UC Irvine

UC Irvine Previously Published Works

Title

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

Permalink

<https://escholarship.org/uc/item/43h51861>

Authors

Fellows, AW
Goulden, ML

Publication Date

2013-02-15

DOI

10.1016/j.agrformet.2012.10.001

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

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

Aaron W. Fellows*, Michael L. Goulden

Department of Earth System Science, University of California, Irvine, CA 92697-3100, USA

ARTICLE INFO

Article history:

Received 27 February 2012

Received in revised form 1 September 2012

Accepted 1 October 2012

Keywords:

Mixed conifer forest

Gross Primary Production

Ecosystem function

Ecotone

Tree mortality

Low elevation forest

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.

© 2012 Elsevier B.V. All rights reserved.

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).

* Corresponding author. Tel.: +1 949 824 9273; fax: +1 949 824 3874.
E-mail address: afellows@uci.edu (A.W. Fellows).

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 $\geq 2.5 \text{ h}$) 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 Evge-Tile59A.03.v2 dataset (USFS, 2007). The location of the flux tower is indicated by the filled circle. The location of the 100 m $\times$ 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

Table 1

Tree density, basal area, and plant functional type.

Species	Density (trees ha ⁻¹)	BA (m ² ha ⁻¹)	Plant functional type
<i>Abies concolor</i> (California White Fir)	10	0.01	Evergreen conifer
<i>Pinus lambertiana</i> (Sugar Pine)	253	4.91	Evergreen conifer
Yellow Pines: <i>P. coulteri</i> (Coulter Pine), <i>P. ponderosa</i> (Pacific Ponderosa Pine), <i>P. jeffreyi</i> (Jeffrey Pine)	153	6.70	Evergreen conifer
<i>Calocedrus decurrens</i> (Incense Cedar)	299	12.13	Evergreen conifer
<i>Quercus chrysolepis</i> (Canyon Live Oak)	252	5.19	Evergreen broadleaf
<i>Q. kelloggii</i> (Black Oak)	166	11.07	Deciduous broadleaf
Total	1132	40.02	–

Density (stand density; tree per hectare) and basal area (BA; m² of tree per hectare) of trees measured at the site. Plant functional type indicates the species' plant functional type.

energy budget before this point. The sensible heat, Q_{sens} , and latent heat, Q_{lat} , stored in the canopy air column between the forest floor and the eddy covariance sensors (Moore and Fisch, 1986) were calculated from the changes in temperature and water vapor concentration. The heat stored in vegetation, Q_{veg} , was calculated assuming the outer 6 cm of each tree responded directly to changes in air temperature (Aston, 1985; Moore and Fisch, 1986; Meesters and Vugts, 1996). The biomass heat storage was calculated as the product of the change in air temperature, the total fresh biomass contained in the outer 6 cm of all trees (Jenkins et al., 2003), and a vegetation heat capacity of 2928 J kg⁻¹ C⁻¹.

We calculated the underestimation of flux associated with the damping of high frequency water vapor and CO₂ fluctuations by our closed-path gas analyzer. We determined the frequency response of the water vapor and CO₂ sampling system by comparison with the simultaneous temperature observations made with the sonic anemometer. We then used this frequency response to simulate the corresponding underestimation of H for each half an hour period, and used this value to correct the water vapor and CO₂ fluxes (Goulden et al., 1996). We corrected the raw sonic anemometer temperature measurements for the effect of humidity on the speed of sound prior to calculating the half an hour covariances (Kaimal and Gaynor, 1991). Radiation measurements are made in the horizontal plane, whereas eddy covariance fluxes are determined for a plane that is tilted by the influence of local topography on wind flow. We therefore adjusted H , LE, NEE, and ET to the horizontal plane to agree with the orientation of the radiation sensors and to ensure that all fluxes were presented per horizontal area.

Including Q_g improved energy budget closure by ~6%. Accounting for Q_{sens} and Q_{lat} , in the canopy air column improved energy budget closure by ~1%. Accounting for Q_{veg} improved the energy budget by ~1%. Accounting for the frequency response of the closed path IRGA improved the energy budget by ~1%. Adjusting the eddy covariance fluxes to the horizontal plane improved the energy budget closure by ~1%. The resulting energy budget closure was 78% ($(H+LE)=0.78 \times AE - 14$; where $AE=Q-Q_g-Q_{\text{sens}}-Q_{\text{lat}}-Q_{\text{veg}}$), which is similar to that reported elsewhere (Wilson et al., 2002).

The remaining underestimation of turbulent flux (~22%) may be attributable to horizontal or vertical advection. Advection can lead to large errors in flux estimates (Aubinet et al., 2010). This problem is potentially greatest at night in sloped terrain, where cold-air drainage transports gas and energy beneath the eddy covariance sensors. Efforts to quantify transport by advection are difficult, expensive, and not always reliable (Aubinet et al., 2010). Our focus on daytime fluxes and use of a friction velocity filter to consider just turbulent periods was intended to minimize errors associated with advection. Additionally, we adjusted the carbon dioxide and water vapor fluxes to account for the remaining underestimation of turbulent flux (Twine et al., 2000).

2.4. Matric potential and soil moisture

We measured the volumetric soil moisture in the top 30 cm of soil using four Frequency Domain Reflectometers (Campbell Scientific; CS616) inserted vertically into the soil surface. We measured the soil matric potential (ψ_s) at 5, 10, 25, 100, and 200 cm depth using thermal dissipation probes (Campbell Scientific; CS229). The CS229 probes were installed in 3.8-cm diameter hand-augered holes that were subsequently backfilled with the original soil from each depth, such that the profile was preserved. The soil probes were measured and recorded at 30-min intervals using a data logger.

The matric potential sensors measure the change in temperature (δT) that results from passing a fixed current through a heating element embedded in a porous ceramic cylinder. δT is then related to ψ_s following Flint et al. (2002), which requires a calibration based on the δT measured when the sensor is completely dry and also completely saturated. We initially planned to use measurements of dry and wet δT for each sensor that were determined in the lab prior to installation. However, the late-summer field-observed δT s often exceeded the dry lab values, and we therefore adopted an ad hoc calibration for each sensor that set the maximum and minimum δT s observed in the field to -10 MPa and 0 MPa. The matric potentials sensors were insensitive to changes in matric potential under extremely dry conditions. This lack of sensitivity and our ad hoc calibration precluded us from resolving the soil matric potential between different sensors under particularly dry soil conditions. The ψ_s s we report are therefore useful for determining the relative patterns at the site, but not the absolute magnitude of the soil matric potential, and should not be used for comparison with observations reported in other studies.

We combined the CS616 and CS229 measurements to calculate the total water stored in the upper 2 m of soil. We calculated an empirical relationship between the observations of depth-integrated ψ_s made with the upper three CS229 probes and the simultaneous soil moisture measured with the CS616 probes. The relationship between ψ_s and volumetric water storage did not rely on assumptions used in our ad hoc CS229 calibration; scaling ψ_s to -1000 MPa instead of -10 MPa changed the calculated soil water by less than 5%. We then applied the empirical relationship to the ψ_s s measured at all depths, and integrated vertically to calculate the total soil moisture stored in the upper 2 m (S_{0-200}).

2.5. Forest inventory

We established a 200 m × 100 m inventory plot that was oriented lengthwise into the dominant wind direction and that began at the eddy covariance tower. We also established a 100 m × 10 m subplot that began at the eddy covariance tower along the centerline of the large plot. We recorded the Diameter at Breast Height (DBH; 1.37 m) of all trees with a DBH greater than 50 cm in the 2 ha

plot, and the DBH of all trees and saplings that were taller than 1.37 m in the 0.1 ha subplot.

2.6. Leaf area

We measured the Leaf Area Index (LAI) 8 times during 2009 using comparisons of the light field above and below the canopy (Licor LAI-2000). Each LAI observation was made shortly after sunrise and consisted of 10 spot measurements along the centerline of the inventory plot. We extrapolated LAI over the 3 year study based on an empirical relationship between the LAI-2000 observations and the local Enhanced Vegetation Index (EVI) pixel obtained by the Moderate Resolution Imaging Spectroradiometer (MODIS; $\text{LAI} = 5.0724 \times \text{EVI} + 0.0416$; $r^2 = 0.68$; EVI downloaded March 2010 from <http://daac.ornl.gov/>; MODIS product was MOD13Q1 Collection 5).

2.7. Leaf-level gas exchange

We selected 5–9 focal trees of the main tree species at the site for intensive leaf level measurements in 2009. We pooled Ponderosa and Coulter Pine into a yellow pine group. Our sample included individuals representing the dominant species, size classes, and topographic positions in the tower footprint. We measured carbon assimilation (A_{max}) on the most recent fully expanded leaves of each focal tree using a portable gas exchange system (Licor 6400). Measurements were made within 2.5 h of solar noon on freshly clipped or non-clipped branches. Comparisons of leaf gas exchange before and after clipping indicated a change in leaf gas exchange of less than 10% for all species except Black Oak. We therefore restricted our Black Oak measurements to intact branches. Chamber CO_2 mixing ratio was controlled at 380 ppm and chamber photon flux density was controlled at $1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Temperature and humidity varied with ambient conditions. We were careful to minimize needle overlap and chamber leaks for conifers. We collected the leaves that were positioned in the chamber following each measurement and subsequently determined the projected area using an optical scanner. We then recalculated leaf gas exchange using the corresponding leaf area for each observation.

We extrapolated the leaf-area-based gas exchange observations to a ground-area based CO_2 exchange for comparison with the tower-based observations by (1) averaging the observed leaf-level A_{max} within each species, (2) calculating a species-weighted A_{max} for the tower footprint ($A_{\text{max w}}$) by summing the product of each species' A_{max} and that species' basal area divided by the total basal area, and (3) multiplying $A_{\text{max w}}$ by LAI.

2.8. Plant water potential

We measured predawn (ψ_{pd}) and midday (ψ_{md}) water potentials on the focal trees using a Scholander pressure chamber. Predawn water potential was measured on 1–2 twigs from each tree. Samples were clipped 2–3 h before sunrise, sealed in plastic bags, stored in a cooler, and analyzed within 2 h. Midday water potential was measured on 1 twig from each tree. Midday measurements were made immediately after clipping.

2.9. Calculations and data analysis

We determined the half-hourly response of GEE to K and T . We minimized the confounding effects of seasonal changes in LAI and soil moisture stress by separating the winter and spring observations (January–June 10 in 2007–2009), when LAI was low and the soil was wet, from the early summer observations (July–August in 2008–2009), when LAI was consistently high and the soil had

not completely dried. We further filtered these observations to isolate the GEE response to light by excluding observations that were impacted by low ($T < 8^\circ\text{C}$) or high ($T > 21^\circ\text{C}$) temperature. Similarly, we isolated the GEE response to T by excluding observations with low light ($K < 500 \text{ W m}^{-2}$). We binned the observations by the meteorological conditions, and homogenized the early summer time period to the winter and spring interval based on the ratio of maximum GEE observed during the two intervals.

We summarized the limitations on GPP imposed by low and high temperature using a regression approach. We calculated the potential GEE ($\text{GEE}_{\text{potential}}$) that would be predicted based on K and T :

$$\text{GEE}_{\text{potential}} = T_{\text{low}} \times T_{\text{high}} \times \text{GEE}(K)$$

where T_{low} and T_{high} are the temperature scalars determined by normalizing the GEE response to T . T_{low} accounts for temperature constraints on GEE below 8°C and T_{high} accounts for temperature constraints on GEE above 21°C . $\text{GEE}(K)$ is the GEE determined as a function of K based on the least squares rectangular hyperbola fit during periods with $8^\circ\text{C} < T < 21^\circ\text{C}$. $\text{GEE}(K)$ was calculated at half-hourly intervals from October 1 to June 10 (winter) using gap-filled K and a regression based on January through June 10 observations. $\text{GEE}(K)$ was calculated for June 10 to September 30 (summer) using a regression based on July through August observations. $\text{GEE}(K)$ was then multiplied by the T scalars to calculate $\text{GEE}_{\text{potential}}$. This approach compared well with observed GEE (observed $\text{GEE} = 0.85 \times \text{GEE}_{\text{potential}} + 0.16$; $r^2 = 0.47$; $P < 0.01$). We determined the annual limitation to GPP imposed by cold T as: $\Sigma \text{GEE}(K) - \Sigma T_{\text{low}} \times \text{GEE}(K)$. Similarly, we determined the annual limitation to GPP imposed by high T as: $\Sigma \text{GEE}(K) - \Sigma T_{\text{high}} \times \text{GEE}(K)$.

We calculated the A_{max} -weighted day of the water year centroid (DOY_A) as: $\Sigma(\text{day of water year} \times A_{\text{max}}) / \Sigma(A_{\text{max}})$. Finally, we determined the difference between groups or years using a one-way analysis of variance. Reported confidence intervals are 95% CI unless otherwise stated.

3. Results

3.1. Meteorological conditions

The local climate was montane Mediterranean, with most P falling from October to May (Fig. 2). Temperature was highest from June to September and the last spring day with frost ranged from mid-April to May (Table 2). Warm and dry summers resulted in increased vapor pressure deficits (VPD), which averaged $\sim 1.8 \text{ kPa}$. Water vapor mixing ratios were typically higher in summer than winter, and the increased VPD during summer was tightly correlated with warmer temperatures. Mean summer temperature and VPD were consistent from year to year (Table 2).

The 1943–2010 mean P at the nearby Idyllwild, CA weather station was $648 \pm 256 \text{ mm}$ (mean $\pm$ stdev; <http://www.wrcc.dri.edu/>, accessed on February 9, 2011). Precipitation during our study varied markedly from year to year; 2007 was the second driest water year on record, with 227 mm; 2008 was about average, with 616 mm; 2009 was drier than average, with 464 mm.

3.2. Forest composition

The site was an oak and pine dominated mixed-conifer forest located near the shrubland to forest ecotone (Fig. 1). Two oaks contributed the largest fraction of basal area: *Quercus kelloggii*, a deciduous oak, and *Quercus chrysolepis*, an evergreen oak (Table 1). Four pines contributed a large fraction of basal area: *Pinus lambertiana*, *Pinus coulteri*, *Pinus ponderosa*, and scattered *Pinus jeffreyi*.

Table 2
Interannual variability.

Year	P (mm)	ET (mm)	T (°C)	T_s (°C)	VPD _s (kPa)	D_{frost} (day)	LAI _{peak} (day)	LAI _s (m ² m ⁻²)
2007	227	469	13.36	20.91	1.84	111	161	1.73
2008	616	674	13.06	21.42	1.77	146	209	1.91
2009	464	671	13.75	20.51	1.77	106	161	1.78

P (mm) is the water-year (October 1 to September 30) P measured at Idyllwild, CA. ET (mm) is the water-year evapotranspiration. T (°C) is the mean annual air temperature measured at the top of the eddy covariance tower. T_s (°C) is the mean summer (June 10 to September 30) air temperature measured at the tower. VPD_s (kPa) is the mean summer VPD. D_{frost} (day) is the last day of the calendar year that the temperature was below 0 °C. LAI_{peak} (day) was the day of the year that peak LAI occurred. LAI_s (m² m⁻²) was the mean summer LAI.

Calocedrus decurrens and a few *Abies concolor* also occurred in the tower footprint. There was a sparse shrub understory of *Ceanothus* spp. and *Arctostaphylos* spp.

The site experienced substantial tree mortality in the early 1990s, and again from 2002 to 2004, in both cases following a series of particularly dry years (Savage, 1994; Walker et al., 2006; Fellows and Goulden, 2012). Substantial tree mortality did not follow the extremely dry year in 2007. The comparative lack of mortality in 2007–2009 relative to 2002–2004 may be attributable to a difference in antecedent conditions. The lack of precipitation in 2002 (~35% of the climatic average), which apparently triggered the large scale mortality, followed 3 years with a mean P that was ~60% of the climatic mean. In contrast, 2007, which was about as dry as 2002, followed 3 years with precipitation that was nearer to the climatic mean. Alternatively, the lack of 2007–2009 mortality may be attributed to natural forest thinning during the 2002–2004 mortality, which may have eliminated many weaker trees and reduced overall LAI.

3.3. Soil matric potential

Soil matric potential (ψ_s) in 2009 remained high in spring and began to decline in June and July (Fig. 3). The shallow soil ψ_s declined first, and deep soil ψ_s declined ~30 days later. A small, early October storm increased shallow soil ψ_s slightly, whereas ψ_s

at 2-m depth did not recover until January 2010, when a cumulative total precipitation of 248–302 mm had fallen (Figs. 2 and 3).

3.4. Predawn and midday water potential

Predawn (ψ_{pd}) and midday (ψ_{md}) plant water potentials varied seasonally (Fig. 4). ψ_{pd} and ψ_{md} began to decline in all species by mid-July. The decline continued through summer, with the lowest ψ_{pd} s recorded in late October. Mean ψ_{pd} in late October ranged from –1.8 MPa in the yellow pines (*P. coulteri* and *P. ponderosa*) to –2.5 MPa in *C. decurrens*. The seasonal patterns of ψ_{pd} generally followed those of ψ_s . A more quantitative comparison between ψ_{pd} and ψ_s was precluded by the uncertain ψ_s calibration.

3.5. Leaf A_{max} and GEE

All evergreen species were photosynthetically active year-round and the seasonal patterns of A_{max} in 2009 were broadly similar. A_{max} gradually increased during the winter and spring, reached a transient peak around June, and then declined through the summer (Fig. 5).

The leaf A_{max} measurements weighted by species basal area ($A_{\text{max w}}$) paralleled the light saturated GEE (GEE_{max}) observed by eddy covariance (Fig. 6). Moderate rates of $A_{\text{max w}}$, $A_{\text{max w}} \times \text{LAI}$, and GEE_{max} were observed throughout the winter despite relatively cold days (Fig. 2). Photosynthesis increased in late spring and early summer coincident with warmer days and the growth of new leaves (Figs. 2 and 6), and peaked around June. Photosynthesis in 2009 declined through the late summer and early autumn, coincident with reductions in soil water content, reductions in plant water potential, elevated temperature, and elevated VPD (Figs. 2–4).

Fig. 2. Environmental data time series at site: (a) daily mean temperature (T ; °C; gap-filled), (b) daily mean vapor pressure deficit (VPD; kPa; gap-filled), (c) cumulative precipitation (ΣP ; mm) at Idyllwild, CA, and (d) daily mean volumetric soil moisture in the surface 30 cm (Soil Moisture; %).

Fig. 3. Soil matric water potential (ψ_s) at 5-cm (triangle), 10-cm (diamond), 25-cm (circle), 100-cm (inverted triangle), and 200-cm (square) depth.

Fig. 4. Predawn (ψ_{pd} ; filled circle) and midday (ψ_{md} ; filled triangle) xylem water potential (mean $\pm$ 95% CI) for (a) *Abies concolor*, (b) *Pinus lambertiana*, (c) *Pinus* spp. (*coulteri* or *ponderosa*), (d) *Calocedrus decurrens*, (e) *Quercus chrysolepis*, and (f) *Quercus kelloggii*.

Longer-term averages (60 days) were used to more clearly identify the year-to-year differences in GEE (Fig. 7). 60-Day average GEE_{max} increased in late spring of each year, reaching annual maxima of $\sim 12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in early May 2007 and early July 2008 and 2009. GEE_{max} declined markedly in July 2007, reaching a low of $\sim 4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the late 2007 and early 2008 water years. The interannual variation in summer and fall GEE_{max}

paralleled the interannual precipitation patterns. Precipitation was unusually low in 2007 (Table 2), as were the late summer rates of GEE_{max} in water year 2007 and the fall rates of GEE_{max} in early water year 2008 (Fig. 7). Precipitation was comparatively high in 2008 (Table 2), as were the summer rates of GEE_{max} in water year 2008 and the fall rates of GEE_{max} in early water year 2009.

Fig. 5. Leaf level carbon assimilation (A_{max} ; mean $\pm$ 95% CI) for (a) *Abies concolor*, (b) *Pinus lambertiana*, (c) *Pinus* spp. (*coulteri* or *ponderosa*), (d) *Calocedrus decurrens*, (e) *Quercus chrysolepis*, and (f) *Quercus kelloggii*.

Table 3
Constraints on Gross Primary Production.

Year	GPP	GPP(K)	$T_{low, lim}$ ($\text{gC m}^{-2} \text{yr}^{-1}$) (%)	$T_{high, lim}$ ($\text{gC m}^{-2} \text{yr}^{-1}$) (%)
2007	958	1265	43 (3%)	61 (5%)
2008	1148	1286	43 (3%)	60 (5%)
2009	1153	1272	28 (2%)	60 (5%)

GPP is the Gross Primary Production ($\text{gC m}^{-2} \text{yr}^{-1}$) calculated for each water year by summing the eddy covariance observations. GPP(K) is the sum of GEE calculated from the light response curves ($\text{gC m}^{-2} \text{yr}^{-1}$) without the temperature scalars; GPP(K) provides a measure of GPP in the absence of temperature and drought limitation. $T_{low, lim}$ ($\text{gC m}^{-2} \text{yr}^{-1}$ and percent relative to GPP(K)) is the reduction in annual GPP attributable to cold temperature. $T_{high, lim}$ ($\text{gC m}^{-2} \text{yr}^{-1}$ and percent relative to GPP(K)) is the reduction in annual GPP attributable to high temperature.

Table 4
Conifer leaf gas exchange.

ψ group	ψ range (MPa)	A_{max} ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)	g ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$)	A_g^{-1} ($\mu\text{mol CO}_2 \text{mol H}_2\text{O}^{-1}$)	DOY _A (day)
Wet ($n = 10$)	−0.86 to −1.00	6.84 (0.94) ^a	0.086 (0.017) ^a	93 (8) ^a	April 10 ^a
Average ($n = 10$)	−1.00 to −1.14	6.07 (0.82) ^{a,b}	0.062 (0.008) ^b	107 (7) ^b	April 7 ^{a,b}
Dry ($n = 9$)	−1.14 to −1.78	5.19 (0.97) ^b	0.053 (0.010) ^b	107 (9) ^b	March 31 ^b

ψ group indicates the relative annual range of conifer tree ψ_{pd} , and n indicates the number of trees in each group. ψ range (MPa) is the annual range of mean predawn water potential. A_{max} ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) is the mean ($\pm 95\%$ CI) carbon assimilation. g ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$) is the mean ($\pm 95\%$ CI) stomatal conductance. A_g^{-1} ($\mu\text{mol CO}_2 \text{mol H}_2\text{O}^{-1}$) is the mean ($\pm 95\%$ CI) water use efficiency. DOY_A (day) is the A_{max} -weighted day of year for all leaf gas measurements. Letters indicate significant differences between groups.

GEE declined with decreasing temperatures below 8°C and with increasing temperatures above 21°C (Fig. 8). Higher summer temperatures were correlated with increased evaporative demand and VPD. Previous physiological work has established that plant photosynthesis responds to several aspects of the physical environment that covary closely. High temperature may decrease NEE by decreasing photosynthesis or increasing respiration (Yuan et al., 2011). Similarly, high evaporative demand may cause stomatal closure and reduced photosynthesis as mediated by changes in VPD, relative humidity, transpiration, or leaf water potential (Jarvis, 1976; Mott and Parkhurst, 1991). Given the tight correlation between these various aspects of meteorology and associated problems with multicollinearity, we were unable to separate the possible metabolic effect of temperature on either photosynthesis or respiration from the possible effects of VPD, relative humidity, transpiration, or leaf water potential on stomatal aperture. We therefore use the term “high temperature limitation” to represent a lumped constraint that is mechanistically caused by one or more aspects of the environment that are correlated with

warmth. The constraint on annual GPP imposed at high temperature was similar to that imposed by low temperature (Table 3). Cold air temperatures reduced annual GPP by $28\text{--}43 \text{ gC m}^{-2} \text{yr}^{-1}$ (2–3% of GPP(K); Table 3) and high temperatures reduced GPP by $60\text{--}61 \text{ gC m}^{-2} \text{yr}^{-1}$ (5% of GPP(K)).

3.6. Soil water balance

The total moisture in the upper 2 m of soil (S_{0-200}) began to decline in mid-April 2009, immediately after the last large rainfall of the water year (Fig. 9). The rate of S_{0-200} decline remained quantitatively similar to, or slightly less than, the accumulated evaporative loss of water vapor through July, at which point S_{0-200} remained nearly constant while ET continued. Almost no precipitation was observed from April 20 to September 30 (Figs. 2 and 9), while S_{0-200} declined by $\sim 200 \text{ mm}$ and cumulative ET was greater than $\sim 400 \text{ mm}$.

Average ET was 605 mm yr^{-1} over the three study years, which exceeded the 436 mm mean P observed during the same period (Table 2). Average annual ET during 2007–2009 was 93% of the long-term mean P in Idyllwild, CA.

Fig. 6. (a) Mean leaf-level carbon assimilation weighted by each species' proportional basal area ($A_{max,w}$ ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$); mean $\pm$ standard error), (b) LAI ($\text{m}^2 \text{m}^{-2}$), and (c) the product of $A_{max,w}$ and LAI (solid black squares) and the daily eddy covariance GEE (open inverted triangles; mean $\pm$ standard error) averaged for periods with incoming solar radiation greater than 500 W m^{-2} .

Fig. 7. Gross Ecosystem Exchange for observations with incoming solar radiation greater than 500 W m^{-2} for the 2007, 2008, and 2009 water years (averaged for 60-day intervals; GEE ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)). Markers indicate the midpoint of each interval.

Fig. 8. Relationship between Gross Ecosystem Exchange (GEE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; mean $\pm$ 95% CI) and air temperature (T ; $^{\circ}\text{C}$) for observations with $K > 500 \text{ W m}^{-2}$. Winter and spring periods (January–June 10) are indicated with black triangles and summer periods (July–August) with open circles. July–August observations were normalized to the January–June 10 observations by multiplying by the ratio of the maximum GEE observed during January–June to the maximum GEE observed during July–August.

Fig. 9. Cumulative water balance during 2009. Storage in the top 2 m of soil calculated from the matric potential sensors (bold line; mm; a reduction in stored water indicates the withdrawal of water from the soil). ΣET is the cumulative evapotranspiration calculated from the eddy covariance observations (dashed line; mm; a negative ET indicates a loss of water vapor to the atmosphere). ΣET was set equal to storage in the upper 2 m of soil at the beginning of the summer drought. ΣP is observed cumulative precipitation (thin solid line; mm; a positive P indicates the input of precipitation to the land surface).

4. Discussion

4.1. Limitations on forest productivity

Cold winter temperatures, high summer temperatures, and the depletion of soil water all constrained GEE and GPP.

4.1.1. Cold temperature

The evergreen species at the site did not enter dormancy in winter and remained photosynthetically active year-round (Fig. 5). The impact of cold on evergreen GEE was restricted to an immediate, presumably kinetically mediated, decline at air temperatures below $\sim 8^{\circ}\text{C}$ (Fig. 8). The winters were characterized

by large temperature swings (Fig. 2), with occasional cold days that reduced or prevented CO_2 uptake. Most winter daytime periods were above 8°C , and the cold constraint on evergreen GPP was consequently minor, decreasing carbon uptake by $28\text{--}43 \text{ gC m}^{-2} \text{ yr}^{-1}$, or 2–3% (Table 3).

Cold temperatures may also have limited GPP by affecting deciduous leaf out and senescence. The main deciduous species at the site, Black Oak, accounted for $\sim 25\%$ of the overall basal area and contributed $\sim 0.45 \text{ m}^2 \text{ m}^{-2}$ of LAI during the summer (Table 1; Fig. 6). Black Oak A_{max} during the early summer was $\sim 10 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fig. 5), implying that a 1 day delay in leaf out might reduce GPP by $\sim 1 \text{ g m}^{-2}$. The timing of Black Oak leaf out coincided with seasonal warming; peak LAI occurred 50–63 days after the last frost (Table 2). Black Oak's growing season length was probably influenced by spring temperatures, along with additional factors such as photoperiod. However, a quantitative analysis of the GPP limitation imposed by the timing of deciduous tree leaf out is not possible without an improved understanding of the local controls on leaf phenology and aging.

4.1.2. High temperature

High temperatures were associated with a GPP limitation of $\sim 60 \text{ gC m}^{-2} \text{ yr}^{-1}$, or 5% (Table 3). These GEE reductions may have been caused by one or more factors, including the metabolic effect of warmth on photosynthesis (Yuan et al., 2011) or respiration (Mahecha et al., 2010), stomatal closure associated with the direct effect of VPD or humidity on stomata (Jarvis, 1976), or the indirect effect of evaporative demand on transpiration or leaf hydration (Mott and Parkhurst, 1991).

4.1.3. Soil water drought stress

The effect of soil water depletion varied from year to year coincident with P variability (Table 2; Figs. 2 and 7). The leaf gas exchange and plant water potential measurements were made in 2009, which was a moderately dry year. The Mediterranean climate drove a clear seasonal pattern of soil water availability and leaf gas exchange in 2009, with declines in ψ_s , ψ_{pd} , ψ_{md} , A_{max} , and GEE during the summer drought (Figs. 4–7). The decline in ψ_{pd} was both longer and more extreme than that reported for mid and upper montane forest in the Sierra Nevada (Royce and Barbour, 2001), a pattern that is consistent with our site's location near the dry and warm limit of Californian conifer forest. Reductions in GEE were less in the comparatively wet 2008 water year, when high rates of carbon uptake continued into the late summer and early fall (Fig. 7). These patterns indicate that soil water depletion was at least partly responsible for the declines in carbon uptake during summer periods.

The effect of soil drought on GEE was especially pronounced during the severe drought in 2007 (Table 2; Fig. 7). Annual P in 2007 was 227 mm, which is much less than the range of ET at the site (469–674 mm). Soil moisture measurements are not available for 2007, but it is unlikely that the winter rains moistened the soil beneath 2 m during that year (Figs. 2 and 3). The water balance observations in 2009 indicate withdrawal from the upper 2 m of soil supports ET through July, at which point deeper water sources became important (Fig. 9). GEE in 2007 was markedly reduced beginning in July, a pattern that we attribute to the depletion of water in the upper 2 m and the lack of accessible water beneath 2 m that resulted from the dry previous winter.

4.2. Factors contributing to forest persistence near the low elevation ecotone

We believe three factors contribute to the persistence of large trees and closed-canopy forest at the site: (1) lateral water and mass transport that create favorable microsites and reduce the effect of

low P , (2) high rates of GEE at low air temperatures that reduce the photosynthetic limitation by cold, and (3) deep rooting that allows access to soil water and reduces the effect of summer drought.

4.2.1. Favorable microsites

The variability in leaf-level gas exchange within a conifer species generally exceeded the variability between species (Fig. 5). Moreover, the between-individual differences in gas exchange were associated with between-individual differences in ψ_{pd} and presumably soil water access. We pooled all the conifers, irrespective of species, into three categories based on ψ_{pd} (Table 4). The individuals that had systematically higher ψ_{pd} s also had higher A_{max} s and stomatal conductances, lower water use efficiencies ($A g^{-1}$), and continued high rates of photosynthesis later into the summer (a greater DOY_A). Several of the least water-stressed trees were located near a local topographic low in the plot. This microsite may have had an improved water balance, either because of lateral water input or because of material deposition and deeper soils. The occurrence of favorable microsites that either had deeper soil or received lateral water subsidies presumably contributed to the persistence of individual trees at the site.

The overall tower footprint may on average receive a net input of water as surface or subsurface flow from upslope areas to the east (Fig. 1). Average ET exceeded P over the study (Table 2; Fig. 9). This pattern may have resulted from lateral water input to the footprint, and possibly also from a long-term depletion of deep soil water associated with a series of below average P years. The vegetation in the area was a complex mosaic of shrubland and forest. The ecotone was locally obvious (a sharp transition from shrubs to trees), but the precise location of the ecotone did not map onto a single elevation. Hence, the 1650–1700 m elevation band around our site was about half shrubland and half forest (Fig. 1), and it is possible that the areas with tall, persistent forest were hydrologically more favorable, either because of lateral water input or deeper soils.

4.2.2. Low temperature GEE

Photosynthesis by the evergreen canopy appeared unusually well adapted to cold. The relationship between GEE and temperature showed high CO_2 uptake at air temperatures down to $8^\circ C$. Yuan et al. (2011) determined the minimum temperature that net daytime CO_2 uptake occurred (T_b) in 42 evergreen needleleaf forests. We calculated T_b at our site following Yuan et al. for our non-gap filled observations. The observed T_b at our site was $-1^\circ C$, which is lower than that reported for any other site (Fig. 10).

The daytime winter temperatures at our site were typically 5 – $10^\circ C$. We hypothesize that evergreen vegetation that experiences extended periods in this thermal range will be strongly selected to maintain high rates of photosynthesis near freezing (e.g. Waring and Franklin, 1979), resulting in unusually low T_b s. Ecosystems in climates that are warmer than ours would be expected to contain species with photosynthetic capabilities adapted to higher temperatures. Ecosystems in climates that have colder winters than ours would be expected to contain species that are winter dormant and well adapted to the warmer parts of the year. Hence, evergreen boreal trees, which are dormant in winter, exhibit higher T_b s than we observed, despite much lower annual air temperatures (Goulden et al., 1997). A similar non-linear relationship between air temperature and cold adaptation mediated by phenological shifts was described by Kimball et al. (2010).

4.2.3. Deep soil water access

Vegetation withdrew water stored in the soil, saprolite, and fractured granitic bedrock to support transpiration and CO_2 uptake during the dry summer (Figs. 6, 7 and 9). Most P fell from October to April, and infrequent and small convective rainstorms contributed little over the rest of the year. Just 7 mm fell in 2009 from April

Fig. 10. Low temperature compensation point (T_b , the temperature at which an ecosystem shifts from a carbon sink to a source with decreasing temperature) for the main study site (black bar) and for 42 evergreen needle leaf forests investigated by Yuan et al. (2011) (gray bars; N is the number of T_b estimates in each temperature bin). The T_b at the study site was calculated following Yuan et al.'s protocol for non-gap filled observations.

20 to September 30; ET during this period exceeded the sum of water withdrawal from the top 2 m of soil and P by ~ 200 mm. ET continued after the water in the upper 2 m of soil was depleted, implying transpiration from July to late October was supported by sources beneath 2 m. An analysis of soil in the upper 2 m indicated texture was consistent with depth. If we assume similar soil properties beneath 2 m, this implies the plants accessed soil water to a depth of at least 4 m. A decrease in soil volumetric water holding capacity beneath 2 m associated with increasing coarse and rocky material would imply even deeper rooting.

Previous reports have also indicated deep rooting in mixed conifer forest. Arkley (1981) analyzed the water balance in the nearby San Bernardino Mountains and concluded that “highly productive forests of California survive through the frequent dry summers by using water stored deep in the decomposed granite or fractured rock substrate.” Similarly, fractured bedrock provided at least 70% of the water transpired during the growing season in a low elevation Sierra Nevada forest (Witty et al., 2003). Soil water stored in deep soils may buffer the large interannual P fluctuations at our site. Interannual ET variability was less than P variability, and ET exceeded P in 2007 and 2009. Some of the ET in dry years may have been supported by a net withdrawal of deep soil water. This long-term buffering may allow the growth and survival of a plant community that uses most of the long-term average P , and that is partly decoupled from interannual P variability (see also Goulden et al., 2012).

4.3. Are low elevation mixed conifer forests vulnerable to climate change?

In principle, climate warming at our site could (a) increase GPP by facilitating winter photosynthesis, (b) decrease GPP by increasing summer thermal stress, evaporative demand, or soil drying, or (c) cause offsetting increases in winter GEE and decreases in summer GEE. We used a simple regression approach to estimate the net effect of a $3^\circ C$ warming on $GEE_{potential}$. The associated reduction in cold stress increased winter carbon uptake by $24 g C m^{-2} yr^{-1}$, and

the associated increase in high temperature stress decreased summer uptake by $56 \text{ gC m}^{-2} \text{ yr}^{-1}$. We note that this approach does not account for the indirect effects of warming on plant physiological processes including deciduous phenology, or for the possibility that warming will accelerate ET and cause an earlier onset of drought. Nonetheless, the analysis indicates that the direct effect of warming on GPP is not expected to be extreme, and that the winter and summer responses may largely offset.

A more dramatic impact of climate change on the local forest may be associated with an increased frequency of severe drought, which could cause tree mortality at the site and ultimately shift species composition and structure. We attributed the persistence of forest at the site to deep soil water access and also possible surface or subsurface water inputs. GEE was markedly reduced in summer 2007, presumably as a result of deep soil drying and a lack of full soil recharge during the preceding winter. The vertical input of water into the deep soil column, as well as the lateral flow of water down a hillslope, require soil saturation. It appears unlikely that the soil at the site is recharged beneath 2 m depth in unusually dry years. Episodic tree mortality in the San Jacinto Mountains has occurred with prolonged droughts over the past 100 years (Savage, 1994; Walker et al., 2006; Fellows and Goulden, 2012). An increase in the frequency of particularly dry years caused by increased P variability, decreased mean P , or increased ET could promote deep soil drying and cause more frequent mortality at the site. In particular, the vegetation at the site may prove vulnerable to a series of unusually dry years that deplete deep soil moisture, reduce lateral flow, and drive sustained reductions in GEE and GPP (McDowell et al., 2008).

Acknowledgements

We thank Ray Anderson, Anne Kelly, Scot Parker, and Greg Winston for help with the setup, maintenance, collection, and processing of the eddy covariance data. The Kearney Foundation and the U.S. Department of Energy Terrestrial Ecosystem Science Program provided funding for this research.

References

- Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* 106 (17), 7063–7066.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol. Manage.* 259 (4), 660–684.
- Arkley, R.J., 1981. Soil moisture use by mixed conifer forest in a summer-dry climate. *Soil Sci. Soc. Am.* 45, 423–427.
- Aston, A.R., 1985. Heat-storage in a young eucalypt forest. *Agric. Forest Meteorol.* 35 (1–4), 281–297.
- Aubinet, M., Feigenwinter, C., Heinesch, B., Bernhofer, C., Canepa, E., Lindroth, A., Montagnani, L., Rebmann, C., Sedlak, P., Van Gorsel, E., 2010. Direct advection measurements do not help to solve the night-time CO_2 closure problem: evidence from three different forests. *Agric. Forest Meteorol.* 150, 655–664.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* 102 (42), 15144–15148.
- Cayan, D., Maurer, E., Dettinger, M., Tyree, M., Hayhoe, K., 2008. Climate change scenarios for the California region. *Climatic Change* 87 (0), 21–42.
- Fellows, A.W., Goulden, M.L., 2012. Rapid vegetation redistribution in Southern California following the early 2000s drought. *J. Geophys. Res.* 117, G03025.
- Finnigan, J., 2008. An introduction to flux measurements in difficult conditions. *Ecol. Appl.* 18 (6), 1340–1350.
- Flint, A.L., Campbell, G.S., Ellett, K.M., Calissendorff, C., 2002. Calibration and temperature correction of heat dissipation matrix potential sensors. *Soil Sci. Soc. Am. J.* 66 (5), 1439–1445.
- Goulden, M.L., Anderson, R.G., Bales, R.C., Kelly, A.E., Meadows, M., Winston, G.C., 2012. Evapotranspiration along an elevation gradient in California's Sierra Nevada. *J. Geophys. Res.* 117, G03028.
- Goulden, M.L., Daube, B.C., Fan, S.-M., Sutton, D.J., Bazzaz, A., Munger, J.W., Wofsy, S.C., 1997. Physiological responses of a black spruce forest to weather. *J. Geophys. Res.* 102 (D24), 28987–28996.
- Goulden, M.L., Munger, J.M., Fan, S.-M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biol.* 2, 169–182.
- Goulden, M.L., Winston, G.C., McMillan, A.M.S., Litvak, M.E., Read, E.L., Rocha, A.V., Rob Elliot, J., 2006. An eddy covariance mesonet to measure the effect of forest age on land-atmosphere exchange. *Global Change Biol.* 12 (11), 2146–2162.
- Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philos. Trans. R. Soc. Lond. B* 273, 593–610.
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. *Forest Sci.* 49 (1), 12–35.
- Kaimal, J.C., Gaynor, J.E., 1991. Another look at sonic thermometry. *Bound. Lay. Meteorol.* 56, 401–410.
- Kelly, A.E., Goulden, M.L., 2008. Rapid shifts in plant distribution with recent climate change. *Proc. Natl. Acad. Sci. U.S.A.* 105 (33), 11823–11826.
- Kimball, S., Angert, A., Huxman, T., Venable, D., 2010. Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Global Change Biol.* 16 (5), 1555–1565.
- Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A., Ackerly, D.D., 2008. Climate change and the future of California's endemic flora. *PLoS ONE* 3 (6), e2502.
- Leuning, R., van Gorsel, E., Massman, W.J., Isaac, P.R., 2012. Reflections on the surface energy imbalance problem. *Agric. Forest Meteorol.* 156, 65–74.
- Mahecha, M.D., Reichstein, M., Carvalhais, N., Lasslop, G., Lange, H., Seneviratne, S.I., Vargas, R., Ammann, C., Arain, M.A., Cescatti, A., Janssens, I.A., Migliavacca, M., Montagnani, L., Richardson, A.D., 2010. Global convergence in the temperature sensitivity of respiration at ecosystem level. *Science* 329 (5993), 838–840.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yeepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178 (4), 719–739.
- Meesters, A.G.C.A., Vugts, H.F., 1996. Calculation of heat storage in stems. *Agric. Forest Meteorol.* 78, 181–202.
- Minnich, R.A., 2007. Southern California conifer forests. In: Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), *Terrestrial Vegetation of California*. University of California Press, Berkeley, CA, pp. 502–538.
- Moore, C.J., Fisch, G., 1986. Estimating heat storage in Amazonian tropical forest. *Agric. Forest Meteorol.* 38, 147–169.
- Mott, K.A., Parkhurst, D.F., 1991. Stomatal responses to humidity in air and helox. *Plant Cell Environ.* 14, 509–515.
- Parnesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421 (6918), 37–42.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58 (6), 501–517.
- Royce, E.B., Barbour, M.G., 2001. Mediterranean climate effects. I: conifer water use across a Sierra Nevada Ecotone. *Am. J. Bot.* 88 (5), 911–918.
- Savage, M., 1994. Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest in California. *Can. J. Forest Res.* 24 (6), 1149–1159.
- Seager, R., Vecchi, G.A., 2010. Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proc. Natl. Acad. Sci. U.S.A.* 107 (50), 21277–21282.
- Twine, T.E., Kustas, W.P., Norman, J.M., Cook, D.R., Houser, P.R., Meyers, T.P., Prueger, J.H., Starks, P.J., Wesely, M.L., 2000. Correcting eddy-covariance flux underestimates over a grassland. *Agric. Forest Meteorol.* 103 (3), 279–300.
- USFS, 2007. *EvegTile59A.03.v2*. USFS, McClellan, CA.
- Vargas, R., Allen, M.F., 2008. Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration. *New Phytol.* 179 (2), 460–471.
- Walker, R., Rosenberg, M., Warbington, R., Schwind, B., Beardsley, D., Ramirez, C., Fischer, L., Frerichs, B., 2006. Inventory of Tree Mortality in Southern California Mountains (2001–2004) due to Bark Beetle Impacts. Fire and Resource Assessment Program, California Department of Forestry and Fire Protection, Sacramento, CA.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416 (6879), 389–395.
- Waring, R.H., Franklin, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* 204 (4400), 1380–1386.
- Wilson, K., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Bernhofer, P., Bernhofer, C., Ceulemans, R., Dolman, H., Field, C., Grelle, A., Ibrom, A., Law, B.E., Kowalski, A., Meyers, T., Moncrieff, J., Monson, R., Oechel, W., Tenhunen, J., Valentini, R., Verma, S., 2002. Energy balance closure at FLUXNET sites. *Agric. Forest Meteorol.* 113 (1–4), 223–243.
- Witty, J.H., Graham, R.C., Hubbert, K.R., Doolittle, J.A., Wald, J.A., 2003. Contributions of water supply from the weathered bedrock zone to forest soil quality. *Geoderma* 114 (3–4), 389–400.
- Yuan, W., Luo, Y., Liang, S., Yu, G., Niu, S., Stoy, P., Chen, J., Desai, A.R., Lindroth, A., Gough, C.M., Ceulemans, R., Arain, A., Bernhofer, C., Cook, B., Cook, D.R., Dragoni, D., Gielen, B., Janssens, I.A., Longdoz, B., Liu, H., Lund, M., Matteucci, G., Moors, E., Scott, R.L., Seufert, G., Varner, R., 2011. Thermal adaptation of net ecosystem exchange. *Biogeosciences* 8, 1453–1463.