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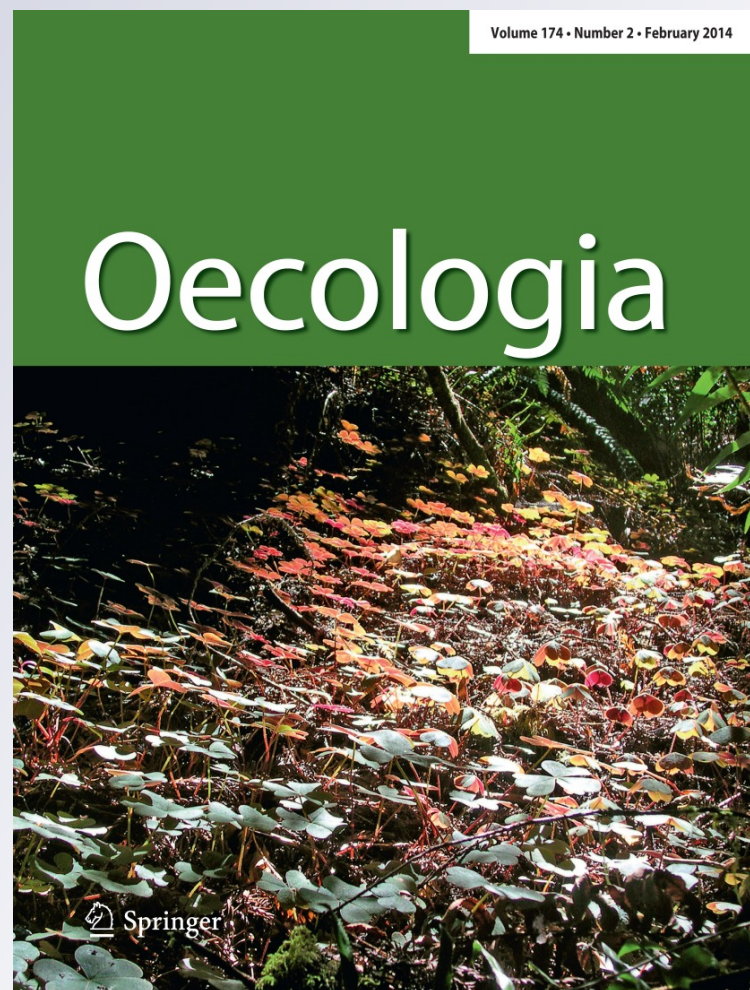
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# Light use efficiency of California redwood forest understory plants along a moisture gradient

Louis S. Santiago · Todd E. Dawson

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**Abstract** We investigated photosynthesis of five plant species growing in the understory at three sites (1,170-, 1,600- and 2,100-mm annual moisture inputs), along the geographical range of coastal California redwood forest, to determine whether greater inputs of rain and fog at northern sites enhance photosynthetic utilization of fluctuating light. Measurements of understory light environment and gas exchange were carried out to determine steady state and dynamic photosynthetic responses to light. Leaf area index ranged from 4.84 at the 2,100-mm site to 5.98 at the 1,170-mm site. Maximum rates of net photosynthesis and stomatal conductance ( $g$ ) did not vary appreciably within species across sites. Photosynthetic induction after a change from low to high light was significantly greater in plants growing in lower light conditions regardless of site. Photosynthetic induction also increased with the rate of  $g$  in diffuse light, prior to the increase to saturating light levels. Post-illumination  $\text{CO}_2$  assimilation was the largest factor contributing to variation in C gain during simulated lightflecks. The duration of post-illumination photosynthetic activity, total  $\text{CO}_2$  assimilation per light received, and light use efficiency during simulated lightflecks increased significantly with moisture inputs in four out of five species. Increasing leaf N concentration with increasing moisture inputs in three

out of five species, coupled with changes in leaf N isotopic composition with the onset of the summer fog season suggest that natural N deposition increases with rain and fog inputs and contributes to greater utilization of fluctuating light availability in coastal California redwood forests.

**Keywords** Community diversity · Fog · Lightfleck · Nitrogen isotope · Photosynthesis

## Introduction

Light is a critical resource for plants, particularly in forest understory environments where long periods of low-intensity diffuse light are interspersed by brief high-intensity lightflecks. Up to 80 % of the annual C gain in some understory plants occurs during lightflecks (Chazdon 1988). The ability of understory plants to maximize C gain during lightflecks depends on: (1) the photosynthetic induction response once a leaf is illuminated, (2) the ability to maintain induction during diffuse-light periods, and (3) the ability to continue photosynthetic activity immediately after a lightfleck (post-illumination  $\text{CO}_2$  assimilation) (Sharkey et al. 1986; Valladares et al. 1997; Montgomery and Givnish 2008). Maximizing C gain may also depend on the overstory canopy structure and its resultant light regime, which determines the temporal distribution of lightflecks, the magnitude of lightflecks, and the total amount of light received by an understory plant (Montgomery and Chazdon 2001). Acclimation and adaptation to low light therefore involve rapid photosynthetic induction in response to sudden increases in light availability and greater light use efficiency (LUE) than that expected by steady state  $\text{CO}_2$  assimilation rates (Chazdon and Pearcy 1986a, b; Valladares et al. 1997; Montgomery

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and Givnish 2008). Yet, resources besides light might also limit the performance of plants in forest understory environments (Coomes and Grubb 2000). For example, nutrient addition has been shown to enhance photosynthesis and growth of tropical forest seedlings, even under severely low light conditions (Burslem et al. 1996; Pasquini and Santiago 2012; Santiago et al. 2012). Furthermore, initial stomatal conductance ( $g_{\text{initial}}$ ) is greater and photosynthetic induction more rapid during wet season than dry season mornings for tropical understory shrubs, illustrating a positive effect of water availability on understory C gain (Allen and Percy 2000). To further test the role of water availability on C gain under low light, we investigated photosynthesis and LUE under fluctuating light environments across a moisture gradient in California redwood forest.

Ecosystem moisture availability is usually evaluated at relatively coarse scales, often represented across landscapes as annual inputs (Stephenson 1990). However, the complete suite of water inputs also includes fog, dew and mist, and other forms of occult precipitation (Cavelier and Goldstein 1989; Andrade 2003; Goldsmith et al. 2012, 2013), which may provide important sources of water, especially if they occur during the dry season when precipitation is uncommon (Dawson 1998). Occult precipitation can be difficult to detect with traditional micrometeorological techniques such as rain gauges, but with prolonged occurrence they can thoroughly saturate plant canopies and soil, thus substantially increasing plant available moisture (Bruijnzeel et al. 1993; Santiago et al. 2000). Clearly water uptake by roots improves plant water status, but for a long time, researchers have known that water absorption by organs other than roots also occurs (Stone et al. 1950; Stone et al. 1956; Vaadia and Waisel 1963; Rundel 1982). Under field conditions (Burgess and Dawson 2004; Oliveira et al. 2005; Breshears et al. 2008; Limm et al. 2009; Eller et al. 2013; Goldsmith et al. 2013), as well as in experimental settings (Simonin et al. 2009), fog interception has been shown to increase plant water status and even photosynthesis, indicating that foliar water uptake can enhance plant physiological function and C gain, potentially contributing to greater LUE and a greater C income under low light conditions.

Coastal California redwood forests receive moisture inputs from two main sources: frontal rain storms during short wet Mediterranean-type winters and summer fog. Precipitation in redwood forests increases from south to north, whereas frequency of fog is greatest in northern California (up to 44 %), and remains high through central California, but declines below 30 % in Oregon and southern California (Johnstone and Dawson 2010). Importantly, coastal fog peaks in August, with the greatest

occurrence from June to September, when the lack of frontal storms promotes otherwise dry conditions. Indeed the extent of redwood forest along the California coast is highly associated with frequency of fog greater than 40 % (Johnstone and Dawson 2010). Furthermore, there is evidence of past declines in abundance of redwood forests during glaciations (Heusser 1998), when coastal upwelling may have been reduced, thus limiting the frequency of summer fog (Ortiz et al. 1997; Herbert et al. 2001; Johnstone and Dawson 2010). It is also thought that summer subsidies of fog contribute to the height of redwood trees through foliar deposition and absorption rather than the trees having to always transport water more than 100 m against gravity (Simonin et al. 2009), making them the tallest tree species in the world. Consequently, the shade cast by redwood trees is severe, producing low light conditions for understory plants (Pfitsch and Percy 1989a, b). Yet, it is important to understand the ecology of understory plants in redwood forest, because they represent the largest contribution to plant biological diversity of the redwood ecosystem as they grow in the dappled light below a mono-canopy of giants. Recent studies demonstrating that foliar water uptake is a common water acquisition strategy for nearly all of the species that comprise the California redwood forest plant community (Dawson 1998; Limm et al. 2009), and that the capacity for foliar uptake varies at the landscape scale within the common redwood forest fern, *Polystichum munitum* (Limm and Dawson 2010), indicate that there is large potential for interactions between moisture availability, foliar absorption and C gain across moisture gradients in California redwood forest.

Based on better-developed forest understory vegetation at northern redwood forest sites under consistently closed canopy conditions, we expected greater photosynthetic utilization of lightflecks in sites receiving greater moisture inputs. We therefore hypothesized that there were two main ways that moisture inputs could influence the ability of understory plants to exploit fluctuating light. One was that increased moisture promotes greater stomatal aperture in low light, thus allowing a more rapid induction following a sudden increase in light availability. The second was that greater rain and fog would promote soil solution conditions that favor N uptake, which would have a positive effect on allocation to photosynthetic enzymes such as ribulose-1,5-bisphosphate carboxylase oxygenase and the light-harvesting complexes of the thylakoid membrane (Evans 1989), leading to greater CO<sub>2</sub> assimilation per quantity of light received. Moreover, the N in rain, and especially fog (Weathers et al. 2000; Ewing et al. 2009; González et al. 2011), could directly provide greater access to this important resource associated with maximizing C gain. Our main objectives were to:



1. Examine how steady state and dynamic understory photosynthesis respond to varying canopy structure across this moisture gradient.
2. Determine the consequences of mean annual rain and fog input on the ability of plants in the redwood forest understory habitat to assimilate C under low light conditions.
3. Understand how LUE varies with moisture availability along this environmental gradient.

## Materials and methods

### Study sites and species

This study was conducted at three sites along a 612-km north–south gradient along the California coast. This study region roughly spans the range of the California coastal redwood forest, which extends from California's border with Oregon in the northern, high-rainfall end, to Monterey County at the southern, drier end where forest begins to grade into chaparral vegetation. The climate of the region is Mediterranean with cool wet winters caused by frontal storms, and otherwise dry summers, except for inputs by coastal summer fog (Dawson 1998). We selected three sites over a range of combined mean annual precipitation and fog inputs of 1,170, 1,600, and 2,100 mm, with minimal changes in elevation and distance to coast. All sites contain mature forest on flat to moderately sloping ( $<4^\circ$ ) topography. The 1,170-mm site is located along Opal Creek in Big Basin State Park, the 1,600-mm site is located along Bull Creek in Humboldt Redwoods State Park, and the 2,100-mm site is located on lower Cal Barrel Road in Prairie Creek State Park. Emergent canopy trees at the sites range from ~75 m at the 1,170-mm site to  $>110$  m at the 1,600- and 2,100-mm sites. Across the 1,170-, 1,600-, and 2,100-mm sites, interpolated mean annual temperature is 13.1, 10.0 and 11.6 °C, mean relative humidity is 73.3, 74.2, and 74.8 %, mean annual Penman potential evapotranspiration is 1,068, 863, and 920 mm, and the mean annual hours with sunshine is 68.8, 58.5, and 55.1 %, respectively (New et al. 2002).

To compare photosynthetic C gain of understory plants across sites, we selected the five most common understory species across all sites, including saplings ~2 m height of California coast redwood (*Sequoia sempervirens*; dominant canopy tree), and tan oak (*Notholithocarpus densiflora*; understory to mid-canopy tree), 1- to 2-m-tall huckleberry (*Vaccinium ovatum*; understory shrub), 5- to 20-cm-tall sorrel (*Oxalis oregana*; understory herb) and 0.5- to 1-m tall western sword fern (*Polystichum munitum*; fern). We refer to all species by generic names hereafter.

### Light environment

Hemispherical photographs were used to quantify the light environment for each plant in which photosynthetic light response curves and induction curves were measured. Photographs were taken using a digital camera (Coolpix 4500; Nikon, Japan) and a fisheye converter lens (FC-E8; Nikon) with an exposure time of 1/125 and an aperture of 2.8 (Engelbrecht and Herz 2001). The camera was oriented horizontally 15–20 cm above the plant and toward north using a compass. All photographs were taken with overcast skies late in the afternoon to maximize contrast between foliage and sky. Estimation of percent direct and diffuse canopy light transmittance from hemispherical photographs was accomplished with the Gap Light Analyzer program (Frazer et al. 1999), and summed to provide total percent canopy light transmittance.

The average canopy cover for each site was measured with a plant canopy analyzer late in the afternoon in September 2005 (LAI-2000; Li-Cor Biosciences, Lincoln, NE). Two canopy analyzers that had been inter-calibrated and synchronized were used for all measurements. One unit was placed in a large clearing for above-canopy measurements, and the second unit was carried along a 30-m transect at each site. To minimize the influence of understory vegetation, LAI-2000 measurements were taken ~1 m above the ground (Deblonde et al. 1994). The LAI-2000 measures light using five concentric light-detecting silicon rings, sampling five concentric sky sectors with central zenith angles of 7°, 23°, 38°, 53°, and 68°. We only used the first four rings because, due to the tall nature of trees in this forest, and rolling hills near the horizon, the 68° ring was often not exposed to sky. Leaf area index (LAI) was estimated by an inversion model comparing the transmittances, calculated simultaneously for each sky sector, measured above and below the canopy (Cutini et al. 1998).

### Community composition

Plant community composition of the understory was evaluated in ten 30-m transects with five 0.25-m<sup>2</sup> plots randomly chosen along each transect. Within each plot, each individual was identified and recorded and a visual assessment of percent cover was determined. Other species present near transects, but not falling in a measurement plot, were recorded for total species richness per site. Community composition was evaluated as plant density, species richness, evenness and the Shannon–Wiener Function for diversity (Krebs 1989).

### Photosynthetic light response

Photosynthetic CO<sub>2</sub> assimilation (A) and g in response to light were measured on newly formed mature understory leaves from three to four individuals per species

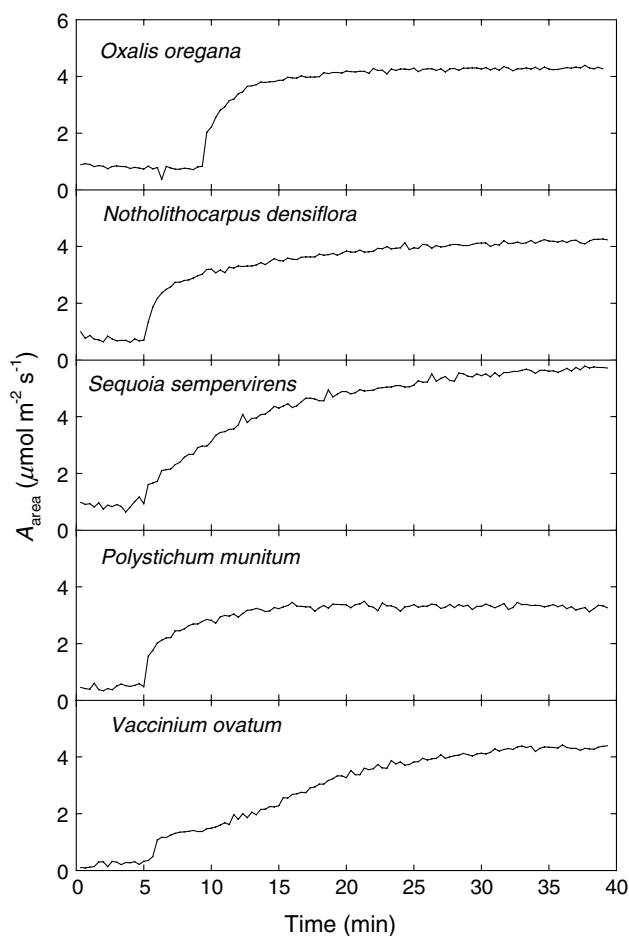
at each site across a range of photon flux density (PFD; 0–1,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) in July and August 2005. We first measured  $A$  at 1,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PFD, before light was decreased in a stepwise fashion for a total of ten measurement points to 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Measurements were conducted with a portable gas exchange system equipped with an infrared gas analyzer for quantifying precise changes in  $\text{CO}_2$  and  $\text{H}_2\text{O}$  vapor concentrations inside a cuvette containing a functional leaf (Li-6400; Li-Cor Biosciences); the cuvette was also outfitted with a red/blue light source (Li-Cor 6400-02B no. SI-710; Li-Cor Biosciences), with  $\text{CO}_2$  concentration maintained at 400  $\mu\text{mol mol}^{-1}$ , and ambient relative humidity (47.0–73.9 %), and air temperature (16.8–29.0 °C). Parameters for light response curves were fit to a non-rectangular hyperbola (Sims and Pearcy 1991).

### Photosynthetic induction state

The capacity for understory species to respond to increasing PFD, was measured as the time course of  $A$  and  $g$  after a step increase in PFD from diffuse levels (10  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) to light-saturated levels (300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) with the same portable gas exchange system cited above (Li-6400; Li-Cor Biosciences) in July and August 2005 (Fig. 1). Measurements were conducted on leaves that had been acclimated to ambient light (10–15  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), but had not been exposed to lightflecks for at least 30 min.  $g_{\text{initial}}$  prior to transfer from low to high light and the time to reach 90 % of a fully induced value of  $\text{CO}_2$  assimilation ( $T_{90}$ ) were recorded. Induction state of the leaf is defined as the percent of fully induced photosynthetic assimilation rate at 60 s since the time of illumination ( $A_{60}$ ) (Chazdon and Pearcy 1986a, b).

### Lightfleck experiments

During March and April 2005, photosynthesis during and following short-duration, high-intensity lightflecks was measured with a portable infrared gas analyzer (Li-Cor 6400; Li-Cor Biosciences), by exposing a leaf to diffuse light (10  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for 5 min, then exposing it to saturating (400  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) lightflecks of different length (2, 4, 8, 32, 64 s) (Pfitsch and Pearcy 1989a, b). A period of 120 s of diffuse light preceded and followed each lightfleck. Total  $A$  during each lightfleck, post-illumination  $\text{CO}_2$  assimilation ( $A_{\text{post}}$ ), the duration of post-illumination  $\text{CO}_2$  fixation ( $T_{\text{post}}$ ), and total  $\text{CO}_2$  assimilation per PFD received during the lightfleck and during the post-illumination assimilation period ( $A/\text{PFD}$ ) were calculated.  $T_{\text{post}}$  was defined as the time for photosynthesis to decrease to within 1 SD of diffuse light values after the step decrease from saturating to diffuse light levels (Fig. 2). LUE was defined as total assimilation during the lightfleck (including post-illumination  $\text{CO}_2$  fixation) divided by the amount of assimilation that would

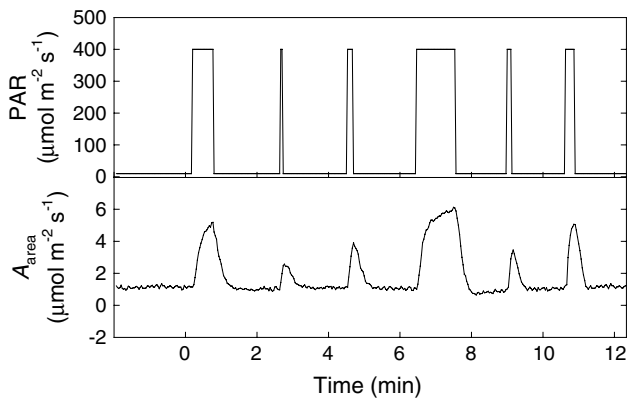


**Fig. 1** Representative time course of induction of photosynthetic  $\text{CO}_2$  assimilation per area ( $A_{\text{area}}$ ) of five species growing in the redwood forest understory at the 1,170-mm site (Big Basin State Park, CA). Low-light-acclimated leaves experienced 5–10 min of diffuse light (10  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) before saturating light (300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was applied for 30–45 min

occur if the leaf responded instantaneously to changing light (Chazdon and Pearcy 1986a, b; Valladares et al. 1997).

### Leaf structure and chemistry

Leaves were collected following photosynthetic measurements in spring (March and April) and summer (July and August) 2005, and transported to the laboratory where the leaf area sampled for gas exchange was recorded. Leaves were dried for 48 h at 65 °C, and weighed for determination of specific leaf area (SLA) so that  $A$  could be expressed per area ( $A_{\text{area}}$ ) and per mass ( $A_{\text{mass}}$ ). Dried leaves were ground to a fine powder and all leaves from the same individual plant were pooled for chemical analysis. Leaf C and N concentrations and stable isotopic composition of C ( $\delta^{13}\text{C}$ ) and N ( $\delta^{15}\text{N}$ ) were determined with an elemental analyzer (ANCA-SL; PDZ Europa Scientific, Manchester, UK),



**Fig. 2** Representative time course of photon flux density (*PAR*) during lightfleck experiment (*upper panel*) and response of  $A_{\text{area}}$  to saturating lightflecks ( $400 \mu\text{mol m}^{-2} \text{s}^{-1}$  *PAR*) of varying duration (*lower panel*) for a *Sequoia sempervirens* sapling at the 2,100-mm site (Prairie Creek State Park, CA). Each lightfleck was separated by 2-min intervals of diffuse light ( $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ )

interfaced with a continuous flow isotope ratio mass spectrometer (PDZ Europa 20/20; PDZ Europa Scientific), and reported in delta notation relative to the Pee Dee belemnite standard at the Center for Stable Isotope Biogeochemistry. Long-term external precision for the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses are  $\pm 0.22$  and  $0.25 \text{‰}$ , respectively.

#### Statistical analysis

Data were averaged for each species within a site, and the average site-specific values for species were analyzed for variation in light environment, photosynthetic parameters and leaf chemistry as dependent variables. General linear models were used to evaluate variation among dependent variables with species and sites as categorical independent variables in SAS version 9.2 (SAS Institute, Cary, NC). When significant variation was detected, differences among species or sites were assessed with post hoc Duncan's multiple range tests. The bivariate relationship between  $T_{90}$  and  $g_{\text{initial}}$  was evaluated with non-linear regression in SAS version 9.2 (SAS Institute). The bivariate relationship between  $A_{60}$  and total canopy transmittance was assessed using standardized major axis regression using (S)MATR version 1.0 (Falster et al. 2003), because both  $x$  and  $y$  are random variables and  $x$  is not under the control of the experimenter (Sokal and Rohlf 1995).

## Results

### Light environment

The three sites varied in their understory light environment. LAI was significantly greater at the 1,170- and 1,600-mm

**Table 1** Light environment characteristics in the understory of coastal California redwood forest sites that vary in annual moisture inputs

	Big Basin State Park (1,170 mm)	Humboldt Redwoods State Park (1,600 mm)	Prairie Creek State Park (2,100 mm)
LAI	$5.98 \pm 0.10$ a	$5.58 \pm 0.29$ a	$4.84 \pm 0.21$ b
Total transmission (%)			
<i>Notholithocarpus densiflora</i>	$12.5 \pm 3.9$ a	$10.9 \pm 1.5$ a	$13.0 \pm 1.4$ a
<i>Oxalis oregana</i>	$11.8 \pm 1.3$ a	$6.0 \pm 0.5$ a	$8.3 \pm 0.5$ a
<i>Polystichum munitum</i>	$9.8 \pm 1.1$ a	$8.6 \pm 3.9$ a	$10.4 \pm 1.2$ a
<i>Sequoia sempervirens</i>	$14.0 \pm 2.0$ a	$5.9 \pm 0.6$ b	$8.4 \pm 2.2$ b
<i>Vaccinium ovatum</i>	$13.9 \pm 2.2$ a	$12.3 \pm 1.3$ a	$8.1 \pm 1.8$ a

Values for total transmission are based on canopy photographs above individual plants ( $n = 3\text{--}5$ ). Values for leaf area index (LAI) are based on site means ( $n = 30$ ). Values are means  $\pm 1$  SE. LAI values or total transmission values within species that do not share the *same letter* were significantly different ( $P < 0.05$ )

sites than at the 2,100-mm site (Table 1). Despite the greatest LAI at the 1,170-mm site, the mean canopy light transmittance of measurement species of 12 % at the 1,170-mm site was significantly greater than the values of  $\sim 9$  % at the two wetter sites ( $P < 0.05$ ), indicating that individuals of these five species grew in slightly higher light environments in the driest site. Within species, this difference was only significant for *Sequoia* (Table 1).

### Community composition

Mean plant density (individuals  $\text{m}^{-2}$ ) was lowest at the 1,170-mm site (3.3), peaked at the 1,600-mm site (92.96), and was intermediate at the 2,100-mm site (68.24; Table 2). Mean percent cover increased with increasing moisture inputs from 7.4 % at the 1,170-mm site to 31.0 % at the 1,600-mm site, and 99.6 % at the 2,100-mm site, because of larger sizes of individuals at the latter. Species richness in measurement plots varied from a low of four at the 1,170-mm site, to a high of 15 at the 1,600-mm site, and to 11 at the 2,100-mm site. Total species observed at a site increased with moisture inputs and was 13, 20, and 24 for the 1,170-, 1,600-, and 2,100-mm sites, respectively. The Shannon diversity index revealed that diversity was greatest at the 1,600-mm site (1.12), followed by the driest site (0.76), and lowest at the wettest site (0.43). Evenness, an important component of the Shannon diversity index, played an important role in structuring variation in diversity across the sites and was greatest at the 1,600-mm site



**Table 2** Density of individuals for each California redwood forest understory plant species encountered in transects at three sites that vary in mean annual moisture inputs (1,170 mm, Big Basin State Park; 1,600 mm, Humboldt Redwoods State Park; 2,100 mm Prairie Creek State Park)

Species	Family	Density (individuals m <sup>-2</sup> )		
		Big Basin	Humboldt Redwoods	Prairie Creek
<i>Adenocaulon bicolor</i>	Asteraceae			0.32
<i>Anemone deltoidea</i>	Ranunculaceae		2.72	0.88
<i>Blechnum spicant</i>	Polypodiaceae			0.56
<i>Calypso bulbosa</i>	Orchidaceae			0.08
<i>Claytonia palustris</i>	Portulacaceae		1.12	
<i>Dentaria californica</i>	Brassicaceae		0.64	
<i>Galium spp.</i>	Rubiaceae		0.16	
<i>Pleuropogon hooverianus</i>	Poaceae		1.12	
<i>Hierochloa occidentalis</i>	Poaceae		1.60	
<i>Iris douglasiana</i>	Iridaceae		0.32	
<i>Notholithocarpus densiflora</i>	Fagaceae	0.13	0.32	
<i>Oxalis oregana</i>	Oxalidaceae	2.53	67.36	62.88
<i>Polystichum munitum</i>	Polypodiaceae	0.13	0.80	2.00
<i>Pteridium aquilinum</i>	Polypodiaceae			0.16
<i>Rosa gymnocarpa</i>	Rosaceae		0.16	
<i>Rubus parviflorus</i>	Rosaceae		10.24	
<i>Smilacina racemosa</i>	Convallariaceae			0.16
<i>Trientalis latifolia</i>	Primulaceae		0.96	0.56
<i>Trillium ovatum</i>	Convallariaceae			0.40
<i>Vaccinium ovatum</i>	Ericaceae	0.53		0.24
<i>Vancouveria planipetala</i>	Berberidaceae		0.48	
<i>Viola sempervirens</i>	Violaceae		4.96	

(0.41), followed by the driest site (0.32), with the wettest site having the lowest evenness (0.18) due to the prevalence of *Oxalis*, which comprised 72 % of all individual plants in the plots.

#### Photosynthetic leaf traits

Among sites, *Oxalis* was the only species that showed variation in  $A_{\text{area}}$ , with lower values at the wettest site ( $F_{2,6} = 4.32$ ;  $P < 0.05$ ; Table 3). There were no significant differences in  $A_{\text{mass}}$  or maximum  $g$  ( $g_{\text{max}}$ ) within any species among sites ( $P > 0.05$ ). Leaf N increased significantly with increasing moisture in *Notholithocarpus*, *Oxalis* and *Polystichum*, but not in *Sequoia* or *Vaccinium* (Table 3). *Oxalis* was the only species that showed variation in SLA among sites, with greater values at the two wetter sites compared with the driest site ( $F_{2,6} = 7.3$ ;  $P < 0.05$ ; Table 3).

Across all sites, saplings of the two tree species, *Sequoia* and *Notholithocarpus*, exhibited greater values of  $A_{\text{area}}$  ( $F_{4,32} = 13.4$ ;  $P < 0.0001$ ) and  $A_{\text{mass}}$  ( $F_{4,32} = 77.5$ ,  $P < 0.0001$ ), than the low-statured species, *Oxalis*, *Polystichum*, and *Vaccinium*. Mean  $g_{\text{max}}$  across species varied from  $67.5 \pm 11.8$  mmol m<sup>-2</sup> s<sup>-1</sup> in *Notholithocarpus*

to  $4.35 \pm 3.4$  mmol m<sup>-2</sup> s<sup>-1</sup> in *Polystichum*, but was not significantly different among species ( $F_{4,32} = 1.35$ ;  $P > 0.05$ ). Leaf N ( $F_{4,32} = 112.5$ ;  $P < 0.0001$ ) and SLA ( $F_{4,32} = 365.2$ ;  $P < 0.0001$ ) showed significant variation among species.

#### Photosynthetic induction

Induction periods during photosynthetic responses to an increase in PFD before steady state photosynthetic rates were reached varied from 5 to 40 min depending on the species (Fig. 1). The shape of the response function varied from a hyperbolic shape in *Oxalis*, *Notholithocarpus*, and *Polystichum*, to a more gradual response in *Sequoia* and *Vaccinium* (Fig. 1). Mean  $A_{60}$  varied from 21 to 56 % ( $43 \pm 3$  %  $\bar{x} \pm 1$  SE), and did not differ significantly among species or sites ( $P > 0.05$ ), but decreased with increasing canopy light transmittance (Fig. 3), indicating that plants growing under lower light availability showed faster induction.  $T_{90}$  was shorter in leaves that had a greater  $g_{\text{initial}}$  (Fig. 4), and was significantly lower at the 1,600-mm site ( $9.1 \pm 2.4$  min) compared to the 1,170-mm site ( $14.3 \pm 1.9$  min) and the 2,100-mm site ( $15.3 \pm 1.9$  min) ( $F_{2,26} = 4.61$ ;  $P < 0.05$ ). Values for  $g_{\text{initial}}$  were not

**Table 3** Maximum stomatal conductance ( $g_{\max}$ ), maximum photosynthetic CO<sub>2</sub> assimilation rate per area ( $A_{\text{area}}$ ), maximum photosynthetic CO<sub>2</sub> assimilation rate per mass ( $A_{\text{mass}}$ ), leaf N concentration, and specific leaf area (SLA) for five species studied along a moisture gradient in coastal redwood forest in California, USA

	Big Basin State Park (1,170 mm)	Humboldt Redwoods State Park (1,600 mm)	Prairie Creek State Park (2,100 mm)
$g_{\max}$ (mmol m <sup>-2</sup> s <sup>-1</sup> )			
<i>N. densiflora</i>	50.9 ± 10.2 a	83.8 ± 29.9 a	67.8 ± 28.4 a
<i>O. oregana</i>	78.5 ± 16.2 a	53.5 ± 14.8 a	44.7 ± 6.5 a
<i>P. munitum</i>	48.7 ± 2.8 a	44.2 ± 10.4 a	35.8 ± 6.0 a
<i>S. sempervirens</i>	52.0 ± 7.6 a	49.9 ± 1.1 a	59.7 ± 1.6 a
<i>V. ovatum</i>	35.0 ± 10.7 a	71.7 ± 45.5 a	43.4 ± 15.5 a
$A_{\text{area}}$ (μmol m <sup>-2</sup> s <sup>-1</sup> )			
<i>N. densiflora</i>	4.6 ± 0.4 a	5.5 ± 0.8 a	5.4 ± 0.7 a
<i>O. oregana</i>	4.5 ± 0.3 a	3.4 ± 0.2 ab	3.1 ± 0.2 b
<i>P. munitum</i>	3.9 ± 0.1 a	3.5 ± 0.3 a	3.2 ± 0.2 a
<i>S. sempervirens</i>	5.0 ± 0.7 a	5.0 ± 0.3 a	5.5 ± 0.1 a
<i>V. ovatum</i>	3.1 ± 0.7 a	3.3 ± 0.1 a	3.1 ± 0.9 a
$A_{\text{mass}}$ (nmol g <sup>-1</sup> s <sup>-1</sup> )			
<i>N. densiflora</i>	45.0 ± 2.2 a	62.7 ± 8.6 a	62.0 ± 21.3 a
<i>O. oregana</i>	201.2 ± 28.0 a	193.5 ± 15.5 a	165.5 ± 6.6 a
<i>P. munitum</i>	63.1 ± 6.3 a	66.2 ± 5.4 a	58.1 ± 6.3 a
<i>S. sempervirens</i>	41.3 ± 7.6 a	41.1 ± 0.6 a	46.8 ± 0.7 a
<i>V. ovatum</i>	44.1 ± 12.8 a	32.0 ± 1.1 a	40.3 ± 16.3 a
Leaf N (mg g <sup>-1</sup> )			
<i>N. densiflora</i>	9.3 ± 0.0 a	10.6 ± 0.8 a	13.0 ± 1.2 b
<i>O. oregana</i>	19.7 ± 0.5 a	24.2 ± 2.0 b	22.9 ± 1.6 ab
<i>P. munitum</i>	12.6 ± 0.1 a	13.9 ± 0.2 b	15.1 ± 0.5 c
<i>S. sempervirens</i>	7.1 ± 0.9 a	7.9 ± 0.8 a	9.0 ± 1.4 a
<i>V. ovatum</i>	9.9 ± 1.4 a	8.2 ± 0.8 a	9.7 ± 1.0 a
SLA (cm <sup>2</sup> g <sup>-1</sup> )			
<i>N. densiflora</i>	99.0 ± 7.7 a	113.7 ± 4.0 a	110.8 ± 23.0 a
<i>O. oregana</i>	442.6 ± 35.7 a	570.2 ± 10.1 b	534.8 ± 24.9 b
<i>P. munitum</i>	162.5 ± 13.5 a	189.5 ± 16.1 a	180.1 ± 9.7 a
<i>S. sempervirens</i>	82.7 ± 7.4 a	82.4 ± 3.4 a	85.8 ± 0.2 a
<i>V. ovatum</i>	134.5 ± 17.0 a	97.2 ± 0.3 a	125.4 ± 15.4 a

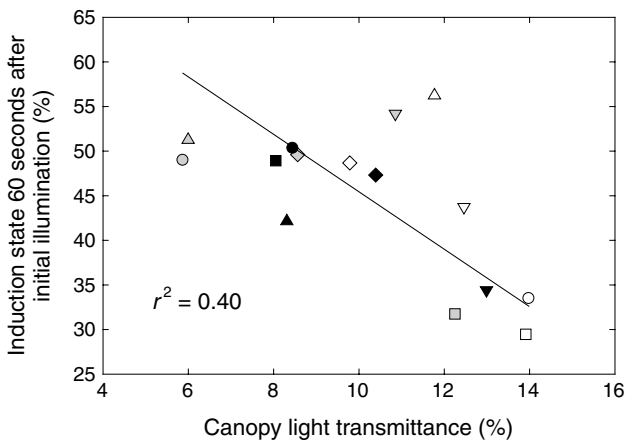
Values are mean ± 1 SE for three to five individuals per site. Values with different letters within the same species are significantly different (ANOVA,  $P < 0.05$ )

significantly different among sites ( $P > 0.05$ ), but among species, they were significantly greater for *Notholithocarpus* than *Sequoia* and *Vaccinium*, with *Oxalis* and *Polystichum* showing intermediate values ( $F_{4,31} = 2.91$ ;  $P < 0.05$ ).

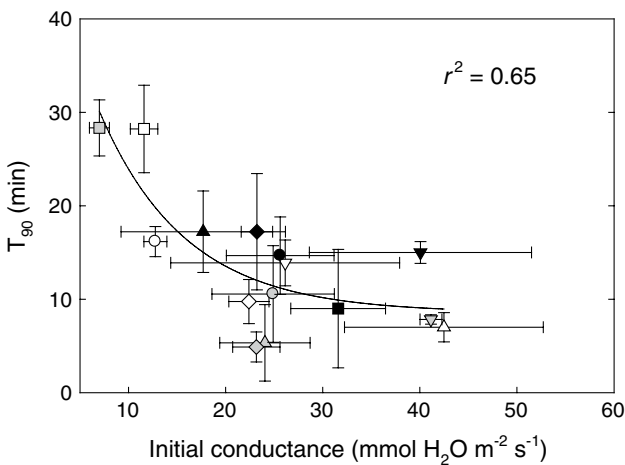
### Lightfleck experiments

Mean photosynthetic CO<sub>2</sub> assimilation during illumination in experimental lightflecks ranged from  $6.15 \pm 0.37 \mu\text{mol m}^{-2}$  during 2-s lightflecks to  $164.45 \pm 9.38 \mu\text{mol m}^{-2}$  during 64-s lightflecks. Mean  $T_{\text{post}}$  for all lightflecks was 22.3 s and thus  $A_{\text{post}}$  contributed 11–94 % of total C gain caused by experimental lightflecks. There was no significant variation among sites in the amount of CO<sub>2</sub> assimilated during illumination in lightfleck experiments ( $P > 0.05$ ). However,  $T_{\text{post}}$  was greater at the 2,100-mm site ( $26.1 \pm 0.9$  s) than at the 1,170- and 1,600-mm sites ( $20.0 \pm 0.6$  and  $21.7 \pm 0.6$  s, respectively;  $F_{2,232} = 23.5$ ;  $P < 0.0001$ ; Fig. 5).

Among species, there were large differences in  $T_{\text{post}}$  with *Polystichum* showing the longest mean  $T_{\text{post}}$  of  $25.1 \pm 0.7$  s and *Oxalis* showing the shortest of  $17.9 \pm 0.6$  s, and other species exhibiting intermediate values ( $F_{4,232} = 10.0$ ;  $P < 0.0001$ ; Fig. 5).  $A_{\text{post}}$  averaged across lightflecks of different length increased with increasing moisture inputs and was significantly greatest at the 2,100-mm site, intermediate at the 1,600-mm site, and significantly lower at the 1,170-mm site ( $F_{2,232} = 18.6$ ;  $P < 0.0001$ ; Fig. 5).  $A/\text{PFD}$  was significantly greater at the 2,100- and 1,600-mm sites compared to the 1,170-mm site ( $F_{2,232} = 3.74$ ;  $P < 0.05$ ; Fig. 5). The one species that showed an exception to the general statistical trend of increasing  $T_{\text{post}}$ ,  $A_{\text{post}}$ , and  $A/\text{PFD}$  with increasing moisture was *Oxalis*, which caused significant site × species interactions in these three variables ( $P < 0.05$ ; Fig. 5). The total amount of CO<sub>2</sub> assimilation caused by experimental lightflecks was significantly related to  $T_{\text{post}}$  for all lightfleck lengths (Fig. 6). This relationship was strongest for 2-s



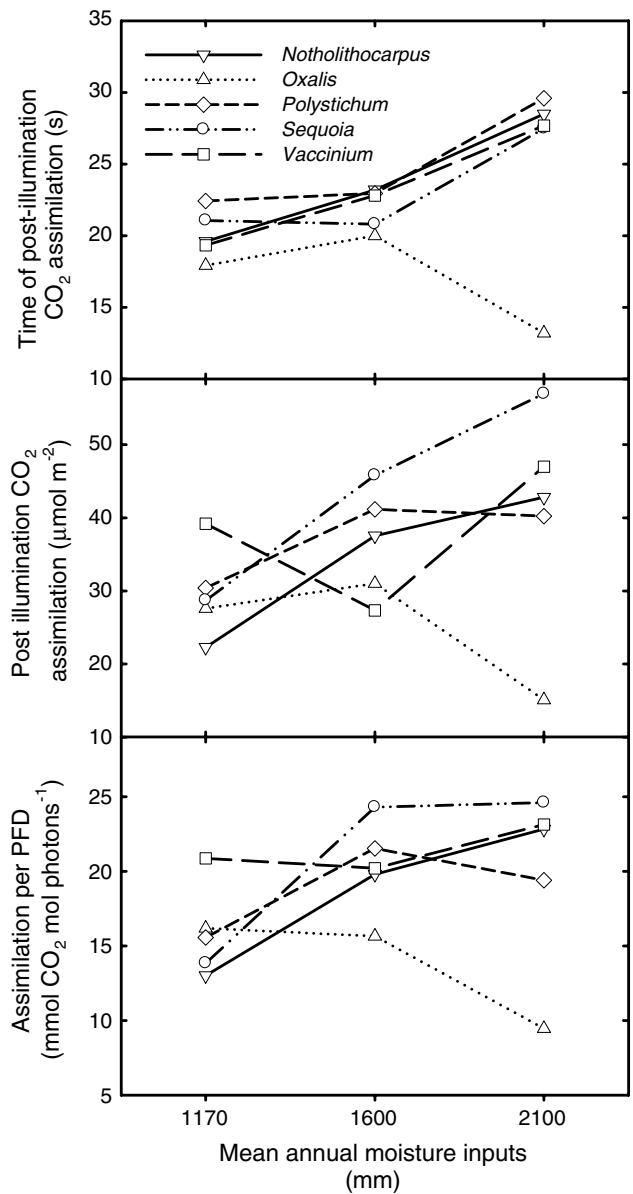
**Fig. 3** Induction state as a function of canopy light transmittance for five species of redwood forest plants growing in the understory [*Notholithocarpus densiflora* (inverted triangles), *Oxalis oregana* (triangles), *Polystichum munitum* (diamonds), *Sequoia sempervirens* (circles), *Vaccinium ovatum* (squares)]. Each point represents the mean of each species at one of three sites along a moisture input gradient. Solid symbols Plants from the 2,100-mm site, gray symbols plants from the 1,600-mm site, open symbols plants from the 1,170-mm site. Leaf induction state was calculated as the percent of maximum photosynthetic rate reached after 60 s of exposure to high light following 5–10 min in diffuse light. The line represents the best-fit standard major axis regression line ( $y = -3.22x + 77.6$ ;  $P = 0.01$ )



**Fig. 4** Time to reach 90 % of maximum photosynthetic rate after illumination with high light ( $T_{90}$ ) as a function of initial stomatal conductance of the leaf under diffuse light prior to exposure to high light ( $g_{\text{initial}}$ ). Points are means  $\pm$  1 SE. Symbols as in Fig. 3. The fitted line represents the equation  $y = 47.4e^{(-0.113x)} + 8.56e^{(-0.0000000000327x)}$

lightflecks, and the strength of this relationship decreased with increasing lightfleck length (Fig. 6).

Mean LUE across species also increased with increasing moisture inputs and was significantly greater at the 2,100-mm site ( $277 \pm 28$  %) than at the 1,170-mm site ( $177 \pm 16$ ), with the 1,600-mm site ( $226 \pm 20$  %) showing intermediate

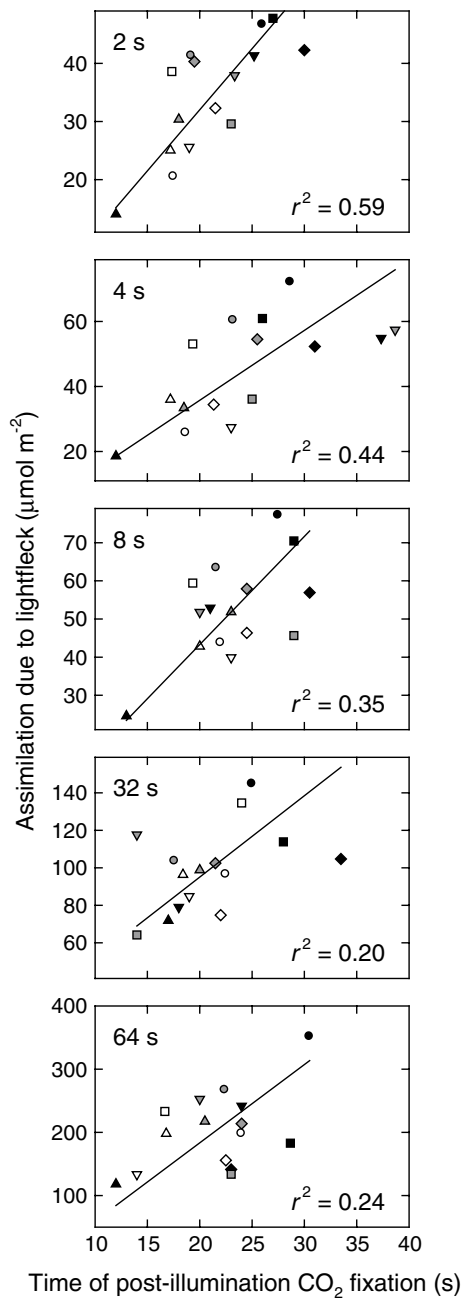


**Fig. 5** Mean time of post-illumination  $\text{CO}_2$  assimilation (upper panel), mean post-illumination  $\text{CO}_2$  assimilation (middle panel), and total assimilation caused by lightfleck per unit PFD received during the lightfleck and the post-illumination  $\text{CO}_2$  assimilation period (lower panel), for five species of redwood forest understory plants from three sites along a moisture input gradient

values ( $F_{2,232} = 4.09$ ;  $P < 0.005$ ). LUE decreased with increasing lightfleck duration in all species (Fig. 7). These leaves which were induced by diffuse light, exhibited LUEs as high as 800 % for 2-s lightflecks (Fig. 7).

Leaf stable isotopic composition

Leaf  $\delta^{13}\text{C}$  across species was significantly greater at the 2,100-mm site ( $-32.5$  ‰) than at the 1,600-mm ( $-33.1$  ‰)



**Fig. 6** Total CO<sub>2</sub> assimilation caused by lightfleck during illumination and during the post-illumination CO<sub>2</sub> assimilation period as a function of the time of post-illumination CO<sub>2</sub> assimilation activity for five species of redwood forest understory plants from three sites along a moisture input gradient. The panels reflect lightflecks of different duration from 2 to 64 s. Symbols as in Fig. 3. Lines represent the best-fit standard major axis regression line (2 s  $y = 2.10x - 9.99$ ,  $P < 0.001$ ; 4 s  $y = 2.15x - 7.28$ ,  $P < 0.01$ ; 8 s  $y = 2.84x - 13.5$ ,  $P < 0.05$ ; 32 s  $y = 4.34x + 8.24$ ,  $P < 0.1$ ; 64 s  $y = 12.4x - 64.7$ ,  $P = 0.05$ )

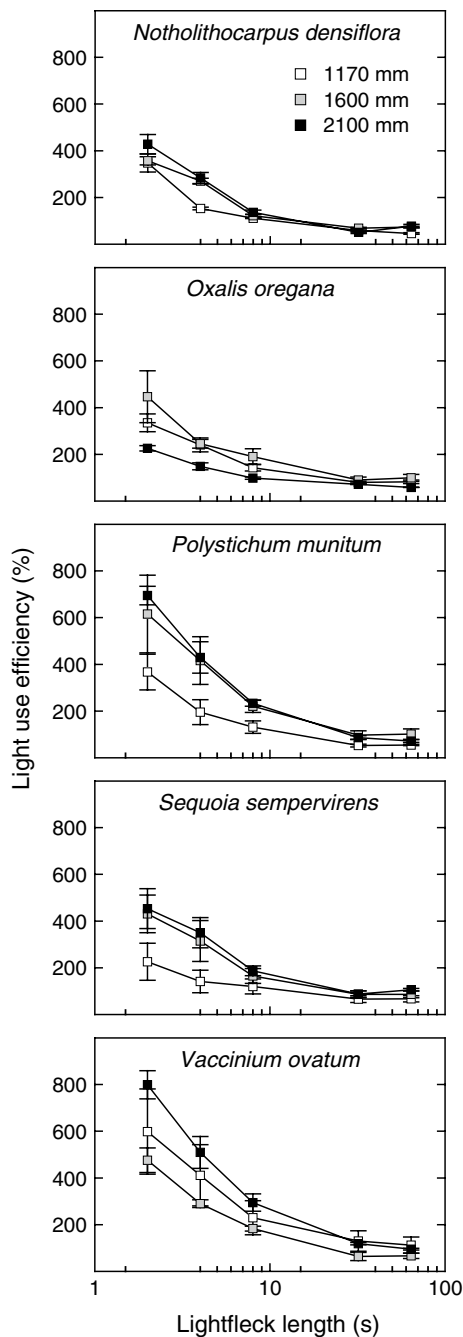
and 1,170-mm ( $-33.3\%$ ) sites ( $F_{2,58} = 5.49$ ;  $P < 0.01$ ), although the total range of values was small. Leaf  $\delta^{15}\text{N}$  decreased significantly with increasing moisture among

sites in the March–April rainy season ( $F_{2,58} = 16.28$ ;  $P < 0.0001$ ) and during the July–August fog season ( $F_{2,53} = 16.74$ ;  $P < 0.0001$ ; Fig. 8). The wettest site also produced an appreciable change in  $\delta^{15}\text{N}$  with the onset of the summer fog season, as  $\delta^{15}\text{N}$  dropped precipitously, whereas in the two drier sites, the change from the spring rainy season to the summer fog season was within the SE of the zero value (Fig. 8).

### Discussion

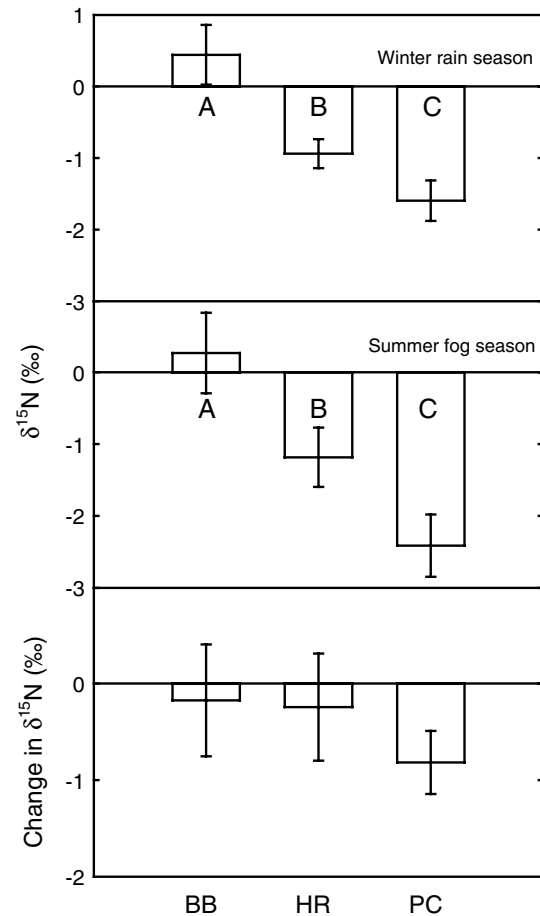
We tested the ability of plants in the redwood forest understory to assimilate CO<sub>2</sub> in constant and fluctuating light in response to a gradient of moisture inputs. Our data demonstrate that overall, understory plants conduct post-illumination CO<sub>2</sub> fixation for a longer time (greater  $T_{\text{post}}$ ), show greater  $A$  during the post-illumination period (greater  $A_{\text{post}}$ ), and obtain more CO<sub>2</sub> per total light received during experimental lightflecks (greater A/PFD), with increasing moisture inputs. Our data also indicate that greater  $g$  at the onset of photosynthetic induction ( $g_{\text{initial}}$ ) reduces the time to reach 90 % of the fully induced value of CO<sub>2</sub> assimilation ( $T_{90}$ ) following transfer from low to high light. Furthermore, increasing LUE with increasing moisture inputs integrates the importance of departures from steady state photosynthetic light responses and highlights the extent to which post-illumination CO<sub>2</sub> fixation can be important in maximizing C gain in an environment where both water and light can be limiting. However, we did not find evidence that plants in wetter sites showed greater induction state measured as the percent of fully induced photosynthetic assimilation rate 60 s after illumination ( $A_{60}$ ). Thus, our data indicate that C gain during short-duration lightflecks increases with moisture inputs along the range of California redwood forests and is consistent with two out of three of the well-known ways in which plants are known to maximize C gain in low light (Sharkey et al. 1986; Valadares et al. 1997; Montgomery and Givnish 2008). Our data are also consistent with increased understory C gain as a mechanism enhancing greater understory plant density and percent cover in northern high-moisture sites relative to drier southern sites across the span of California redwood forest.

Although our data indicate significant increases in  $T_{\text{post}}$ ,  $A_{\text{post}}$  and A/PFD with increasing moisture inputs across this gradient when all species are considered, the response of *Oxalis* was strikingly different (Fig. 5). In contrast to the other four species which show a pattern of increasing post-illumination CO<sub>2</sub> fixation with increasing moisture, values of  $T_{\text{post}}$ ,  $A_{\text{post}}$  and A/PFD in *Oxalis* actually decreased with moisture inputs. These counterintuitive results are likely caused by the low stature of *Oxalis* (<20 cm), and



**Fig. 7** Light use efficiency as a function of lightfleck duration (log scale) of induced leaves for five species of redwood forest understory plants from three sites along a moisture input gradient (1,170, 1,600 and 2,100 mm year<sup>-1</sup>). Solid symbols Plants from the 2,100-mm site, gray symbols plants from the 1,600-mm site, open symbols plants from the 1,170-mm site. Points are mean  $\pm$  1 SE

the progressively increasing vegetation cover as moisture inputs increase toward northern humid sites. This finding is relevant because although *Oxalis* individuals appear to become increasingly shaded at wetter sites, they also increase in abundance with moisture inputs (Table 2),



**Fig. 8** Site means ( $\pm 1$  SE) of five species of redwood forest understory plants for leaf N isotopic composition ( $\delta^{15}N$ ) measured during spring and summer, and the difference between seasons. Means with different letters are significantly different at  $P \leq 0.05$ . BB Big Basin State Park, HR Humboldt Redwoods State Park, PC Prairie Creek State Park

supporting the notion that moisture enhances the ability of this species to thrive in low light. Interestingly, *Oxalis* shows the lowest amount of foliar water uptake among ten common redwood forest plant species (Limm et al. 2009), suggesting that *Oxalis* is highly dependent on soil water uptake in order to maintain stomatal apertures that minimize  $T_{90}$ . These data are also consistent with the findings of Pfitsch and Percy (Pfitsch and Percy 1989a, b), whose work on *Adenocaulon bicolor* demonstrates the importance of  $g_{initial}$  and rapid photosynthetic induction (*Oxalis*; Fig. 1) for maximizing C gain in the redwood forest understory environment.

Our data also indicate that although understory vegetation density and cover increase with moisture inputs, canopy coverage did not vary substantially and was actually slightly lower at the 2,100-mm site. This difference is likely due to the immense size of trees at the 2,100-mm site, which have a strong effect on canopy structure and



light transmittance. The large vertical orientation and minimal branching low in the canopy of the giant trees along Cal Barrel Road at the 2,100-mm site (Sawyer et al. 2000), transmit light to the understory in a manner that may be better described as “sun swaths” rather than sunflecks (L. S. Santiago, personal observation). Canopy light conditions may also be associated with greater foliar  $\delta^{13}\text{C}$  values at the 2,100-mm site compared to the two drier sites, consistent with reports of increasing  $\delta^{13}\text{C}$  values of Redwood forest understory plants with increasing daily PFD (Percy and Pfitsch 1991), as well as other studies demonstrating greater  $\delta^{13}\text{C}$  values with increasing light availability (Ehleringer et al. 1987; Zimmerman and Ehleringer 1990). However, Percy and Pfitsch (1991) show  $\delta^{13}\text{C}$  variation of over 3 ‰, whereas our complete variation is 0.8 ‰ and our values are in a range suggesting influence by respired  $\text{CO}_2$  from soil, which is always more negative than source air (Sternberg et al. 1989; Buchmann et al. 1997), thus limiting our ability to place too much emphasis on the physiological implications of these values. Furthermore, understory light conditions represent a combination of canopy light interception and sky conditions, and the 2,100-mm site receives approximately 12 % fewer hours of sunshine than the 1,170-mm site (New et al. 2002), as well as a greater frequency of fog (Johnstone and Dawson 2010). Therefore, lower light conditions likely prevail with increasing northern exposure along this gradient, even though individual plants can show substantial variation in terms of their location and light habitats in the heterogeneous forest understory, making it difficult to distinguish the effects of climate and canopy light effects on photosynthetic performance of a particular species or plant community. Nonetheless, our study species exhibited increasing  $A_{60}$  with decreasing light transmittance, consistent with other studies that characterize the dependence of induction state on light habitat (Chazdon and Percy 1986a, b; Valladares et al. 1997; Montgomery and Givnish 2008). Additionally, greater LUE at the wettest site is consistent with adaptations well suited to enhance plant performance under low light conditions. Thus, although the presence of fog reduces the amount of sunshine, the associated moisture inputs also appear to provide conditions that favor C gain during lightflecks, thus buffering redwood understory plant species in northern sites from extremely low C budgets.

Variation in foliar N concentration and  $\delta^{15}\text{N}$  among sites is also noteworthy. The increase in leaf N in three out of five species with increasing moisture inputs is in line with the idea that fog and rain contribute to plant N uptake. However, the mechanism is unknown. One possibility is that greater fog and rain deposition in northern sites promote solubility of plant-available N forms in soil. Another possibility is that because rain, and especially fog contain N (Weathers and Likens 1997; Weathers et al.

2000; Ewing et al. 2009; González et al. 2011), greater inputs of rain and fog at wetter sites may simply represent an increase in plant available N inputs. The timing of seasonal change in foliar  $\delta^{15}\text{N}$  at the 2,100-mm site corresponds to the change from spring frontal rains to summer fog, suggesting that the shift in foliar  $\delta^{15}\text{N}$  corresponds to a change in source N. A 5-year study in redwood forest in the middle of the redwood range shows that most dissolved inorganic N is delivered to the forest floor as  $\text{NO}_3^-$ , and that forest throughfall N is seven times greater during the fog season compared to the rain season (Ewing et al. 2009), consistent with the possibility that the change in foliar  $\delta^{15}\text{N}$  with the onset of the fog season at the foggiest site represents a shift to fog-based N forms. Furthermore, at the same site as the Ewing et al. (2009) study,  $\delta^{15}\text{N}$  of fog  $\text{NO}_3^-$  was not significantly different from rain ( $-1.2 \pm 0.68$  ‰), but  $\delta^{15}\text{N}$  of  $\text{NH}_3$  in throughfall ( $+3.37 \pm 0.69$  ‰) was more depleted than in fog ( $+10.04 \pm 1.56$  ‰) (Templer et al. 2006), also supporting the idea that foliar  $\delta^{15}\text{N}$  changes with the arrival of fog signify a shift to fog-based N forms. Preliminary data collected at the 2,100-mm site show that mean  $\delta^{15}\text{N}$  of two samples of August 2005 fog  $\text{NO}_3^-$  ( $-1.7$  ‰) was more depleted than one sample of March 2005 rain ( $+4.4$  ‰; L. S. Santiago, unpublished data), consistent with the depletion in foliar N at this site at the onset of the summer fog season. However, there simply are not enough data on  $\delta^{15}\text{N}$  of fog N to confirm whether the seasonal shift in foliar  $\delta^{15}\text{N}$  at the 2,100-mm site is caused by a shift of plant use of fog N, or whether greater amounts of fog N in foggy redwood forests are the reason for enhanced LUE.

Overall, our data demonstrate that plants growing under lower light conditions show rapid induction once transferred to high light, and that the ability to maintain stomata relatively open during diffuse light periods is associated with rapid attainment of maximum steady state photosynthesis when exposed to high light. The main difference among sites was the ability to continue photosynthetic activity immediately after a lightfleck, with four out of five species exhibiting increased photosynthetic parameters associated with post-illumination  $\text{CO}_2$  fixation with increasing moisture. Greater foliar N with increasing moisture inputs in three species and the large seasonal change in leaf  $\delta^{15}\text{N}$  at the foggiest site suggest that N inputs associated with fog also increase plant-available N that can be allocated to photosynthetic light-harvesting complexes and carboxylating enzymes to enhance C gain in low light (Evans 1989; Pasquini and Santiago 2012). Yet, further N isotopic work is clearly needed to nail down this hypothesis. These results highlight the potential for variation in resource availability along environmental gradients to influence C gain opportunities for plants in low light habitats.

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