growing season. Access to a reliable supply of moisture deep in the soil and regolith appears critical for the survival of large trees at the site. These trees may prove vulnerable to climate change if increasing evaporation rates or interannual precipitation variability causes a more frequent or severe depletion of deep regolith moisture.

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1. Introduction

Air temperatures in the Southwestern United States are projected to rise 1.5–4.5 °C by 2070–2099 with global climate change (Cayan et al., 2008). Precipitation (*P*) projections for the Southwestern US are less certain, though several recent analyses indicate declining mean *P* (Seager and Vecchi, 2010). Warming and drying are expected to move the spatial patterns of climate poleward and upslope, with concomitant shifts in vegetation distribution (Loarie et al., 2008; Parmesan and Yohe, 2003; Walther et al., 2002). Vegetation growing near its southern or low elevation range limit may prove especially vulnerable to mortality and displacement with climate change, underscoring the need to better understand the mechanisms that contribute to the resilience, resistance and persistence of these ecosystems.

Widespread tree mortality was observed throughout western North America in the last decade coincident with severe drought and warmer temperatures (Allen et al., 2010; Breshears et al., 2005; Raffa et al., 2008; Walker et al., 2006). This mortality has been

causally linked to severe drought, the outbreak of insects including bark beetles, and possibly a warming climate (Adams et al., 2009; Allen et al., 2010). There has been speculation this mortality mimics what would be expected with climate change: episodic tree death that is increased in frequency or intensity by decreasing mean *P*, increasing frequency of drought, and increasing thermal stress (Allen et al., 2010).

Southern California's montane forest provides an excellent study system to investigate the relationship between climate and semiarid forest physiological activity. These forests experience a montane Mediterranean climate, with cold wet winters and warm dry summers; in principle, their growing season length may be limited by winter cold and/or summer drought (Goulden et al., 2012). Southern California's forests occur near the southern limit of several important tree species, including Pacific Ponderosa Pine, Jeffrey Pine, California White Fir and Sugar Pine. Southern California's mountains experienced marked tree and shrub mortality in 2002–2004 that was similar to that reported elsewhere in the Southwestern US (Minnich, 2007; Fellows and Goulden, 2012). The mortality in Southern California's San Jacinto and Santa Rosa Mountains was concentrated in the lower parts of species' ranges, which contributed to a 37–65 m upslope movement of plant distribution (Kelly and Goulden, 2008; Fellows and Goulden, 2012).

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We used micrometeorological and plant physiological observations to investigate the controls on photosynthesis by a stand growing near the lower forest ecotone in Southern California's San Jacinto Mountains. We focused on forest CO₂ uptake (referred to as Gross Ecosystem CO₂ Exchange at half-hourly intervals (GEE), and Gross Primary Production at annual intervals (GPP)), which is presumably linked to tree survival, persistence, and stress evasion through the availability of carbohydrates for growth and also the avoidance of stomatal closure (Adams et al., 2009). We focused on four questions: (1) What is the relative importance of drought, summer warmth, and winter cold in limiting growing season length and GPP? (2) Does the forest exhibit strategies that maximize growing season length and GPP? (3) Would climate change be expected to (a) increase growing season length and GPP by facilitating winter photosynthesis, (b) decrease growing season length and GPP by increasing summer drought and heat stress, or (c) cause offsetting changes in the beginning and end of the growing season? (4) What climatic stress or combination of stresses would be expected to have the greatest effect on growing season length and GPP?

2. Methods

2.1. Site

Our field site was located in the US Forest Service Hall Canyon Research Natural Area at 1708 m on the western flank of the San Jacinto Mountains (33°48'28"N, 116°46'18"W). The eddy-covariance tower is registered in the Ameriflux network (Oak Pine Forest/US-SCf), and the installation is part of the Southern California Climate Gradient, an eddy covariance mesonet (Goulden et al., 2006, 2012) of six sites deployed along an elevation and climatic gradient in Southern California. The Hall Canyon site was dominated by evergreen and deciduous oaks, several pine species, white fir and a sparse shrub understory (Table 1). The site was near the mixed forest to shrubland ecotone; chaparral shrubland was increasingly dominant at lower elevations (Fig. 1; Fellows and Goulden, 2012). The canopy was heterogeneous and rough, with a mix of gaps, shorter evergreen and deciduous oaks, and taller conifers. The topography was complex, with both local slopes associated with drainages, and a general east to west slope associated with the mountain front. The site was unburned since ~1880, and selective logging in the area ended in the early 1900s.

2.2. Eddy covariance

We used eddy covariance to determine the controls of weather on GEE and GPP. We focused on GPP because it provides a measure of the carbon available for plant growth and respiration, and also because it provides an indication of plant stress and stomatal closure.

Measurements of the meteorological conditions (incoming solar radiation (K), net radiation (Q) and temperature (T)), and the net exchanges of carbon dioxide (NEE), water vapor (ET), and sensible heat (H) were made at the top of a 26-m telescoping aluminum tower (Goulden et al., 2006, 2012). Data gaps in the time series were caused by power loss, equipment failure, and non-turbulent atmospheric conditions ($u^* \leq 0.30 \text{ m s}^{-1}$). Short gaps (<2.5 h) in the meteorological records were filled by interpolation. Longer gaps (gaps ≥ 2.5 h) were filled with the mean for the corresponding time of day calculated at 25-day intervals. Respiration (R) was determined at 25-day intervals by extrapolating to darkness the best fit rectangular hyperbola between NEE and K . GEE was calculated by assuming a constant 25-day R and adding it to NEE. Missing GEE and ET observations were filled using the gap-filled K and the relationships between K and GEE or ET determined for 25-day intervals.

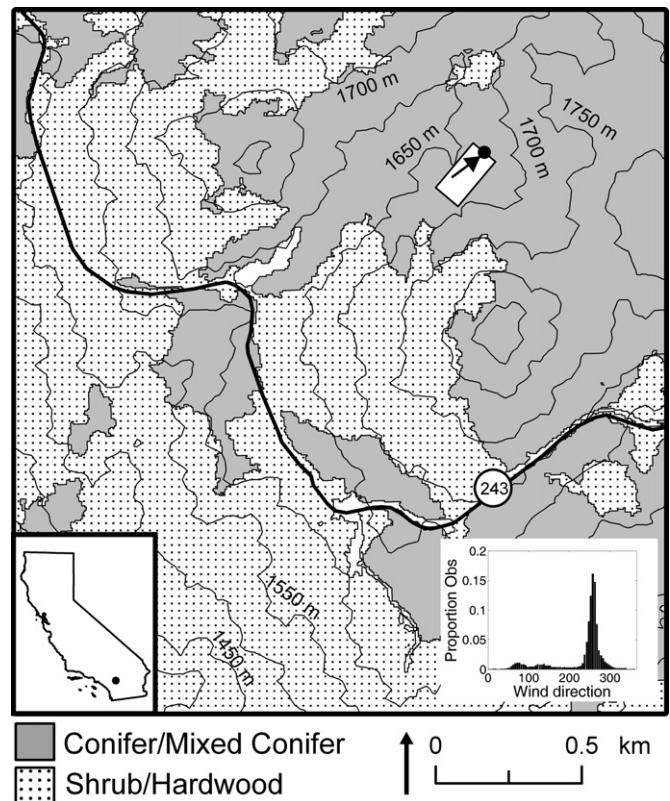


Fig. 1. Map of the study area. Conifer and mixed conifer forest is designated by uniform gray polygons; shrub and hardwood cover is designated by stippled polygons. Vegetation cover is from the life form class (WHRLIFEFORM) in the Evg-Tile59A.03.v2 dataset (USFS, 2007). The location of the flux tower is indicated by the filled circle. The location of the 100 m × 200 m sample plot is indicated by the white rectangle. The arrow at the field site indicates the daytime mean observed wind direction. The histogram indicates the proportion of daytime wind observations for individual direction bins, with 0 indicating due North.

2.3. Energy budget

Complex wind flows may reduce the accuracy of eddy covariance measurements in mountainous terrain (Finnigan, 2008). We investigated the local energy budget to assess the reliability of the eddy covariance measurements. Energy budget closure was determined as the slope of the linear regression between available energy (AE) and the sum of H and latent heat fluxes (LE). A large and systematic discrepancy in the energy budget may indicate the eddy covariance measurements are unreliable.

Several factors may cause a lack of energy budget closure, including: inadequate accounting for energy stored in the soil, air column, and vegetation; inadequate accounting of high frequency eddy transport due to poor instrument response; inadequate accounting for humidity when calculating temperature from the sonic anemometer speed of sound measurement; differences in the reference planes for the radiation and turbulent flux measurements; and horizontal or vertical advection (Leuning et al., 2012). We considered, and, where possible, accounted for each of these uncertainties.

We calculated the energy stored in the soil, air column, and vegetation at half an hour intervals. Soil heat storage, Q_g , was calculated by vertically integrating the change in temperature measured at 5, 10, 25, 100, and 200 cm-depth. The soil heat capacity was calculated from observations of water content and a soil bulk density of 1.05 g cm^{-3} (Vargas and Allen, 2008). The observations of soil temperature needed to calculate soil heat storage were only available beginning in 2009, and we were unable to analyze the

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