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Dynamic and complex microclimate responses to warming and grazing manipulations

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Abstract

Synthesis efforts that identify patterns of ecosystem response to a suite of warming manipulations can make important contributions to climate change science. However, cross-study comparisons are impeded by the paucity of detailed analyses of how passive warming and other manipulations affect microclimate. Here we document the independent and combined effects of a common passive warming manipulation, open-top chambers (OTCs), and a simulated widespread land use, clipping, on microclimate on the Tibetan Plateau. OTCs consistently elevated growing season averaged mean daily air temperature by 1.0–2.0 °C, maximum daily air temperature by 2.1–7.3 °C and the diurnal air temperature range by 1.9–6.5 °C, with mixed effects on minimum daily air temperature, and mean daily soil temperature and moisture. These OTC effects on microclimate differ from reported effects of a common active warming method, infrared heating, which has more consistent effects on soil than on air temperature. There were significant interannual and intragrowing season differences in OTC effects on microclimate. For example, while OTCs had mixed effects on growing season averaged soil temperatures, OTCs consistently elevated soil temperature by approximately 1.0 °C early in the growing season. Nonadditive interactions between OTCs and clipping were also present: OTCs in clipped plots generally elevated air and soil temperatures more than OTCs in nonclipped plots. Moreover, site factors dynamically interacted with microclimate and with the efficacy of the OTC manipulations.

These findings highlight the need to understand differential microclimate effects between warming methods, within warming method across ecosystem sites, within warming method crossed with other treatments, and within sites over various timescales. Methods, sites and scales are potential explanatory variables and covariables in climate warming experiments. Consideration of this variability among and between experimental warming studies will lead to greater understanding and better prediction of ecosystem response to anthropogenic climate warming.

Keywords: alpine, climate warming, experimental grazing, experimental warming, global change, microclimate, open-top chambers, rangelands, Tibetan Plateau, tundra

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Introduction

Field-based climate warming manipulations provide information about ecosystem responses to climate change under relatively controlled conditions allowing the identification and quantification of mechanisms controlling variable responses. Scientists use both active and passive experimental designs to simulate climate warming. Active warming methods include buried heating cables (Melillo *et al.*, 2002) and overhead infrared (IR) heaters (Harte *et al.*, 1995; Bridgham *et al.*, 1999; Wan *et al.*, 2002), while passive warming methods include closed greenhouses (Hobbie & Chapin, 1998) and open-top chambers (OTCs) (Marion *et al.*, 1997).

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Recently, researchers have attempted to synthesize broad patterns of ecosystem responses to climate warming manipulations (Arft *et al.*, 1999; Cornelissen *et al.*, 2001; Rustad *et al.*, 2001). However, there are several sources of variation that can obscure understanding of ecosystem responses to climate warming when synthesizing results among studies. First, a given climate manipulation can have different effects on microclimate across ecosystems or under different abiotic and biotic conditions. Second, different warming techniques used in the same ecosystem or under sites with similar abiotic and biotic conditions can have different microclimate effects on that system. Third, the presence of additional treatments or site factors in the study could interact with simulated warming to alter microclimate in nonadditive or unexpected ways. Finally, climate manipulations may alter microclimate in ways that vary over inter and intra-annual timescales.

Here, we document detailed microclimate effects of OTCs in an alpine ecosystem on the northeastern Tibetan Plateau. More than six of Asia's major river systems originate on the Tibetan Plateau and on the order of 10^9 people live on or downstream of the Tibetan Plateau.

Several lines of evidence indicate the Tibetan Plateau is experiencing climatic warming (Thompson *et al.*, 1993, 2000; French & Wang, 1994). Moreover, the region is predicted to experience 'much greater than average' increases in surface temperatures in the future (Giorgi *et al.*, 2001). Concurrent with climate changes, there are profound changes to the pastoral land-use dynamic on the Tibetan Plateau. Over the past 15 years, commonly held rangelands are being privatized and a traditionally nomadic people are being made sedentary (Miller, 1999). Studies of similar situations in other rangeland systems demonstrate how these policies result in increased grazing pressures on the rangelands (Williams, 1996).

In this paper, we report on the OTC effect on 24 h air and soil temperature measurements averaged over month and growing season for 2 consecutive years. We also examine OTC effects on daily gravimetric soil moisture. We compare the independent and combined microclimate effects of the OTCs and clipping because grazing is a widespread land use on the Tibetan Plateau. We overlay experimental warming and clipping on a backdrop of sites representing different habitats crossed with different grazing histories to examine the specificity of OTC effects on microclimate variables. Ultimately we seek to evaluate those ecosystem conditions that most strongly control the effect of OTCs on microclimate.

The specific questions we address are: How do OTCs affect air and soil temperature and soil moisture in this alpine tundra ecosystem? How does the OTC effect on microclimate compare to clipping and how do these factors interact? How do the independent and combined treatment effects change over monthly, growing season and interannual time scales? How do the independent and combined OTC and clipping effects on microclimate change with habitat and grazing history? Which ecosystem characteristics are most strongly associated with OTC-induced changes in microclimate? In the discussion section of this paper, we compare our results to the results reported from the two most common warming techniques used in grassland/tundra ecosystems: OTCs and IR heaters.

Materials and methods

Study region and site description

We conducted our research at the Haibei research station (HARS), a facility run by the Northwest Plateau Institute of Biology, Chinese Academy of Sciences. HARS is situated at latitude 37°37′N, longitude 101°12′E (Fig. 1). Mean annual temperature is −2 °C, mean annual precipitation is 500 mm, over 80% of which falls during the summer monsoon season. Mean elevation of the valley bottom is 3200 m. A detailed site description can be found in Zhao & Zhou (1999).

There are two main habitats in the region: winter-grazed meadow situated along the valley floor, and summer-grazed shrubland situated on the higher slopes encircling the valleys. The meadow is dominated by an assemblage of forbs and graminoids; the shrubland is dominated by a deciduous shrub, *Potentilla fruticosa*. Forbs, grasses and sedges occur in all sites; however, the specific vegetative assemblages depend on habitat and grazing history. The alpine meadow and shrub vegetation which occur in this region comprise approximately 35% of the area of the Tibetan Plateau (Zhao & Zhou, 1999). In $75 \times 75\,\mathrm{cm}^2$ plots, there average 30 plant species (Klein *et al.*, 2004). Most plants are C3 and 87% are perennial.

We established our experiment in both the meadow and shrubland habitats. Within each habitat, we identified sites with 'low' and 'high' grazing intensity histories, for a total of four sites: high grazing intensity history meadow site (HG meadow), low grazing intensity history meadow site (LG meadow), high grazing intensity history shrubland site (HG shrubland) and low grazing intensity history shrubland site (LG shrubland). Both the grazing intensity and grazing duration differed among grazing history sites. Within each habitat, the low and high grazing history sites were similar in other features – such as slope, aspect, soil type, and distance to the river.

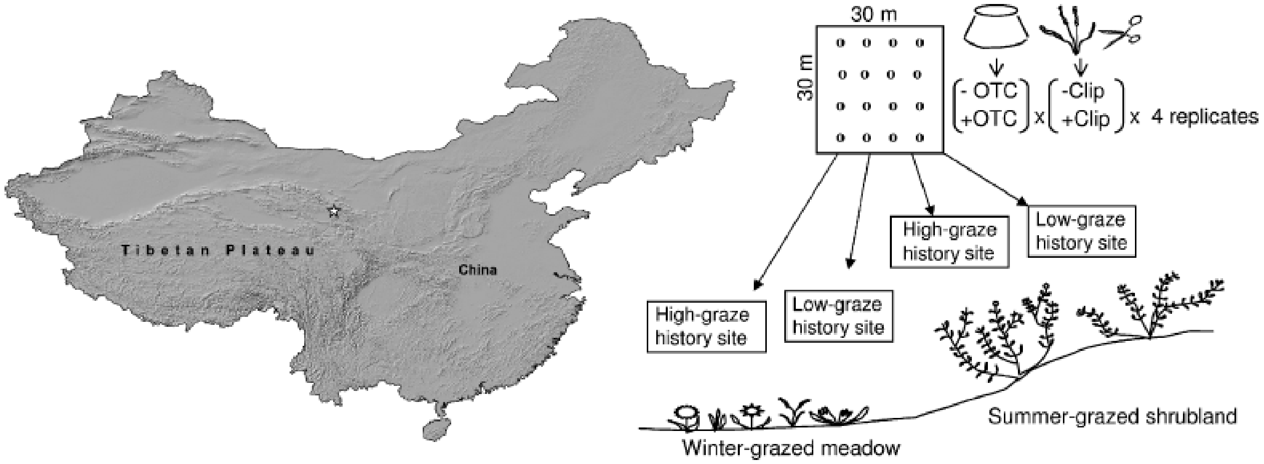

Fig. 1 Left side: study site region. The asterisk indicates the approximate location of the experiment. Right side: experimental design. We conducted this study in two habitats: a summer-grazed shrubland and a winter-grazed meadow. Within each habitat, we identified sites with 'low' and 'high' grazing intensity historics, for a total of four study sites. In each site, we fenced a $30 \times 30\,m^2$ area, within which we established a fully factorial experimental design, with 'OTCs' and 'clipping' as our main treatments. We had four replicates per treatment for a total of 16 plots per site × 4 sites = 64 plots.

Experimental design

We fenced each of the four $30 \times 30\,m^2$ sites within which we laid out 16 plots in a 4 × 4 matrix (for a total of 64 plots). Within each site, we established a complete factorial experimental design where we simulated warming using OTCs and the defoliation effects of grazing through clipping (Fig. 1). We placed the conical OTCs on the plots in September 1997. The OTCs, which were 1.5 m in diameter and 40 cm in height, were constructed of Sun-Lite HP (Solar Components Corporation, Manchester, NH, USA) 1.0 mm thick fiberglass reinforced with a surface and internal resin matrix to prevent chemical breakdown and deterioration over time. This material has high solar transmittance in the visible wavelengths (86%) and low transmittance in the infrared (<5%). The OTCs remained on the plots year round. All plots were spaced 2 m apart. OTCs are used by the International Tundra Experiment (www.itex-science.net) and are commonly employed to study the effects of climate warming on ecosystems (Marion *et al.*, 1997; Arft *et al.*, 1999; Hollister & Webber, 2000).

We began the defoliation treatments in the spring of 1998. In the winter-grazed meadows, traditionally grazed during the winter months, we clipped the plots prior to initiation of growth in the early spring. In the summer-grazed shrublands, traditionally grazed during the summer months, we clipped the plots in mid-July. We clipped plots to approximately 3 cm in height, which is the height of the vegetation outside of our fenced plots in the sites with a high grazing history. We removed approximately 30% of total live peak above-ground (AG) biomass in the shrubland sites and 15% of total peak AG biomass in the meadows. We did not clip plants that yak and sheep do not graze (such as *Oxytropis* spp., and *Stellara chamaejasme*). We plucked the shrub leaves and stem tips to simulate sheep browsing.

Response variables

Air and soil temperature. During the 1999 and 2000 growing seasons, we measured air and soil temperatures with HoboPro dataloggers (Onset Computer Company, Pocasset, MA, USA). Air sensors were centered in the plot 10 cm above the soil surface. The sensors were covered with white PVC elbows which were open at the ends (to allow free flow of air across the sensor) but angled in a way that avoided sensor contact with direct and back radiation. Soil sensors were 5 cm from center and 12 cm below the soil surface. Dataloggers recorded instantaneous air and soil temperature every hour from June to September in 1999 and from May to October in 2000. We present information on monthly averaged and growing season averaged daily (24 h) mean, maximum and minimum air temperatures, and the diurnal range in air temperatures (T_{air_av}, T_{air_max}, T_{air_min}, T_{air_range}, respectively) and daily mean soil temperature (T_{soil_av}).

Soil moisture. In 1999, we placed blocks (approximately 2 cm in diameter and 3 cm in height), which consisted of gypsum cast around two concentric, stainless-steel electrodes (Delmhorst Instrument Co., Towaco, NJ, USA) in the plots. Each block was situated 5 cm from the center of each plot 12 cm below the soil surface. We took manual measurements with a Delmhorst KS-D1 Digital Soil Moisture Tester once per day between 13:00 and 14:00 hours Beijing Standard Time (solar noon occurs during this time period in the summer). We recorded soil moisture from June to September in 1999 and from May to October in 2000. The meter converts measurements from 0.1 to 15 bars tension to an arbitrary 0–100 scale. To calibrate the measurements to our specific soil conditions and to convert the meter measurements to accepted measures of soil moisture, we simultaneously took soil cores and Delmhorst readings. We calculated the gravimetric soil moisture content for those cores and obtained a nonlinear regression fit between the meter readings and the gravimetric moisture on a gram of water per gram of soil basis. The best fit regression equation was: gravimetric soil moisture $= 0.20 \times e^{(0.01) \times \text{meter moisture}}$, $n = 59$, $R^2 = 0.62$, $P < 0.0001$. We also computed a bulk density measurement from each plot by collecting three soil cores per plot, removing the roots, rocks and moisture from the cores and calculating bulk density (g soil cm^{-3} soil). We averaged the three subsamples to obtain a plot level bulk density estimate. We calculated soil volumetric moisture content by multiplying the plot daily mass moisture content by the plot bulk density. When we discuss site soil moisture differences, we present results from both the volumetric and mass measurements, as these results were different. For treatment effects, however, the two measures yielded the same results. Therefore, in these sections we present the results from the mass measurements only. We refer to absolute differences in soil moisture content (%). That is, if the control plots yield a soil moisture content of 20% and treatment plots yield a soil moisture content of 25%, we state the treatment increased soil moisture by 5%. We present data on monthly and growing season averaged daily soil moisture values ($M_{\text{soil\_av}}$).

Data analysis

To compare microclimate variables among sites, we used data from the control plots only (no OTC, no clip) and conducted repeated-measures ANOVAS where 'year' was the repeated measure and 'habitat' and 'grazing history' were the main factors. For this analysis, we used data from the same dates in 1999 and 2000. To examine growing season averaged and monthly averaged treatment effects on microclimate, we used the full datasets available for 1999 and 2000. For this analysis, we conducted a repeated-measures ANOVA, separately by each site, where 'year' was the repeated measure and 'OTC' and 'clip' were the main factors. To examine within-growing season treatment effects, we conducted a repeated-measures ANOVA, separately by site, for 2000 where 'month' was the repeated measure and 'OTC' and 'clip' were the main factors. We followed up on significant effects by conducting pairwise comparisons with the Tukey test for multiple comparisons. For all ANOVAS, reported results are significant at $P < 0.05$, unless stated otherwise.

Our treatments were: T_{CON} = CONTROL (no OTC, no clip); T_{WM} = WARM (+OTC, no clip); T_{CL} = CLIP (no OTC, +clip); $T_{\text{WM} \times \text{CL}}$ = COMBINED (+OTC, +clip). If there was no warm × clip interaction, we refer to an overall warming effect, where the 'warming effect' $= [(T_{\text{WM}} + T_{\text{WM} \times \text{CL}})/2 - (\text{T}_{\text{CON}} + \text{T}_{\text{CL}})/2]$. This scenario compares the average effects of warming, in both the presence and absence of clipping. If a warm × clip interaction was present, we present the effects of 'warm (no clip)' $= (T_{\text{WM}} - T_{\text{CON}})$ and 'warm (+clip)' $= (T_{\text{WM} \times \text{CL}} - T_{\text{CL}})$ separately. We follow the same convention for the clipping effects: we present overall clipping effects if interactions were absent, or clip (no warm) and clip (+warm) effects, if interactions were present. The 'combined effects of warming and clipping' $= (T_{\text{WM} \times \text{CL}} - T_{\text{CON}}) = [(T_{\text{WM}} - T_{\text{CON}}) + (T_{\text{CL}} - T_{\text{CON}})]$ + Interaction Effect. This is the effect of combined OTC and clip plots vs. non-OTC, nonclip plots. If an interaction was present (interaction effect $\neq 0$), we compare the direction and magnitude of the combined effect (additive effect plus interaction) to the strictly additive treatment effects.

To evaluate which site conditions influence the efficacy of the OTCs, we conducted two separate analyses. First, we conducted simple linear regressions with the change in $T_{\text{air\_av}}$, $T_{\text{soil\_av}}$, $M_{\text{soil\_av}}$ ('treatment' minus 'control') as the dependent variables and with site characteristics in the 'control' plots as the independent variables. We conducted these analyses separately for clipped and nonclipped plots. We used growing season-averaged values from 2000 for all variables. The independent variables we included in the models were: $T_{\text{air\_av}}$, $T_{\text{soil\_av}}$, $M_{\text{soil\_av}}$, standing biomass, and litter areal coverage (AC). For each analysis, $n = 4$. We also conducted regressions with $T_{\text{air\_av}}$, $T_{\text{soil\_av}}$, $M_{\text{soil\_av}}$ as the dependent variables and with OTC treatment and site characteristics ($T_{\text{air\_av}}$, $T_{\text{soil\_av}}$, $M_{\text{soil\_av}}$, standing biomass, litter AC, and total species richness) as the independent variables. We conducted separate analyses for clipped and nonclipped plots. We aggregated all the sites ($n = 32$) and also conducted the analysis by site ($n = 8$). If there was a significant OTC treatment × site characteristic interaction, we conducted a separate regression analysis for OTC and non-OTC plots with respect to that site characteristic ($n = 16$ for all sites together and $n = 4$ for the analysis by site). If the relationship between a given site characteristic and a microclimate variable was significantly different in the presence of OTCs as compared with the relationship in the absence of the OTCs, this suggests there is a relationship between the site variable and the OTC effect on microclimate.

Results

Control plots: year and site comparisons

Interannual effects. The 1999 growing season was warmer and drier than the 2000 growing season. T_{air_av} was approximately 0.5 °C larger, T_{soil_av} was 1.2 °C larger, and M_{soil_av} was 2% lower in 1999 as compared with 2000.

Habitat effects. The meadow sites were generally warmer than the shrubland sites. Within the low graze history sites, T_{air_av} was 0.9 °C warmer at the meadow than at the shrubland site, with no differences at the high graze history sites (Fig. 2a). T_{soil_av} was 2.0 °C larger at the meadow sites than at the shrubland sites, regardless of grazing history (Fig. 2b). The meadow sites were 3% drier on a mass basis (Fig. 2c), but 12% moister on a volumetric basis.

Grazing history effects. The high graze history sites were generally warmer and drier than the low graze history sites. At the shrubland sites, T_{air_av} at the high graze history site was 0.7 °C larger than at the low graze site, with no differences at the meadow sites. T_{soil_av} was 2.0 °C larger at the high graze history sites than at the low graze history sites, regardless of habitat. The high graze history sites were 3% drier on a volumetric basis with no grazing history differences on a mass basis.

Treatment effects: growing season averages

OTC effects. OTCs increased T_{air_av} by 1.0–2.0 °C, T_{air_max} by 2.1–7.3 °C, T_{air_range} by 1.9–6.5 °C, with few significant effects on T_{air_min}. The range of observed responses was generated by variability among sites, between years and between the nonclipped and clipped plots (Tables 1 and 2). At most sites, the overall OTC effect on T_{air_av} was insensitive to interactions with year or clip; this explains the relatively small range in the effect size. However, at the HG meadow site, there was a year × OTC × clip interaction, the effects of which were idiosyncratic (Table 2). For both T_{air_max} and T_{air_range}, there were often OTC interactions with year and with clip. Generally, when an OTC × year interaction was present, the treatment effect was larger in 1999 (the warmer and drier year) than in 2000. For example, at the LG sites OTCs increased T_{air_max} by 5.2 °C (meadow) and 4.3 °C (shrubland) in 1999 and by 3.3 °C (meadow) and 2.1 °C (shrubland) in 2000. When an OTC × clip interaction was present, the OTC effect was generally greater in presence of clipping than in the absence of clipping (the only exception being the HG meadow site in 1999). For example, at the LG shrubland site, warm (no clip) increased T_{air_range} by 1.7 °C, while warm (+ clip) increased T_{air_range} by 4.2 °C. OTC effects on T_{soil_av} and M_{soil_av} were generally absent or small (Tables 1 and 2). The only significant increase in T_{soil_av} with OTCs (+ 1.9 °C) occurred in clipped plots at the HG meadow site in 2000. The OTC effect on M_{soil_av} was inconsistent among sites and years. Regardless of the direction, the magnitude of a significant treatment effect was consistently small (3% or less on a mass basis).

Clipping effects. Clipping effects on microclimate often demonstrated a pattern opposite to OTC effects on microclimate (Table 2). Clipping generally had no effect on T_{air_av}, decreased T_{air_max} by 1.7–4.4 °C and T_{air_range}

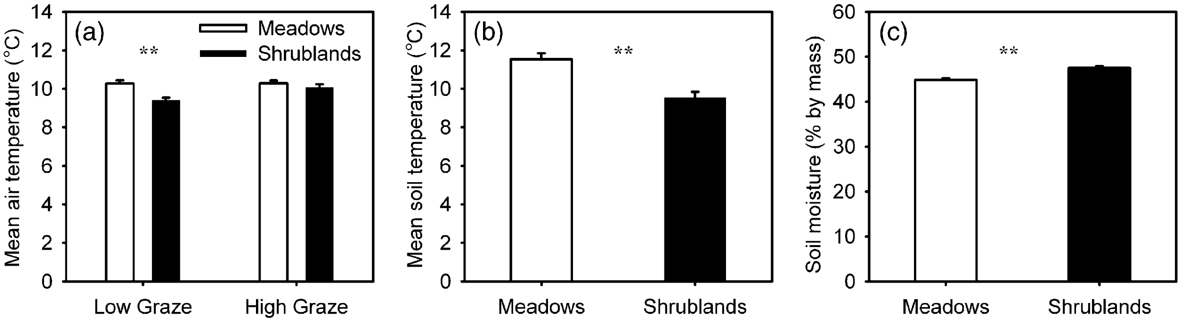

Fig. 2 Meadow vs. shrubland (control plots only) mean growing season averaged microclimate variables: (a) air temperature, (b) soil temperature and (c) soil moisture on a mass basis. For air temperature, there was a habitat × grazing history interaction. **Significant difference at $P < 0.05$.

Table 1 Results from repeated-measure ANOVAs conducted separately for each site

Variable	Site	Model	MS	*F*	*P*
$T_{\text{air\_av}}$	HG meadow	YR × OTC × CL	5.15	6.99	0.01
	LG meadow	OTC	27.26	4.88	0.03
	HG shrubland	OTC	28.05	5.20	0.03
		COMB	15.45	3.06	0.09
	LG shrubland	OTC	14.37	2.65	0.10
		COMB	13.30	2.74	0.11
$T_{\text{air\_max}}$	HG meadow	YR × OTC × CL	49.91	10.01	0.00
		COMB	46.00	6.59	0.02
	LG meadow	OTC × CL	18.29	2.25	0.10
		YR × OTC	24.14	3.42	0.07
		COMB	53.38	5.76	0.02
	HG shrubland	YR × OTC × CL	40.05	8.03	0.01
		YR × COMB	52.79	7.61	0.01
	LG shrubland	YR × OTC	33.88	5.66	0.02
		CL	59.87	5.43	0.02
		YR × COMB	20.96	4.44	0.04
$T_{\text{air\_min}}$	HG meadow	YR × CL	5.09	2.42	0.13
	LG meadow	YR × OTC × CL	10.58	3.48	0.07
		COMB	0.53	3.85	0.10
	HG shrubland	COMB	0.82	17.18	0.01
$T_{\text{air\_range}}$	HG meadow	YR × OTC × CL	61.58	6.19	0.02
		COMB	22.55	5.92	0.02
	LG meadow	YR × OTC × CL	30.80	2.47	0.12
		COMB	45.55	9.92	0.00
	HG shrubland	YR × OTC × CL	53.64	7.84	0.01
		YR × COMB	44.03	4.49	0.04
	LG shrubland	YR × OTC	28.76	3.98	0.05
		OTC × CL	21.48	4.44	0.04
		YR × COMB	15.34	2.42	0.13
$T_{\text{soil\_av}}$	HG meadow	YR × OTC × CL	2.55	3.39	0.07
	LG meadow	CL	41.96	13.94	0.00
	HG shrubland	YR × CL	4.15	10.50	0.00
		YR × COMB	3.13	6.82	0.01
	LG shrubland	CL	40.10	6.60	0.01
		COMB	35.10	3.43	0.08
$M_{\text{soil\_av}}$	HG meadow	OTC	91.96	8.29	0.01
		COMB	52.80	4.46	0.04
	LG meadow	OTC × CL	21.26	2.41	0.13
		CL	205.41	16.65	0.00
	LG shrubland	YR × OTC × CL	37.15	3.15	0.08

In the first analysis, year (YR) was the repeated measure and OTC and clip (CL) were main factors. In the second analysis, YR was the repeated measure and combined treatments (COMB) was the main factor.

HG meadow, LG meadow, high and low grazing intensity history meadow sites; HG shrubland, LG shrubland, high and low grazing intensity history shrubland sites; OTC, open-top chamber.

by 1.3–4.0 °C, with few effects on $T_{\text{air\_min}}$. The only exception to this was at the LG shrubland site, where clipping increased $T_{\text{air\_max}}$ by 2.0 °C and increased $T_{\text{air\_range}}$ by 1.2 °C (no OTC) and 3.7 °C (+OTC). Unlike the OTCs, clipping consistently increased $T_{\text{soil\_av}}$ by 1.0–1.7 °C at most sites and years. Similar to the OTCs, clipping had small ($<3\%$ by mass) effects on $M_{\text{soil\_av}}$.

Combined treatment effects. While the independent effects of OTCs and clipping on microclimate were often in the opposite direction, combined treatments often resulted in increased air and soil temperatures. When there was an OTC × clip interaction (Table 1), combined effects were generally larger than the strictly additive treatment effects. Moreover, when there was a significant combined treatment × year interaction (Table 1) the effect was generally larger in 1999 than in 2000. Combined treatments increased $T_{\text{air\_av}}$ by 1.3–1.5 °C at the shrubland sites, with no effects at the meadow sites. Combined treatments elevated $T_{\text{air\_max}}$ by 2.4–6.5 °C, $T_{\text{air\_range}}$ by 1.7–6.4 °C with no effect on $T_{\text{air\_min}}$. Combined treatments either had no effect or increased $T_{\text{soil\_av}}$ by approximately 1.5–2.2 °C. Combined treatments had small, but idiosyncratic effects on $M_{\text{soil\_av}}$.

Treatment effects: monthly averages for 2000

Air temperature. A month × OTC × clip interaction was present at the meadow sites where the OTC increase in $T_{\text{air\_av}}$ in the absence of clipping was greatest in May and decreased throughout the growing season to October; by contrast, the OTC increase in $T_{\text{air\_av}}$ in the presence of clipping was relatively constant over the growing season. For example, at the HG meadow site, warm (no clip) increased $T_{\text{air\_av}}$ by approximately 1.5 °C in May and June, by 1.0 °C in July and August, and by 0.5 °C in September and October. By contrast, warm (+clip) elevated $T_{\text{air\_av}}$ by 1.5–2.0 °C throughout the entire growing season (Fig. 3a). A similar pattern occurred at the LG meadow site. At the shrubland sites, where only an OTC × month interaction was present, the pattern of warming throughout the growing season was similar to the warm (no clip) pattern at the meadow sites.

Clipping effects on $T_{\text{air\_av}}$ also varied by month. The strongest effects generally occurred during the middle to the end of the growing season, near peak vegetative biomass. At the meadow sites, in some months, clip (no OTC) decreased $T_{\text{air\_av}}$, while clip (+OTC) increased $T_{\text{air\_av}}$. At the shrubland sites, the effect of clipping on $T_{\text{air\_av}}$ varied by month, but was insensitive to the presence or absence of warming. For example, at the LG shrubland site, clipping increased $T_{\text{air\_av}}$ by 0.4–1.1 °C in most months, with the largest effects in July and August.

There was a combined treatment × month interaction at all sites except the HG meadow site. At these sites, the

Table 2 Treatment effects on growing season averaged microclimate variables for all four sites based on results from Table 1 followed by a Tukey test

Variable	Site	Year	*W*	*W*(−CL)	*W*(+ CL)	Year	CL	CL(−*W*)	CL(+ *W*)	Year	COMB
T_{air_av}	HG meadow	1999		**2.0**	**1.2**				−1.0		
		2000		**1.0**	**1.9**			−0.7		1999 and 2000	1.1
	LG meadow	1999 and 2000	**1.4**							1999 and 2000	1.2
	HG shrubland	1999 and 2000	**1.4**							1999 and 2000	***1.5***
	LG shrubland	1999 and 2000	**1.0**							1999 and 2000	***1.3***
T_{air_max}	HG meadow	1999		**7.3**	**4.6**			**−1.7**	**−4.4**	1999 and 2000	**2.4**
		2000		**3.1**	**5.3**			**−3.4**	−1.1		
	LG meadow	1999 and 2000		**3.1**	**5.4**	1999 and 2000		**−2.6**		1999 and 2000	**2.8**
		1999	**5.2**								
		2000	**3.3**								
	HG shrubland	1999		**6.7**	**5.9**			0.5		1999	**6.4**
		2000		2.2	**5.8**			**−3.3**	0.6	2000	***2.6***
	LG shrubland	1999	**4.3**			1999 and 2000	**2.0**			1999	**6.5**
		2000	***2.1***							2000	**4.1**
T_{air_min}	HG meadow	1999									
		2000					**0.6**				
	LG meadow	1999		0.6							
		2000		−0.6	**1.6**			**−1.8**			
T_{air_range}	HG meadow	1999		**6.5**	**4.1**			***−1.6***	**−4.0**	1999 and 2000	**1.7**
		2000		***1.8***	**5.1**			**−4.2**	−0.9		
	LG meadow	1999		**3.0**	**6.3**			**−3.0**		1999 and 2000	**2.6**
		2000		**3.2**	**2.4**			−0.5	**−1.3**		
	HG shrubland	1999		**6.1**	**5.5**					1999	**5.8**
		2000		1.3	**6.0**			**−3.7**	1.0	2000	***2.3***
	LG shrubland	1999 and 2000		**1.7**	**4.2**			***1.2***	**3.7**		
		1999	**4.0**							1999	**6.4**
		2000	**1.9**							2000	**4.3**
T_{soil_av}	HG meadow	1999			0.5				***1.0***		
		2000			**1.9**			−1.0	0.9		
	LG meadow	1999 and 2000					**1.7**			1999 and 2000	**2.0**
	HG shrubland	1999					0.6			1999	0.6
		2000					**1.3**			2000	**1.5**
	LG shrubland	1999 and 2000					**1.6**			1999 and 2000	**2.2**
M_{soil_av}	HG meadow	1999 and 2000	**−2.4**							1999 and 2000	**−2.6**
	LG meadow	1999 and 2000		***1.3***	**−1.7**			***1.4***	**−1.7**		
	LG shrubland	1999		***1.6***	−0.9			**2.7**			
		2000			***2.1***			***−2.3***	−0.5		

W, warming; *W*(−CL), warm (no clip); *W*(+ CL), warm (+ clip); CL, clipping; CL(−*W*), clip(no warm); CL(+ *W*), clip(+ warm); COMB, observed combined effect. For italicized and bold numbers, $P_{adj} < 0.1$; for bold numbers, $P_{adj} < 0.05$. We omit nonsignificant ($P_{adj} > 0.1$) differences less than 0.5 units.

largest OTC × clip interactions generally occurred in August, when the interaction effect was approximately 1.0 °C larger than the strictly additive treatment effect.

Soil temperature. Treatments effects on growing season averaged soil temperatures mask important treatment effects on within-growing season soil temperatures. OTC × month and clip × month interactions were present at most sites. The largest OTC increases in T_{soil_av} occurred early in the growing season. OTCs increased T_{soil_av} by approximately 1.0 °C in May at all sites, including the LG shrubland site (Fig. 3b). Similar to air temperatures, when an OTC × clip interaction was present, soil temperatures remained elevated over a greater duration of the growing season under the warm (+ clip) scenario as compared with the warm (no clip) scenario (Fig. 4). Clipping similarly caused the largest increases in T_{soil_av}, from 1 to 3.0 °C, in May. At most sites, combined treatments elevated soil

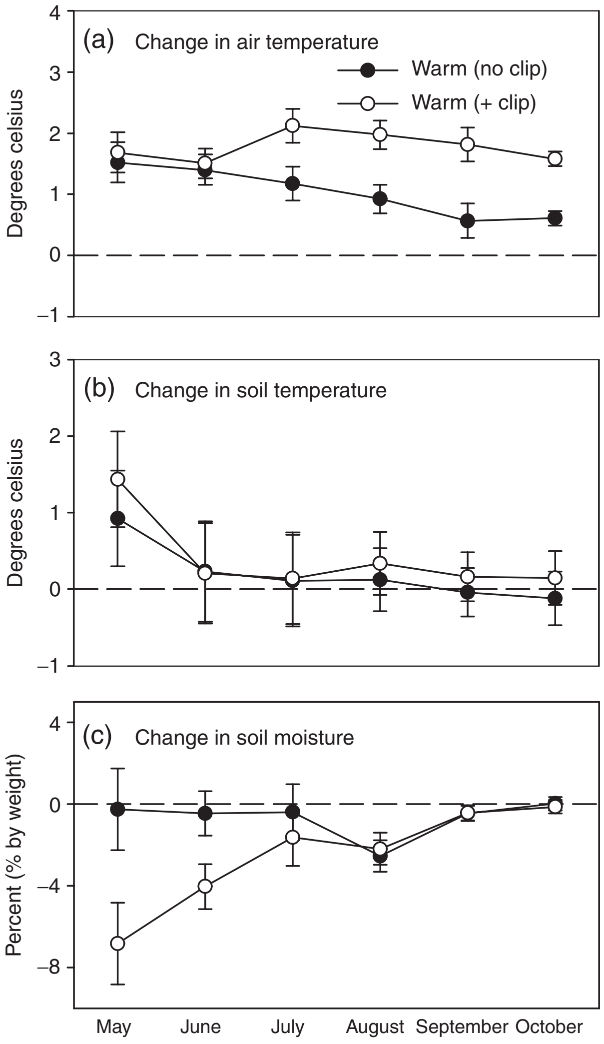

Fig. 3 Monthly averaged warm (no clip) and warm (+ clip) effects on (a) $T_{\mathrm{air\_av}}$ at the HG meadow site, (b) $T_{\mathrm{soil\_av}}$ at the LG shrubland site and (c) $M_{\mathrm{soil\_av}}$ at the HG meadow site. Circles represent mean treatment differences and bars represent standard errors.

temperature by 2.2–3.4 °C in May with a tapering to 1.0–1.3 °C by October.

Soil moisture. Treatment × month interactions were present at most sites, with the HG meadow site exhibiting larger treatment effects on $M_{\mathrm{soil\_av}}$. At this site, although warm (no clip) had no season averaged effect on $M_{\mathrm{soil\_av}}$, warm (no clip) decreased $M_{\mathrm{soil\_av}}$ by 2.5% in August. Also at this site, warm (+ clip) decreased season averaged $M_{\mathrm{soil\_av}}$ by 2.5%, with the largest declines occurring in May (−7%) and June (−4%, Fig. 3c). At the shrubland sites, OTC × month interactions were present at the HG site, but not at the LG site. The effects of clipping and of combined treatments on $M_{\mathrm{soil\_av}}$ were similarly mixed and varied by month, site and the presence or absence of warming.

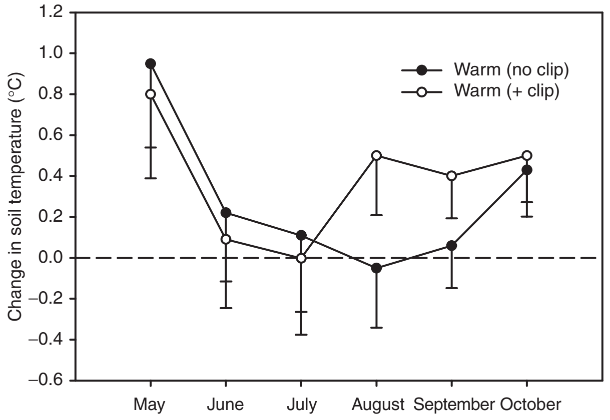

Fig. 4 Monthly averaged OTC effects on $T_{\mathrm{soil\_av}}$ at the HG shrubland site in 2000, where an OTC × clip × month interaction was present. OTCs elevated soil temperature in May and October, both in the presence and absence of clipping. Warm (+ clip) also elevated soil temperatures in August and September. Circles represent mean treatment differences and bars represent standard errors.

Relationship between site abiotic and biotic characteristics

The change in air temperature was positively related to litter AC in the nonclipped plots ($R^2 = 0.99$, $P = 0.001$, $n = 4$) and to soil temperature in the clipped plots ($R^2 = 0.90$, $P = 0.05$, $n = 4$), although the higher OTC air temperatures most likely drove the higher soil temperatures. Increases in soil moisture on a mass basis were positively related to air temperature in the clipped plots, but this was not significant ($R^2 = 0.70$, $P = 0.16$, $n = 4$); this finding is, however, supported by results presented below. There was a negative relationship between OTC air and soil warming and standing biomass (Fig. 5a, b). Under the OTC treatments, the relationship between litter cover and soil temperature was unimodal: from approximately <40% litter cover, there was a positive relationship between litter cover and OTC increases in soil temperature; by contrast, from approximately >40% litter cover, there was a negative relationship between litter cover and OTC increases in soil temperature (Fig. 5c, d). Within the clipped plots at the LG meadow site, fewer species were associated with greater OTC increases in soil moisture (+ OTC $R^2 = 0.95$, $P = 0.03$, no OTC $R^2 = 0.10$, $P = 0.69$). Also at the meadow sites, warmer temperatures were associated with larger OTC effects on soil moisture (LG meadow: + OTC $R^2 = 0.91$, $P = 0.04$, no OTC $R^2 = 0.65$, $P = 0.4$; HG meadow: + OTC $R^2 = 0.98$, $P = 0.01$, no OTC $r^2 = 0.01$, $P = 0.89$).

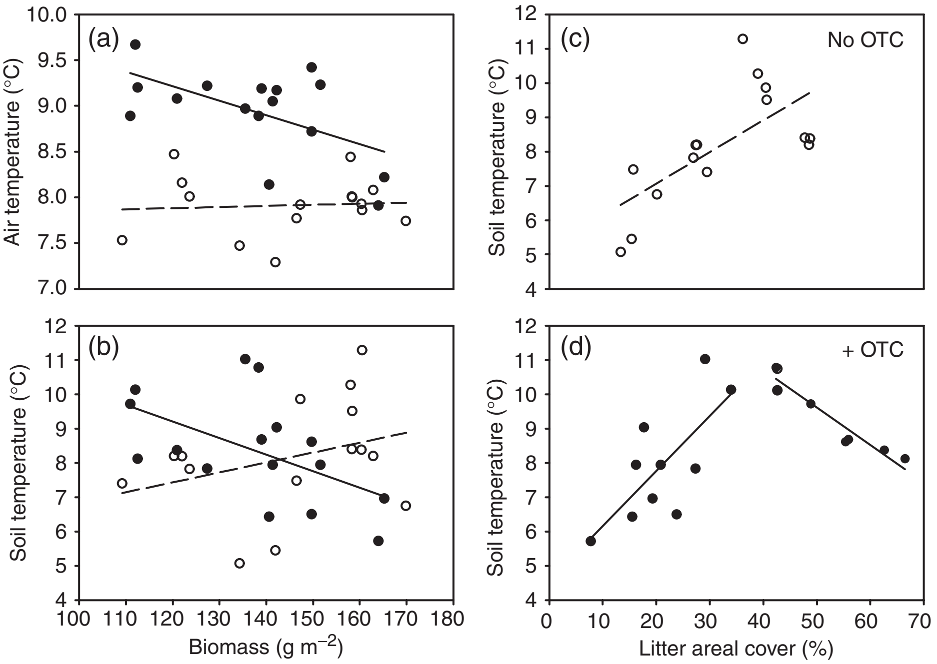

Fig. 5 Relationship between growing season averaged standing biomass and (a) air temperature and (b) soil temperature for non-OTC (open circle) and + OTC (closed circle) plots. For both analyses, there was a significant OTC × biomass interaction. The regression statistics for biomass vs. air temperature were: non-OTC $R^2 = 0.00$, $P = 0.8$; + OTC $R^2 = 0.32$, $P = 0.02$. The regression statistics for biomass vs. soil temperature were: non-OTC $R^2 = 0.11$, $P = 0.24$; + OTC $R^2 = 0.29$, $P = 0.03$. Relationship between litter AC and soil temperature (c) without and (d) with OTCs. There was a significant OTC × litter AC interaction. In the non-OTC plots, there was a positive, linear relationship between litter cover and soil temperature ($R^2 = 0.46$, $P = 0.005$). In the OTC plots, there was a unimodal relationship described by a quadratic fit ($R^2 = 0.58$, $P = 0.004$). All plots are nonclipped plots.

Discussion

OTC effects on microclimate

Published reports of OTC effects on microclimate in arctic tundra systems document a similar magnitude of air warming to that which we observed in our study: 1–2 °C at 10 cm AG. However, some of these other sites report night-time cooling (Marion *et al.*, 1997) – a phenomenon we did not observe. Some researchers working at tundra sites report an increase in diurnal air temperature range (Marion *et al.*, 1997); we similarly observed an increase in diurnal temperature range. We conclude that OTCs increase both growing season averaged mean daily air temperatures and the diurnal range in air temperature.

In our study, OTC effects on growing season averaged soil temperature were less consistent than the effects on air temperature. Likewise, the reported effects of OTCs on soil temperature in arctic and alpine sites are mixed (Marion *et al.*, 1997). The OTC effects on soil temperature have mostly been documented in arctic tundra sites, where growing season soils are moist, where permafrost is present at depth, and where there is often a high bryophyte cover. We observed a positive correlation between the amount of OTC air warming and soil temperature. Moreover, biomass was negatively related to soil warming. The degree to which these abiotic and biotic factors differ between sites could explain some of the variability in both the strength and direction of the OTC effect on soil temperature. Moreover, the presence of permafrost could override the relatively smaller heat flux produced by passive OTC warming. Sampling inconsistency among sites could also explain the reported mixed effects of OTCs on soil temperature. The documentation of OTC effects on soil temperature lack temporal resolution, replication and are inconsistent with respect to temperature sensor placement (Marion *et al.*, 1997; Totland, 1997; Walker *et al.*, 1999). This sampling inconsistency could cause more perceived rather than actual variability across study sites.

Given the consistent increases we observed in air temperature throughout the growing season, we believe our results may be biased against finding an OTC effect on soil temperature because our soil sensors were relatively deep in the soil profile. There likely were stronger changes to soil temperature closer to the soil surface than our sensors recorded at 12 cm depth. Despite our sensor placement, OTCs did increase soil temperatures early in the growing season at all of our study sites and were more likely to increase soil temperature when combined with clipping. OTC soil warming was enhanced under conditions of low standing biomass, and intermediate levels of litter AC. Under these conditions, OTCs may also affect belowground processes such as nutrient availability and soil carbon storage and turnover.

While we did observe some statistically significant OTC effects on soil moisture, they are likely not ecologically significant. In our study region, which is dominated by the Asian monsoon, 80% of precipitation occurs during the summer growing season. At all sites, soil moisture during all months of the growing season ranged from approximately 35–50% on a mass basis. Therefore, the soil moisture recharge through precipitation may have negated any more significant decreases in soil moisture with OTC warming. Warmer air and soil conditions can enhance OTC effects on soil moisture. To our knowledge, there is no published report on the effect of OTCs on soil moisture at other sites that employ OTC warming.

OTC vs. IR heater effects on microclimate

Reports of IR heating document either no increase in air temperature (Saleska *et al.*, 2002) or night-time only increases in air temperature (Wan *et al.*, 2002). By contrast, most of the air warming from OTCs occurs during the daytime. Wan *et al.* (2002) reported decreased diurnal air temperature range with IR heating; OTCs generally increase the diurnal air temperature range. IR heating causes significant and consistent increases in soil temperature over the growing season, as this can be controlled by adjusting the wattage on the heaters (Harte *et al.*, 1995; Bridgham *et al.*, 1999; Wan *et al.*, 2002). By contrast, OTC effects on soil temperature are less consistent. IR heaters caused significant soil drying or advanced snowmelt with repercussions for late growing season soil drying (Harte *et al.*, 1995; Wan *et al.*, 2002). In our study, any potential OTC soil drying was compensated for by precipitation.

These contrasting microclimate effects between active IR and passive OTC manipulations may be attributed to the different mechanisms driving the temperature changes. With the sides of the OTCs inclined by 60° with respect to horizontal, the OTCs passively trap the IR radiation. Heat is trapped AG within the walls of the chamber. This air is not mixed with ambient air except as it escapes through the opening in the chamber. Marion *et al.* (1997) report the smaller the opening, the greater the temperature enhancement effect of the OTCs. With IR heaters, there is an insufficient amount of IR-absorbing gas in the path from the heaters to the ground for the air to absorb a significant amount of IR. The air could warm by convection from the warmed soil, but air advection dilutes that effect. It is possible that IR heaters and OTCs have more similar effects on leaf temperature than on air temperature; however, data are not available to test this hypothesis. IR heaters direct heat downward to the ground where it is absorbed and heats the soil. With OTCs, the temperature gradient is not strong enough to produce a significant heat flux into the soil, especially in the presence of high biomass or litter cover. These findings suggest that comparing ecosystem responses in studies using similar or different warming methods depends on whether the variable of interest is most sensitive to changes in air temperature, soil temperature or soil moisture. Comparison of results within OTC warming studies, or between OTC and IR studies, requires careful and detailed documentation of the manipulation's effects on microclimate.

Independent and combined OTC and clip effects on microclimate

The effects of clipping were often in the opposite direction as the effects of OTCs on microclimate. Moreover, OTCs had stronger and consistent effects on air temperature, while clipping had stronger and consistent effects on soil temperature. These results highlight the potential confounding effects present when interpreting results from factorial studies of multiple global changes. Nonadditive combined treatment effects were present in our study. When an OTC × clip interaction was present, the interaction generally increased the air and soil temperature effects relative to the strictly additive treatment effects. These results indicate that assuming an additive effect from single global change studies can lead to misleading results. Rather, factorial studies can provide a more realistic estimation of co-occurring global change effects.

Temporal dynamics

We observed significant inter and intragrowing season temporal variation in OTC effects on microclimate. The warming effect often persisted later into the growing season when combined with clipping. Moreover, May was the only month in which all of the sites had elevated soil temperatures with OTCs. As OTC effects on microclimate depend on solar radiation, wind speed, site microclimate and vegetative biomass status, dynamic changes in the OTC effects over time would logically occur as these other factors change. For example, we observed a negative relationship between biomass and both air and soil temperature. As biomass develops over the growing season, and varies between years (in response to both interannual temperature differences and to multiyear climate manipulations) we would expect this biomass feedback to alter soil temperature and the OTC effect on microclimate over time. Other studies have similarly found biotic influences on warming manipulation microclimate effects (Harte *et al*., 1995; Bridgham *et al*., 1999). We also found a positive relationship between OTC increases in air temperature and litter AC; this is another dynamic feature of the landscape.

Understanding how warming manipulations affect microclimate over time helps to interpret the results of warming studies. For example, Arft *et al*. (1999) found OTC warming accelerated plant development in the spring, but did not impact senescence at the end of the season. They hypothesized that leaf bud burst may be more sensitive to temperature change whereas senescence may be more responsive to photoperiod. However, our results in the warm (no clip) scenario show that (1) the OTC air warming effect is greatest early in the growing season and weakest at the end of the growing season; and (2) an increase in soil temperature occurs only early in the growing season. These OTC effects on air and soil temperature over the growing season provide a plausible explanation for the Arft *et al*. (1999) phenology results if they found similar patterns of warming at the sites included in their meta-analysis. The meta-analysis also found increases in vegetative growth the first 3 years of the study and then no effect in year 4. They propose this could be a response to increasing N limitations. However, the warming-induced increase in growth over the first few study years may feedback to decrease the OTC warming effect in subsequent years. Based on the data presented in their analysis, this hypothesis cannot be eliminated. Rustad *et al*. (2001) found an increase in ANPP over 5 years; the effect did not decline over time. While the Arft *et al*. studies all employed OTC warming methods, the Rustad *et al*. meta-analysis included studies using both active and passive warming devices. Warming caused by a method such as buried soil cables would be less sensitive to biomass changes than warming caused by OTCs. Thus, the presence or absence of a biomass feedback to the effectiveness of the warming method could explain these disparate results between meta-analyses.

Our results demonstrate the importance of monitoring and reporting the treatment effects on microclimate over the exact time that the study is occurring. For example, had we only measured soil temperature in May, we may have erroneously reported that the OTCs increased soil temperatures over the entire growing season. This also suggests it is important to know exactly when the OTCs were placed on the plots and how this relates to microclimate. For example, if we had put our OTCs on the plots on June 1, we would not have caused a significant soil warming effect during a crucial time for vegetative growth and nutrient dynamics.

Site factors that influence OTC effects on microclimate

Biotic and abiotic site factors interact with microclimate and with the efficacy of the OTC manipulations. Even within our relatively limited geographic study region, grazing history and habitat established the initial abiotic and biotic conditions that affected how OTCs influenced microclimate. For example, the microclimate treatment responses at the LG shrubland site often differed from the responses at the other sites. Shrub AG biomass in the control plots of the LG site was almost twice that of the HG site ($+57\,\mathrm{g\,m^{-2}}$, $P<0.0005$). At this site, the extensive shrub canopy shades the air close to the soil surface. Therefore, altering the shrub canopy (through warming or clipping) can have strong indirect microclimate effects. OTCs had a relatively larger effect and clipping had a relatively smaller effect on soil temperature at the HG meadow site as compared with the other sites. The HG meadow site was the warmest and driest of all of the sites (on a moisture mass basis) with comparatively lower biomass in the control plots. Clipping had smaller effects because the clipping treatment removed less biomass from this site. Moreover, the warmer and drier site conditions were more conducive to larger OTC effects on microclimate variables.

Our findings indicate warmer conditions enhance OTC effects on temperature and moisture. Low biomass may result in more OTC soil warming, for reasons we have already discussed. Lower species richness is associated with larger OTC effects on soil moisture, indicating fewer species may decrease the buffering potential of the vegetation to an external forcing. More litter may also result in more OTC air warming. Litter may absorb radiation, which could heat the surrounding air by convection. Unlike live biomass, litter cannot regulate its temperature through processes such as transpiration. Low levels of litter may also warm the soil through a similar mechanism; however, dense litter cover can be a barrier to heat fluxes into the soil. Intermediate litter cover is, therefore, correlated with larger OTC increases in soil temperature. While it is difficult to decouple cause from effect, our findings suggest that these are the site characteristics that can influence the efficacy of OTCs in addition to grosser features, such as solar radiation, cloud cover and wind speed (Marion *et al*., 1997).

Conclusions

Synthesis efforts that identify patterns of ecosystem response to warming manipulations can make unique contributions to climate change science. However, detailed analysis of OTC effects on an alpine ecosystem microclimate highlights the need to understand the microclimate effects of the warming manipulations at several different scales: (a) between warming methods; (b) within warming method across ecosystem sites; (c) within sites over various timescales; and (d) within warming method and site but crossed with additional treatments. The effects at these various scales should be thoroughly documented and considered as potential explanatory variables and covariables in climate warming experiments.

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