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REGULAR ARTICLE

Temporal and spatial variation in how vegetation alters the soil moisture response to climate manipulation

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Abstract
Aims Soil water balance, key for ecosystem processes, is determined by multiple factors, including precipitation, temperature, slope and vegetation. How these interact with climate change and the relevant time scale of the interactions are poorly understood. We investigated the interplay among climate change, local abiotic conditions (slope) and biotic factors (vegetation or not) on soil water balance in a steppe grassland on the south exposure of a northern Mongolia valley.
Methods We manipulated climate using passive warming open top chambers (OTCs), similar to those used in other systems. Areas of bare ground were created inside the OTCs to explicitly evaluate the effect of vegetation on soil moisture and its dynamics. The experiment was set up at two topographic locations, a steep upper slope and a gentle lower slope. Volumetric soil moisture content was measured throughout each growing season in a small area where vegetation had been removed and where it was left intact both inside OTCs and in control plots. To account for OTCs intercepting some precipitation, we also examined treatment effects on soil drying rates.
Results Vegetation and climate manipulation reduced soil moisture more strongly in the wetter of the two years and just after rains. Similarly, treatment effects were more pronounced on the wetter lower slope. Averaged across the growing season, climate manipulation did not affect soil water differentially in vegetated and unvegetated areas, but seasonal variation in the strengths of treatment effects and interactions between climate and vegetation reflected plant developmental phenology. Soil drying rate was faster on the drier upper slope or with vegetation and faster overall in the drier year. In the dry year 2010, soil drying was slower in OTCs, likely because of wind interception.
Conclusions Monthly or seasonal averages of soil moisture would have provided poor information about the interplay among factors affecting soil water balance in this system. Our study illustrates the utility of experimentally examining the interaction between biotic and abiotic factors and considering relevant time scales when investigating the complex effects of climate change on ecosystem processes.

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Introduction

Soil moisture is an essential driver of most ecosystem processes. It influences the nitrogen cycle, via microbial activity (Stark and Firestone 1995; Barnard et al. 2006) and carbon storage and cycling (Tate and Ross 1997; Flanagan and Johnson 2005; Garten et al. 2009). Soil moisture is an essential resource affecting productivity and hence plant and microbial community composition and diversity (e.g., Clark et al. 2009; Castro et al. 2010). Limited soil water selects for aridity tolerance and drives many biotic interactions (Novoplansky and Goldberg 2001; Pugnaire et al. 2004; Michalet 2006). Finally, soil moisture has consequences for climate itself, by affecting dewpoint temperature and surface thermodynamics with feedbacks to precipitation (Myoung and Nielsen-Gammon 2010).

Climate change is projected to involve not only an increase in average temperatures (2.5°C over this century) but also altered precipitation patterns (Easterling et al. 2000; IPCC 2007). The less frequent but stronger precipitation events forecast for many regions by most models should dramatically affect ecosystem processes and plant community structure and composition (Castro et al. 2010; Dermody et al. 2007; Knapp et al. 2008; Weltzin et al. 2003; Yang et al. 2011). However, the vulnerability and responses of ecosystems to climate change drivers appear contingent on the local conditions and dominant vegetation (Grime et al. 2000; Scholze et al. 2006; Liancourt et al. 2009); responses may differ both in direction and intensity even at small spatial scales (Harte et al. 1995; Klein et al. 2004).

Ecosystem water balance is determined by inputs in the form of precipitation and by outputs through evaporation, transpiration, leaching, and surface runoff. Local inputs and outputs vary substantially both temporally and spatially due to storms, wind, slope, aspect, and vegetation cover and phenology, but little is understood about the interactions of these factors, especially in the context of climate warming (Flanagan and Johnson 2005; Dermody et al. 2007; Engel et al. 2009).

The effect of vegetation on ecosystem water balance, in particular, is complex and may either mitigate or exacerbate the effects of climate change. On one hand, vegetation can increase soil drying through transpiration, but on the other, it can bring water up from deeper soil layers via hydraulic lift (Horton and Hart 1998), lessen runoff on steep slopes (Dunne et al. 1991), and reduce soil evaporation due to shading, as happens in European calcareous (Liancourt et al. 2005) and subalpine grasslands (Gross et al. 2008). Zavaleta et al. (2003) have reported that at the end of the growing season in annual-dominated Mediterranean grasslands, vegetation can offset the effect of climate warming on soil moisture.

We study the interaction between vegetation cover and climate manipulation in the Eurasian steppe, the largest grassland in the world and one that provides crucial services for local herder populations. Specifically, our experiment is set in northern Mongolia, where a substantial rise in temperatures has been observed over the last 40 years (+1.7°C in the Hövsgöl area, Namkhaijanstan 2006). The intensification of grazing observed in the area, because of the decrease in nomadic habits of the local people, potentially makes the system more vulnerable to climate change. The danger is that stress from overgrazing and altered climate may lead semi-arid grasslands to shift catastrophically to desert. To our knowledge, no empirical data based on experimental manipulation of climate are available for the cold and dry northern Mongolian steppe, although some recent studies set in Inner Mongolia, China have considered soil moisture together with climate manipulation (Niu et al. 2008; Liu et al. 2009; Xia et al. 2010).

Our main goal is to evaluate how experimental summer climate manipulation affects soil moisture while taking into account spatial heterogeneity due to topography and vegetation cover and temporal variation in precipitation. We manipulated climate using passive warming open top chambers (OTC), similar to those used in other systems (Marion et al. 1997; Klein et al. 2004) and created areas of bare ground inside the OTCs to evaluate explicitly the effect of vegetation on soil moisture and its dynamics. Because passive warming chambers alter precipitation and air advection and convection in addition to temperature (Marion et al. 1997), we recognize them as climate manipulators, not solely warming devices (see Dabros et al. 2010). As response variables, we examine standing soil moisture and the rate of soil drying, an approach that compensates for the interception of some precipitation by the climate manipulators. Soil moisture loss is of particular interest because it serves as a key indicator of how abiotic and biotic factors affect the distribution of water within the ecosystem, providing basic information for understanding how climate change will alter the ecology of the region.

Due to the elevated air temperatures achieved, we hypothesized that (i) climate manipulation would significantly increase soil drying rates after precipitation events. Because we expected transpiration to outweigh other effects of plants on soil water, we hypothesized that (ii) the presence of vegetation would also increase the drying rate. We had no *a priori* hypothesis regarding how climate manipulation and vegetation might interact with each other to affect soil drying or how such an interaction might depend on incipient moisture levels. Our daily measures of soil moisture, however, allowed us to assess how interactions among experimental factors varied temporally, both within growing seasons and between 2009 and the drier year of 2010. Finally, we anticipated that (iii) climate manipulation and vegetation would each reduce soil moisture more strongly in locations where soils are inherently wetter and plant productivity is greater, which in our system is lower on the slope.

Materials and methods

Site

The experiment was conducted during two consecutive summers, from June to August 2009 and 2010, on a south-facing slope of steppe grasslands in the Dalbay river valley, on the eastern shore of Lake Hövsgöl (51° 01.405′ N, 100° 45.600′ E; ranging from 1670 m to 1800 m in elevation), northern Mongolia. The average annual air temperature is −4.5°C, with the coldest average monthly temperature of −21°C (January) and warmest of 12°C (July) (Nandintsetseg et al. 2007). The average annual precipitation measured for the last 40 years, averaged for three weather stations south (Hatgal), west (Renchinlhumbe) and north (Hankh) of Lake Hövsgöl, was 265 mm (Namkhaijanstan 2006). In 2008, we installed a year-round meteorological station approximately a third of the way up the south-facing slope in order to measure precipitation, temperature, wind speed and insolation. Overall, Jan.–Dec. 2009 was wetter (270 mm) than Jan.–Dec. 2010 (246 mm). Summer rainfall (June to Aug.) was also greater in 2009 (201 mm) than in 2010 (178 mm), when most of it fell between Aug. 11 and 17; 42 mm occurred in a single storm on Aug. 12, 2010.

Permafrost is not present on the south-facing slope but is found in a nearby riparian zone and on north-facing slopes under the taiga forest, which consists of *Larix sibirica* and *Pinus sibirica*. The steppe vegetation is a mixture of sedges (e.g., *Carex pediformis*, *Carex dichroa*), grasses (e.g., *Festuca lenensis*, *Koeleria macrantha*, *Agropyron cristatum*, *Helictotrichon schellianum*, *Stipa krylovii*) and short forbs (e.g., *Aster alpinus*, *Potentilla acaulis*, *Artemisia commutata*, *Thymus gobicus*). The vegetation differs both in composition and in total cover between the upper and lower slope, the two locations of experimental climate manipulation chambers. In 2009, the lower slope (elevation 1670 ma.s.l.) had a total vascular plant cover of 78% and the upper slope (elevation 1800 ma.s.l.) 64%. *Carex pediformis* is the most common species on the lower slope and *Potentilla acaulis* on the upper. Lichen cover is also greater on the upper slope. The soil is sandy loam texture, of alluvial origin, and classified as a non-carbonated Dark Kastanozem (Aridic Boroll or Typic Ustolls). Bedrock consists of Cenozoic volcanic deposit (Batkhishig 2006).

The experiment and statistical analysis

Fifteen 9×9 m experimental blocks were established on the south-facing slope and fenced to exclude grazing livestock. Eight were located lower on the slope (gentle to flat slope) and seven on the upper part of the slope (incline ~20°). Each block enclosed plots in which summer climate is manipulated in a factorial design with precipitation addition treatments on the upper slope and exposure to grazing on the lower. Here we report data and analyses from control plots without added precipitation or grazing. The climate manipulation was accomplished with hexagonal passive, open-top chambers (OTC) measuring 1.0 m wide at the top, 1.5 m at the bottom and 40 cm tall, and made of Sun-Lite® HP fiberglass glazing (Marion et al. 1997). Each of the six side panels was mounted on a clear Lexan frame and attached to the next with hinges. An area of the same footprint and dimensions was delineated in each block as a control. Both OTCs and controls were placed in the same locations both summers. Detailed monitoring of the climate manipulation performance of the OTCs found that over the course of the 2009 and 2010 summer seasons, mean daytime air temperatures at 15 cm height were 1.5°C warmer in the chambers, maximum daytime air temperatures were 3.3°C warmer, and mean nighttime air temperatures were 0.3°C cooler (unpublished data). Differences in soil temperatures at 10 cm depth were not found to be statistically different between control plots and OTCs, but volumetric soil moisture content was 1.6 to 4.1 percentage points less in OTCs compared to control plots (unpublished data). As a check, photosynthetically active radiation (PAR) measurements were made horizontal to the soil, at the ground surface either under the vegetation or in the non-vegetated plots between 11:00 a.m. and 12:00 p.m. (solar noon) on a cloudless day. For the control treatment, PAR was 1140±65 mmol m^{-2} s^{-1} in the vegetated areas and 1630±26 mmol m^{-2} s^{-1} in the unvegetated areas. In the OTCs, PAR was 963±88 mmol m^{-2} s^{-1} in the vegetated areas, and 1452±75 mmol m^{-2} s^{-1} in the unvegetated areas. Measures of PAR differed significantly between vegetated and non-vegetated areas ($P<0.05$; OTCs and controls combined). The results suggest that vegetation, and to a less extent OTCs, intercept light and could therefore decrease evaporation and drying rates.

In order to understand the effect of climate treatment and its interaction with vegetation (i.e.,

Table 1 Results of the repeated measures ANOVA for the effect of slope, climate treatment, vegetation, time and their interaction on volumetric soil moisture content (θ) during the summers 2009 and 2010

Source of variation	2009			2010		
	df	Mean square	Variance components (%)	df	Mean square	Variance components (%)
Climate	1	3777.83***		1	11624.1***	
Vegetation	1	534.78**		1	80.54^{ns}	
Slope	1	30142.82***		1	18009.2***	
Climate × Vegetation	1	29.14^{ns}		1	0.01^{ns}	
Climate × Slope	1	2.18^{ns}		1	1169.13***	
Vegetation × Slope	1	176.04^{ns}		1	187.50*	
Climate × Vegetation × Slope	1	49.82^{ns}		1	69.69^{ns}	
Time	38	898.73***		70	2021.04***	
Climate × Time	38	21.21***		70	57.79***	
Vegetation × Time	38	27.07***		70	6.64***	
Slope × Time	38	24.90***		70	31.36***	
Climate × Vegetation × Time	38	14.89***		70	6.27***	
Climate × Slope × Time	38	4.80^{ns}		70	4.02**	
Vegetation × Slope × Time	38	12.23***		70	4.84***	
Climate × Vegetation × Slope × Time	38	8.04***		70	2.28^{ns}	
Block[Slope]	13	204.91	13.23	13	168.51	12.29
Climate × Block[Slope]	13	56.71	7.21	13	20.72	0
Vegetation × Block[Slope]	13	38.19	3.36	13	37.25	0
Climate × Vegetation × Block[Slope]	13	20.91	6.97	13	71.99	16.50
Time × Block[Slope]	494	5.27	2.10	910	3.76	7.83
Climate × Time × Block[Slope]	494	4.01	2.06	910	2.24	5.90
Vegetation × Time × Block[Slope]	494	4.48	5.79	910	2.24	5.90
Residual	494	3.75	59.30	910	1.82	51.60

Asterisks indicate significant effect with *$P\leq0.05$, **$P\leq0.01$ and ***$P\leq0.001$. ns indicates non-significant results.

transpirational water loss) on volumetric soil moisture content (θ), we created a triangular area of 0.55 m^2 of bare soil within each plot by removing the above-ground vegetation in one corner formed by two sides of the chamber and in an area of the same dimension in the control plot. Two sides of the hexagon were oriented N-S. We removed the vegetation from the west-side triangle of half the chambers or control plots selected at random, and from the east-side triangle in the other half of the chamber or control plots. We used a serrated knife (20 cm long) to remove vegetation and trench around the area in order to exclude roots from surrounding vegetation, and we kept these areas vegetation-free by weekly hand weeding. The 1×0.5 m area in the center of the hexagon was left undisturbed for annual vegetation censuses, and so was not part of this study. Preliminary measurements of soil moisture at the onset of the vegetation removal showed no significant differences between the three areas within each plot (data not shown).

Volumetric soil moisture content (θ) of the surface soil was measured between 10:00 a.m. and 11:00 a.m. on almost every rainless day in 2009 and daily in 2010, regardless of precipitation events. Two measurements were taken randomly and pooled within each triangular area where the vegetation was removed and in the corresponding vegetated area on the opposite side of the hexagon, using a portable probe (WET-2 sensor, Delta-T Devices Ltd) at a depth of approximately 6 cm.

Volumetric soil moisture content data was analyzed for each year separately using univariate repeated-measures ANOVA. The fixed factor of slope (location), climate, and vegetation were fully crossed, and time was the repeated factor. Block was a random factor nested within slope; the analyses included interactions between block and climate, vegetation and time. We also performed Tukey's tests to evaluate the fixed effects and their interactions on θ on particular dates.

Because the chambers themselves reduce the amount of precipitation reaching the plots (unpublished data), the rate of soil moisture loss is likely to be a stronger indicator of how climate alteration within OTCs affected soil moisture. Thus, we examined how slope, climate, vegetation and their interactions affected the dynamics of soil moisture after each rainfall event, calculated as the soil drying rate. For each experimental and control plot and for each year, we modeled variation in θ over rainless days following each rainfall event as an exponential decay:

$$\theta_t = \theta_0 e^{-kt}$$

where θ_0 is the volumetric soil moisture immediately after a rainfall event and t the number of rainless days following the rainfall event. We call these sequences of precipitation and subsequent rainless days 'time intervals.' We worked with five separate time intervals in 2009, when sufficient continuous data was available, and 11 intervals in 2010 (Appendix 1). The

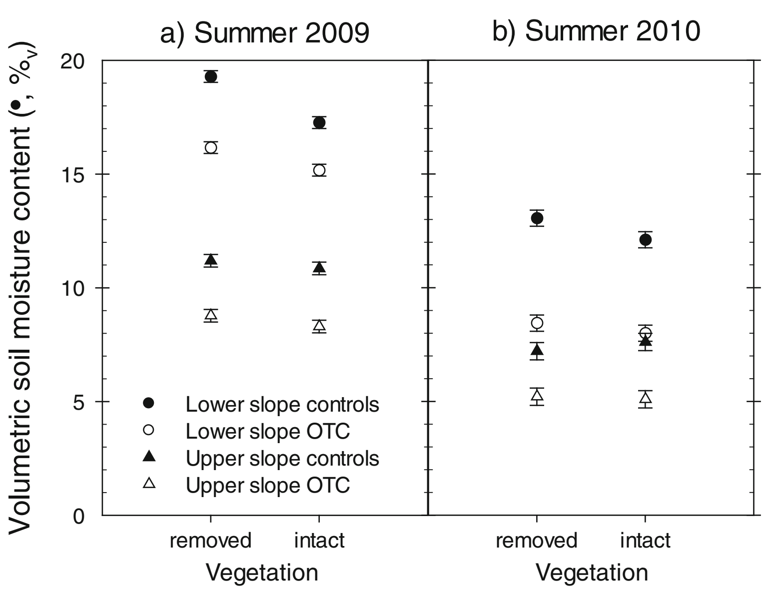

Fig. 1 Seasonal averages and standard errors for volumetric soil moisture content (θ,$\%_v$) during the summer 2009 (**a**) and the summer 2010 (**b**), for the lower (*circles*) and upper (*triangles*) slope positions, in the control (*closed symbols*) and OTC (*open symbols*) treatments with intact and removed vegetation. Sample sizes: n=8 for lower slope and n=7 for upper slope

parameter k was estimated by fitting the model $ln\ \theta_t - ln\ \theta_0 = kt$ as a linear regression of $ln\ \theta_t - ln\ \theta_0$ versus t with the intercept constrained to zero. ANOVAs were conducted separately for each year with k as the dependent variable and slope, climate, vegetation and time interval as fixed factors and fully crossed. Similar to the previous analyses, block was a random factor nested within slope; the analyses included interactions with climate, vegetation and time intervals (Table 2). For graphical data presentation, the finite soil drying rate, Δ soil moisture (Fig. 5), which is the percent loss per day was calculated as:

$$\Delta \text{ soil moisture} = 1 - e^{-kt}$$

All statistical analyses were performed using JMP v8.0 (SAS institute 2008).

Results

Volumetric soil moisture content (θ)

Both slope and climate treatment had consistent significant effects on θ in both years (Table 1), where θ was 42% drier at the upper slope location than at the lower slope in 2009 and 40% drier in 2010 (Fig. 1). Soil in the OTC was 17% drier than in the control in 2009 and 33% drier in 2010. Vegetation, as a main effect, was significant in 2009 (7% drier in

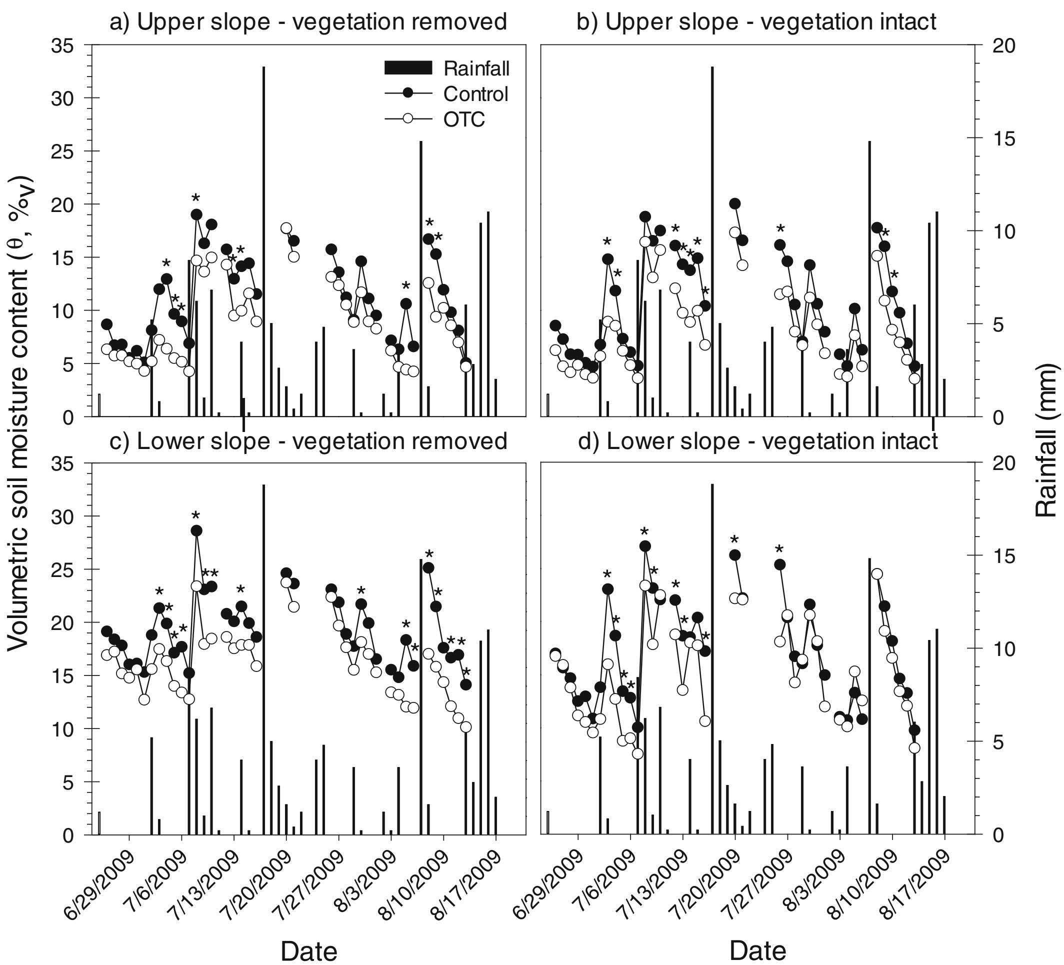

Fig. 2 Variation in average volumetric soil moisture content (θ, $\%_v$) across the 2009 vegetation season for control (*closed symbols*) and OTC (*open symbols*) treatments at the lower and upper slope, and with intact or removed vegetation. *Bars* represent rainfall events in mm. *Stars* above symbols indicate a statistically significant difference in θ between control and the OTC (Tukey tests, $p<0.05$)

vegetated areas) but not in 2010, when vegetation reduced θ at the lower slope only (7% drier in vegetated area; significant slope × vegetation interaction; Table 1, Fig. 1b). The climate × vegetation interaction and the climate × vegetation × slope interaction were not significant either year, indicating that over the whole summer, the OTCs did not differentially affect moisture loss from vegetated vs. bare soil at either slope location. The interaction climate × slope was significant just in 2010 (Table 1), when the OTC reduced soil moisture by 35% at the lower slope and 30% at the upper slope.

Slope, vegetation and climate treatment showed complex interactions with time in affecting θ both years. Temporal soil moisture dynamics were, not surprisingly, driven by the timing of rainfall events and the duration of intervening rainless periods but were also affected by our experimental manipulations (Fig. 2 and 3). The effects of climate treatment and vegetation on θ were smallest during rainless periods, and this results in significant climate × time and vegetation × time interactions each year. The significant slope × time interaction each year reflects a faster change in θ values during rainfall events and intervening rainless periods at the upper slope (see also Δ soil moisture below). The vegetation × slope × time interaction was significant both years because vegetated areas show a stronger decrease in θ at the lower slope, mainly in the middle of the summer. The significant climate × slope ×

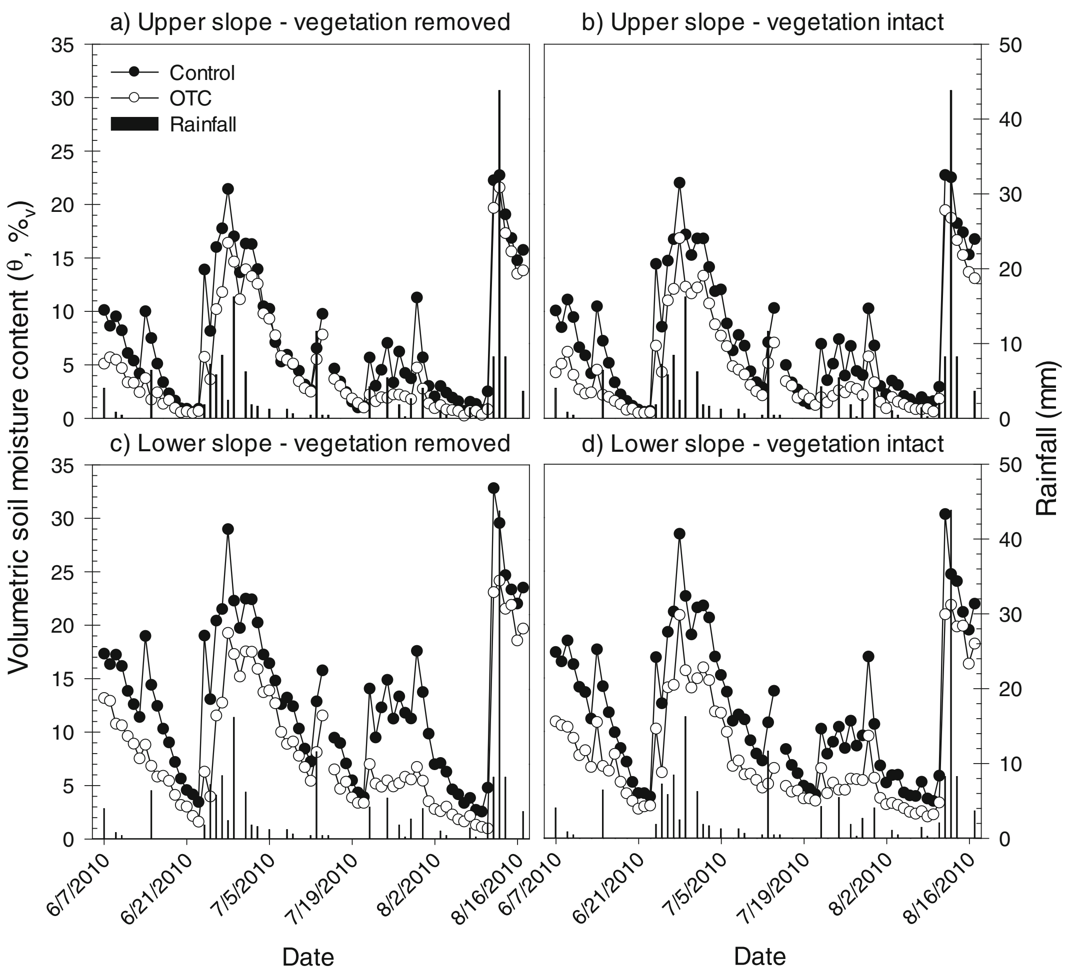

Fig. 3 Variation in average volumetric soil moisture content (θ, $\%_v$) across the 2010 vegetation season for control (*closed symbols*) and OTC (*open symbols*) treatments at the lower and upper slope, and with intact or removed vegetation. *Bars* represent rainfall events in mm

time interaction in 2010 indicates temporal variation in how the two slope locations responded to climate treatment; climate treatment more often lowered θ on the lower slope.

The effect of climate treatment on θ changed over time between intact vegetation and bare ground (significant climate × vegetation × time interaction, Table 1) in both 2009 and 2010. These interactions are more clearly illustrated in 2010 when there was no climate × vegetation × slope × time interaction as there was in 2009 (Table 1, Fig. 4). Vegetation reduced θ the most in OTCs in the middle of the summer. In 2010, for example, OTCs reduced θ more in the presence of intact vegetation than in bare areas during the three first weeks of July (Fig. 4). In contrast, OTCs reduced θ less in the presence of intact vegetation than in bare areas at the end of the season (Fig. 4). The significant four-way interaction of climate × vegetation × slope × time for 2009 and Tukey's tests show that at the end of the 2009 growing season, climate treatment did not significantly affect θ at the lower slope in plots where the vegetation was left intact (Fig. 2).

Out of 39 days of measurement in 2009, there were only three dates (July 10th, Aug. 8th and Aug. 9th) when soil moisture was significantly greater in the presence of vegetation than in bare areas. This positive effect of vegetation on soil moisture was only observed on the day following a precipitation event and only in the OTCs at the lower slope (Tukey's test, $P<0.05$). In 2010, a positive effect of vegetation on soil moisture was observed within OTCs toward the beginning and end of the season, as well as just after or during a rainy day (June 24th and 26th, July 30th and Aug. 11th).

Soil drying rate (Δ soil moisture)

The soil drying rate was overall greater on the upper slope both years, but effects of climate manipulation and vegetation were not consistent between years. The soil drying rate did not differ between climate treatments in 2009, but it was slower in the OTCs than in control plots in 2010. Soil drying rate increased with vegetation in 2009 but showed no effect of vegetation in 2010 (Table 2, Fig. 5).

The soil drying rate varied significantly among the time intervals in each of the two years, but no seasonal trends or consistent patterns were identified. In 2009, there were significant interactions for vegetation × time and climate × vegetation × time indicating variation in how vegetation and its interaction with climate affected the drying rate of soil over time (Table 2). In 2010, the only significant two-way interaction was slope×time, indicating temporal variation in how much faster the upper slope dried.

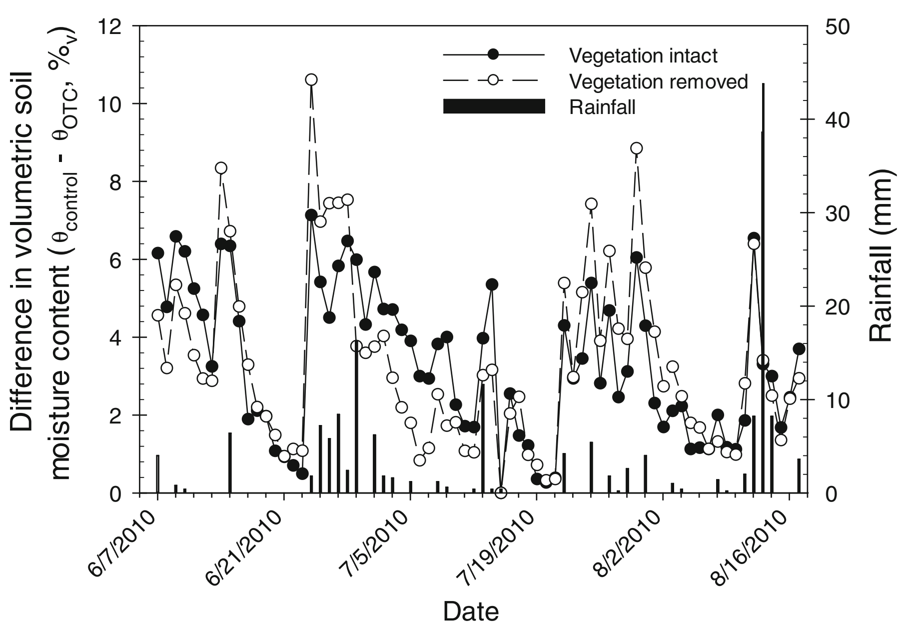

Fig. 4 Difference in average volumetric soil moisture content (θ,$\%_v$) between controls and OTC across the 2010 vegetation season for intact vegetation (*solid line*, *closed symbols*) and removed vegetation (*dashed line*, *open symbols*). *Bars* represent rainfall events in mm

Table 2 Results of the ANOVA for the effect of slope, climate treatment, vegetation, time intervals and their interactions on the exponential decay constant (k) used to model volumetric soil moisture content after rainfall events for the summers 2009 and 2010

Source of variation	2009			2010		
	df	Mean square	Variance components (%)	df	Mean square	Variance components (%)
Climate	1	0.1697^{ns}		1	1.2348*	
Vegetation	1	1.2582***		1	0.1592^{ns}	
Slope	1	0.7544**		1	2.2508***	
Climate × Vegetation	1	0.0067^{ns}		1	0.000038^{ns}	
Climate × Slope	1	0.0085^{ns}		1	0.5067^{ns}	
Vegetation × Slope	1	0.00878^{ns}		1	0.1327^{ns}	
Climate × Vegetation × Slope	1	0.00083^{ns}		1	0.0031^{ns}	
Time interval	4	0.3729***		10	2.7974***	
Climate × Time interval	4	0.0306^{ns}		10	0.1429^{ns}	
Vegetation × Time interval	4	0.1128*		10	0.1018^{ns}	
Slope × Time interval	4	0.1020^{ns}		10	0.9118***	
Climate × Vegetation × Time interval	4	0.1122*		10	0.2066^{ns}	
Climate × Slope × Time interval	4	0.0229^{ns}		10	0.1355^{ns}	
Vegetation × Slope × Time interval	4	0.0225^{ns}		10	0.1254^{ns}	
Climate × Vegetation × Slope × Time interval	4	0.0456^{ns}		10	0.0463^{ns}	
Block[Slope]	13	0.0473	0	13	0.1206	0
Climate × Block[Slope]	13	0.0379	0	13	0.2015	0
Vegetation × Block[Slope]	13	0.069	0.821	13	0.1288	0
Climate × Vegetation × Block[Slope]	13	0.0489	1.722	13	0.0629	0
Time interval × Block[Slope]	52	0.0455	2.162	130	0.1129	0
Climate × Time interval × Block[Slope]	52	0.0248	0	130	0.1787	0
Vegetation × Time interval × Block[Slope]	52	0.0342	0.064	130	0.0975	0
Residual	52	0.0274	95.23	130	0.1073	100

Asterisks indicate significant effect with *$P \leq 0.05$, **$P \leq 0.01$ and ***$P \leq 0.001$. ns indicates non-significant results.

Discussion

Our experiment produced several key results. First, if there is an effect of vegetation on soil moisture (2009 only), then it is negative. This result is consistent with our expectation that moisture loss through transpiration or evaporation directly from foliage must more than balance any positive effect of vegetation on soil moisture relative to controls, as might occur from shading or hydraulic lift (Liancourt et al. 2005; Pugnaire et al. 2004). While our climate treatment also reduced soil moisture, on average over the whole season, combined effects of climate treatment and vegetation (2009 only) are additive; there is no interaction between the two. Third, OTCs (2010 only) and vegetation had opposite effects on the soil drying rate, with OTCs reducing it and vegetation increasing it (2009 only). Fourth, important experimental effects differed between years, such as the effect of the vegetation or whether slope interacted significantly with vegetation or climate manipulation. Finally, within a growing season, interactions among slope, climate treatment, and vegetation changed in complex ways over time to affect soil moisture.

Identifying the relevant time scale when climate change, especially warming, interacts with other environmental factors is of primary importance for understanding its impact on ecosystem processes (Shaver et al. 2000). We identified two such time scales: (1) yearly differences, probably due primarily to differences in precipitation between the two summers, and (2) seasonal variation, which seems to

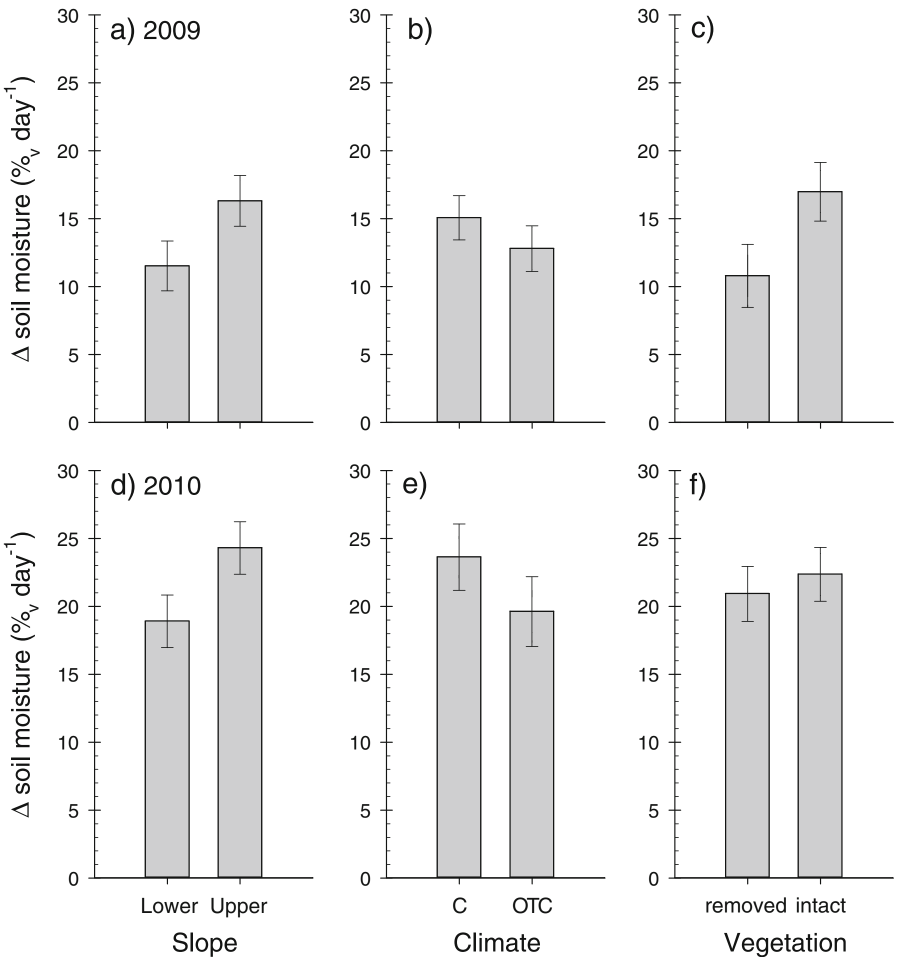

Fig. 5 Effects of slope position, climate treatment and vegetation on soil drying rate (Δ soil moisture, $\%_v$ day^{-1}) for the 2009 (**a**, **b** and **c**) and 2010 (**d**, **e** and **f**) vegetation seasons. *Error bars* represent 95% confidence intervals on the mean, calculated using standard errors reported in JMP printout and $t_{0.05,13}$

reflect both the developmental phenology of the plants (see Nord and Lynch 2009) and variation in baseline soil moisture attributable to the timing and amount of precipitation events (Noy-Meir 1973). These within-season changes in interactions among experimental treatments would have been obscured if soil moisture had only been evaluated as monthly or seasonal averages, rather than daily measurements.

Climate treatment and vegetation did interact to affect soil moisture at some time points during both growing seasons. In general, vegetation further decreased soil moisture in OTCs during the middle of the season (July) but mitigated or even counterbalanced OTC effects toward the end of the season. This result is likely related to plants having more active growth, and apparently maximal transpiration, in July (Suzuki et al. 2003) and reduced transpiration concomitant with senescence at the end of the season (Suzuki et al. 2003; Zavaleta et al. 2003). Increased shading by well-developed vegetation late in the season might also have reduced evaporation directly from the soil. Our findings regarding a late season reduction in the impact of vegetation on soil moisture agree with those of Zavaleta et al. (2003) in Californian grasslands but are not as dramatic. That study differed from ours in using infrared lamps to produce warming and not explicitly removing vegetation.

Besides a seasonal trend likely related to the phenology of the vegetation, we also found that all experimental effects—climate treatment, vegetation, and slope—were more pronounced during or after rainfall events and in 2009, the wetter year (see Figs. 2 and 3). That vegetation and OTCs effects on soil moisture were more common on the lower slope may also be related to that location being wetter, consistent with other studies showing a less pronounced effect of climate manipulation in drier locations (Klein et al. 2004; see also Harte et al.

1995). However, other differences between the two slope locations, such as plant cover and species composition, may be equally important. Regardless, our results show that topography should be considered in empirical studies of climate change, when it seldom is (Dunne et al. 2004).

There were also important differences between years in how experimental treatments affected the soil drying rate. Vegetation increased soil drying as a main effect in 2009, which suggests a higher transpiration rate in the wetter year. In 2010, when climate treatment was a significant main effect, the soil drying rate was slower within OTCs, compared to controls. Since OTCs increase temperature and evaporation should increase as a function of temperature, this opposite result in 2010 suggests an important effect that year in wind interception by this passive warming device (Marion et al. 1997). Moreover, when the soil drying rate inside OTCs is equal to or lower than controls, the lower soil moisture levels inside OTCs must be due primarily to their intercepting precipitation, inherent to their design.

The OTC design has been infrequently used in arid or semi-arid systems, such as steppe in northern Mongolia. Longer running studies in wetter systems such as those in the arctic carried out in conjunction with the International Tundra Experiment (ITEX) and on the Tibetan Plateau report only minor effects of OTCs on soil moisture averaged across the growing season (Marion et al. 1997; Klein et al. 2004; but see Aerts 2006; Dabros et al. 2010). We would use some caution in comparing our results, which are based on measurements taken off-center where there would be more interception of precipitation, to those from other studies in which moisture measurements were made in the center of OTCs. Our estimates of soil drying rates, however, take into account initial levels of soil moisture and thus the differences between OTCs and control plots in rates of soil drying are not due to the amount of precipitation reaching the points of measurement.

Averaging soil moisture over the entire growing season, as climate studies often do, makes it difficult to understand how well experimental manipulations simulate likely climate change scenarios and also how they operate at finer time scales with potentially greater biological relevance (Shaver et al. 2000). Given the temporal variation we uncovered, particularly in relation to OTC effects on volumetric soil moisture content (θ), species that inherently differ in phenology could respond very differently to changing climate (Cleland et al. 2006; Sherry et al. 2007). Along these lines, recent eco-hydrological models better account for seasonal changes in vegetation cover or vegetation activity (e.g., Kondoh and Higuchi 2001; Tague et al. 2009; Choler et al. 2010).

Our results, together with those from Zavaleta et al. (2003), illustrate the need for manipulative climate change studies involving multiple factors affecting soil water balance. Understanding where, when, and how these multiple biotic and abiotic factors interplay will help in the construction of more accurate climate change models and in identifying the relevant time scale for examining climate change effects on biological processes of interest.

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Appendix 1

Table 3 Dates for the time intervals (see Table 2)

	Time interval
2009	26–30 June
	03–07 July
	26–28 July
	30 July–01 August
	08–12 August
2010	09–13 June
	14–22 June
	28–29 June
	02–03 July
	04–06 July
	08–10 July
	14–20 July
	22–23 July
	30 July–01 August
	04–06 August
	08–09 August

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