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GLOBAL WARMING AND SOIL MICROCLIMATE: RESULTS FROM A MEADOW-WARMING EXPERIMENT¹

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Abstract. We used overhead infrared radiators to add a constant increment of ≈ 1.5 W/m², over 2 yr, to the downward heat flux on five 30-m² montane meadow plots in Gunnison County, Colorado, USA. Heating advanced snowmelt by ≈ 1 wk, increased summer soil temperatures by up to 3°C, and reduced summer soil moisture levels by up to 25% compared to control plots. Soil microclimate response to heating varied with season, time of day, weather conditions, and location along the microclimate and vegetation gradient within each plot, with the largest temperature increase observed in daytime and in the drier, more sparsely vegetated zone of each plot. Day-to-day variation in the daily-averaged temperature response to heating in the drier zone was negatively correlated with that in the wetter zone. Our experimental manipulation provides a novel and effective method for investigating feedback processes linking climate, soil, and vegetation.

Key words: climate; ecosystem manipulation; global warming; meadow; Rocky Mountains; soil microclimate; soil moisture; soil temperature; subalpine; vegetation.

INTRODUCTION

Climate warming due to anthropogenic increases in greenhouse gases is projected to increase Earth's average surface temperature by 2–5°C during the next 50–100 yr (Hansen et al. 1981, IPCC 1992). Direct and dramatic ecological responses to this impending warming are expected (Peters and Lovejoy 1992), as are feedback effects whereby ecological responses generate additional climatic impacts by modifying transfer rates of energy, water, and trace greenhouse gases at the planetary surface (Rosenberg et al. 1983, OIES 1992).

In terrestrial ecosystems, changes in soil moisture and soil temperature influence ecosystem processes such as nutrient cycling, primary productivity, plant survival and recruitment, and succession (Field et al. 1992). Soil microclimate is, in turn, controlled not only by exogenous climate parameters such as insolation, downward infrared radiation due to atmospheric greenhouse gases, and precipitation, but also by the effect of biotic characteristics such as vegetation cover and species composition on endogenous climate parameters such as the surface albedo and transpiration rates (Dickinson 1983). Therefore, understanding how climate warming will affect terrestrial ecosystems requires

knowledge of how soil microclimate is influenced by site-specific biotic and physical characteristics. Such knowledge, combined with data characterizing direct ecosystem responses to climate change, will provide a basis for quantifying the feedback mechanisms linking climate and ecosystems.

The ecosystem warming experiment described here was designed to improve understanding of the linkages among soil microclimate (temperature and moisture), biogeochemical processes (greenhouse gas fluxes, carbon storage, nutrient pool sizes and transformation rates), and biotic responses (phenology, productivity, and distribution of vegetation, and soil mesofaunal abundance). Here we describe the experimental strategy and the effects of artificial warming on the timing of snowmelt and on soil microclimate. Our results provide insight into the role vegetation and ambient soil microclimate play in modulating soil microclimate response to increased infrared radiation. Subsequent papers will address biotic and ecosystem-level responses to the warming and the feedback processes coupling climate, soil biogeochemistry, and vegetation.

Both experimental and theoretical approaches have been used to predict responses of terrestrial ecosystems to global warming. Theoretical approaches include both mechanistic mathematical models (Pastor and Post 1986, Parton et al. 1988, Rastetter et al. 1991) and correlation analyses (Emmanuel et al. 1985, Lashof

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1989, Overpeck et al. 1991). The ability of mechanistic models to elucidate ecosystem responses to climate change is currently limited by an absence of empirical information, from field or laboratory manipulations, about the dependence of critical rate constants on climate parameters (Anderson 1991). Correlation analyses have assumed that existing patterns of spatial association between climate and species composition or climate and soil characteristics will remain valid as climate changes over time. Studies of the poleward movement of vegetation types during the last glacial retreat support this assumption over paleoclimatic time scales (Overpeck et al. 1991), but no evidence exists that changes in biogeochemical processes, such as adjustment of soil chemistry to new climatic conditions, and biotic changes, such as species migration, will occur on the time scale of decades that characterizes anthropogenic global warming.

Experimental studies have focused on controlled-climate laboratory studies (Billings et al. 1983) or on experimental field manipulations using either plastic enclosures (Shaver et al. 1986) or buried electric-resistance wires (Van Cleve et al. 1990, Peterjohn et al. 1993) to achieve soil warming. Enclosures have the advantage of low cost and ease of application, but they alter microclimate in many unintended ways. Underground wires permit precise control over soil temperatures and are relatively easy to maintain. On the other hand, they unrealistically heat the soil surface from below and produce sharp soil temperature gradients in the close vicinity of the wires. Moreover, they do not heat the aboveground vegetation, they influence snowmelt in an unrealistic manner, and they require at least some degree of physical disturbance of the soil for their installation, possibly altering water percolation into the soil (NSF 1992).

Our experiment uses infrared radiators suspended above the study site. We chose this approach, rather than enclosures or underground wires, because it more closely simulates an actual mechanism by which anthropogenic greenhouse gases warm the ground—augmentation of the downward infrared flux. We chose not to manipulate precipitation at the site because of the large uncertainty in the magnitude and even the sign of impending changes in regional precipitation rates. Moreover, since we expected our manipulation to advance the time of snowmelt and increase evapotranspiration rates, we anticipated the opportunity to investigate the ecological effects of altered soil moisture without manipulating precipitation rates.

Our experimental site is an open subalpine meadow on the western slope of the Colorado Rocky Mountains. Montane ecosystems are likely to be especially responsive to global warming for several reasons. First, climate change will make montane regions vulnerable to invasion because of the sharp vegetational gradients that occur there. Second, climate warming is expected to raise soil temperature, reduce soil moisture, and ad-

vance the timing of snowmelt, thereby changing critical factors in montane plant productivity, phenology, and succession. In this regard, snow-albedo feedback will greatly enhance the physical response of montane regions to global warming because solar intensity in montane regions at the time of spring snowmelt and first autumn snow cover is high relative to lower elevations. Third, even small changes in the cool late spring and autumn soil temperatures and in summer soil moisture levels could influence nitrogen availability (McGill et al. 1981, Addiscott 1983), often a limiting factor in high-elevation terrestrial ecosystem productivity (Lee et al. 1983).

The experimental site spans an ecotone containing both scrub-steppe (West 1988) and montane meadow (Peet 1988) communities, and thus provides an opportunity to study changes that could affect major North American life zones. Moreover, the species diversity within the study area (nearly 100 angiosperm species) may allow for more rapid shifts in vegetational composition in response to warming than would be expected in sites with lower plant species diversity. Because these communities are geographically widespread, contain considerable stores of soil organic carbon (Schlesinger 1977), and are a sizable sink for atmospheric methane (M. Torn and J. Harte, *unpublished manuscript*), their biogeochemical responses to climate change could feed back upon atmospheric levels of carbon dioxide and methane, two important greenhouse gases. Moreover, the vegetational responses of scrub-steppe and montane grassland ecosystems to climate change will affect their use as rangeland, with implications for an important land use practice in montane regions throughout the world.

METHODS

Site characterization

Our study site is located at the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado (latitude 38°53' N, longitude 107°02' W, elevation 2920 m). It is in the upper Canadian, or montane, life zone as defined by Merriam (1890). This life zone is widespread at moderately high elevations and latitudes of North America (Vankat 1979, Barbour and Billings 1988). In Colorado, the montane zone supports a mosaic of habitats, including mixed conifer forest, aspen forest, and open meadow. The RMBL area is especially biologically diverse because its steep, glaciated topography causes dramatic vegetation species transitions on small spatial scales and because it is located at the upper elevational boundary of a tongue of Great Basin desert scrub.

Annual precipitation over the past decade has averaged 700 mm, with over 80% as snow. Snowmelt typically concludes in May. Mean daily-averaged summer air temperature is $\approx 10^{\circ}\text{C}$. Climate data for the period May–September for the two years relevant to

TABLE 1. Weather data from the National Dry Deposition Network weather station, Gothic, Colorado. Monthly averages of humidity, temperature, and solar flux derive from hourly readings, 24 h/d.

Month	Total precipitation (cm)		Average relative humidity (%)		Average air temperature (°C)		Average solar flux (W/m ²)	
	1991	1992	1991	1992	1991	1992	1991	1992
May	0.5	2.01	47.0	63.8	4.41	5.54	260.8	247.9
June	1.62	1.12	63.4	50.4	8.66	8.96	264.4	275.4
July	5.58	5.3	73.1	60.2	11.06	10.24	260.9	247.6
Aug	2.8	4.33	64.6	64.6	11.24	9.84	226.2	202.8
Sept	2.42	7.98	59.9	60.0	7.57	8.28	197.1	202.5

this paper, 1991 and 1992, were obtained from a National Dry Deposition Network weather station located 150 m south of the experimental site (Table 1). Total snowfall at RMBL during 1990–1991 and 1991–1992 was 0.69 m and 0.47 m (water equivalent), respectively (B. Barr, *personal communication*). Soil at the study site is a cryoboroll (R. Amundson, *personal communication*) consisting of deep, rocky, non-calcareous, glacial till. Below a sparse litter layer, the soil is remarkably uniform in color and texture down to at least 50 cm. Organic content averages $\approx 10\%$ at a soil depth of 5 cm below the litter layer and drops to $\sim 6\%$ at 50 cm, as estimated by loss in mass of sieved (2-mm mesh) and oven-dried soil upon ignition at 500°C. Site soils have an average pH of 6.3, as measured potentiometrically in a 1:1 soil: water slurry.

The experimental site spans an uphill–downhill gradient of soil moisture and vegetation. The lower, middle, and upper zones are designated L, M, and U, respectively (Fig. 1a). Zone L is relatively flat and lush; its soils tend to be moist because the zone lies roughly 1 m in elevation above a willow swale that is swampy throughout most of the summer. Zone M is relatively steep (average slope of 15°), dry, and sparsely vegetated, while zone U, which extends to a ridge top, is relatively flat, dry, and sparsely vegetated.

Sagebrush (*Artemisia tridentata*) and a diverse assemblage of forbs and graminoids, including *Mertensia fusiformis*, *Vicia americana*, *Lathyrus leucanthus*, and *Festuca thurberi* are found within the drier zone U. The shrub *Pentaphylloides floribunda* (*Potentilla fruticosa* of various authors) and a comparably diverse assemblage of forbs and graminoids, including *Claytonia lanceolata*, *Erythrocoma triflora*, *Rhodiola integrifolia*, and *Melica spectabilis* occur in the moister zone L. As is true of vegetation in many high elevation and high latitude regions, there are few annual species (Barrell 1969; D. Inouye, *personal communication*).

Experimental design

Ten 3 × 10 m plots were laid out in June, 1990, with the long axis of each plot spanning the ecotone described above (Fig. 1b). The tops of the plots extend to a moraine ridge line, to ensure that no uphill snowmelt runoff could influence the plots. A slight arc in the ridge results in an average difference in the ori-

entation of adjacent plots of 4°, with the long axis of the southernmost plot (no. 1) oriented at 88° E and that of plot 10 oriented at 126° E. The elevational difference between the east and west edges of the plots ranges from 1.5 m to 2.2 m.

We chose an alternating assignment of control and treatment plots to facilitate statistical isolation of treatment–control differences from north–south gradient effects (Hurlbert 1984). A 3 m wide gap between plots ensured that controls are not influenced by the infrared radiation (IR) flux from the heaters, and that plots are relatively isolated from one another hydrologically.

Electric heaters (Kalglo) 1.6 m in length and 12 cm wide were suspended 2.5 m above the ground from steel cables supported by four 4 m tall steel towers placed at the corners of a rectangle surrounding the ten plots. Two heaters per plot were located directly over the centers of zones L and U and parallel to the 10 m long midline. The shape of the reflectors above the heating elements was designed to optimize within-plot uniformity of the radiation field in the direction transverse to the heaters, resulting in a nearly uniform additional heat flux of approximately 15 W/m² over 80% of the lower and upper thirds (zones L and U) of the heated plots. The additional heat flux was only about 5 W/m², however, in 1 m wide strips at the top and bottom of the plots and in the center of zone M (where the zone M temperature and moisture probes are located), and for that reason we emphasize here the results for zones L and U. We estimated the relative distribution of infrared radiation flux on the plots and between plots by infrared thermometry measurements of uniform ceramic tiles placed at the soil surface and by direct measurement of downward IR flux (Everest Interscience infrared thermometer 210 AL).

The incremental IR flux of 15 W/m² was selected because it is comparable to the mid-range estimate of the additional downward IR flux (direct plus feedback effects) expected from a doubling of atmospheric carbon dioxide (Ramanathan 1981). The heaters produce no visible radiation. In the far red (700–800 nm) region, where plant morphogenesis may be affected (Morgan and Smith 1981), they contribute at ground level $\approx 10^{-6}$ of solar input.

TABLE 2. Date of snowmelt and soil microclimate data from a year-round field experiment at Gothic, Colorado (averaged over depth and growing season). For all means, $N = 5$ plots. Heated plots were warmed by suspended electric heaters.

	Lower zone						Upper zone					
	Date of snowmelt (day of year)		Soil temperature (°C)		Soil moisture (% dry mass)		Date of snowmelt (day of year)		Soil temperature (°C)		Soil moisture (% dry mass)	
	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992
Control plots												
1	146.6	121.4	13.35	12.25	33.2	37.4	137.3	120.8	14.36	12.84	23.3	31.1
3	150.4	121.7	12.39	11.65	40.9	43.1	139.3	123.6	14.11	12.73	17.9	26.6
5	146.7	120.6	14.06	12.54	31.4	35.7	137.5	120.4	12.79	11.82	25.1	33.2
7	134.6	118.7	12.82	11.89	33.0	35.5	133.5	117.8	14.04	13.06	17.6	25.8
9	131.6	110.7	12.44	11.78	30.2	38.3	129.4	104.7	13.44	12.83	19.5	25.5
Mean	142.0	118.6	13.01	12.06	33.7	38.0	135.4	117.5	13.75	12.65	20.7	28.4
SE	3.7	2.1	0.31	0.18	1.9	1.4	1.8	3.3	0.27	0.22	1.5	1.6
Heated plots												
2	141.3	121.7	13.46	12.52	30.7	36.6	134.4	119.5	14.91	13.55	17.4	25.7
4	134.6	118.6	13.36	12.30	32.6	33.6	133.5	119.8	14.8	13.68	17.5	26.4
6	130.5	116.6	12.62	11.75	35.4	39.0	132.6	118.7	15.14	13.68	21.7	27.7
8	130.3	103.8	13.18	12.58	29.1	35.1	127.6	100.6	13.74	12.79	16.9	24.0
10	127.6	102.8	12.42	11.88	32.6	37.8	125.5	100.6	14.82	13.83	16.9	24.7
Mean	132.9	112.7	13.01	12.23	32.1	36.4	130.7	111.8	14.68	13.52	18.1	25.7
SE	2.4	3.9	0.21	0.17	1.1	1.0	1.8	4.6	0.24	0.19	0.9	0.7

Experimental methods

To avoid stepping on plots, we carry out all field sampling and in-plot measurements from moveable, raised platforms.

Monitoring soil microclimate.—Beginning in January, 1991, when the heaters were turned on, we have monitored soil temperature and moisture every 2 h, year round, at 5 cm, 12 cm, and 25 cm depth in the centers of zones L, M, and U of each of the ten plots (90 locations). Soil temperature and soil moisture are measured with copper-constantan thermocouples and gypsum blocks, respectively, wired to multiplexers and data loggers (Campbell Scientific, CR10) for automated data collection. We calibrated the gypsum blocks in the laboratory using intact soil cores from the site and gravimetric determination of soil moisture as mass of

water per unit soil dry mass, expressed as a saturation ratio (Gardner 1986). Our soil moisture data are reported here as absolute fraction by mass.

Each spring, 6 or so of the wires from the 90 moisture probes had to be repaired due to damage from rodents. For that and other reasons, $\approx 1\%$ of the soil moisture data were judged to be spurious (negative readings or far outliers) and were discarded. Moreover, during the 1991 and 1992 study period described here, data logger problems (including a lightning strike in late 1992) resulted in ≈ 6 wk with incomplete soil temperature and moisture data.

Characterization of vegetation biomass.—To estimate aboveground graminoid and forb biomass at the approximate time of maximum aboveground biomass (at the end of the second week of August, 1992), all aboveground forb and graminoid biomass in a 0.25×2 m patch within each of zones L and U of each plot was clipped, oven-dried at 60°C to constant mass, and weighed. No temperature or moisture probes are located within the clipped patches and virtually all vegetative matter was returned to the patch of origin after drying and weighing.

Shrub biomass could not be measured by harvesting without permanently destroying the shrubs, so we used seasonal shoot production (in the same patches that were clipped for forb and graminoid production) as an indicator, even though this measure of seasonal aboveground shrub production underestimates total aboveground shrub biomass. We estimated shoot production by measuring the correlation of dry mass with length for 50 new shoots clipped from each patch (ten plants per patch, five shoots per plant) and then measuring the length of all the new shoots in each of the 0.25×2 m patches. The Pearson correlation coefficients were

TABLE 3. Factors affecting date of snowmelt* in a field experiment at Gothic, Colorado: results of analysis of covariance, with north-south position (Plot no.) as covariate.† Treatment plots were warmed by suspended electric heaters.

Source of variation	ss	df	F	P
Year	4034.1	1	269.9	<0.001
Plot no.	1086.3	1	72.7	<0.001
Treatment	195.7	1	13.1	0.001
Zone	72.1	1	4.82	0.036
Zone $\times$ Year	28.1	1	1.88	0.181
Zone $\times$ Treatment	14.0	1	0.94	0.340
Zone $\times$ Year $\times$ Treatment	10.7	1	0.72	0.404
Year $\times$ Treatment	3.19	1	0.21	0.647
Error	463.4	31		

* Date when soil temperature at 5 cm depth reached $+1^\circ\text{C}$.

† For each zone/year combination, homogeneity of treatment group slopes is satisfied at $F_{1,6} < 4.2$, P (falsely rejecting homogeneity assumption) > 0.1 .

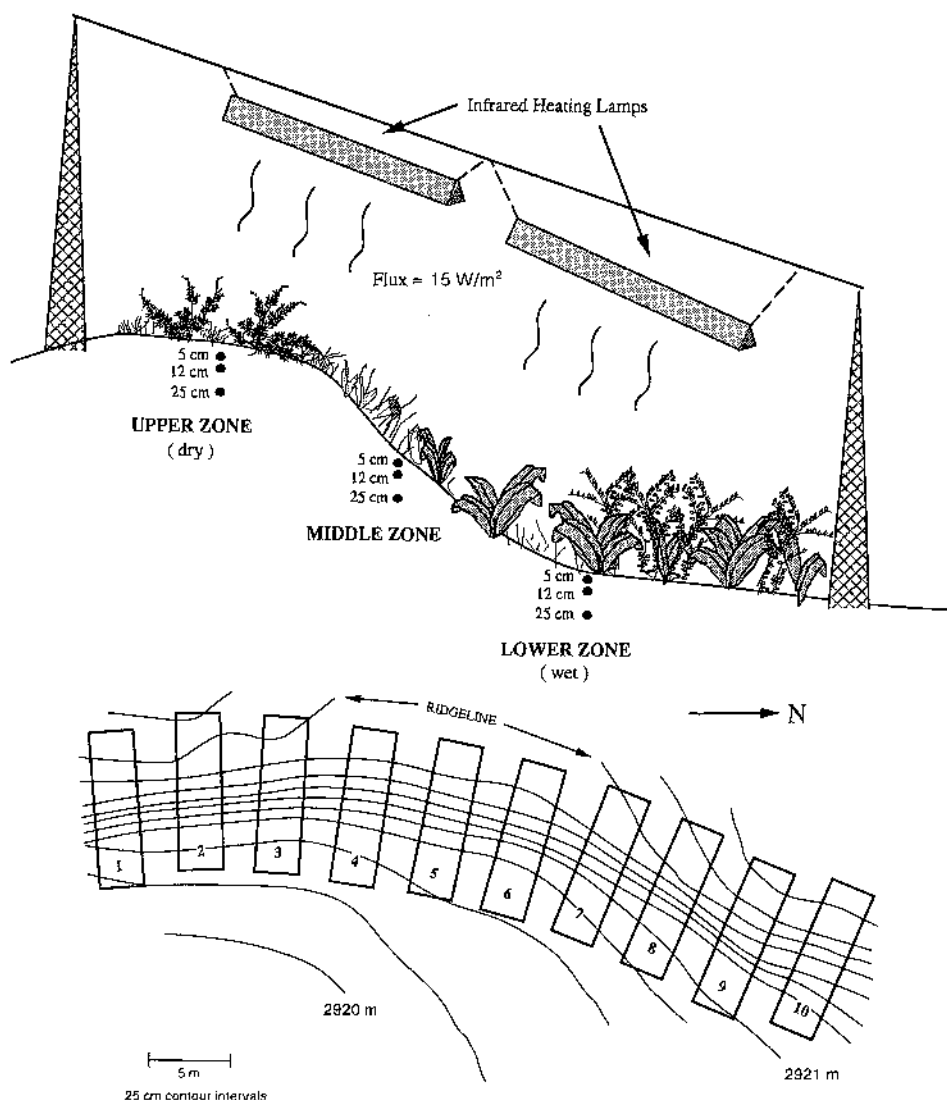


FIG. 1. Typical heated-plot experimental profile (not to scale); control plots are similar but lack the suspended electric heaters. Layout of the plots is shown below.

always >0.65 , averaging 0.882 for *P. floribunda* for zone L of plots 1–10 and 0.787 for *A. tridentata* for zone U of plots 1–10.

SOIL MICROCLIMATE RESULTS

The annual soil microclimate data are grouped below into three intervals: the snowmelt period (typically late April through May), a subsequent late-spring and summer period, designated here as the growing season, and a period from September to early spring, characterized by dormancy of most of the vegetation. Weather conditions during 1991 and 1992 differed considerably, with 1992 being, in general, cooler and wetter (Table 1).

The snowmelt period

We define melt date (the date of completion of snowmelt) for an individual plot and zone to be when the

soil temperature at 5-cm depth reaches $+1^{\circ}\text{C}$. Heating advanced melt date by an average of 9.9 and 4.7 d in zones L and U, respectively, in 1991, and 5.9 and 5.7 d in 1992. Within each treatment group, snowmelt generally proceeded from north to south and zone U generally melted earlier than zone L (Table 2).

An analysis of covariance (ANCOVA), using plot number for the covariate of plot orientation (Fig. 1b), shows snowmelt date to be significantly dependent on treatment ($P = 0.001$), as well as on zone, year, and plot number, but not on interaction terms such as zone $\times$ treatment (Table 3). Using a similar ANCOVA but with year as a repeated measure, the effect of treatment on date of snowmelt is significant ($P = 0.042$), as are the effects of year and plot number, but the effect of zone is no longer significant ($P > 0.05$). In a split-plot ANCOVA, with each plot split into two zones and each of the two years treated separately, treatment and zone

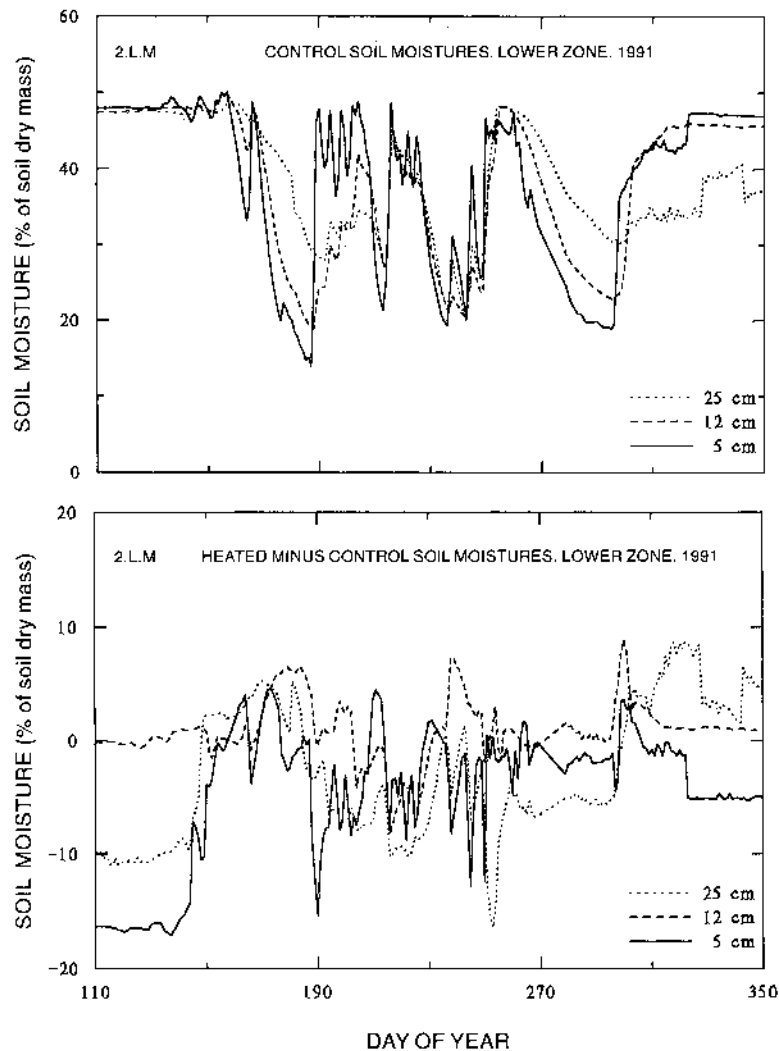


FIG. 2. Daily-averaged soil microclimate data from a field soil-warming experiment in central Colorado for the period 20 April–16 December 1991; all data are averaged over $n = 5$ plots within treatments. 2.L.T, zone L temperature; 2.U.T, zone U temperature; 2.L.M, zone L moisture; 2.U.M, zone U moisture. (Figure continues on pages 138–140.)

are significant factors in 1991 ($P = 0.009$ and 0.006 , respectively) but not in 1992 ($P = 0.238$ and 0.405 , respectively).

The largest temperature difference between heated and control plots occurred during the snowmelt period, in late April or May, when there was sharply increased absorption of sunlight in the exposed soils of the heated plots but not in the soils of the snow-covered control plots. During the period of final snowmelt in all plots, which occurred during days 125–160 of the year (5 May–9 June) in 1991 and days 100–140 (9 April–14 May) in 1992, temperatures in the soils of the heated plots averaged 2–5°C higher than in the control plots.

Graphs of the treatment-averaged temperature and moisture data (Fig. 2) clearly indicate the progression of snowmelt in the control and warmed plots. The end

of the snowmelt period in the first control plot to melt occurred when the average control plot temperature began to rise above 0°C; similarly, the end of the snowmelt period in the first treatment plot to melt is marked by the beginning of the sharp rise in the temperature differences between heated and control plots (Fig. 2, parts 2.L.T, 2.U.T). Control and treatment plot moisture levels in zone U rose gradually to the same saturation level (42% by mass) during the period of snowmelt (Fig. 2, part 2.U.M). The initial moisture excess in the heated plots on day 110 (due to greater melting in those plots during the winter and early spring) rapidly decreased when snowmelt later occurred in the control plots. In zone L, control plot moisture levels remained at saturation (48% of dry soil mass) throughout the snowmelt period, while heated plot soils remained drier than control plot soils at 5- and 25-cm depth, but not

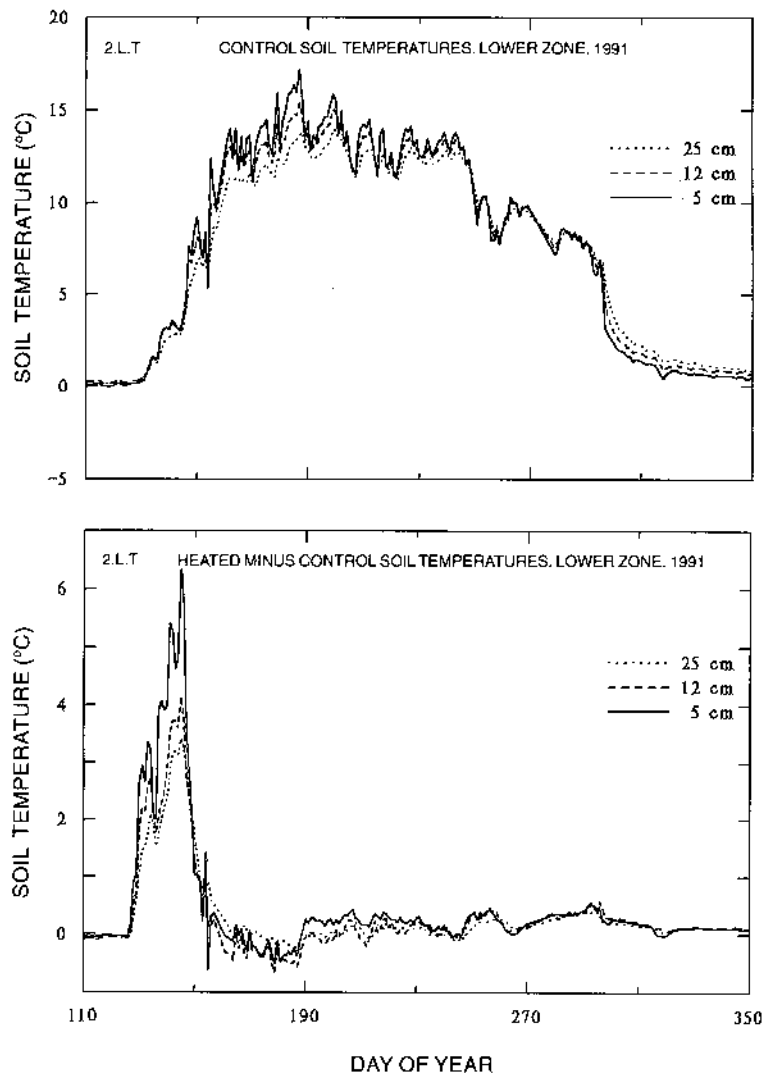


FIG. 2. Continued.

at 12-cm depth (Fig. 2, part 2.L.M). Similar patterns characterize the 1992 data.

During the snowmelt period of 1991, the depth-averaged total soil difference in temperature sum (with 0°C as baseline for degree-days) between replicate-averaged heated and control plots was 73 and 62 degree-days in zones L and U, respectively, while in 1992 it was 67 and 41 degree-days.

Daily-averaged soil-temperature differences between adjacent control and treatment plots reached values as high as 12°C during the period when a treatment plot had melted and the adjacent control had not. The treatment-averaged data (Fig. 2, parts 2.L.T and 2.U.T) do not show such a large effect because the temperature differences between adjacent pairs of plots peaked at different times. Thus the treatment-averaged data in Fig. 2 portray a warming effect during snowmelt that is longer in duration and less intense in magnitude than pairwise comparisons suggest.

In 1991, subzero air temperatures occurred during several nights when most of the heated plots were nearly snow-free and control plots were snow-covered. On those occasions, soil temperatures at 5-cm depth in the heated plots dropped as low as -5°C, whereas control plot temperatures hovered within one-half degree of 0°C.

The growing season: daily-averaged data

The results discussed here refer to daily-averaged soil temperature and moisture data for the period of days 161–243 (10 June–31 August) in 1991 and days 141–244 (20 May–31 August) in 1992. We denote temperature and moisture values by T and M , and heated-minus-control values of temperature and moisture by ΔT and ΔM , respectively, specifying in each of the following analyses whether we are referring to seasonally-averaged, depth-averaged, and/or replicate-averaged data.

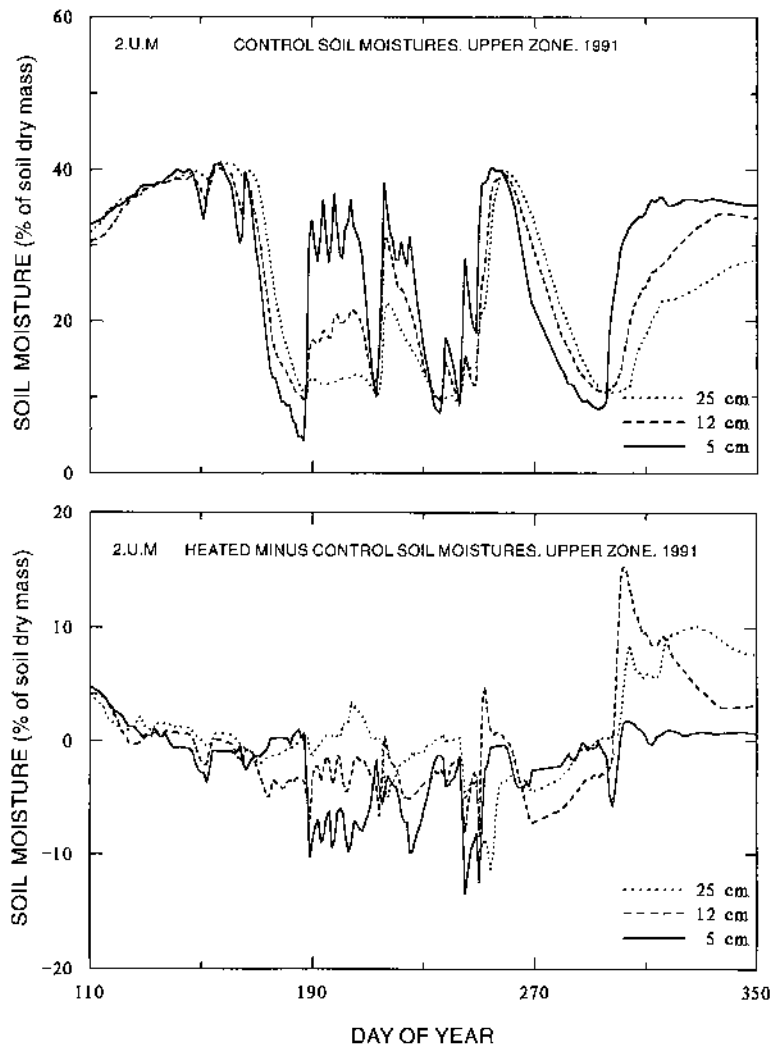


FIG. 2. Continued.

Soil microclimate of individual plots.—Results in this subsection refer to values of T and M for all 20 plot/zone combinations (10 plots, zones L and U), averaged over both depth and growing season (Table 2). Fig. 3 (parts 3.T and 3.M) shows the range of values of T and M for the individual plots, and indicates that the data for 1991 and 1992 were highly correlated with each other (T : $r = 0.954$, $P < 0.001$; M : $r = 0.970$, $P < 0.001$). Note that in every case the soils were wetter and cooler in 1992 than in 1991. In contrast to the dependence of date of snowmelt on the covariate of plot number (Table 3), regressions of the temperature and moisture data in Table 2 against plot number show no significant dependence; in particular, for all year and zone combinations, the coefficients of determination are < 0.3 and the probabilities of observing the data if the slopes were zero are > 0.1 .

An analysis of variance, with year as a repeated measure and zone and treatment as categorical variables,

indicates that temperature depends more significantly on treatment ($P = 0.039$) than does moisture ($P = 0.099$) and both depend significantly on zone and year ($P < 0.001$) (Table 4). We also tested, with analysis of covariance, the effect of treatment, zone, and above-ground biomass (Table 5) on 1992 soil temperature and moisture. Whereas treatment is not a significant explanatory variable for soil moisture in the ANOVA model (Table 4), both moisture ($P = 0.034$) and temperature ($P = 0.002$) do depend on treatment in the ANCOVA model. Moreover, temperature ($P = 0.011$), but not moisture ($P = 0.139$), is significantly dependent on biomass, and both temperature and moisture depend significantly on zone ($P < 0.001$).

To explore in more detail the effect of biomass on temperature and moisture in the two zones, we used a multivariate regression model, with treatment, biomass, and zone $\times$ biomass as explanatory variables (ter Braak and Looman 1987). The results (Table 6) indicate

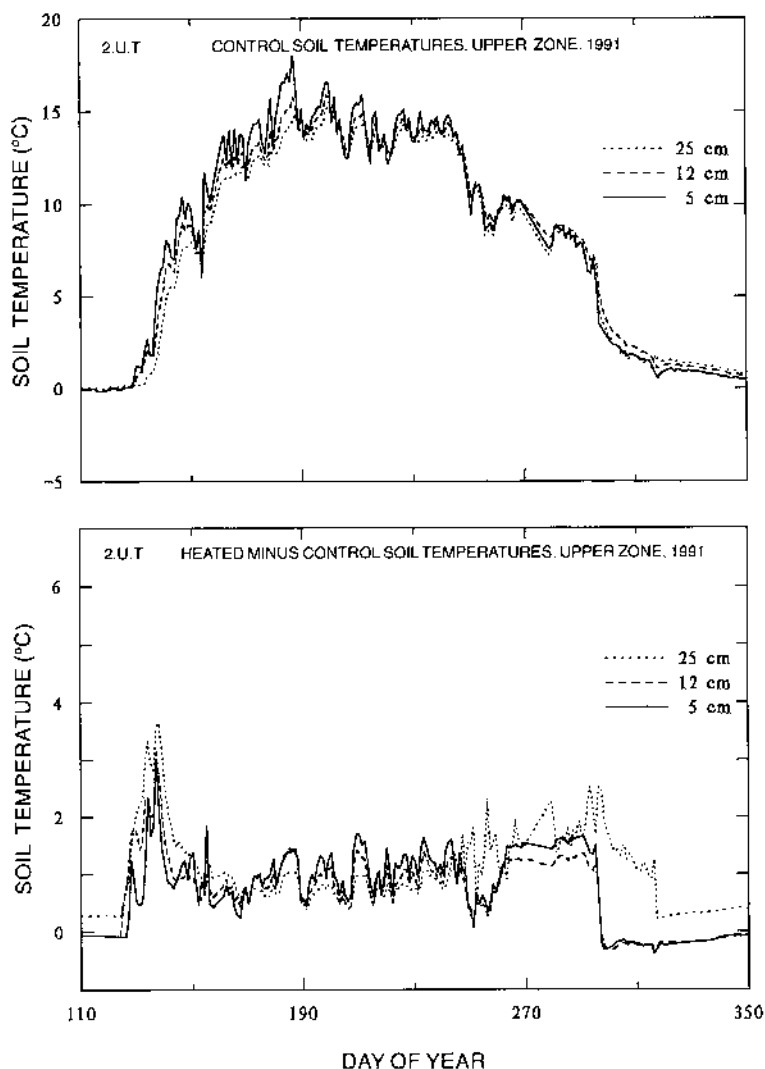


FIG. 2. Continued.

zone-L temperatures considerably more depressed by biomass than zone-U temperatures, and that moisture is enhanced by biomass in zone L and depressed by biomass in zone U.

Magnitude of the replicate-averaged effects.—Heated minus control temperatures (ΔT) during the 1991 growing season (days 160–240 of the year) were greater at all depths in the drier, less-densely vegetated, zone U, where ΔT was $\approx 0.9^\circ\text{C}$ (Fig. 2, part 2.U.T), than in the moister, more-densely vegetated, zone L, where ΔT was $\approx 0.1^\circ\text{C}$ (Fig. 2, part 2.L.T). In zone U, the magnitude of ΔT decreased with depth from 1.03°C at 5 cm to 0.90°C at 12 cm and 0.76°C at 25 cm. In zone L there was no systematic dependence of ΔT on depth. The average magnitude and the depth-dependence of ΔT in 1992 were similar to that in 1991 for both zones.

During the growing seasons of 1991 and 1992, the depth-averaged total degree-day difference (with 0°C as baseline for degree-days) between replicate-aver-

aged heated and control plots was 72 and 85 degree-days, respectively, while in zone L, it was 10 and 17 degree-days, respectively.

The effect of heating on soil moisture at 5- and 12-cm depth was irregular over time, but greater in zone U than in zone L, whereas at 25 cm, heating dried zone L more than it did zone U (Fig. 2, parts 2.U.M, 2.L.M). In both 1991 and 1992, the seasonally- and depth-averaged value of ΔM in zone U and the 25 cm value in zone L was $\sim 15\%$ of control plot M . At 5 cm in zone L, ΔM averaged $\sim 5\%$ of control M , while at 12 cm in zone L, ΔM was $\sim 3\%$ of control plot M .

Correlations over the growing season among daily- and replicate-averaged data.—There was a strong negative correlation between the daily values of control plot T and control plot M in both the lower and upper zones (Table 7). ΔT was correlated with control plot values of T and M from day to day, but, unexpectedly, the sign of the correlation was opposite in the two

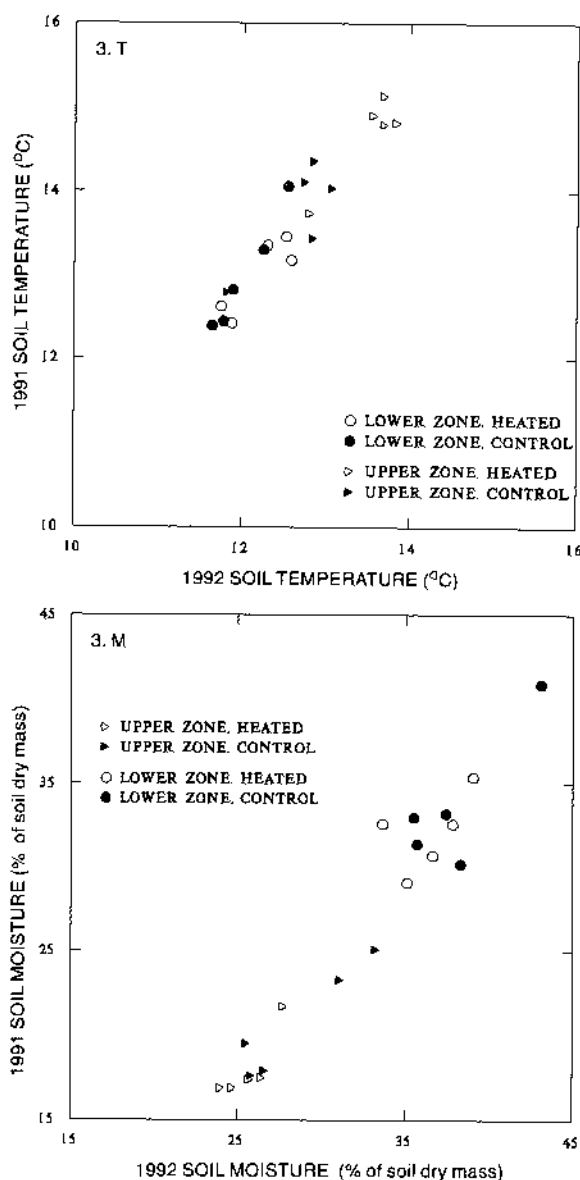


FIG. 3. Interannual comparison of growing-season temperature and moisture values for each of the ten plots, averaged over the three soil depths and over the growing season (10 June–31 August 1991; 20 May–31 August 1992). 3.T, soil temperatures; 3.M, soil moistures.

zones. In zone U, ΔT was larger at higher control temperatures and lower control moistures at all depths in both 1991 and 1992; in contrast, in zone L ΔT was larger at lower control temperatures and higher control moistures (Fig. 4, Table 7).

In contrast to the consistent pattern of strong correlation between ΔT and T or ΔT and M , daily variation in ΔM was only weakly, but positively, correlated with control T in zone U at all three depths and in both years. Moreover, the sign of the correlation of ΔM with control T in zone L and with control M in both zones

showed no simple pattern with respect to year and depth (Table 7).

The correlation between zone-L and zone-U values was positive for both the control T and control M data at every depth and in both years (Table 8). Values of ΔT were correlated negatively between the two zones, in all depth/year combinations, while values of ΔM correlated positively except for 12-cm depth in 1991 (Table 8).

The growing season: two-hourly data

Data collected at 2-h intervals exhibited a diurnal cycle in both control and heated plot temperatures; as expected the amplitudes decreased, and the time of maximum temperature lagged, with increasing depth. Fig. 5 (parts 5.L.T, 5.U.T, 5.L.M, and 5.U.M) illustrates the diurnal variation in temperature and moisture for the replicate-averaged control plot data for a typical week in early August, 1991 (3 August–9 August). Very similar patterns characterized the 1992 data.

The data also reveal a strong and unexpected diurnal variation in the difference between replicate-averaged heated and control plot temperatures. In the upper zone, in 1991, ΔT was maximum at all depths in early to mid afternoon, and at 5 cm reached values $>3^{\circ}\text{C}$ on some days during the growing season (Fig. 5, part 5.U.T). In the lower zone, in 1991, the diurnal variation was more complex, with the 5-cm data exhibiting double peaks in ΔT each midday (Fig. 5, part 5.L.T). In 1992, a similarly complex pattern of diurnal variation in the 5-cm data characterized both the upper and lower zones. Thus, this more complex diurnal variation occurred in the wetter zone (L) in both years and in the wetter year (1992) in both zones. A prominent midday dip in ΔT , to negative values, was also observed at 12 cm in zone L in both years.

To examine the possibility that the midday peak in ΔT was due to the slight dependence of plot orientation (and therefore of average replicate orientation) on plot number, the diurnal variation in the replicate averages of data from plots 2 through 9, only, was calculated. Analyzed that way, the midday peak is actually slightly more prominent than that shown in Fig. 5, part 5.U.T, indicating that this feature of the data is not a spurious effect resulting from differences in plot orientation.

Diurnal variation in ΔM was highly irregular in all zone/depth/year combinations.

The dormancy period

During late summer and autumn, 1991, the daily- and depth-averaged values of ΔT increased in both zones, rising to 2 and 0.5°C in zones U and L, respectively (Fig. 2, parts 2.U.T and 2.L.T). ΔT was largest during periods when snow had accumulated on the control, but not the heated, plots. The temperature response to heating was depth-dependent only in zone U, where ΔT was greatest at 25 cm and large positive values persisted long after snow covered both control and

TABLE 4. Factors affecting soil temperature and moisture: results of repeated-measures analysis of variance for 1991 and 1992 temperature and moisture data, averaged over depth and growing season.

Source of Variation	Temperature				Moisture			
	ss	df	F	P	ss	df	F	P
Zone	11.79	1	24.79	<0.001	1401.03	1	92.25	<0.001
Treatment	2.41	1	5.07	0.039	46.08	1	3.034	0.099
Treatment $\times$ Zone	1.61	1	3.38	0.085	2.74	1	0.18	0.677
Year	10.30	1	236.01	<0.001	359.22	1	234.4	<0.001
Year $\times$ Zone	0.14	1	3.24	0.091	28.78	1	18.78	0.001
Year $\times$ Treatment	0.01	1	0.16	0.699	0.002	1	0.001	0.973
Year $\times$ Treatment $\times$ Zone	0.05	1	1.06	0.319	0.03	1	0.021	0.887
Error (between treatments)	7.61	16			243.00	16		
Error (within treatments)	0.70	16			24.52	16		

treatment plots. The patterns of diurnal variation and of correlations among microclimate variables were qualitatively similar to growing-season patterns.

For the entire dormancy period from day 244 (1 September) of 1991 to day 99 (8 April) of 1992, the difference in depth-averaged, soil-temperature heat sums between heated and control plots was 25 degree-days in zone L and 92 degree-days in zone U. In the late autumn of both years, the soils of the heated plots were wetter than those of the control plots because accelerated snowmelt after the first snowfall provided more moisture to the soils in the heated plots (Fig. 2, parts 2.U.M and 2.L.M).

DISCUSSION

There are four prominent features in the observed response of soil microclimate to the warming treatment:

1) The infrared heaters raised soil temperatures more in the drier, less vegetated, zone U than in the moister, more densely vegetated, zone L (Fig. 2).

2) The daily-averaged temperature responses to heating in zone L and zone U were negatively correlated over the growing season (Table 8). In zone U, ΔT was positively correlated with control T and negatively correlated with control M , while the sign of correlation was reversed in zone L (Table 7, Fig. 4). This reversal occurred despite the strong positive correlation in both

control plot temperatures and control plot moisture levels between the two zones.

3) The infrared heaters dried the soils in zone U more than in zone L at 5-cm and 12-cm depth, but at 25-cm depth the drying was comparable in the two zones (Fig. 2).

4) The diurnal variation of ΔT in zone U shows a large midday peak at all depths, but especially at 5-cm depth (Fig. 5, part 5.U.T).

Zone L differs from zone U in two major ways that could explain the different soil microclimate responses to the heat treatment in the two zones. First, the soils of zone L are wetter (Fig. 3, Table 2) because it is down-slope of zone U and closer to a swampy area. Second, zone L is more densely vegetated than zone U.

Soil moisture increases the heat capacity of soil and influences how absorbed energy is distributed between raising soil temperature and causing evaporation. We denote this influence on soil microclimate as the "moisture effect". (In meteorology, this phenomenon is described by the Bowen ratio—Campbell 1986.) Other factors being equal, higher soil moisture implies that the additional infrared radiation from the heaters goes less into raising soil temperature and more into drying the soil. To the extent that the moisture effect dominates over other processes regulating soil microclimate, we expect ΔT to be smaller in the more moist zone L than in the drier zone U, consistent with observation (1) above.

Vegetation cover can also influence ΔT because denser vegetative cover shades the soil from the additional IR flux and therefore might lead to reduced soil warming. We call this process the "vegetation effect". To the extent that the vegetation effect influences the soil response to heating, we expect ΔT in the more vegetated zone L to be smaller than ΔT in the less vegetated zone U. This is again consistent with observation (1).

The effects of moisture and vegetation effect on soil microclimate are interrelated, of course, because the density of vegetation both influences soil moisture (through transpiration) and is influenced by it (through moisture limitation on plant establishment, survival, and productivity). Nevertheless, observation (2) above

TABLE 5. Aboveground dry biomass (g/m^2) on 15 August 1992. Forb and graminoid biomass measured directly; shrub biomass estimated from new shoot length. For all means, $N = 5$ plots. Neither the zonal nor treatment differences are significant at the 0.05 level (Student's t test).

Control plots			Heated plots		
Plot	Lower zone	Upper zone	Plot	Lower zone	Upper zone
1	149.3	141.5	2	312.4	122.8
3	184.2	105.5	4	241.5	202.9
5	115.1	268.7	6	492.8	168.3
7	138.5	158.2	8	248.9	258.9
9	213.4	210.4	10	185.9	225.2
Mean	160.1	176.8	Mean	296.3	195.62
SE	17.4	28.5	SE	53.1	23.4

TABLE 6. Results of a multiple regression of soil temperatures (*T*) and moistures (*M*) in the upper zone (U) and the lower zone (L) of each individual plot, averaged over depth and 1992 growing season.

Variable	Partial regression coefficient		Standard error of partial reg. coefficient		Standard partial reg. coefficient		P (2-tailed)	
	<i>T</i>	<i>M</i>	<i>T</i>	<i>M</i>	<i>T</i>	<i>M</i>	<i>T</i>	<i>M</i>
Constant	12.744	33.118	0.265	1.876	0	0	<0.001	<0.001
Treatment	0.815	-3.601	0.205	1.483	0.599	-0.315	0.001	0.027
Biomass	-0.0025	0.0018	0.0013	0.0096	-0.313	0.026	0.083	0.857
Zone × Biomass	0.0018	-0.0221	0.0005	0.0033	0.589	-0.864	0.001	<0.001

* Categorical variables were assigned as follows: zone L = -1, zone U = +1, control = -1, heated = +1. The coefficients of determination for the temperature and moisture models are 0.702 and 0.787, respectively. *N* = 20 for each regression and all tolerances exceed 0.5. Note that the overall dependence of *T* on biomass has a coefficient of $-0.0025 - 0.0018 = -0.0043$ for zone L, and $-0.025 + 0.0018 = -0.0007$ for zone U.

may offer insights into the relative contributions of the two effects within each of the two zones. Dominance of the moisture effect within a zone would imply that wetter soils should lead to smaller temperature increases in the heated plot; in other words, ΔT should be negatively correlated with soil moisture, as observed in zone U. But in zone L, ΔT is positively correlated with soil moisture, suggesting that the moisture effect may be less influential there. That, plus the higher vegetation density in zone L, suggests that the vegetation effect dominates the soil response to heating there.

The differential impacts of vegetation on zones L and U can be further analyzed through consideration of observation (3) above. Comparison of the depth-dependence of ΔM in the two zones suggests that the major cause of heater-induced soil drying in zone L is increased transpiration rather than evaporation, while in zone U increased evaporation rather than transpiration is more likely responsible for heater-induced soil drying. In particular, in the more densely vegetated zone L, soil drying in the heated plots relative to the controls is greatest at 25-cm depth, and this effect is most pronounced in the second half of the growing season, after day 210 (29 July) in 1991 (Fig. 2, part 2.L.M) and day 190 (8 July) in 1992. This may be a

consequence of plant roots taking up more of their moisture at 25-cm than at 5- or 12-cm depth, with the moisture loss more noticeable later in the growing season when plant cover and moisture stress are greatest. Visual inspection of root architecture in two 80 cm deep and 75 cm long trenches dug adjacent to the plots (10 m north of zone L, plot 10, and 10 m south of zone U, plot 1) indicated that the greatest density of root matter occurs between 15- and 40-cm depth, thus supporting this interpretation. In addition, early in the growing season, when plant cover has not attained its summer maximum, there is direct augmented surface evaporation from zone L, which shows up in Fig. 2, part 2.L.M, as downward spikes at 5-cm depth (but not 25-cm depth) in the ΔM data. Later in the growing season, when vegetation is most dense, these downward spikes do not occur, but they reoccur at the start of the dormancy period around day 240.

In contrast to zone L, incremental soil drying in zone U is least at 25-cm depth, and occurs throughout, rather than just early in, the growing season. Zone U is also characterized by drying spikes at 5-cm depth throughout the growing season (Fig. 2, part 2.U.M), supporting the interpretation that augmented evaporation from the

TABLE 7. Pearson correlation coefficients for daily-averaged soil microclimate data, averaged over treatment during the growing season. *T* = control-plot temperature; *M* = control-plot moisture; ΔT = heated- minus control-plot temperature; ΔM = heated- minus control-plot moisture. **P* < 0.05; ***P* < 0.01; ****P* < 0.001 for observing the data if slope were zero.

Year	Zone	Depth (cm)	<i>M</i> vs. <i>T</i>	ΔT vs. <i>T</i>	ΔT vs. <i>M</i>	ΔM vs. <i>T</i>	ΔM vs. <i>M</i>	ΔM vs. ΔT
1991	lower	5	-0.31**	-0.52***	0.63***	-0.01	-0.58***	-0.40***
		12	-0.49***	-0.50***	0.25*	0.39***	-0.63***	-0.69***
		25	-0.64***	-0.46***	0.36***	-0.39***	0.27*	-0.40***
	upper	5	-0.36***	0.65***	-0.56***	-0.30	-0.56***	0.02
		12	-0.62***	0.60***	-0.50***	-0.23*	0.50***	-0.11
		25	-0.85***	0.02	-0.02	-0.27*	-0.36***	0.04
	lower	5	-0.57***	-0.52***	0.29**	0.03	-0.30**	-0.24*
		12	-0.67***	-0.75***	0.01***	-0.35***	0.22*	0.35***
		25	-0.66***	-0.74***	0.50***	-0.53***	0.37***	0.20*
1992	upper	5	-0.68***	0.80***	-0.72***	-0.17	-0.01	0.06
		12	-0.73***	0.66***	-0.52***	-0.24*	0.32***	-0.33***
		25	-0.90***	0.36***	-0.22*	-0.35***	0.21*	0.25*

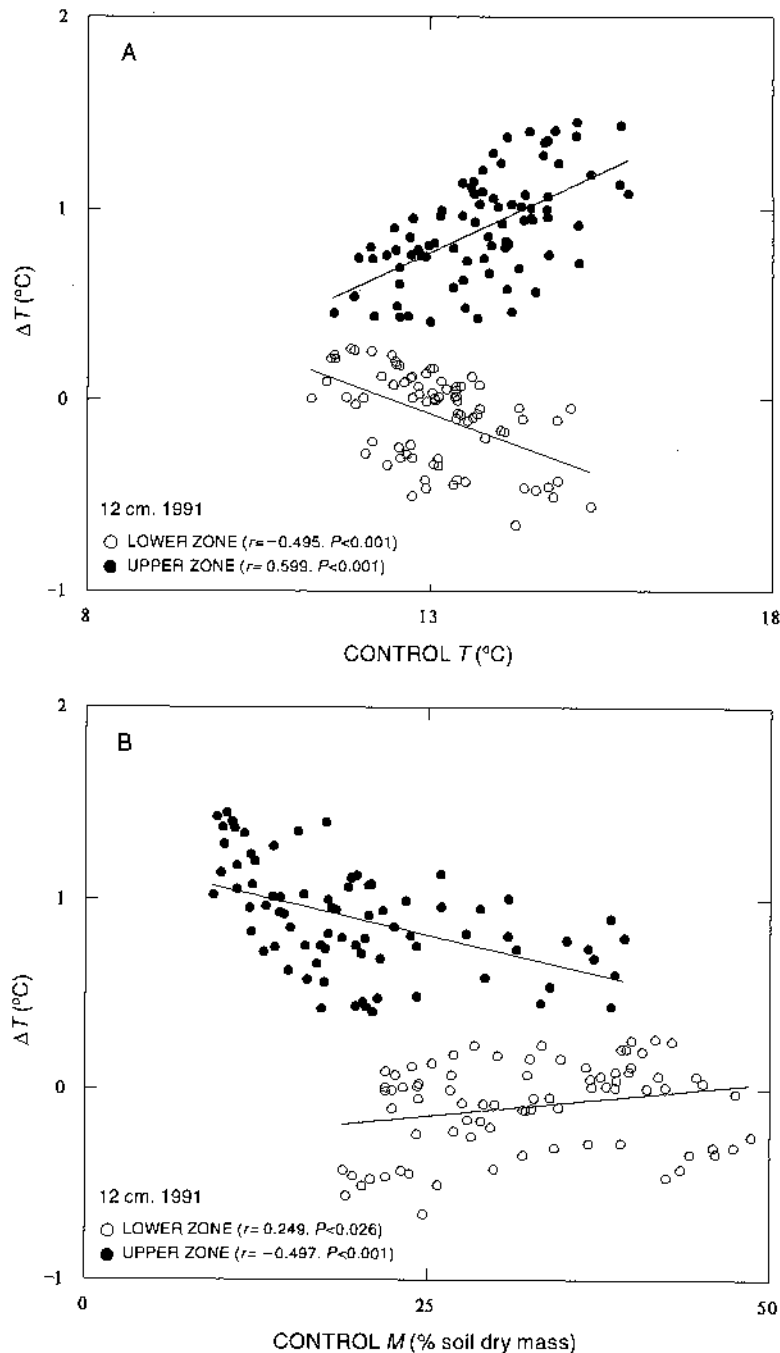


FIG. 4. Correlations between daily-averaged incremental temperatures (ΔT , the difference between control and heated plots) and control-plot temperatures (T) and moistures (M) at 12-cm soil depth, during the 1991 growing season (10 June–28 August). r = Pearson correlation coefficient; P = probability of observing the data if the slopes were zero.

soil surface is the most important process leading to heater-induced soil drying there.

Additional evidence that the vegetation effect is dominant in zone L comes from the multivariate regression (Table 6), which suggests that vegetation density explains more of the plot-to-plot variance of temperatures in zone L than in zone U.

The evidence presented above suggesting that the moisture and vegetation effects dominate within zones U and L, respectively, does not bear directly on the question of why the soils of zone U are warmer than those of zone L. Results of the multivariate general linear model (Table 6), however, suggest the existence of a zonal effect on temperature that is distinct from

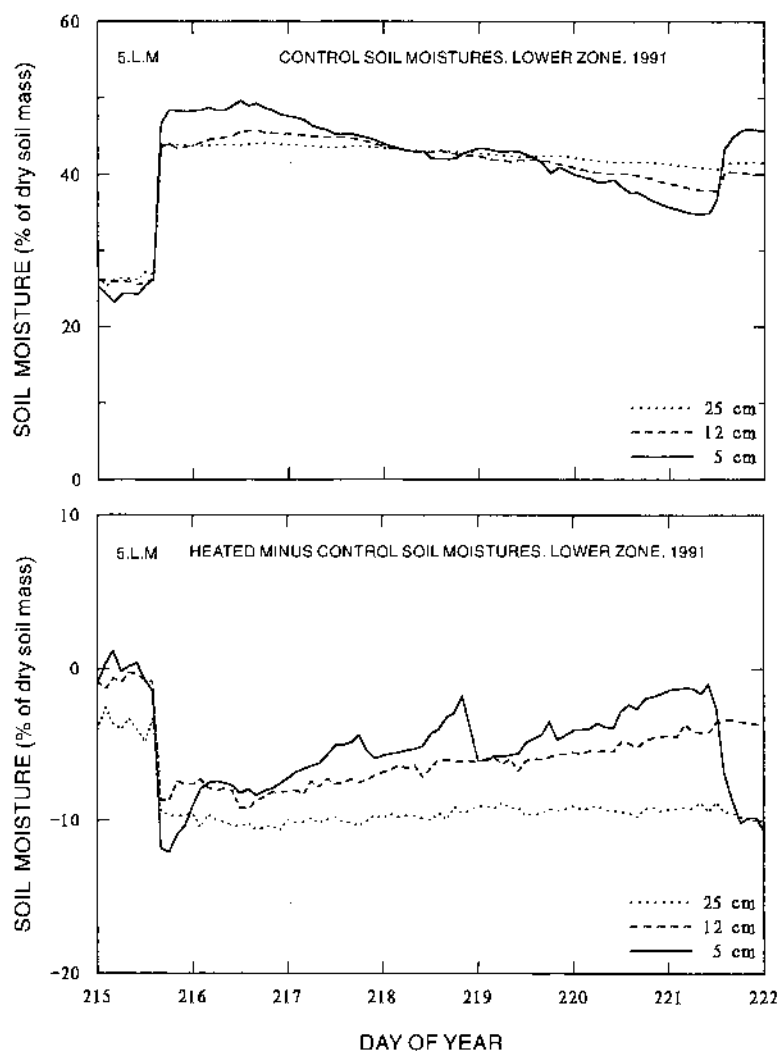


FIG. 5. Two-hourly soil-microclimate data, averaged over $n = 5$ plots within treatments, for the period 3 August–9 August 1991. 5.L.T, zone L temperature; 5.U.T, zone U temperature; 5.L.M, zone L moisture; 5.U.M, zone U moisture. (Figure continues on pages 146–148.)

the vegetation effect. In particular, the interzonal vegetation difference explains less than half the interzonal soil temperature difference. The moisture effect is a more likely explanation, with interzonal moisture differences driven in part, at least, by topography.

TABLE 8. Pearson correlation coefficients, zone L versus zone U, for temperature and moisture data; symbols are defined as in Table 7.

Year	Depth (cm)	T	M	ΔT	ΔM
1991	5	0.951***	0.969***	-0.244*	0.613***
	12	0.868***	0.946***	-0.433***	-0.098
	25	0.936***	0.932***	-0.191*	0.384***
1992	5	0.992***	0.971***	-0.421***	0.231**
	12	0.992***	0.947***	-0.601***	0.218*
	25	0.994***	0.848***	-0.078	0.355***

To understand the surprising observation of a large midday peak in the diurnal variation of ΔT in zone U [observation (4) above], we return to the moisture effect. A higher soil moisture level does not only cause more of the additional infrared radiation from the heaters to evaporate water instead of raising soil temperature; it also influences how the incoming solar radiation is partitioned between raising soil temperature and drying soil. To the extent that the heaters dry the soil, more of the incoming solar radiation will be available in the heated plots, relative to the control plots, for raising soil temperature. Thus, a relatively small decrease in soil moisture (due to the heaters) can result in a large effect on soil temperature on sunny days.

In zone U, the heaters do induce soil drying and therefore the temperature response of the heated plots to insolation should exceed that of the moister control

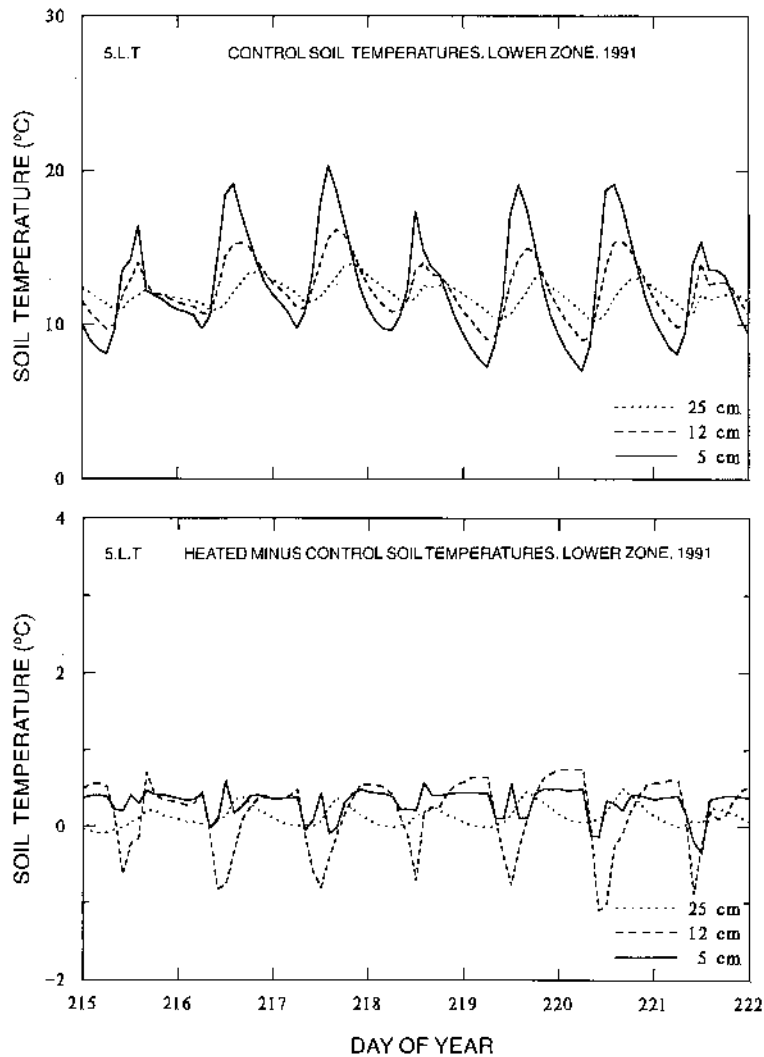


FIG. 5. Continued.

plots. In other words, when the sun is shining the soil temperature response to incoming solar radiation is magnified by the incremental drying induced by the heaters. This, we suggest, leads to the midday peak in ΔT in zone U.

This explanation of the diurnal variation in ΔT in zone U is supported by the positive correlation between that zone's daily-averaged values of ΔT and control plot temperatures (Table 7), both of which are strongly correlated with daily maximum values of insolation measured at the weather station. Decreased soil moisture also generally increases soil albedo, however, and this would tend to operate in the opposite direction, causing a daytime dip in ΔT . Our results suggest, therefore, that the latent heat effect dominates the soil albedo effect. A mathematical model of energy and water transfer in our plots supports this and simulates the correct phase and approximate magnitude of the midday peak in ΔT (Shen and Harte, *unpublished data*).

A possible alternative explanation of the diurnal variation in ΔT in zone U is that aboveground vegetation is responsible; plots with less vegetation will be less shaded and therefore should exhibit greater midday soil warming. This explanation can be ruled out both because the aboveground vegetation is actually slightly denser in the heated plots than in the control plots of zone U (Table 5) and because strong diurnal variation shows up very shortly after snowmelt when aboveground vegetation is scant.

The different relative effects of transpiration and evaporation on soil drying, and the different relative effects of vegetation and moisture on soil temperature, provide some insight into why the diurnal pattern of variation in soil temperature is more complex in zone L than in zone U. If increased plant transpiration is the major direct mechanism by which the heaters influence soil microclimate in zone L, it follows that there should be a daytime drawdown of moisture levels in the root

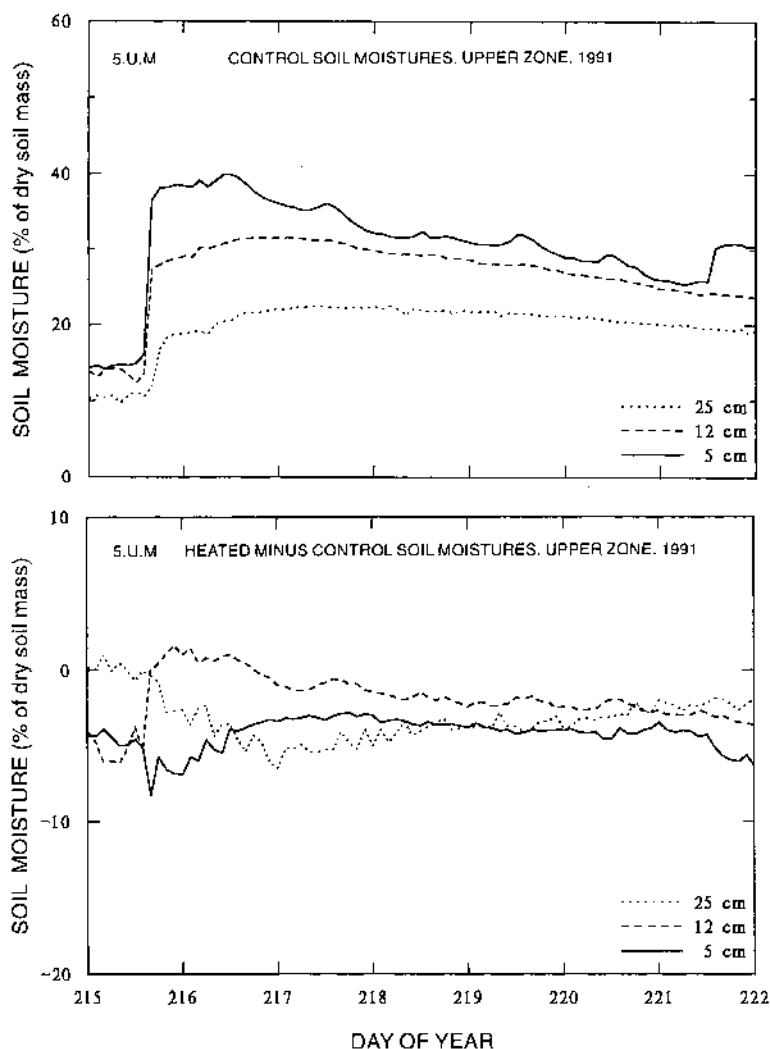


FIG. 5. Continued.

zone rather than in the shallower soils. The effect of this drawdown on shallow-soil moisture levels (which determine the strength of sunlight enhancement of soil temperature by the mechanism discussed above) will be delayed by the transport time for moisture flow within the soil column. While we cannot be more precise without a mathematical modeling of this unsaturated-flow transport process, we suggest that the complex pattern of diurnal variation of ΔT at all depths in zone L is the result of the time delay in moisture transport between the root zone and the shallow soil.

Additional mathematical modeling will be needed to understand whether our observation of a midday peak in ΔT is of regional or global significance. Models can be used, for example, to determine whether the midday peak induces differential daytime vs. nighttime atmospheric responses to increasing greenhouse gas levels.

CONCLUSION

We demonstrated that an ecosystem-warming manipulation using overhead infrared radiators as a heat

source provides an effective way to study the responses of soil microclimate to warming. We observed unexpected responses, including a sharp daytime peak in the temperature increment between heated and control plots in the drier, less-vegetated zone, and a negative correlation between the microclimate responses to heating in that zone and the wetter, more densely vegetated, zone. These and other observed responses illustrate the complexity of soil-vegetation-climate system and the potential for unexpected responses to global warming.

We have interpreted the patterns of response to the heat treatment in the two zones in terms of two regulatory mechanisms that derive from differences in soil moisture content and vegetation cover. Further exploration of this interpretation needs to be carried out with mathematical models of the physical soil environment.

Our choice of an ecotone for the study site has assisted and enriched interpretation of data. In particular, the gradient of ecological conditions within each plot

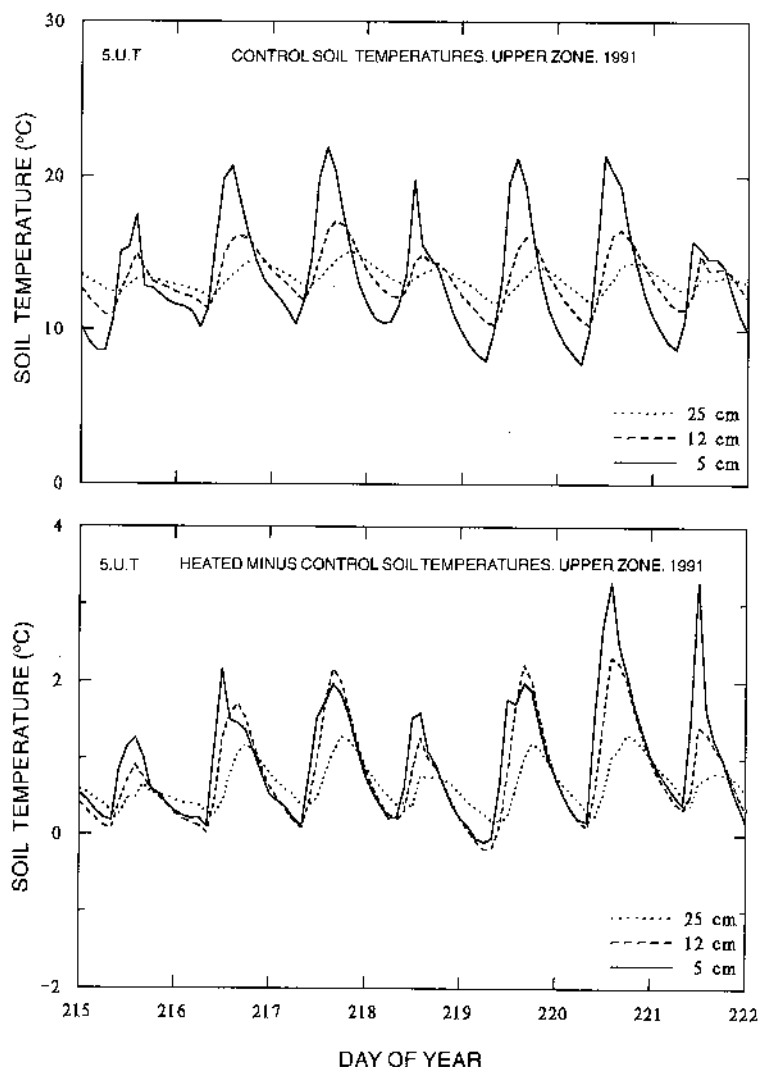


FIG. 5. Continued.

has provided a means of identifying mechanisms shaping the soil microclimate response to warming. In subsequent analyses of the full suite of ecosystem data from our warming experiment, we will examine the ways in which a wide range of ecosystem properties depend not only on the heat treatment but also on intraplot gradients, on year-to-year variation in regional climate, and on the interplot variation in date of snowmelt. In this way we expect to be able to elucidate contingent ecosystem responses to climate change.

Our results highlight the prominent role that vegetation will play in influencing future soil microclimate responses to enhanced IR flux. More generally, the large soil microclimate data set that our study is yielding provides an opportunity to test hypotheses and models of soil microclimate response to climate change.

Thus, our results have implications for ecologists and climatologists. First, they serve as a reminder that the

simple generalizations about soil microclimate response to warming that follow from general circulation models (such as statements about average increase in soil temperature or decrease in soil moisture content) may obscure as much as they reveal for ecologists. For example, the large diurnal variation in temperature increment that we observed may have implications for rates of nutrient cycling, greenhouse gas fluxes, and vegetation productivity and distribution. Second, while it is well known that the bi-directional linkages among climate, vegetation, and soil can lead to feedback mechanisms that alter climate and ecosystems, our experimental design offers a useful way to actually develop a quantitative and potentially predictive understanding of the nature of these mechanisms. To derive the most benefit from experimental manipulations such as this, both localized mathematical models of soil-climate-vegetation linkages and techniques for extrapolating local results to regional and global scales are needed.

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ERRATUM

In an article by J. L. Lindquist, D. Rhode, K. J. Puettmann, and B. D. Maxwell ("The influence of plant population spatial arrangement on individual plant yield," *Ecological Applications* **4**(3):518–524), several values shown in Table 2 were erroneous. The corrected table is shown below. Four sentences in the *Results* section of the article that refer to values reported in Table 2 should be changed to reflect the corrected values.

TABLE 2. Least squares nonlinear regression models using four independent variables (N , DD , AD^6 , and DI). S = biomass production (the dependent variable), M = mean dry biomass of five individuals grown in the absence of competition (10.1 and 66.8 g for experiments 1 and 2, respectively), N = neighborhood density (=16 plants, excluding the target individual), Θ = the weighting variable, c = the single estimated parameter, and r^2 = the coefficient of determination.

Model	Experiment 1			Experiment 2		
	Θ	c	r^2	Θ	c	r^2
1. $S = \frac{M}{(1 + c \cdot N)}$	...	0.17*	0.0	...	0.53*	0.0
2. $S = \frac{M}{(1 + c \cdot N \cdot DD)}$	0.45	0.30*	0.37	0.35	0.97*	0.19
3. $S = \frac{M}{(1 + c \cdot N \cdot AD^6)}$	1.2	0.26*	0.20	1.0	0.71*	0.29
4. $S = \frac{M}{(1 + c \cdot N \cdot DI)}$	0.45	0.42*	0.57	0.4	1.29*	0.51

* Indicates the parameter estimate (c) is significantly different from 0 at $P < 0.05$.