



RESEARCH ARTICLE

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Key Points:

- Examined the vadose zone water balance response to imposed climate warming treatments
- Warming increased spring ET, but decreased summer ET, with no significant difference annually
- Warming had no effect on mean annual groundwater recharge in this climate

Supporting Information:

- README_auxiliary material
- Table S1

Correspondence to:

L. A. Pangle,
lpangle@email.arizona.edu

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Rainfall seasonality and an ecohydrological feedback offset the potential impact of climate warming on evapotranspiration and groundwater recharge

Luke A. Pangle¹, Jillian W. Gregg², and Jeffrey J. McDonnell³

¹Water Resources Graduate Program, Oregon State University, Corvallis, Oregon, USA, ²Terrestrial Ecosystems Research Associates, Corvallis, Oregon, USA, ³School of Environment and Sustainability, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

Abstract The potential impact of projected climate warming on the terrestrial hydrologic cycle is uncertain. This problem has evaded experimentalists due to the overwhelming challenge of measuring the entire water budget and introducing experimental warming treatments in open environmental systems. We present new data from a mesocosm experiment that examined the combined responses of evapotranspiration (ET), soil moisture, and potential groundwater recharge (R ; lysimeter drainage) to a 3.5°C temperature increase in a grassland ecosystem experiencing a Mediterranean climate. The temperature increase was applied both symmetrically throughout the day, and asymmetrically such that daily minimum temperature was 5°C greater than ambient and daily maximum temperature was 2°C greater than ambient. Our results span 3 water years and show that symmetric and asymmetric warming-enhanced ET during the spring. However, this increase in ET reduced soil moisture more rapidly, resulting in less ET during the summer than occurred under ambient temperature, and no difference in total ET during the combined spring and summer (March to October). Groundwater recharge was reduced during late-spring storms relative to the ambient temperature treatment, but these reductions were less than 4% of total annual R , and were offset by slightly greater R in the fall under both warming treatments. The results highlight the potential for local interactions between temperature, vegetation, and soils to moderate the hydrological response to climate warming, particularly in environments where precipitation is seasonal and out of phase with the vegetation growing season.

1. Introduction

Empirical evidence suggests that detectable intensification of the hydrologic cycle has occurred over the last several decades, whereby long-term records of evapotranspiration, specific humidity, precipitation, and runoff show increasing trends at global [Huntington, 2006] and continental scales [Groisman *et al.*, 2004]. These changes are correlated with increases in air temperature, and raise questions about the potential impact of future climate warming on the terrestrial hydrologic cycle. However, at regional and subregional scales these trends vary qualitatively and quantitatively, or may be unapparent [Groisman *et al.*, 2004]. Other components of the hydrologic cycle (e.g., groundwater recharge) are critical in some ecosystems, but their response to past climate variability has been poorly monitored, and their potential response to future climate warming remains uncertain [Green *et al.*, 2011]. The interactions and feedbacks between local climate, vegetation, and soils may strongly influence how future climate warming alters water fluxes in specific ecosystems, yet these interactions and feedbacks are poorly understood [Norby and Luo, 2004; Wu *et al.*, 2011].

So what projections can be made about the impact of future climate warming on the annual water budget in specific ecosystems? One hypothesis is that warmer air temperatures would enhance evapotranspiration by increasing incoming long-wave radiation and increasing the vapor-pressure gradient from the land surface to the atmosphere. If there is no change in total precipitation, then to conserve mass, an increase in evapotranspiration should cause a reduction in groundwater recharge and direct runoff. This has been the underlying hypothesis for many water budget models to date. For example, *Budyko* [1974] postulated that the ratio of average-annual evapotranspiration to precipitation for large basins is controlled by an aridity index (based on temperature and the surface energy balance), and that the remaining fraction of average-

annual precipitation contributes to runoff (including surface and groundwater contributions to river discharge, and assuming water storage in the landscape was constant over long time periods). Budyko developed a quantitative model based on these principles that provided a good fit to calculated values of these ratios for many catchments, and thus provided a framework for evaluating the climate sensitivity of the annual water budget through interbasin comparison. However, subsequent analyses of this hypothesis revealed a systematic error; catchments in which precipitation was seasonal, and temporally out of phase with temperature, commonly had greater runoff and less evapotranspiration than predicted [Milly, 1994]—highlighting the important influence that local precipitation regimes may have on the overall water budget response to changing temperature [Luo *et al.*, 2008; Porporato *et al.*, 2004; Wu *et al.*, 2011].

The singular use of climatic indices for projecting the water budget response to climate warming may also be compromised at intraannual time scales because this approach does not account for seasonal regulation of transpiration by plant stomata that can result from phenological change and insufficient soil water [Donohue *et al.*, 2007]. Furthermore, simultaneous increases in atmospheric CO₂ can enable greater water-use efficiency of leaf-level photosynthesis [Fredeen *et al.*, 1997]—an effect that may offset potential increases in evapotranspiration caused by warmer air temperature. An example of the importance of seasonal regulation of transpiration can be observed in Mediterranean climates where maximum-daily temperatures during the summer cooccur with daily evapotranspiration rates that may be well below maximum due to a limited soil-water supply. Peak photosynthesis and in these systems occurs during the spring [Ma *et al.*, 2007; Phillips *et al.*, 2011], when high evapotranspiration may also reduce soil-water storage and inhibit groundwater recharge during precipitation events. However, the magnitude of evapotranspiration during the spring may be reduced under elevated atmospheric CO₂ concentrations—an effect that has been shown to delay the onset of soil-moisture deficits in other Mediterranean climates [Field *et al.*, 1997; Fredeen *et al.*, 1997].

Despite theoretical expectations of increased evapotranspiration and reduced groundwater recharge and runoff in response to warmer temperatures, experimental examination of this problem has been lacking. Accurate measurement of the terrestrial hydrologic cycle continues to be a major challenge for hydrologists [Beven, 2006] and catchment-sized units that are used in observational studies of hydrological processes are beyond the spatial scale accessible for experimental control and manipulation. Small-scale manipulative experiments have improved our understanding of how some water budget components respond to projected temperature increases associated with global climate warming [Bell *et al.*, 2010b; De Boeck *et al.*, 2006; Dermody *et al.*, 2007; Fay *et al.*, 2002; Morgan *et al.*, 2004; Zavaleta *et al.*, 2003a, 2003b]. However, these studies have not captured the entire water budget; most often they omit subsurface flow processes, such as groundwater recharge, which is potentially the most important water budget component for consumptive water use by humans. Subsurface water flow is not directly controlled by air temperature, however, evapotranspiration and groundwater recharge are interdependent, since both fluxes depend on soil moisture [Porporato *et al.*, 2004; Rodriguez-Iturbe *et al.*, 1999]. To date, there is little experimental evidence to suggest how climate-induced changes in evapotranspiration could affect groundwater recharge [Green *et al.*, 2011; Kundzewicz *et al.*, 2007; Taylor *et al.*, 2012].

Here we present a mesocosm experiment that examines how projected climate warming impacts evapotranspiration, soil moisture, and groundwater recharge in a grassland ecosystem experiencing a Mediterranean rainfall regime in the Pacific Northwest region of the USA. Average-annual temperature in this region is projected to increase by 3.0°C by the year 2080, with no significant change in annual precipitation, based on the mean simulation results from an ensemble of 19 Global Climate Models driven by three CO₂ emissions scenarios [Mote and Salathe, 2010]. We focus on two main objectives: (1) to quantify how increased temperature affects seasonal trends of evapotranspiration and (2) to quantify how warming-induced changes in evapotranspiration influence seasonal and annual groundwater recharge. We test three hypotheses: (1) increased temperature will increase evapotranspiration, specifically due to greater evapotranspiration occurring earlier in the spring season; (2) warming-enhanced evapotranspiration will reduce groundwater recharge during the spring due to lower soil moisture prior to precipitation events; and (3) warming-enhanced evapotranspiration will cause lower soil moisture preceding the onset of the rain season, thus requiring greater total precipitation to initiate recharge. The combined result of 2 and 3 would be an overall reduction of recharge at the annual time scale. Note that, while simultaneous increases in atmospheric CO₂ concentration could, to some extent, offset the hypothesized evapotranspiration/recharge responses, our experiment examines responses to

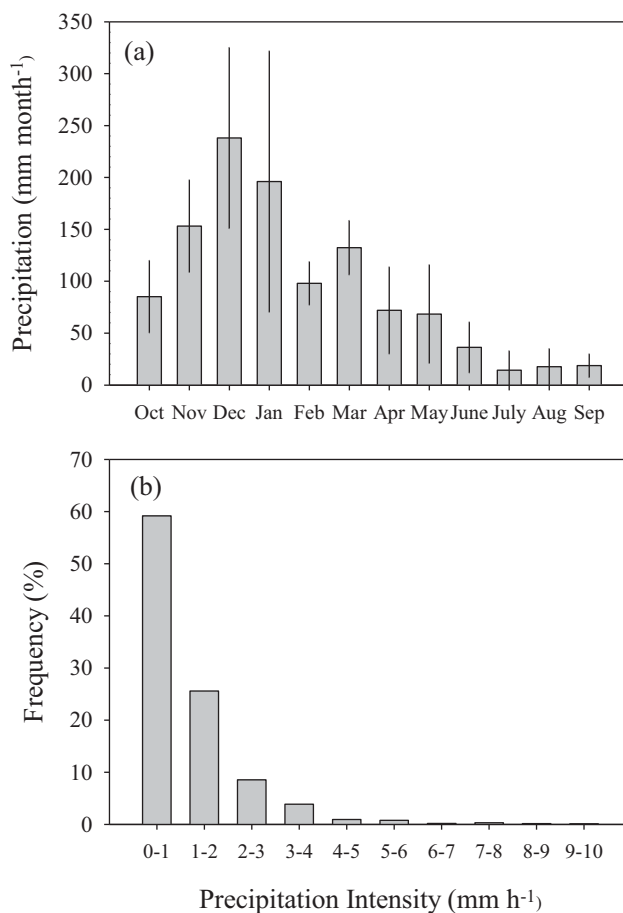


Figure 1. (a) Average precipitation that occurred each month over the study period (October 2007 to August 2010). Error bars represent plus and minus one standard deviation ($n = 3$, except $n = 2$ for August and September). (b) The frequency distribution of precipitation intensity during the same period (calculated based on hourly totals grouped into 1 mm increments).

with a southerly aspect. The terracosms have an aluminum frame with three walls and a roof made of clear Teflon film, and a north-facing wall made of Plexiglass (Figure 2). They are essentially closed systems, though the chamber front and control valves are opened periodically to aid with climate control. A 2.3 m³ polypropylene tank underlies each terracosm and acts as a nonweighing lysimeter. The lysimeter depth ranges from 1 to 1.3 m along a sloping base that enables drainage. The lysimeters were insulated (0.15 m of foam insulation, R value 60) and placed within larger steel containment structures in the soil.

The lysimeters were filled with soil that was excavated from a nearby prairie that had previously been undeveloped park lands. The soil is in the Dixonville series—moderately deep, well-drained soils formed in clayey colluvium, and basalt-derived residuum (NCSS Soil Characterization Database, 2012, <http://ncsslabsdata-mart.sc.egov.usda.gov/>). The soil was excavated during the summer of 2005 in five 0.2 m depth increments and large materials were removed using a 0.0245 m sieve. Particle size analysis using the pipette method [Gee and Bauder, 1986] showed that the textural class was silty clay loam at 0–0.6 m depth (29–38% clay), silt loam at 0.6–0.8 m depth (26% clay), and loam at 0.8–1.0 m depth (23% clay). Pea gravel was used to fill the base of the lysimeter and to provide a flat surface, and a layer of landscaping cloth was placed on top of the pea gravel to minimize root growth into the gravel and lysimeter plumbing. Soils were then back filled into the terracosms and packed using a uniform tamping procedure for each increment, yielding a soil profile with 1 m depth and bulk density of approximately 1.1 g cm⁻³.

Three annual forbs, eight perennial forbs, and three perennial grass species were planted in each terracosm to simulate a plant assemblage that resembled natural grasslands found in Oregon’s Willamette Valley.

warming alone, applied in symmetric and asymmetric patterns (see section 2), and therefore suggests potential maximum hydrologic responses.

2. Materials and Methods

2.1. Climate

This work was conducted at the terracosm facility (<http://www.teraglobal-change.org>) that is located in Corvallis, OR, USA (44.57, -123.29; 77 m.a.s.l.). The climate is “wet Mediterranean” with mild temperatures and seasonal precipitation. Average temperature is 4.1°C in January and 19°C in August. Average annual precipitation is 1085 mm and is almost entirely rainfall (Hyslop Farm Climate Station; <http://cropandsoil.oregon-state.edu/hyslop/handbook>). The majority of rainfall occurs during the winter months with a prolonged dry period during the summer (Figure 1a). Rainfall intensity is low—rates of 3 mm h⁻¹ or less occurred during more than 90% of the hours with any recorded rainfall during the study period (Figure 1b).

2.2. Site Description

The terracosm facility consists of 12 sun-lit climate-controlled chambers (referred to as terracosms). Each terracosm covers a flat-ground-surface area of 2 m² (1 × 2 m); the height ranges from 1.5 to 1.7 m along a sloping roof



Figure 2. A photograph of the terracosms in an open field in Corvallis, Oregon, and a drawing illustrating the enclosed aboveground chamber, underlying lysimeter, and irrigation system. Additional photographs and diagrams can be viewed at www.teraglobalchange.org.

Plants were started in a greenhouse during the summer of 2005, left over winter in a lath house, and transplanted into the terracosms after the last frost during April 2006. Sixteen individuals of each species were transplanted into each terracosm in a randomized design that was replicated between terracosms. The plants grew on the repacked soils for 1 year under ambient environmental conditions before the chamber tops were installed and temperature treatments initiated on 17 April 2007. Here we report on data collected from 1 October 2007 until a temporary cessation of temperature treatments on 26 July 2010.

2.3. Climate Control and Experimental Treatments

The terracosms' interior climate was monitored and controlled at a 1 min frequency. Detailed descriptions of the climate control features have been published previously [Phillips *et al.*, 2011; Tingey *et al.*, 1996]; here we summarize the controls most relevant to the hydrological processes being studied. Three temperature treatments were imposed ($n = 4$ per treatment). The ambient temperature treatment maintained the same temperature as measured at an adjacent climate station; the symmetric warming treatment maintained a temperature that was constantly 3.5°C greater than ambient; and the asymmetric warming treatment maintained a temperature that was, on average, 3.5°C greater than ambient, though the minimum dawn temperature was 5°C greater than ambient, while the maximum midday temperature was only 2°C greater (Figure 3a). Soil warming occurred through heat transfer from the temperature-controlled airstream within the terracosm. The air was warmed with a thermal radiator and cooled with a chilling radiator that were located inside an air-handler system. Air was continuously circulated through the terracosms, resulting in an approximate wind speed of 0.35 m s^{-1} above the plant canopy [Tingey *et al.*, 1996], and approaching zero near the soil surface.

Relative humidity (RH) inside the terracosms was measured with Vaisala HMT337 relative humidity sensors (Vaisala, Inc.) and $[\text{CO}_2]$ was monitored with infrared gas analyzers (LI-6262, LI-COR, Inc.). Relative humidity and $[\text{CO}_2]$ were controlled to match ambient conditions measured at the adjacent climate station, and were maintained at the same levels among all temperature treatments. Hence, absolute humidity was greater inside terracosms receiving warming treatments. The vapor-pressure deficit was, on average, 25% greater under both warming treatments than under ambient temperature. Under asymmetric warming, this relative difference varied with temperature, often exceeding 30% during the predawn hours and dropping below 20% during the afternoon (Figure 3b).

2.4. Measurement and Calculation of Water Budget Components

Natural precipitation was captured as it fell on the terracosm roofs and routed to a closed container. After approximately 2 L (1 mm depth equivalent), accumulated water was pumped through a roof-mounted sprinkler system with six low-pressure sprinkler heads over the following 40–60 s. The precipitation amount (P) was calculated as the product of the pump run time (s) and a calibration value (L s^{-1}), then converted to units of depth (mm) by dividing by the 2 m^2 soil-surface area. The system was calibrated approximately monthly.

Five time domain reflectometry (TDR) probes (CS610, Campbell Scientific, Inc.) were installed horizontally in each lysimeter during soil packing, at depths of 0.05, 0.15, 0.35, 0.55, and 0.75 m below the soil surface.

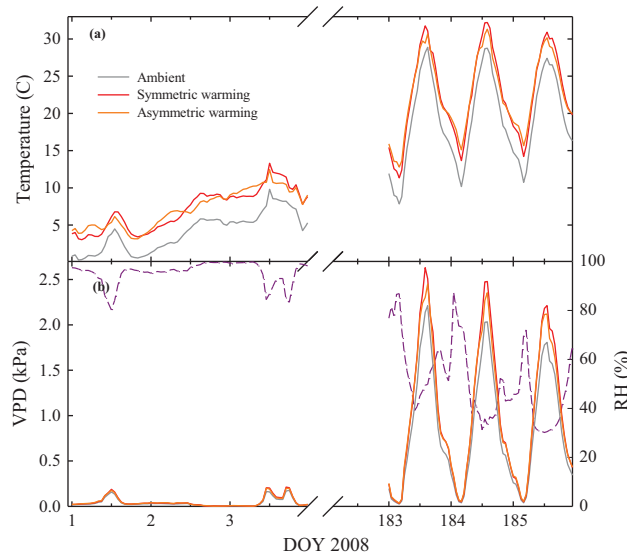


Figure 3. (a) Time series of temperature on days of the year 1 through 3 and 183 through 185 under ambient temperature, symmetric warming, and asymmetric warming. (b) Time series of vapor-pressure deficit over the same time span. The purple dashed line represents relative humidity, which was maintained at ambient levels under all three temperature treatments.

Volumetric water content (θ) was measured at each probe location at a 36 min interval using a Tektronix 1502b TDR Cable Tester (Tektronix, Inc.) that was operated in conjunction with a Campbell CR10 Data Logger and SDM50 Coax Multiplexer. The 36 min sampling interval was the highest frequency achievable given this specific hardware configuration. For reasons that we ultimately could not determine, the TDR system produced time series of data with several types of apparent errors: (1) sporadic measurements that deviated beyond realistic values of θ , (2) values that deviated from preceding θ values by margins that would not occur realistically during rainfall infiltration and drying, and (3) periods when θ values became static due to equipment malfunction.

Any θ values greater than 0.5, or less than 0.1, were omitted from the data

set, as laboratory measurements on soil samples from the terracosms indicated these values as the total porosity and the water content under 300 kPa of applied air pressure, respectively. It was also apparent from reviewing the data that any θ values below 0.1 were erroneous fluctuations, as the vast majority of θ values at all soil depths, and for all individual sensors, were greater than 0.1 even at the end of the summer drought period. Any θ measurement that differed from the previous or following value by more than 0.05 was omitted from the data set. The 0.05 threshold was chosen after manually reviewing the soil-moisture time series specifically during storm events and observing that fluctuations that occurred over the 36 min sampling interval were almost always less than 0.05. Further, a frequency distribution and box plot both showed that differences between subsequent measurements were normally distributed with a mean (μ) of zero and standard deviation (σ) of 0.032, and that differences between consecutive measurements were less than 0.05 94% of the time. Any θ values that differed from the mean of those measured at the same depth and time in the other 11 terracosms by more than 3σ (σ signifies standard deviation) were considered outliers, and omitted. The data were reviewed before and after this editing procedure to verify that erroneous measurements were removed without unnecessarily omitting data from functional probes. To account for short periods when θ measurements were static due to equipment malfunction, any sequence of identical measurements occurring over 3 h or more were omitted from the data set. Identical consecutive measurements were clearly apparent because the numerical θ values generated by the TDR system included more than five decimal places.

Average-daily θ was calculated for each probe based on these edited short-term data (36 min interval, 60 total probes). To compare seasonal trends of soil moisture between each temperature treatment, we calculated treatment averages of the total volumetric water content of the entire soil volume (θ_{tot}) at a daily time step using a weighted averaging scheme:

$$\theta_{tot} = 0.1\theta_5 + 0.15\theta_{15} + 0.2\theta_{35} + 0.2\theta_{55} + 0.35\theta_{75} \quad (1)$$

The weighting coefficients on the right-hand side of equation (1) represent the fraction of the total soil volume that each probe was assumed to represent. The subscripts on the right-hand side of equation (1) indicate the TDR probe depth, and the θ terms they correspond with represent the average volumetric water content measured at that depth among all terracosms receiving a specific temperature treatment. The sample size for each of those averages varied due to missing data that resulted from the editing procedures

described above. These time series are presented in Figure 6b and the soil-moisture data are submitted as supporting information and made available online.

The lysimeter drainage was used as a proxy for potential groundwater recharge (R). We extracted soil cores from each terracosm once annually, and found less than 10% of total root biomass at 0.8–1 m soil depth, which was similar to vertical root distributions reported by *Schenk and Jackson* [2002] for multiple prairie ecosystems. Hence, even if the soil profile was extended to greater depth, it is not likely that water draining beyond 1 m depth would be taken up by plant roots in this ecosystem. Soil water that percolated to the sloped base of the lysimeters drained through an exit pipe to a tipping-bucket gauge where it was measured in 0.004 mm increments. The tipping-bucket gauges were calibrated approximately monthly during the study period. No R data are reported from January 2010, due to equipment replacement during that time. Errors existed in the R data set due to occasional clogs in the outflow pipe and equipment failure. These errors were manually removed using a written record of equipment failure that was maintained throughout the experiment. Linear interpolation was used to fill most of the data gaps. If the data gap was too long to be filled, the data from that terracosm did not contribute to the treatment average for that season or year.

Evapotranspiration (ET) was calculated on a seasonal basis (seasons defined in section 2.6) as the residual component of the water balance (i.e., $ET = P - R - \Delta S$), where P and R represent cumulative-seasonal precipitation and groundwater recharge, respectively, and ΔS represents the seasonal change in total soil-water storage. Cumulative P , R , ΔS , and therefore, ET were calculated individually for each terracosm. The ΔS was calculated as the difference between θ_{tot} on the last day of the season and θ_{tot} on the day prior to the beginning of the season (e.g., 28 February, 17 May, and 30 September 2008, as noted in description of seasons below). For each specific date that was considered when calculating seasonal ΔS , θ_{tot} could not be readily calculated for each terracosm (using equation (1)) because average-daily θ values were not available at all five soil depths due to the data editing procedures described above. If the average-daily θ value was missing from only one soil depth, that value was filled with the average θ value measured at the same depth within the other terracosms receiving the same temperature treatment. The value was then adjusted by adding the mean-absolute difference in θ that existed between the single probe and the average of the other similar probes (considering all days when the average θ of the similar probes was at the same level ∓ 0.01 as the date when a missing data point was filled). If the average-daily θ value was missing from more than one soil depth, θ_{tot} and ΔS were not calculated from that particular terracosm and season, and the terracosm was omitted from the statistical hypothesis testing described in section 2.6. This gap-filling procedure is similar to other correlative methods used for calculating cumulative fluxes at eddy-covariance sites [*Moffat et al.*, 2007] where data continuity is disrupted due to instrument failure, and in our case was used for 6% of the data needed to calculate ΔS and ET.

The slow rate of infiltration and the delayed R response to P events prevented the calculation of ET using the water budget approach at the daily time scale, and lead to unrealistic ET values at the monthly time scale during winter months due to the frequency of P events. Hence, we limited our ET calculations to the months of March through September, which is also the time most relevant to address our hypotheses.

2.5. Calculation of Reference Evapotranspiration

To approximate the *potential* influence of symmetric and asymmetric warming on grassland ET, we calculated reference evapotranspiration (ET_0) for each temperature treatment. These estimates reflect the physical influence of temperature and vapor-pressure deficit (VPD) (Figure 3) in the absence of water limitation. Reference ET was calculated at an hourly time step using a standardized form of the Penman-Monteith model as outlined by *Allen et al.* [1998]. This approach utilized aerodynamic and surface resistance terms that represent a uniform grass canopy of 0.12 m height that is well watered [*Allen et al.*, 1998]. The input data required for the model included solar radiation, temperature, relative humidity, and local latitude and longitude. Hourly solar radiation data from a pyranometer (LI-200, LI-COR, Inc.) were obtained from the Agrimet climate station (<http://www.usbr.gov/pn/agrimet/agrimetmap/crvoda.html>) located approximately 10.5 km northeast of our study site. The temperature and relative humidity data were those measured within the terracosms. Seasonal values of ET_0 for each temperature treatment were calculated over the same time spans as actual ET.

2.6. Data Analysis

We used a single-factor analysis of variance (ANOVA) to test for the effect of temperature on ET and R . We also included a block effect in the ANOVA model, and used the Brown-Forsythe test [*Kutner*

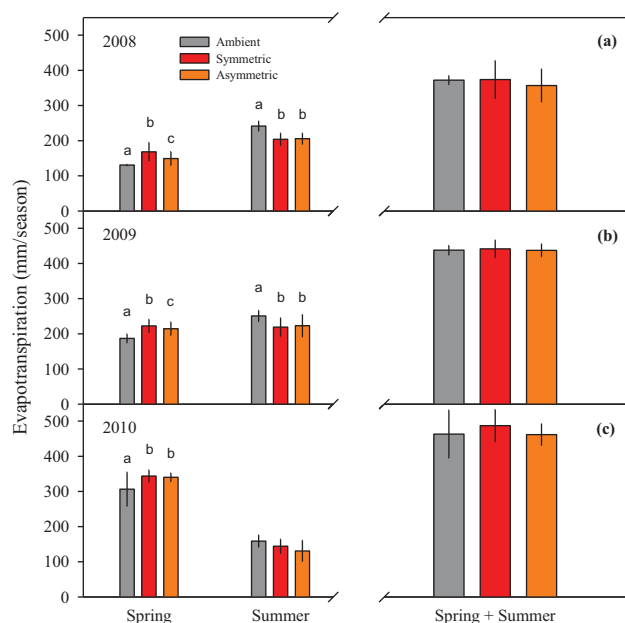


Figure 4. (a–c) Cumulative ET during spring (1 March until cessation of recharge), summer (time following spring until 30 September), and spring and summer combined for 2008–2010. Evapotranspiration totals during 2010 do not include August or September, as treatments temporarily ceased on 26 July 2010 during plant dormancy. Error bars indicate 90% confidence intervals. Where present, letters indicate differences among temperature treatments associated with a p value of 0.1 or less.

et al., 2005] to confirm the assumption of equal variances among treatment groups. Temperature and block were treated as fixed effects. We tested for differences in cumulative ET among treatments during the “hydrological spring” (hereafter referred to as spring), which we defined as the period from 1 March until the last day during which R was greater than zero for at least one temperature treatment; the “hydrological summer” (hereafter referred to as summer), defined as the period from the cessation of R until 30 September; and for the combined spring and summer period. The last day during which R was greater than zero (i.e., the last day of spring for our purpose) was not exactly the same among treatments in some years. However, any additional R that occurred after the specified date was negligible for any treatment (0.1 mm or less). We tested for dif-

ferences in cumulative R during the initial recharge period during the fall (November to December), during the spring, and for the entire water year (1 October to 30 September).

Gaps in the ET and R data due to equipment malfunction resulted in an unbalanced experimental design for some comparisons. We accounted for this by utilizing a regression approach to ANOVA [Kutner *et al.*, 2005], whereby a “full” linear statistical model (i.e., one that contains a term describing temperature effects) is compared to a “reduced” model that omits the term describing the temperature effects. The reduced model represents the null hypothesis that temperature had no statistically significant impact on the response variable. The alternative hypothesis of a significant temperature effect is accepted if the full model accounts for a significantly greater fraction of the total variance. For any ANOVA that yielded a type-one error probability of 0.1 or less (i.e., p value ≤ 0.1), we proceeded with Tukey’s procedure for multiple-pairwise comparisons of factor level means to specify which temperature levels were significantly different.

3. Results

3.1. Evapotranspiration

Evapotranspiration was greater under both warming treatments (ET_{sym} and ET_{asy}) during the spring, but less during the summer, resulting in no significant difference in total ET between either warming treatment and the ambient temperature treatment (ET_{amb}) over the combined spring and summer period (Figures 4a–4c). The spring period (defined as 1 March until the cessation of R) lasted until 15 May, 22 May, and 16 June in 2008, 2009, and 2010, respectively. Cumulative ET_{sym} and ET_{asy} during spring were, on average, 37 mm (20%) and 27 mm (13%) greater than ET_{amb} , respectively (Figures 4a–4c, p values were 0.10, 0.002, and 0.04 in 2008, 2009, and 2010, respectively). ET_{sym} was significantly greater than ET_{asy} during spring of 2008 and 2009 (Tukey multiple-mean comparison, $\alpha = 0.1$), but not in 2010. Evapotranspiration under ambient temperature during the summer was, on average, 28 mm (14%) and 31 mm (17%) greater than ET_{sym} and ET_{asy} , respectively (Figures 4a–4c, p values were 0.004 and 0.04 in 2008 and 2009, respectively). A similar trend was emerging during 2010, though cumulative ET for this summer period did not include the months of August and September since the temperature treatments were temporarily stopped during this period

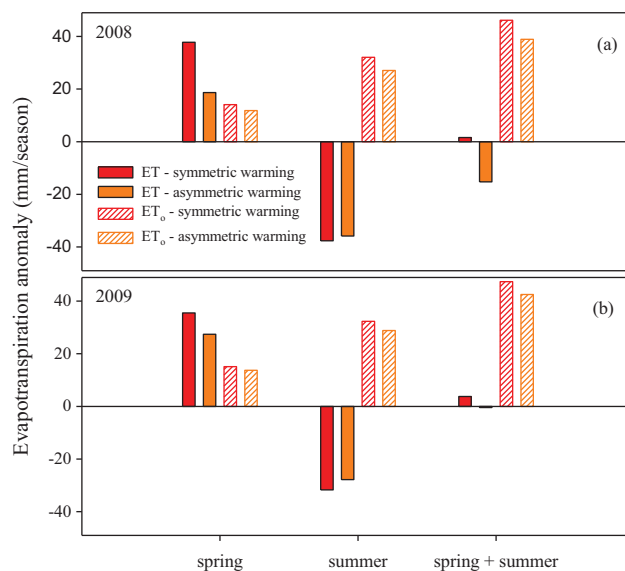


Figure 5. The magnitude of the warming effect on actual ET (i.e., $ET_{sym} - ET_{amb}$ and $ET_{asy} - ET_{amb}$) and reference ET_o (i.e., $ET_{o,sym} - ET_{o,amb}$ and $ET_{o,asy} - ET_{o,amb}$) during spring, summer, and the combined spring and summer periods of (a) 2008 and (b) 2009. The reference ET_o values were calculated using the method of Allen *et al.* [1998]—representing potential ET for a reference crop under no water limitation (described further in section 2).

(0.2) and 28 mm (1.2) greater than $ET_{o,amb}$ ($n = 2$ years), whereas actual ET_{sym} and ET_{asy} were 28 mm (12) and 31 mm (4.6) less than ET_{amb} , respectively (Figures 5a and 5b).

3.2. Soil Moisture

Total soil-water storage followed a seasonal cycle controlled by precipitation (Figures 6a and 6b). There was a transition from dry to wet conditions at the onset of precipitation in the fall, persistently wet conditions throughout the winter, and a transition from wet to dry conditions during the spring as precipitation decreased. During 2008, the minimum θ_{tot} (calculated as average θ_{tot} for the last 7 days of September) was 0.18, 0.17, and 0.17 for the ambient, symmetric, and asymmetric warming treatments, respectively; in 2009 these values were 0.18, 0.17, and 0.18. During the spring, θ_{tot} declined to lower values earlier under symmetric and asymmetric warming than under ambient temperature (Figure 6b). The maximum difference in θ_{tot} between ambient and warming treatments was 0.05 and 0.04 for symmetric and asymmetric warming, respectively, and occurred in late May or early June of each year. In general, the trajectory of θ_{tot} decline under ambient temperature lagged that observed under warming treatments by 1–2 weeks. For example, on 1 June 2009, θ_{tot} was 0.26 and 0.27 under symmetric and asymmetric warming treatments, though θ_{tot} under ambient temperature did not decline to 0.27 until 14 June (Figure 6b). A similar comparison beginning at 1 July 2009 showed a time lag for soil drying in the ambient chambers of 8 days.

3.3. Groundwater Recharge

Groundwater recharge was initiated during November or December (Figure 6c). The cumulative precipitation required to initiate R was nearly identical among temperature treatments in 2007, 61 and 23 mm less under symmetric and asymmetric warming compared to ambient temperature in 2008 ($p = 0.13$), and 30 and 17 mm less under symmetric and asymmetric warming compared to ambient temperature in 2009 ($p = 0.08$, Figure 7). These differences in cumulative precipitation typically occurred over the course of several hours during a single heavy rainstorm, and there was great variability among individual terracosms within any temperature treatment (Figure 7).

Groundwater recharge was marginally greater under both warming treatments than under ambient temperature during fall (November to December), though these differences were only significant in fall 2009 ($p = 0.04$, Figures 8a–8c). Recharge was similar among all treatments throughout the remainder of the winter. During spring, the last large storm that caused R resulted in greater R under ambient temperature than

when vegetation was dormant. These contrasting spring and summer trends resulted in no significant difference in ET between any temperature treatment during the combined spring and summer period (Figures 4a–4c, p value of 0.45 in 2008 and 0.99 in 2009).

The warming-treatment effects on ET (i.e., $ET_{sym} - ET_{amb}$ and $ET_{asy} - ET_{amb}$) were greater than the projected effects on reference ET_o (i.e., $ET_{o,sym} - ET_{o,amb}$ and $ET_{o,asy} - ET_{o,amb}$) during the spring, and less during the summer (Figures 5a and 5b). Averaged over three spring seasons, cumulative ET_{sym} and ET_{asy} were 37 mm (1.2) and 27 mm (7.6) greater than ET_{amb} ($n = 3$ years, σ in parentheses), respectively, whereas $ET_{o,sym}$ and $ET_{o,asy}$ were 17 mm (3.7) and 16 mm (5.4) greater than $ET_{o,amb}$. During the summer, projected $ET_{o,sym}$ and $ET_{o,asy}$ remained, on average, 32 mm

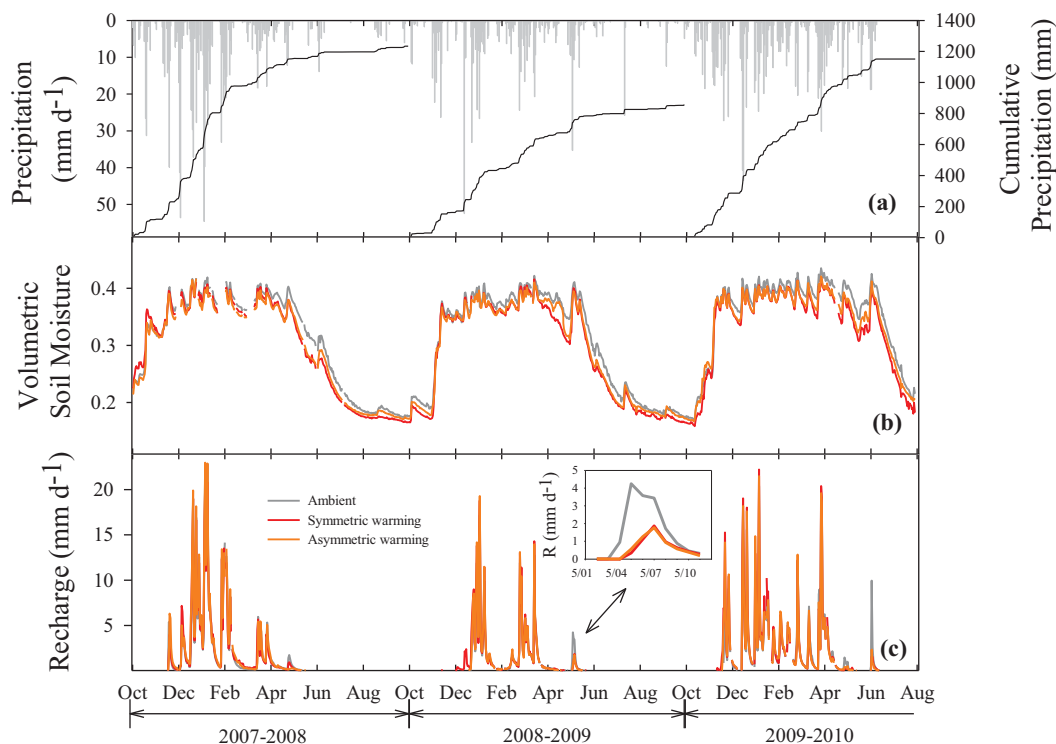


Figure 6. (a) Daily P from 1 October 2007 to 31 July 2010 and cumulative P for each water year. (b) Average-daily volumetric water content for each treatment during the same period. Each value is the treatment average of the volumetric water content of the entire soil volume, calculated using equation (1). (c) Average-daily R for each treatment. The inset graph highlights an example of the differences in R observed among treatments during the final R event of the spring (here expanded only for 2009).

under both warming treatments (Figure 6c). For example, average R from 4 to 23 May 2009 was 16.6 mm (2.85), 6.35 mm (3.36), and 8.42 mm (2.30) under ambient temperature, symmetric warming, and asymmetric warming, respectively ($n = 4$; σ in parentheses). Similar differences were observed in June 2010, and smaller differences in April 2008 (Figure 6c). However, the reductions in R that occurred during these late-spring storm events had a small relative effect—they represented 4%, or less, of total annual R that occurred under ambient temperature in any year. Cumulative R over the entire spring period was significantly reduced by warming treatments only during 2010 (Figure 8c, p values were 0.87, 0.34, and 0.07 in 2008, 2009, and 2010, respectively). There were no significant differences in average-annual R between any temperature treatments across all 3 years (Figures 8a–8c, p values were 0.55, 0.22, and 0.70).

4. Discussion

Contrary to our hypothesis, we found that a 3.5°C increase in temperature did not significantly reduce R over the entire water year, nor did it alter total ET that occurred during the spring and summer seasons. While the timing and magnitude of ET and R were affected at seasonal time scales, these effects were both positive and negative, depending on the season, resulting in no net difference in either flux at the growing season to annual time scale, respectively. In the following discussion, we assess which factors are responsible for the contrasting seasonal patterns of ET and R, and how the vegetation, climate, and soils specific to this experiment affect the general inference that can be made from our results.

4.1. What Caused the Contrasting Seasonal Patterns of ET Observed Under Warming Treatments Versus Ambient Temperature?

Evapotranspiration was greater under warming treatments than under ambient temperature during the spring (Figures 4a–4c), which was consistent with our first hypothesis. The comparison of ET_0 with actual ET helped to distinguish the relative importance of warming-induced changes in the physical environment (temperature and VPD) and the ecological effect of earlier peak-physiological activity by the vegetation.

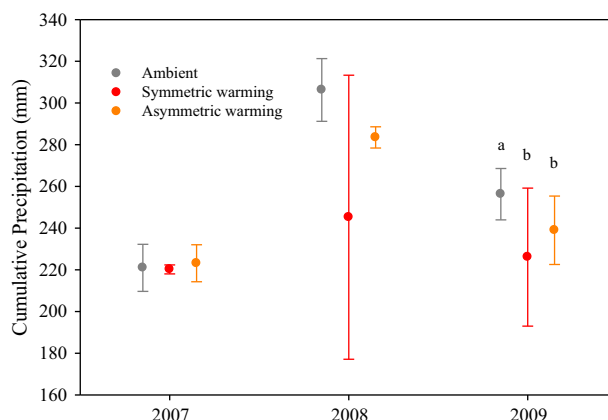


Figure 7. The cumulative P (beginning 1 October) required to initiate 1 mm d^{-1} of R during the fall season of each year. Error bars represent 90% confidence intervals. Different lower-case letters indicate differences among treatments with $p = 0.1$ or less.

Specifically, ET_o provides an estimate for the potential change in ET expected in response to the warming influence on VPD in the absence of water limitation. Differences in the magnitude of the warming effect on actual ET versus ET_o then reflect the relative contribution of plant canopy growth, photosynthesis, and stomatal conductance to the overall ET response (the plant functions that dictate the resistance parameters in the Penman-Monteith model, but are held constant when estimating ET_o). In both 2008 and 2009, the warming treatments enhanced actual ET during the spring (relative to ambient temperature) by a margin that was greater than projected using the ET_o calculations. This discrepancy was likely due to acceleration of the

timing of peak-seasonal photosynthesis that accompanied the increases in VPD. *Phillips et al.* [2011] showed that warming treatments accelerated the timing of peak-daily photosynthesis within the terracosc grasslands by an average of 2 weeks—from mid-May to late-April 2009. In a similar Mediterranean grassland ecosystem in California, *Zavaleta et al.* [2003a] also showed a warming-induced acceleration in the timing of canopy greenness and the absorption of radiant energy in the photosynthetically active range. Our results, considered alongside those of *Phillips et al.* [2011], suggest that warming-induced changes in the timing of peak photosynthesis augmented the warming-enhanced VPD to increase ET during the spring season in this Mediterranean climate.

Evapotranspiration was drastically reduced during the summer in response to limited soil moisture, as illustrated by the stark contrast between ET and ET_o (Figure 5). The decline in ET occurred earlier under warming treatments compared to ambient temperature and paralleled similar observed declines in photosynthesis [*Phillips et al.*, 2011]. As θ diminishes, uptake of soil water by plants is limited, causing reductions in photosynthesis, leaf area, and the overall ET component of the water budget [*Bell et al.*, 2010a, 2010b; *Porporato et al.*, 2004, 2001; *Ryu et al.*, 2008]. In this Mediterranean climate, ET increases steadily throughout the spring at the same time that the frequency and magnitude of precipitation steadily decreases. As a result of these opposing trends, soil moisture declines steadily following the last spring rains toward a seasonal minimum value during the late summer. The warming treatments accelerated ET during the spring, but it came at the cost of earlier water stress and plant senescence at the onset of the summer dry period, whereas plants growing under ambient temperature were able to continue transpiring at a greater rate later into the season. This negative ecohydrological feedback caused a reduction in ET during the summer that offset the enhancement of ET that occurred during spring, resulting in no difference in total ET during the combined spring and summer period. The results of this manipulative experiment support the conclusions of *Angert et al.* [2005], who interpreted hemispherical-scale fluctuations in atmospheric $[CO_2]$ and concluded that enhanced CO_2 uptake by vegetation during warmer spring periods did not lead to greater CO_2 uptake over the entire growing season, presumably due to drought-induced reductions in photosynthetic activity during late summer.

This negative feedback may have had a secondary biophysical effect, where, despite greater temperature and VPD, the rate of bare-soil evaporation after plant senescence was too low to sustain the cumulative increase in ET that had developed under warming treatments during the spring. As the plants senesce, the transpiration component of ET would have decreased concomitant with declining rates of photosynthesis [*Phillips et al.*, 2011; *Ryu et al.*, 2008], while the fraction of ET attributable to bare-soil evaporation was likely to have increased [*Zhongmin et al.*, 2009]. However, the rate of evaporation from the soil was near a water-limited-minimal rate, where evaporation from the soil surface is limited by exceedingly slow unsaturated-liquid-water flow from deeper soil layers. Additionally, senescing plant tissue has been shown to increase

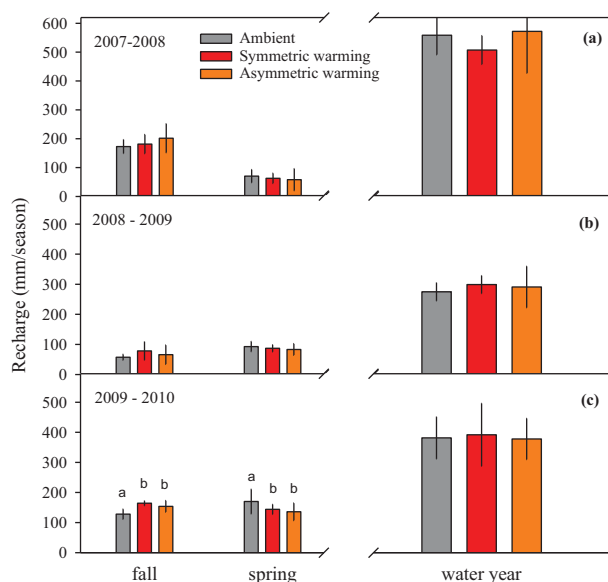


Figure 8. Cumulative R for the fall (November to December), spring (1 March until the cessation of R), and the complete water year for 2007–2010. Error bars indicate 90% confidence intervals. Where present, letters indicate differences among temperature treatments associated with a p value of 0.1 or less. No data were available for January 2010 due to equipment replacement during that time. Hence, the reported R for that water year is less than the actual amount.

the albedo of the land surface in similar grasslands [Baldocchi *et al.*, 2004], and the dense mat of senesced plant tissue that remained after the growing season may have diminished advective vapor transport from the underlying soil surface by the wind, therefore inhibiting evaporation from the soil.

4.2. Why Were There Only Small Seasonal Reductions of R, and No Reduction Over the Entire Water Year?

We anticipated that warming-enhanced ET during the spring season would reduce prestorm soil moisture, thereby causing a decline in R [Lehmann *et al.*, 2007; McMillan, 2012]. While there were reductions in R under warming treatments during the final large precipitation event of each spring (Figure 6c), these reductions were only a marginal fraction of R that occurred across the entire spring season. One exception was a significant seasonal effect during the spring of 2010 (Figure 8c). Differences in the timing and intensity of P—compared

with the timing of soil drying—may help explain why significant warming effects on R emerged only during the spring of 2010. Total precipitation during June 2010 was 63 mm, compared to only 15 mm in 2009 and 29 mm in 2008, and included 47 mm of cumulative P over a 3 day period. This relatively intense P event was sufficient to generate R for all treatments, and occurred after the maximum difference in θ_{tot} had developed between the warming treatments and the ambient temperature treatment during late May. In contrast, the P events that generated the last R in 2008 and 2009 occurred during late April and early May, respectively, before the maximum treatment difference in θ_{tot} had developed. Hence, in Mediterranean climates the impact of warmer air temperatures on R depends on the frequency and intensity of P events during the spring—high-intensity storms occurring late in the spring may generate less R in a warmer climate than similar storms occurring earlier in the spring, as the former are more likely to occur under greater prestorm deficits in soil-water storage.

Contrary to our expectation that warming-enhanced ET would cause lower minimum θ_{tot} at the end of the summer season [Cai *et al.*, 2009], differences in minimum θ_{tot} were only marginally lower under warming treatments than under ambient temperature, and surprisingly, the cumulative P required to initiate R in the fall was significantly less under warming treatments in 2009 (Figure 7). Although highly variable among individual terracosms, this lower threshold P amount contributed to greater cumulative R under warming treatments during the fall, which offset the reduction of R that occurred during the following spring. While minimum θ_{tot} at the end of the summer drought was only marginally lower under warming treatments, the duration of very low θ_{tot} was extended more substantially. For example, θ_{tot} was below 0.2 under warming treatments for 106–117 days in 2008 and 89–103 days in 2009, compared to only 81 and 61 days under ambient temperature. Longer periods of very low soil moisture could have increased the vertical extent of soil cracks in these clay soils, potentially enabling deeper infiltration through preferential flow processes [Jarvis, 2007] and earlier occurrence of R. This effect was recently demonstrated in agricultural soils by Sanders *et al.* [2012], though we have no direct evidence to evaluate this mechanism and can only offer it as speculation.

4.3. How Does the Specific Combination of Climate, Vegetation, and Soil Affect the General Inference That Can be Made From This Manipulative Experiment?

It is important to recognize what conditions may support, or detract from, the general inference that can be made from experiments or model simulations. We were unable to assess potential spatial variability of the

outcomes we observed, though this is undoubtedly important [Tague *et al.*, 2009; Thompson *et al.*, 2011]. The strengths of our approach included precision climate control, well-defined system boundary conditions, and the ability to simultaneously monitor the treatment response of ET, θ , and R—capabilities that could not be matched by observational studies in the open environment—though the intensive nature of the experiment obviously limited the spatial extent and replication.

Most notably, the Mediterranean rainfall regime and associated temporal trends in soil moisture emerged as dominant influences in this study, and exerted important control over seasonal carbon fluxes as well [Phillips *et al.*, 2011]. In environments where rainfall is seasonally out of phase with temperature, the linkage between ET and temperature is less robust [Milly, 1994; Potter *et al.*, 2005; Pumo *et al.*, 2008; Viola *et al.*, 2008]. Different results might be expected in more humid environments where P occurs more uniformly throughout the year or in phase with vegetative growth, and where the frequency and intensity of rainfall determines how often plant stress may result in reduced ET [Porporato *et al.*, 2004, 2001].

The negative feedback mechanism of lower ET during summer resulting from greater ET during the spring under warming treatments may be unique to grassland ecosystems due to the nearly complete senescence of aboveground tissues and suppressed physiological activity during extended drought periods. Further, grassland ecosystems have lower water-use efficiency than forests, and more intensively exploit soil water when it is available [Ponton *et al.*, 2006; Teuling *et al.*, 2010]. Trees may shed part of their foliage during drought and regulate stomatal aperture to limit water loss, but water stress in trees may occur later in the season [Baldocchi *et al.*, 2004] due to their greater water-use efficiency and more expansive root systems. Hence, warming-induced increases in ET during the spring may result in a greater annual total in forests, unlike the response we observed. Last, the negative feedback we observed may be unlikely in grasslands that contain C₄ species that demonstrate greater water-use efficiency and less susceptibility to water stress during drought [Baldocchi, 2011; Morgan *et al.*, 2011, 2004].

The high water-storage capacity of the silty clay loam soils used in this experiment had important effects on the R response to warming. Green *et al.* [2007] completed a unique modeling analysis that examined the interactive effects of vegetation type (forest versus grassland), various soil textures, and prevailing rainfall regime (seasonal versus nonseasonal rainfall) on R. Their work identified important interactions between all three variables that ultimately determined if climate warming increased or decreased R, and to what extent. One salient finding of their work was the importance of soil texture and water-storage capacity; specifically, they showed that finer textured soils consistently buffered the R response (whether positive or negative) to climate alteration and associated changes in ET, whereas more significant R responses occurred in sandy soils with lower storage capacity. Our soils contain a greater clay fraction than any of those simulated by Green *et al.* [2007]. Hence, the warming-enhancement of ET we observed may have had a greater impact on R during the spring given a more coarsely textured soil.

Last, our experiment did not include elevated atmospheric [CO₂], which is expected under future climate conditions. Manipulative experiments in other Mediterranean grasslands have shown that elevated [CO₂] can enhance the water-use efficiency of photosynthesis by reducing stomatal conductance, resulting in less overall transpiration and soil-water depletion due to root uptake [Field *et al.*, 1997; Fredeen *et al.*, 1997]. In particular, Fredeen *et al.* [1997] showed that ET was reduced and soil moisture remained greater under elevated [CO₂] relative to ambient levels, and the decline of soil moisture during the summer drought was delayed by about 10 days. Had elevated [CO₂] been included in our experiment, the warming-induced enhancement of ET during the spring may have been less, and warming-induced declines in soil moisture and ET during the summer may have been delayed.

5. Conclusions

Results of our study demonstrate that the annual partitioning of P to ET and R in a Mediterranean-grassland ecosystem could be unaltered by climate warming. Warming caused greater ET during the spring (relative to ET under ambient temperature), but this led to more rapid depletion of soil moisture and reduced ET during the summer. Despite warming-enhanced ET, reductions in total soil-water storage became great enough to reduce R only during the final storm event of the spring. These reductions in R were marginal relative to total R that occurred during the spring season, and were offset by greater R under warming treatments at the onset of fall rains, which we speculatively attribute to potential warming effects on the hydraulic

properties of the silty clay soils used in this experiment. Our results confirm the general view that interactions and feedbacks between climate, vegetation, and soil moisture ultimately dictate the ecosystem water balance response to climate warming [Angert *et al.*, 2005; De Boeck *et al.*, 2006; Green *et al.*, 2007, 2011; Jung *et al.*, 2010; Zavaleta *et al.*, 2003a].

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