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The effect of experimental ecosystem warming on CO_2 fluxes in a montane meadow

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Abstract

Climatic change is predicted to alter rates of soil respiration and assimilation of carbon by plants. Net loss of carbon from ecosystems would form a positive feedback enhancing anthropogenic global warming. We tested the effect of increased heat input, one of the most certain impacts of global warming, on net ecosystem carbon exchange in a Rocky Mountain montane meadow. Overhead heaters were used to increase the radiative heat flux into plots spanning a moisture and vegetation gradient. We measured net whole-ecosystem CO_2 fluxes using a closed-path chamber system, relatively nondisturbing bases, and a simple model to compensate for both slow chamber leaks and the CO_2 concentration-dependence of photosynthetic uptake, in 1993 and 1994. In 1994, we also measured soil respiration separately. The heating treatment altered the timing and magnitude of net carbon fluxes into the dry zone of the plots in 1993 (reducing uptake by ≈100 g carbon m^{-2}), but had an undetectable effect on carbon fluxes into the moist zone. During a strong drought year (1994), heating altered the timing, but did not significantly alter the cumulative magnitude, of net carbon uptake in the dry zone. Soil respiration measurements showed that when differences were detected in dry zone carbon fluxes, they were caused by changes in carbon input from photosynthesis, not by temperature-driven changes in carbon output from soil respiration. When differences were detected in dry-zone carbon fluxes, they were caused by changes in carbon input from photosynthesis, not by a temperature-driven changes in carbon output from soil respiration. Regression analysis suggested that the reduction in carbon inputs from plants was due to a combination of two soil moisture effects: a direct physiological response to decreased soil moisture, and a shift in plant community composition from high-productivity species to low-productivity species that are more drought tolerant. These results partially support predictions that warming may cause net carbon losses from some terrestrial ecosystems. They also suggest, however, that changes in soil moisture caused by global warming may be as important in driving ecosystem response as the direct effects of increased soil temperature.

Keywords: carbon flux, climate change, CO_2, feedback, greenhouse gas, montane meadow, soil respiration

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Introduction

Global climatic changes due to anthropogenic increases in atmospheric greenhouse gas concentrations are projected to include an increase in the Earth's global average surface air temperature at a rate of several tenths of a degree per decade during the next 100 years (IPCC 1996). The stresses of this warming on ecosystems could be profound, affecting biogeochemical processes, species composition, and plant physiology and production (Mooney *et al.* 1991; Schlesinger 1991; Peters & Lovejoy 1992). Feedback processes, whereby ecological responses generate additional climatic impacts by modifying the

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composition of the atmosphere and the heat transfer at the planetary surface, are also likely to occur (Lashof *et al.* 1997). Of particular importance are ecological feedbacks arising from climate-induced perturbations to the carbon cycle, since such perturbations can directly alter the CO_2 concentration of the atmosphere, and hence, climate (Woodwell & Mackenzie 1995). A number of modelling and observational studies have suggested that global warming will, on average, enhance both soil respiration (carbon loss) and net primary productivity (carbon gain), but most of these studies also conclude that in most systems, the soil respiration enhancement is likely to be larger (Post *et al.* 1982; Raich & Schlesinger 1992; Townsend *et al.* 1992; Schimel *et al.* 1994; Kirschbaum 1995; Raich & Potter 1995; Trumbore *et al.* 1996; but see Gifford 1992 or McKane *et al.* 1997 for different views). These studies therefore suggest that global warming will induce a net loss of carbon from ecosystems, a positive feedback to global climate.

This paper describes an approach to, and results from, *in situ* measurements of the effect of warming on whole-ecosystem CO_2 fluxes in a Rocky Mountain montane meadow. We used overhead heaters to simulate the increase in surface warming of soil and vegetation that would be expected to occur from a doubled-CO_2 global warming (Harte *et al.* 1995). This manipulation mimics important parts of the expected global warming (infrared radiation-induced shifts in surface microclimate and associated changes in snowmelt patterns), but does not include other important changes, such as increases in air temperature, shifts in precipitation patterns, and CO_2 enrichment. The predictions of general circulation models suggest that a variety of factors – including a decrease in the fraction of winter precipitation that falls as snow as opposed to rain, earlier snowmelt, and a possible reduction in summer precipitation – will combine to reduce soil water content during the growing season of mid-latitude continental interiors (Manabe & Wetherald 1986; Roads *et al.* 1994). Since the heating manipulation also tends to cause drier soils in mid-season, some of the interaction of soil moisture effects with soil temperature that may be expected from global climate change are captured in this experiment even in the absence of precipitation manipulation. Other studies conducted at this site include the effect of ecosystem warming on soil microclimate (Harte *et al.* 1995), plant species composition (Harte & Shaw 1995), methane fluxes (Torn & Harte 1996), soil mesofauna (Harte *et al.* 1996), and leaf physiology, including high-temperature tolerance (Loik & Harte 1996), and water relations (Loik & Harte 1997).

There is a large and rapidly growing body of experimental literature on the effects of CO_2 enrichment on plants and ecosystems (Billings *et al.* 1983; Idso & Idso 1994; Korner & Bazzaz 1996), much of it focusing on the effects of changes in CO_2 in the absence of changes in climate. Our study adds to the relatively smaller body of experiments on the whole-ecosystem effects of climate shifts. These experiments have used different manipulation methods, such as plastic enclosures used in arctic tundra (Chapin & Shaver 1996) or buried electric-resistance wires in a mid-latitude temperate forest (Van Cleve *et al.* 1990; Peterjohn *et al.* 1993, 1994).

We used a chamber and a closed-loop infrared gas analysis system for measuring net whole-system (i.e. soil and plants combined) CO_2 fluxes. We used a modified flux calculation to check and account for the dependence of CO_2 fluxes on CO_2 concentration, and also to correct for any slow leaks between the chamber and ambient air. We used a smaller chamber to measure soil (root plus microbial) respiration separately (Norman 1992) in the second year of measurements.

Our results include (i) an evaluation of our CO_2 flux measurement method, (ii) the diurnal and seasonal pattern of CO_2 fluxes during the 1993 and 1994 growing seasons and the effect of heating on those fluxes, and (iii) multiple regression analysis to explore how physiologically important environmental factors and vegetation characteristics control carbon uptake.

Materials and methods

Field site description

The study site is an ungrazed montane meadow at the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado (38°53′N, 107°02′W, elevation 2920 m). The montane life-zone is widespread at moderately high elevations and latitudes of North America (Vankat 1979). In Colorado it supports a mosaic of vegetation types, including mixed conifer forest, aspen forest, and open meadow. RMBL is in the Southern Rockies, at the boundary between high-elevation montane meadow and at lower elevation Great Basin Sagebrush desert scrub. Annual precipitation averages about 750 mm, with over 80% falling as snow.

The study site supports a highly diverse vegetational community, with roughly 80 species of vascular plants in the study plots. This is a result of both its location on the boundary between life zones, and its steep glaciated topography (which causes dramatic physical and vegetational changes on small spatial scales). The study site is dominated by long-lived herbaceous perennials and a few woody species, with only three identified annual species. Most plant biomass is associated with a few species, including the shrubs *Artemisia tridentata* (sagebrush) and *Pentaphylloides floribunda* (*Potentilla fruticosa* of various authors); herbaceous forbs *Erigeron speciosus* (daisy), *Helianthella quinquenervis* (sunflower), *Veratrum*

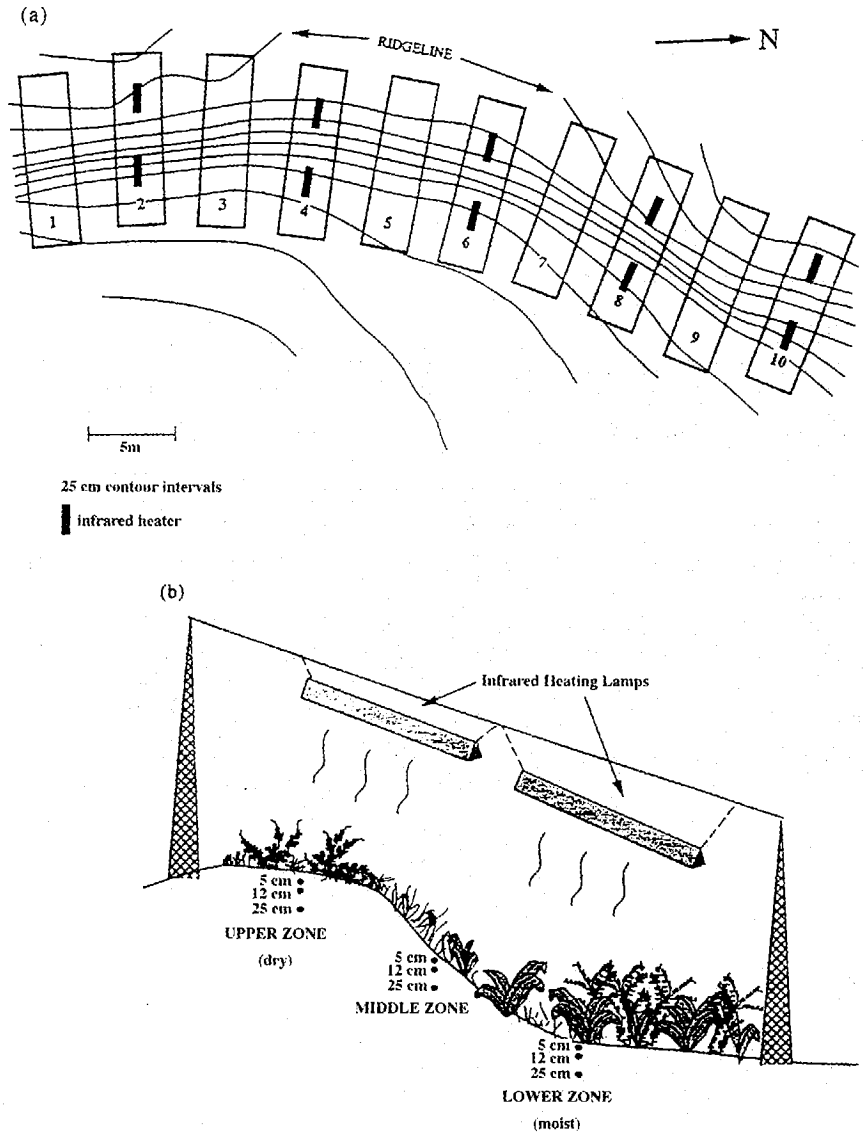

Fig. 1 Experimental design. (a) Arrangement of warming plots. (b) Typical heated plot profile (not to scale).

tenuipetalum (cornlily), *Dephinium nuttallianum* (larkspur), and *Potentilla gracillus*; and graminoids *Festuca thurberi* (fescue) and *Poa* spp. (bluegrass) (Harte & Shaw 1995).

The soil in the study site is a well-drained Cryoboroll formed on a deep, rocky, noncalcareous, glacial till. The soil is relatively uniform in colour and without highly developed soil horizons down to at least 50 cm. Carbon content averages about 5.5% C in the top 10 cm, dropping to about 3% C at 50 cm, as determined by mass spectrometry (Europa Scientific Stable Isotope Analysis System). The soil solution has an average pH of 5.7–6.3, as measured potentiometrically in 1:1 soil–water slurry.

Experimental design

The heating experiment was established in 1990, and consists of 10 3 m × 10 m plots laid out side-by-side along a N–S line, with 3 m between adjacent plots (see Fig. 1a). Each plot is on an incline, and the upper edge extends to a moraine ridge line, ensuring that no uphill snowmelt or precipitation runoff can influence the plots. A slight arc in the ridge (an average of 4° difference in orientation per plot) results in slightly greater southern exposure for the plots at the northern end of the layout relative to those at the southern end. Each plot contains two distinct zones: a dry zone (the upper third of each plot) and a more densely vegetated moist zone (the lower third of each plot; see Fig. 1b). Moister conditions prevail in the lower regions of the plots because they lie roughly a metre above a willow swale that is wet throughout most of the summer.

The heating treatment is applied to 5 of the plots by 1.6-m-long electric heaters (Kalglo, Lehigh, PA) which are suspended 2 m above the ground by cables. Specially

designed reflectors behind the heating elements ensure both a nearly uniform irradiation of heated plots and confinement of the heating flux to those plots, as confirmed by radiometry measurements and the uniformity of the enhanced snowmelt 'footprint' visually observable beneath heaters each spring. The wavelength of heater radiation is in the range 800–1100 nm, hence the heaters produce negligible visible light or photosynthetically active radiation. Heater shadows block ≈0.3% of daily incoming solar radiation on those portions of each plot subject to heater shading (only some portions of each plot are shaded, and for part of each day heater shadows fall outside plot boundaries).

At the onset of heating (January 1991), two heaters per treatment plot were used to achieve a flux of 15 W m^{-2} at the soil surface; we raised this to 22 W m^{-2} in May 1993 via the addition of a third heater. The introduced flux of 22 W m^{-2} is equal to roughly 3% of total average ambient downward radiation. By comparison, the 4 W m^{-2} increase in radiative forcing at the tropopause from doubled-CO_2 is predicted to increase flux at the ground surface by about 12 W m^{-2} because of feedback-enhancement (e.g. by water vapour) of the initial forcing (Ramanathan 1981; IPCC 1996). Our experimentally introduced flux is almost twice this feedback-enhanced surface flux in order to compensate for the absence of air warming in our manipulation and for heat conduction away from heated plots, yet still achieve roughly the level of soil warming expected under a 2 × CO_2 atmosphere.

Microclimate effects

We record soil temperature and soil moisture every two hours, year-round, at 5 cm, 12 cm, and 25 cm depths in the centres of the dry and moist zones of all 10 plots (Harte *et al.* 1995). The heating treatment had a negligible effect on air temperature and relative humidity. The direct microclimate effect of the heating manipulation during the growing season (julian days 160–230) of the years of this study was to warm and dry the soil of the dry zone and to accelerate snowmelt in both zones by one to two weeks (Table 1). In the moist zone, heating had a negligible effect on the growing-season average temperature, and caused smaller percentage reductions in soil moisture, compared to the dry zone. The dry 1994 growing season (summertime precipitation was the lowest in three decades) caused significant reductions in seasonal average soil moisture in both zones (Table 1) compared to measurements taken at our experimental site since 1990.

Growing-season averages of microclimate treatment effects (Table 1) mask effects on shorter timescales that may be important in controlling carbon uptake and release. For example, the effect of heating on dry-zone soil water content ranged from 30% reductions to 20% increases (Fig. 2), depending on conditions (the biggest reductions in soil moisture occurred when control plot soil moisture was at intermediate levels, with relatively smaller treatment effects observed at high and low-moisture) (Harte *et al.* 1995). And, as discussed further below, the apparent absence of any heating effect on temperature in the moist zone (Table 1) is actually due to effects in opposite directions at different times of the season (Fig. 2d).

Table 1 Site microclimate characterization 1993–94

	Dry Zone		Moist Zone	
	control plots	heated plots	control plots	heated plots
Soil Temperature (°C)				
1993	13.7	15.1	12.8	12.8
1994	15.0	16.6	13.9	14.0
Soil Moisture (g H_2O/100 g soil)				
1993	18.8	17.3	29.3	28.6
1994	17.3	15.7	24.0	22.0
Date of Snowmelt (julian day)				
1993	145	132	150	135
1994	133	122	137	130

Soil temperature and moisture values are averages of measurements every 2 hs over 5, 12, and 25 cm depths, from the end of snowmelt to mid-August (date of snowmelt is defined to be the date on which the 5-cm soil temperature reaches 1 °C). Heated plots receive 22 W m^{-2} of infrared radiation from suspended overhead heaters. Source: Harte & Shaw (1995).

The lesser treatment effects on soil microclimate in the moist zone were presumably due to wetter soils and more dense vegetation (Harte *et al.* 1995). Wet soils have both a higher heat capacity and a higher Bowen ratio (latent:sensible heat fluxes) than dry soils, so in wet soils, a given amount of sensible heat input raises temperature less, and a smaller proportion of incoming radiation will contribute to sensible heat in the first place, because a greater proportion is diverted into latent heat (evaporating water). Denser vegetation also reduces the effect of heating on soil temperature due to increased shading of the soil. The shading effect is especially important in the moist zone plots, as illustrated by the seasonal pattern of the temperature treatment effect: for the month after snowmelt (days 160–190) above-ground plant biomass is greater in heated plots due to the head-start in growth allowed by earlier snowmelt. Larger plants shade the soil more than smaller ones, so during this period, the heating treatment actually results in cooler soils (Fig. 2d). After about Day 220 (when above-ground plant biomass is more equal between treatments), moist zone heated plots remain consistently warmer than controls.

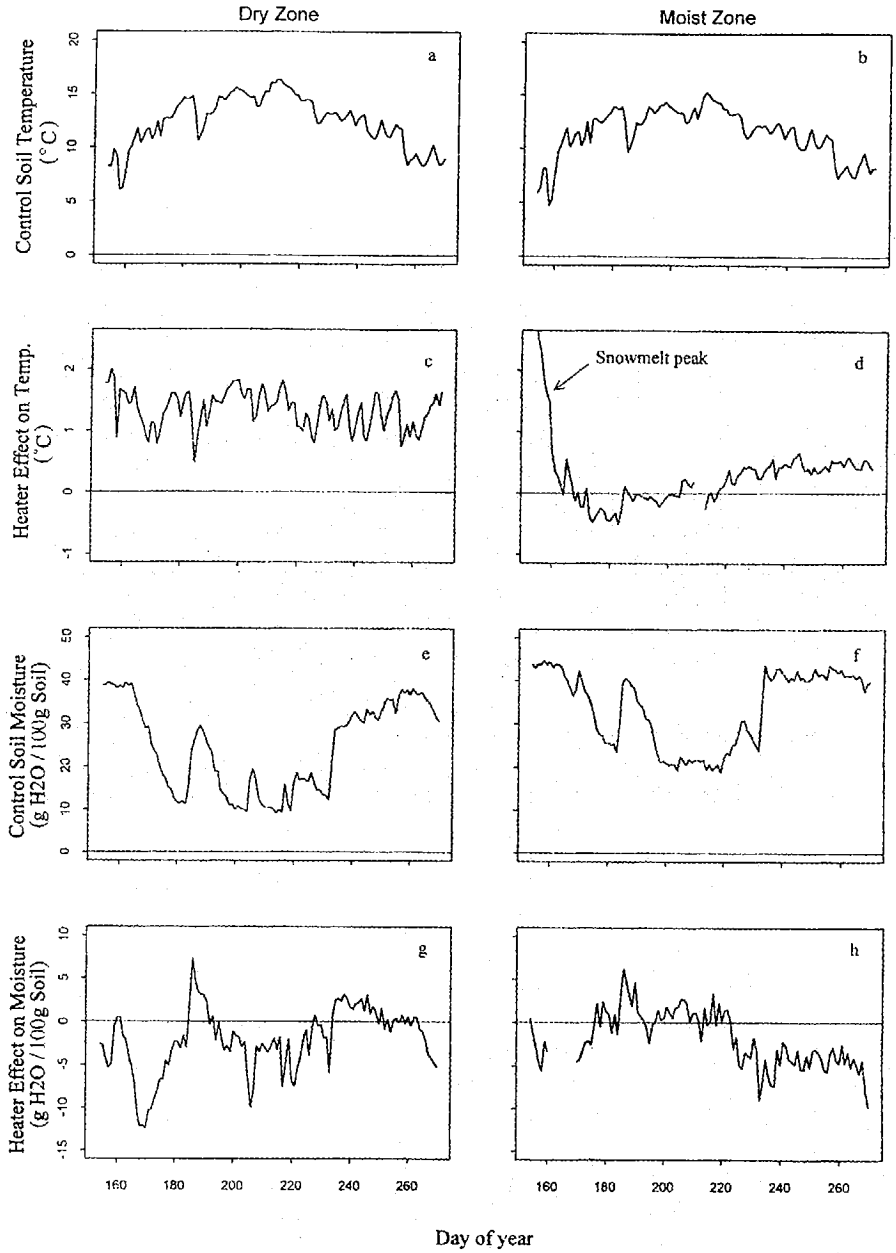

Fig. 2 Daily average 1993 soil microclimate data, days 150–270 (30 May – 27 September): soil temperatures for control plots in the (a) dry-zone, and (b) moist-zone; heater effect on soil temperature (heated minus control plot temperatures) in the (c) dry-zone and (d) moist zone. Soil moisture for control plots in the (e) dry zone and (f) moist zone; heater effect on soil moisture in the (g) dry zone and (h) moist zone. Temperatures are averages of 5, 12, and 25 cm depths, and moisture is from 12 cm depth.

CO_2 flux measurement model

We measured whole-ecosystem CO_2 flux with a passive, real-time closed gas-exchange system modified from those used by Wells *et al.* (1986), Field *et al.* (1989), and Vourlitis *et al.* (1993). We used a square 235 L clear plexiglas chamber, 75 cm on a side and 42 cm in height, which was equipped with Teflon tape on the inside to minimize CO_2 and water exchange with the chamber walls, and two internal fans to ensure thorough mixing of the chamber atmosphere (Fig. 3). To take a flux measurement, the chamber was placed over the measurement area, and the CO_2 concentration in the chamber was measured over a period of 1–2 min with a Li-Cor 6200 portable infrared gas analyser (Li-Cor 1990). A small-diameter tube (3 mm) connected the chamber air to the outside air to avoid pressure gradients which are known to cause substantial bias in flux measurements. We elevated within-chamber CO_2 concentration just prior to taking daytime CO_2 flux measurements by blowing

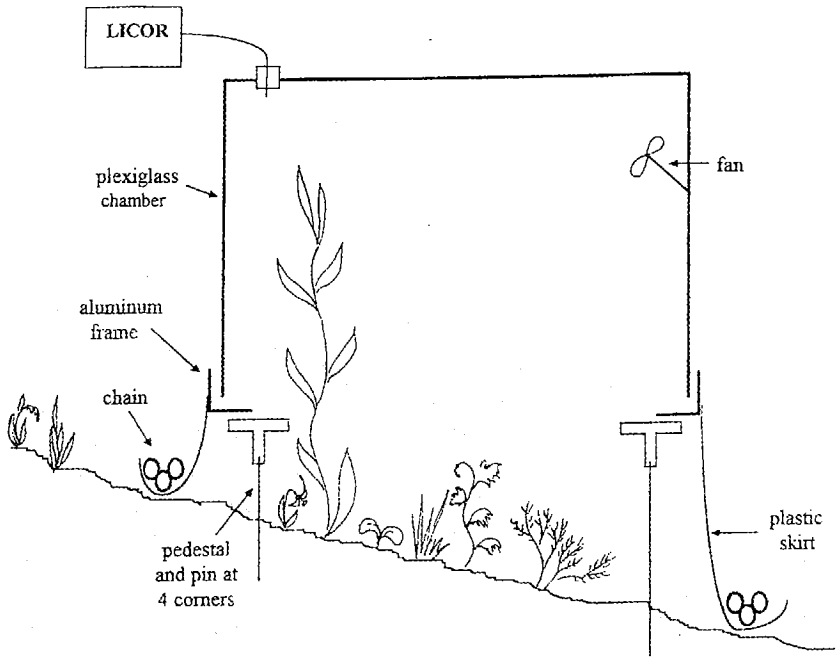

Fig. 3 CO_2 flux-measurement system. The figure shows CO_2 flux measurement in progress on a typical plot. The four metal pins were permanently driven into the ground at the beginning of the season. Metal frames with attached plastic skirts were put in place 12–24 hs prior to the beginning of each measurement, and removed within 24 hs of completing a diurnal measurement cycle. The chamber was put in place for the 1–2 min required to take each measurement, and then taken to the next plot. The volume used in flux calculations was the volume of the chamber plus the volume of the space between the frame and the ground (calculated by multiplying the area of the frame by the average of 9 heights measured on a regular grid over the area of the frame).

CO_2 into the chamber, so that photosynthetic draw-down of chamber CO_2 would cause the concentration to cross ambient levels during the course of the measurement. Initial chamber CO_2 concentrations were not altered at night, because the air flow rate through the Li-Cor CO_2 scrubber (soda lime) was too low to remove significant CO_2 in such a large chamber.

In contrast to the system described by Vourlitis *et al.* (1993), which employed chamber bases permanently installed 10–15 cm into the tundra soil using a serrated knife or chainsaw, we used removable bases which did not cut into the soil and which were in place only during 48 hs surrounding and including each 24-h measurement period. This approach was more practical in our system, where installed bases would, for example, disrupt hydrologic flows down inclined experimental plots, and likely sever the large surface and near-surface roots of plants, particularly *A. tridentata*, in experimental plots.

The removable base consisted of a galvanized steel frame and an attached skirt of plastic sheeting (Fig. 3). The metal frame was placed onto four steel pins which were permanently driven into the ground at the beginning of the season and capped with flat plastic plates that provided a surface to support the metal frame. The frame was supported 10–20 cm above the ground (usually well down into the plant canopy, which, especially in the moist zone, can often rise 20–50 cm above the ground) and the plastic skirt was carefully tucked in between plants so that it rested on the ground directly beneath the frame. The plastic sheeting was held firmly against the soil surface by a metal chain encircling the perimeter of the frame.

Although this method resulted in a fairly leak-tight system, we investigated the possibility that slow leakage could influence the magnitude of the flux measurements. To do this, we developed a simple mathematical model that allowed us to estimate fluxes even when small leaks are present; the same model also allows us to correct for the CO_2 concentration-dependence of photosynthetic uptake. We then compared fluxes estimated with our model with those determined by standard methods which assume no leak and negligibly small changes in flux rate due to changing CO_2 concentrations.

The equation for the flux of net ecosystem productivity (F_{nep}) measured with a (possibly leaking) closed chamber placed over a patch of photosynthesizing and respiring ecosystem is:

$$-\left(\frac{PV}{RT}\right)\frac{dC}{dt} = a\,F_{nep} + (F_{leak} + a\,\Delta F_{photo}), \qquad (1)$$

where C is the concentration of CO_2 in the chamber, t is time, PV/RT is the number of moles of air in the chamber of volume V at ambient temperature and pressure, a is the area covered by the chamber, and F_{nep} is in units of μmol CO_2 m^{-2} s^{-1}. F_{nep} is defined to be positive when the concentration in the chamber is falling due to net uptake. $(F_{leak} + a\,\Delta F_{photo})$ is the 'error' flow out of the chamber due to diffusional leakage (F_{leak}) and due to concentration-induced deviations in photosythetic uptake from the ambient rate ($a\,\Delta F_{photo}$). ΔF_{photo} is expected to be positive when chamber CO_2 concentration is elevated above atmospheric ambient, and negative when chamber concentration is reduced, since the instantaneous photo-

synthetic CO_2 fixation rates of leaves are proportional to atmospheric CO_2 concentrations over moderate ranges (Nobel 1991, p. 438).

The diffusional leak rate will be driven by the difference in CO_2 concentration between the inside and outside of the chamber, i.e. $F_{leak} = \delta\ (C - C_{amb})$, where C_{amb} is the ambient CO_2 concentration of the outside air, and δ is an effective CO_2 diffusion coefficient (in units of moles of air s^{-1}). If the range of the chamber CO_2 concentration over the course of a single measurement is not too great, the effect on photosynthetic uptake can be approximated by a linear function of CO_2 concentration, i.e. $\Delta F_{photo} = \phi\ (C - C_{amb})$, where ϕ is the marginal dependence of photosynthesis on CO_2 concentration. With these substitutions, the two error terms can be written as a function of the CO_2 deviation from ambient, $(F_{leak} + a\Delta F_{photo}) = (\delta + a\phi)(C - C_{amb})$, and (1) becomes:

$$-\left(\frac{PV}{RT}\right)\frac{dC}{dt} = a\,F_{nep} + \varepsilon(C - C_{amb}), \qquad (2)$$

where the diffusional leak coefficient and the CO_2 concentration-dependent photosynthetic deviation coefficient have been combined into a single CO_2 concentration-dependent 'error' coefficient $\varepsilon = (\delta + a\phi)$.

The solution to (2) can be written as:

$$C(t) = (C_0 - C_{ss})e^{-t/\tau} + C_{ss}. \qquad (3)$$

This is an exponentially decaying CO_2 concentration which starts at C_0 (the CO_2 concentration at time $t = 0$ – i.e. the start of the measurement), and approaches the non-zero steady- state value C_{SS} with a characteristic time $\tau = \frac{1}{\varepsilon}\frac{PV}{RT}$. C_{SS} is equal to $C_{amb} - a\,F_{nep}/\varepsilon$, and is that CO_2 concentration where the outside-to-inside chamber gradient, $C_{amb} - C$, is just big enough to cause an inward CO_2 leak that balances the outflow of CO_2 from net carbon uptake.

F_{nep}, the variable of interest, can be estimated by fitting a time-series of CO_2 concentration data to eqn 3 by a nonlinear least squares regression (Stata statistics package). We used Li-Cor output, typically consisting of about 40 data points collected over a period of one minute, to estimate C_0, C_{SS} and τ. F_{nep} can then be calculated from the slope of the CO_2 concentration data at ambient concentration (the local ambient concentration, C_{amb}, was measured just prior to each flux measurement):

$$F_{nep} = \frac{1}{a}\left(\frac{PV}{RT}\right)\frac{\partial C}{\partial t}\bigg|_{C\,=\,C_{amb}} = \frac{C_{amb} - C_{SS}}{a\tau}\left(\frac{PV}{RT}\right). \qquad (4)$$

The flux estimated by this approach corrects for effects of slow leakage and first-order deviations in photosynthetic uptake caused by nonambient chamber CO_2 concentration, but it will not compensate for rapid or abrupt changes in CO_2 concentration which might be caused, for example, by sudden wind gusts.

The same data series can be used to calculate a flux under the standard assumption of no leaks and constant photosynthetic rate. In this case conventional linear least-squares regression methods are used to estimate $\frac{dC}{dt}$, and the standard estimate of F_{nep} is calculated as $\frac{1}{a}\left(\frac{PV}{RT}\right)\frac{dC}{dt}$. A second-order adjustment term accounting for changes in water vapour pressure in the chamber caused by evapo–transpiration (a calculation normally made automatically by the computer- controlled Li-Cor LI-6200, as described in Li-Cor, 1990) was added to both the exponential and straight–line model results to arrive at final estimates of CO_2 flux.

CO_2 flux sampling protocol

We used the measurement methods given above to obtain net whole-system CO_2 fluxes in heated and control plots of both zones for the 1993 and 1994 growing season. In 1993, we measured carbon fluxes over a 24-h period on each of nine days – approximately once every 10 days – beginning on 22 June, and extending through late September. Measurement days were scheduled ahead of time and measurements proceeded as scheduled in sunny or cloudy weather (one set of measurements on one day was interrupted by rain). For each 24-h measurement period, flux data were collected from both zones of each of the 10 plots once every four hours. Thus, we obtained 3 daytime, and 3 night-time measurements per 24-h cycle, except for the last three measurement days, when only two daytime and two night-time measurements were taken due to reduced biological activity on the plots.

In 1994, we repeated the time-series of whole-system flux measurements, except that measurements started immediately after snowmelt, and on each measurement day, only two night-time measurements were made – at 20.00 and 04.00 hours – since the 1993 data showed that the midnight measurement did not differ substantially from the others. Three daytime measurements were made as before. In 1994, we measured soil respiration twice per day on the same days as whole-system flux measurements, with a predawn measurement when soils were at their coldest, and a mid-afternoon measurement when soils were warmest. Soil respiration was measured using a small soil chamber (Norman 1992) that was placed on PVC rings (10 cm diameter) that had been previously installed by pushing them several centimetres into the soil in bare spots between vegetation. Three PVC rings

were installed per plot, and at each measurement time, soil respiration measurements from each of the 3 rings were combined to produce a single plot average.

In both 1993 and 1994, estimates of standing above-ground plant biomass were made for the CO_2 measurement square within each plot within a few days of each CO_2 flux measurement. Estimates were made separately for each of three plant growth forms – shrub, forb, and graminoid – using measurements of leaf area index and areal coverage. The methods for measuring above-ground biomass, and the data obtained thereby are reported in more detail in Harte & Shaw (1995). The same biomass data reported there is used here to interpret the CO_2 flux measurements.

We conducted two kinds of statistical analyses of this data set: simple *t*-tests for differences between heated and control plot CO_2 fluxes, and multiple regression analysis to explore how physiologically important environmental factors and vegetation characteristics control carbon uptake. The regression analysis allowed us to explore the implications of previously observed heating-induced shifts in vegetation growth form (Harte & Shaw 1995) between control and heated plots on carbon storage.

t-tests of differences in CO_2 uptake during a given time period (e.g. individual day, whole-season, etc.) were conducted after first taking the averages over the relevant time-series for each plot separately. To the extent that sequential measurements on a given plot within a day or over the course of the season give some independent information, the method we use here dilutes the statistical power of the test to detect differences by reducing the degrees of freedom. The *t*-tests presented in this paper are therefore likely to be conservative.

Because snowmelt generally proceeds from the more southerly exposed plots at the north end of the plot array to the less southerly exposed at the other end, there is a systematic trend in some variables from one end of the plot array to the other. We therefore used paired *t*-tests when testing for differences in early season CO_2 flux measurements in 1994. Later in the season, after the systematic variation caused by the snowmelt effect had faded, we used the two-sample *t*-test because its greater number of degrees of freedom gave better statistical power.

Regression analyses including multiple measurements from each plot were used to capture the range of variation in different controlling variables. Because the independent variables in the regression were the factors that accounted for most of the difference between control and heated plot fluxes, such as soil microclimate and above-ground vegetation biomass, we assumed that model residuals were randomly distributed across plots.

Results

Measurement model

The comparison of our model for estimating whole-system flux measurements with a conventional straight-line approach is summarized in Figs 4 and 5. The small but noticeable curvatures in the chamber CO_2 concentration trends during measurements (upward during the day and very slightly downward at night, Fig. 4) are indicative of either a slight leak or a CO_2-concentration effect on CO_2 flux. The fit of the exponential model is good, producing residuals that typically deviate from the model fit by less than one ppmv of CO_2 concentration. In both cases shown in Fig. 4, the leak model flux estimate is greater in magnitude than the no-leak estimate. This is because the leak model calculates the flux from the CO_2 slope at the point of the atmospheric ambient (i.e. from $\left.\frac{dC}{dt}\right|_{C = C_{amb}}$), whereas the no- leak model uses the average CO_2 slope of the whole data. When photosynthetic uptake dominates, for example, the slope of the data for concentrations above ambient are too steep, while the slope at subambient concentrations is too shallow. The CO_2 concentration slope during the nighttime measurement, however, is too shallow over the whole range of data, because the CO_2 concentration starts above ambient and rises from there; in this case, the exponential model projects the concentration curve backwards to estimate the slope at the ambient CO_2 concentration.

We compared the flux estimates derived from the exponential model fit to those derived from standard straight-line estimates (Fig. 5). Over the middle range of fluxes, there is close agreement between the two methods. At the extremes, however, the magnitude of straight-line flux estimates can be substantially less than the magnitude of exponential model estimates. This difference is greater and more consistent for negative fluxes (which occur mostly at night or late in the season when photosynthetic fluxes are low or zero), presumably a consequence of CO_2 concentration data that often do not cross ambient CO_2 concentration. This is due to the inability to artificially lower chamber CO_2 concentrations below ambient prior to recording data for a flux calculation. (In contrast, when positive uptake predominates, premeasurement chamber concentrations are easily elevated to ensure the time-series of CO_2 concentration data cross ambient).

The statistical fit of the CO_2 concentration data to the exponential model are consistently significantly better than the fit to the straight-line model. Assuming the exponential model better captures the dynamics of

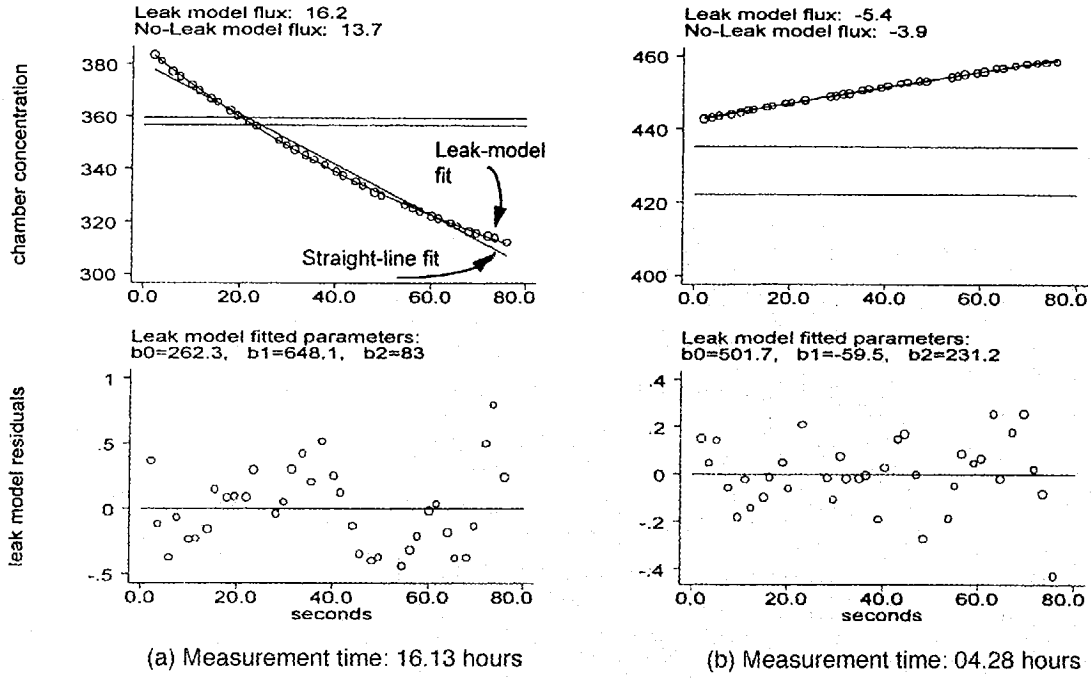

Fig. 4 Results from typical daytime (a), and night-time (b) CO_2 flux measurements on 7/12/93 and 7/13/93, including fits to exponential (leak) model (eqn 3), and the straight-line model.

Notes

(1) The exponential (leak) model is: $[CO_2] = b0 + b1\ exp(-\ t/b2)$ (eqn 3). The fitted parameters $b0$ (eventual steady-state CO_2 concentration), $b1$ (initial deviation from eventual steady-state), and $b2$ (time-constant to approach steady-state) are shown for each of the two measurements. The straight-line (no leak) model is $[CO_2] = C_o + b\ t$

(2) Within-chamber CO_2 concentrations were elevated by blowing CO_2 into the chamber just prior to recording most daytime CO_2 flux data, so that the photosynthetic draw-down of chamber CO_2 would cause the concentration to cross ambient levels during the course of the measurement. Initial chamber CO_2 concentrations were not altered at night, since the flow rate through the Li-Cor CO_2 scrubber was too low to remove CO_2 for a chamber of our size.

(3) Ambient CO_2 concentration was measured just prior to each flux measurement, and is indicated on each of these graphs by two horizontal lines indicating $C_{amb} \pm 1$ s.d. (n = 10 plots) in the measured ambient values. Notice that ambient CO_2 at night is higher (≈430 ppm, as opposed to ≈360 ppm during the day) and more variable than during the day.

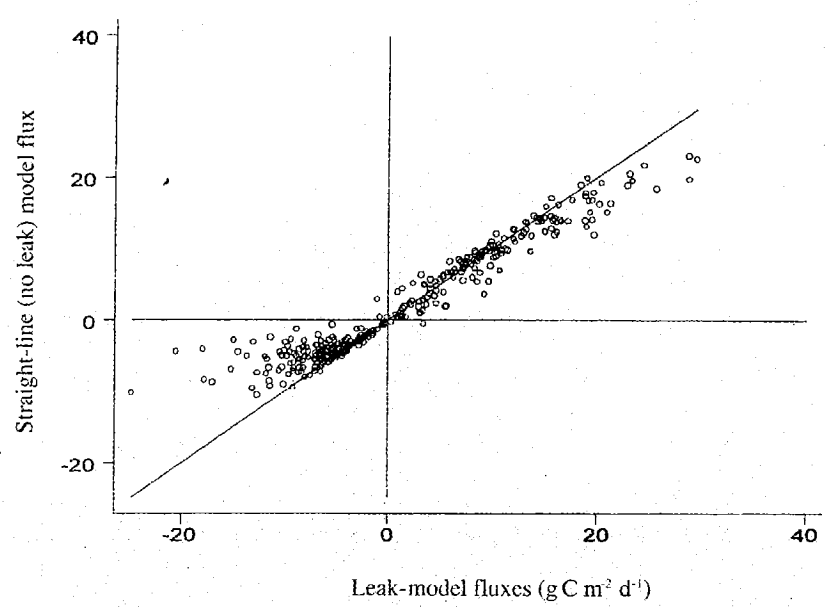

Fig. 5 July 1993 CO_2 fluxes, Straight-line (no-leak) vs. exponential-model estimates. Exponential-model flux estimates are from fitting CO_2 data to $[CO_2] = b0 + b1\ exp(-\ t/b2)$, and taking the slope at the ambient CO_2 concentration. Straight-line model flux estimate is derived from taking the slope of the simple linear regression.

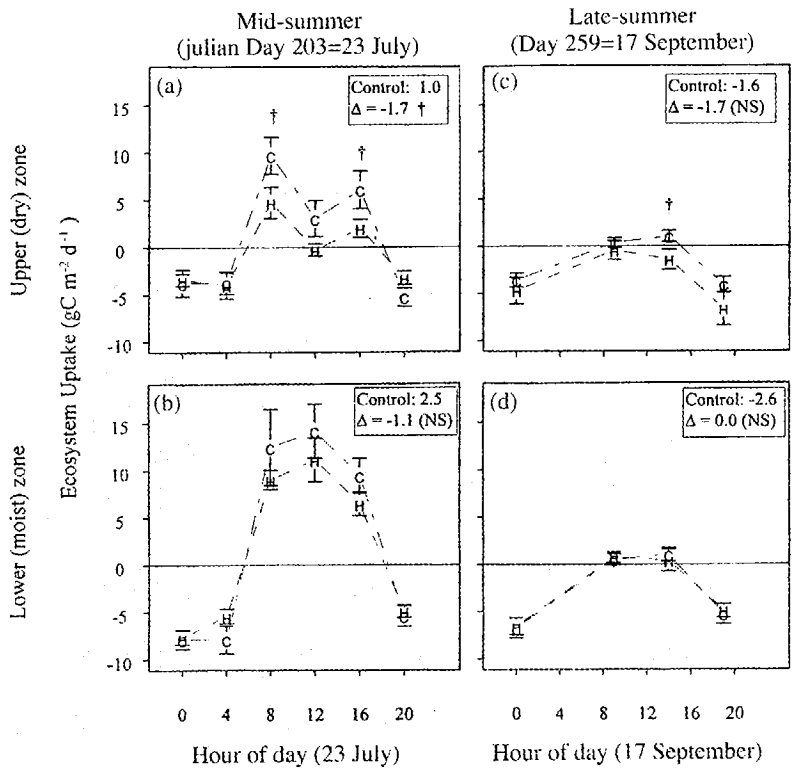

Fig. 6 Diel cycle of net carbon flux on 1993 Julian days 203 (23 July) and 259 (17 September). Ecosystem carbon uptake in heated (H) and control (C) plots: (a) on Day 203 in dry zone plots, and in (b) moist zone plots; (c) on Day 259 in dry zone plots, and (d) in moist zone plots. Error bars are ± 1 SE (n = 5 plots for each treatment). Average control plot uptake for each day is indicated by text in the upper right corner of each graph ('Control'), along with the heating effect on net uptake (Δ). Units are g C m^{-2} d^{-1}. † $P < 0.10$, * $P < 0.05$ (two-sample t-test).

chamber leakage and of concentration-dependent uptake, the straight-line model substantially underestimates 'true' flux magnitudes (especially negative ones), but the degree of underestimation is highly variable. Thus, for the rest of the analyses in this paper, we use the flux estimates arrived at with the exponential model. Using this model helps compensate for any biases which would otherwise be introduced into the flux estimates by the curvature of the CO_2 concentration data.

CO_2 fluxes

Diurnal patterns. The general diurnal pattern is positive net CO_2 fluxes during the day due to photosynthetic uptake, and negative fluxes at night due to respiratory losses (Fig. 6a,b). Late in the season after many of the plant species have senesced, however, daytime fluxes are close to zero, since photosynthesis is much lower (Fig. 6c,d).

Mid-summer daily flux profiles were substantially and negatively affected by heating in the dry zone, but not in the moist zone; they typically exhibit a distinct dip in mid-day carbon uptake in the dry zone (both heated and control), but not in the moist zone (see Fig. 6a for an example of mid-summer dry zone fluxes, Fig. 6b for example of mid-summer moist zone fluxes). This mid-day depression in carbon uptake was characteristic of dry-zone daily flux profiles during the active growing season, and is similar to that observed in carbon fluxes in individual leaves photosynthesizing under conditions of drought stress.

Seasonal patterns. Daily average 1993 CO_2 uptake in both zones (Figs 7a and 8a) was greatest near the beginning of the measurement season, about four weeks after snowmelt was completed. With the onset of plant senescence in early August, fluxes decreased and crossed over to become consistently negative in both treatments and zones.

A similar seasonal pattern was observed in 1994, except for the expected negative values early in the season revealed by the measurements taken immediately following snowmelt (Fig. 9). Because it was the driest summer in recent decades, however, whole-system CO_2 uptake throughout 1994 was substantially depressed compared to 1993, and there was net carbon loss throughout the growing season in both zones.

Heating effects (dry-zone). The heating treatment consistently lowered carbon uptake in the dry zone throughout the 1993 measurement period (Fig. 7a), an effect that is almost entirely due to differences in daytime fluxes

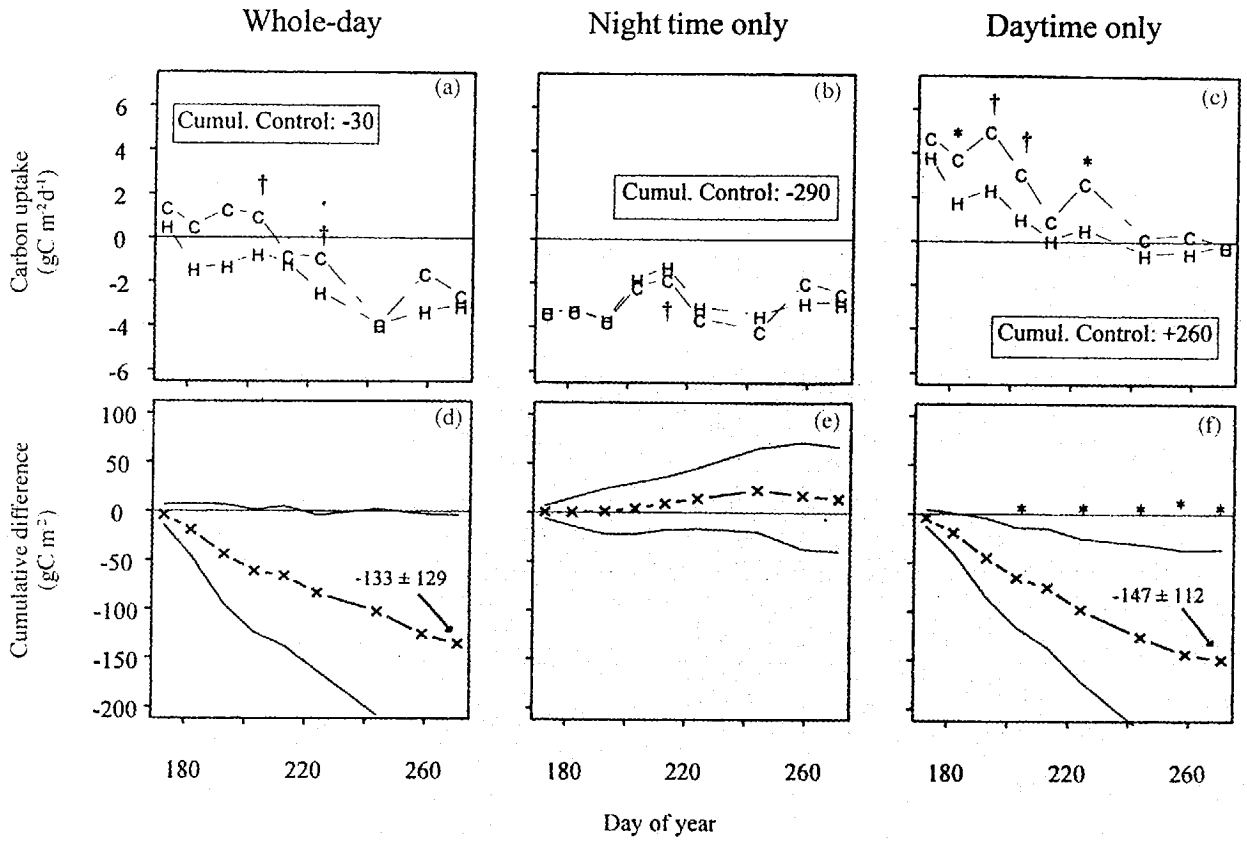

Fig. 7 1993 seasonal trends in net CO_2 fluxes (dry-zone). CO_2 uptake vs. day of year is shown in heated (H) and control (C) plots for (a) whole-day average, (b) night-time only, and (c) daytime only (night- and daytime flux averages were weighted by the fraction of the diurnal cycle which is night or day, so that their simple sum gives the whole-day flux average). Cumulative control plot carbon storage (in gC m^{-2}) over the whole season is indicated by text ('Cumul. control') in a, b, c. Corresponding cumulative differences in seasonal CO_2 uptake (heated minus control plot flux), along with 90% confidence intervals, are shown in graphs (d), (e), and (f). †$P < 0.10$ (not shown on graphs with 90% confidence intervals), * $P < 0.05$. P-values and confidence intervals are based on first averaging over all relevant measurements made on each individual plot within a given measurement day (graphs a–c), or on first integrating carbon flux on each plot to the relevant time (graphs d–f), and then using a two-sample t-test to test for differences between the resultant heated plot ($n = 5$) and control plot ($n = 5$) flux averages.

Note

Out of a potential total of 480 measurements per zone over the whole season, there were 10 bad or missing measurements in the dry zone, and 14 in the moist zone. To avoid the bias that might be introduced by taking simple averages on day with a missing value (e.g. a missing night-time measurement will give a daily average that is too high), the appropriate (i.e. day or night only) non-missing measurements on a given plot from such a day were proportionately weighted to compensate for the missing measurement.

(Fig. 7c). Twenty-four hour average CO_2 uptake was statistically significantly reduced on two of the nine measurement days (Fig. 7a); daytime fluxes (Fig. 7c) were more strongly affected, with uptake significantly reduced on four measurement days.

Perhaps more important than individual day effects from the point of view of the carbon-climate feedback problem, however, is the cumulative effect over the course of the whole season. It is the net effect over the course of the whole growing season (or, ideally, over the course of the whole annual cycle), that matters to atmospheric CO_2 concentration, and hence, to the question of whether there is a feedback to climate. In the case of this first year of carbon flux data from our site, the statistical significance of the integrated effects in the dry upper zone becomes greater as more and more measurements are lumped together, as illustrated in Fig. 7(d)–(f). These graphs show a heated-plot deficit in carbon uptake (Fig. 7d) that grows in magnitude over the course of the season, and reaches –133 gC m^{-2} ($P = 0.09$) by the end of the measurement period.

The effect of heating on carbon balance is due entirely to a reduction in daytime carbon uptake: no statistically detectable effect is observable on whole-season carbon accumulation at night (Fig. 7e), and the accumulated reduction in heated plot daytime uptake by the end of

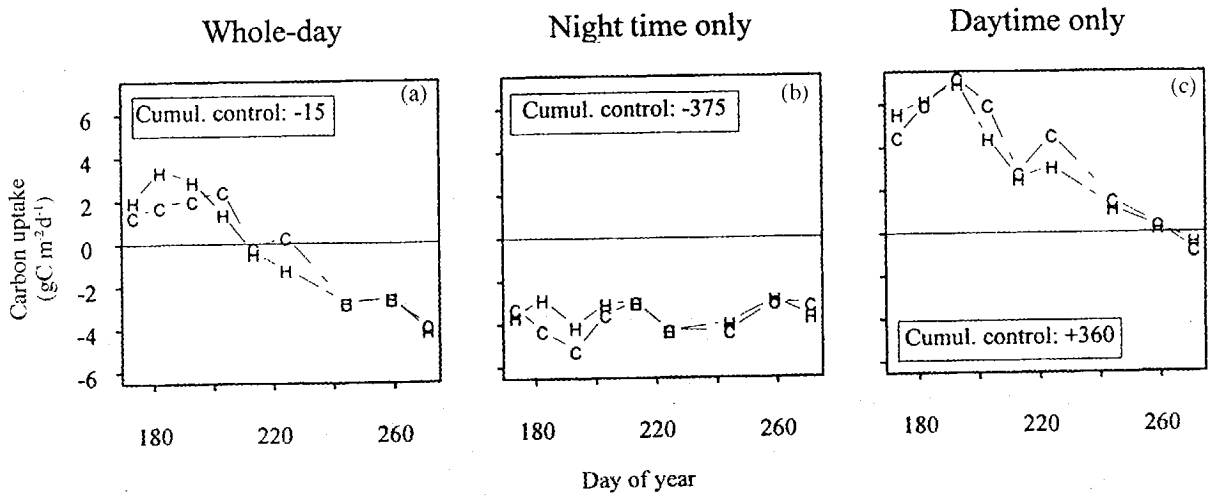

Fig. 8 1993 seasonal trend in net CO_2 fluxes (moist-zone). CO_2 uptake vs. julian day in heated (H) and control (C) plots for (a) whole-day average, (b) night-time only, and (c) daytime only. Cumulative control plot carbon storage (in gC m^{-2}) over the whole season is indicated by text ('Cumul. control'). There were no statistically significant heating effects.

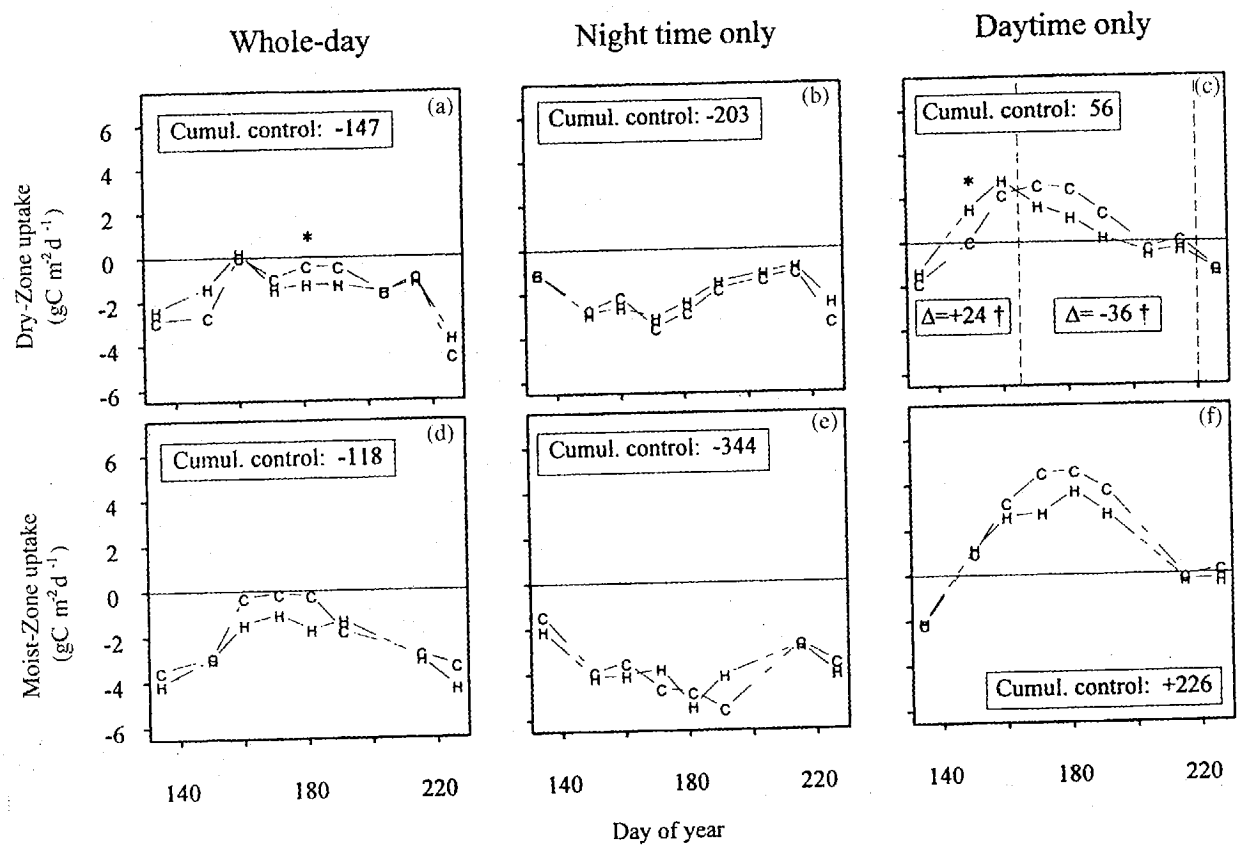

Fig. 9 1994 seasonal trend in net CO_2 fluxes in the upper dry zone (a, b, c), and in the lower moist zone (d, e, f). Cumulative control plot carbon storage (in gC m^{-2}) over the whole season is indicated by text ('Cumul. control'). Cumulative heater-induced differences in early season (days 135–160) and late-season (days 160–215) daytime uptake are shown in c. † $P < 0.10$, *$P < 0.05$ (two sample or paired t-test).

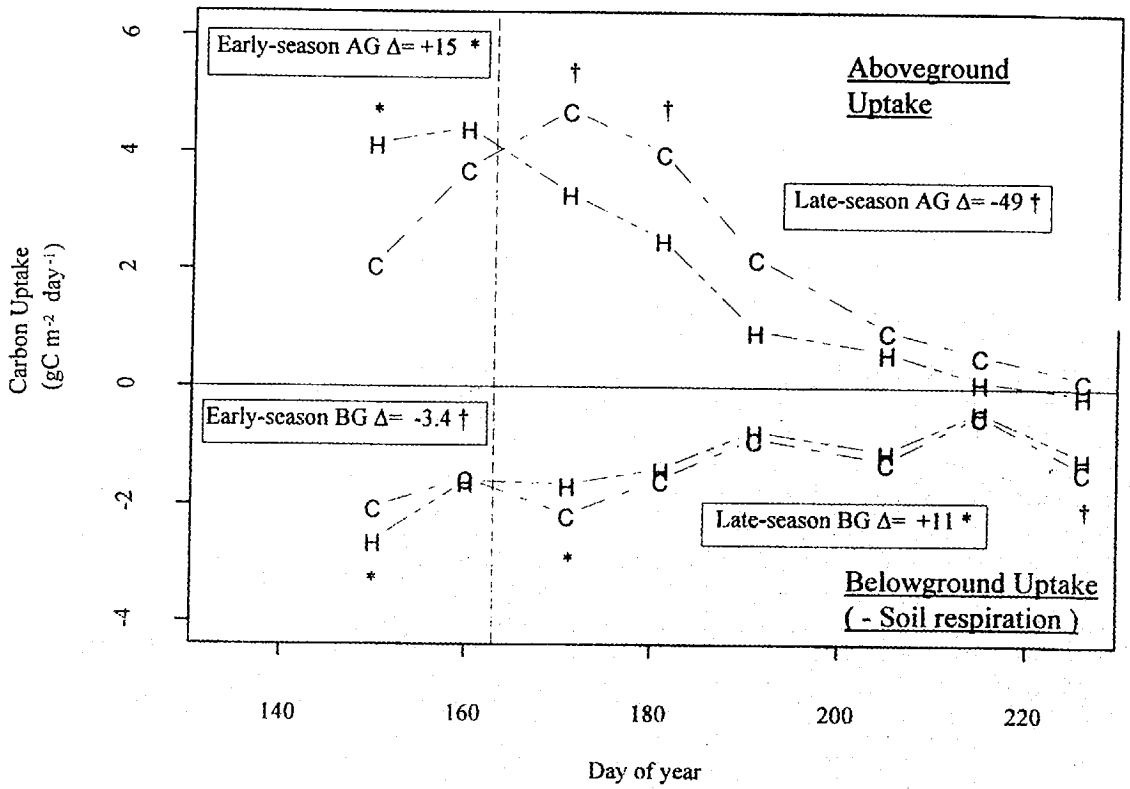

Fig. 10 1994 daytime CO_2 fluxes in the dry-zone (from Fig. 9c, excluding the first measurement on day 134, when no soil respiration measurements were taken), partitioned into above-ground (AG) and below-ground (BG) components. Separate early and late-season cumulative flux differences, Δ (in gC m^{-2}), are shown (separated at the cross-over date indicated by the vertical dotted line). † $P < 0.10$, *$P < 0.05$ (*t*-test).

the season (–147 gC m^{-2}, $P = 0.04$, see Fig. 7f) is larger and more statistically significant than the average whole-day deficit.

The 1994 whole-system CO_2 flux measurements (Fig. 9) began immediately following snowmelt and reveal early season treatment effects in the dry zone that were missed in 1993. As expected, the heater-induced head-start given plants by early snowmelt caused net uptake in heated plots to be greater for the first few weeks of the season in the dry zone (Fig. 9a–c). Approximately 20 days after snowmelt there was a cross-over and the treatment effect is reversed for the rest of the measurement period, as illustrated by the statistically significant cumulative treatment effects on daytime fluxes in opposite directions on either side of the 'cross-over' date (Fig. 9c and Fig. 10). This late-season daytime cumulative heating effect in 1994 (–36 gC m^{-2}, Fig. 9c) is only about 60% the same effect in 1993 (–60 gC m^{-2}, Fig. 7c) integrated over the equivalent time period (from 45 to 90 days after average date of snowmelt).

Because the positive effect of heating on carbon uptake early in the season reversed the negative effect for the rest of the measurement period, there was no statistically significant difference in 1994 cumulative whole-season uptake.

Soil Respiration. Soil respiration measurements in 1994 allowed us to investigate whether the differences that were observed in whole system fluxes were due to changes in above-ground or below-ground processes. The nighttime and whole-day respiration followed the same patterns (in terms of both seasonal trend and treatment effect) as those shown for daytime respiration (Fig. 10), though the nighttime respiration rates were smaller.

The cumulative whole-day soil respiration over the course of the season was –183 gC m^{-2}. The effect of heating was to reduce cumulative whole-season soil respiration by about 15 gC m^{-2} (not significant), an effect which can be split into an early season enhancement (+ 5 gC m^{-2} over days 150–160, $P < 0.05$, paired *t*-test) and a late season reduction (– 20 gC m^{-2} over days 170–226, $P < 0.05$, two-sample *t*-test).

The separate above-ground and below-ground components of daytime net ecosystem exchange are illustrated in Fig. 10 for the dry zone in 1994: soil respiration was elevated in heated plots during the 2 weeks following snowmelt (i.e. heated plots had more negative 'below-ground uptake', as shown in Fig. 10), then experienced a cross-over effect at about the same time as the whole-system fluxes and remained lower in heated plots for the rest of

the measurement period. Thus, the effect of heating on carbon balance was in opposite directions with respect to above and below-ground processes (correlation between above-ground and below-ground treatment effects shown in Fig. 10 on CO_2 uptake: $r = -0.9$, $P = 0.001$, $n = 8$ measurement days), but the above-ground effects were about 3.5 times larger than the below-ground ones (regression of above-ground treatment effect against below-ground effect: coefficient = −3.52, SE = 0.66).

Heating effects (moist zone). The seasonal pattern of CO_2 uptake in the moist lower zone, in contrast to the dry zone, exhibited no statistically detectable effects of heating in 1993 (Fig. 8), irrespective of whether fluxes are split into night- and daytime components (Fig. 8b–c), and irrespective of whether they are considered on individual measurement days separately or integrated over the course of the season (the cumulative heated minus control effect over the whole 1993 measurement period was only + 3 gC m^{-2}).

During the very dry 1994 growing season (Fig. 9d–f), however, measurements of heated-plot CO_2 uptake were consistently (7 out of 8 measurement days) lower throughout the measurement period, resulting in ≈100 gC m^{-2} less uptake in heated plots, although the *t*-test was unable to statistically resolve this apparent effect. The relatively high variance of the 1994 moist-zone CO_2 flux measurements prevents detection of even substantial heating effects; in this case, the effect would have had to reach 200 gC m^{-2} before being detectable at the 90% confidence level.

Inter-zone comparison. Moist zone CO_2 fluxes were usually greater in magnitude than fluxes in the dry zone (Fig. 8 vs. Fig. 7 and Fig. 9d–f vs. Fig. 9a–c): during most diel periods, control fluxes were more negative at night and more positive during the day. The 1993 individual-day zonal differences occasionally approach significance at the $P = 0.1$ level for the day- and night-time fluxes considered separately (data not shown). There was no detectable difference between the zones in integrated carbon accumulation in 1993, possibly because greater moist zone whole-season carbon accumulation during the daytime ($P = 0.12$) was offset by the greater moist-zone whole-season carbon losses at night ($P = 0.09$) (not shown).

Regression analysis

We constructed a series of regressions to model the effect of vegetation composition and physiologically important variables like light and soil microclimate on daytime dry-zone CO_2 uptake (when the clearest heating effects were observed in both 1993 and 1994). The most explanatory simple model was:

$$CO_2\ uptake = a_0 + a_1\,(day\ of\ year) + a_2\,PAR + a_3\,M_{soil} + a_4 M_{soil}^2 + \sum_{\substack{i\,=\,Forb,\\ Shrub,\,Gram}} b_i\,Biomass_i,$$

where 'CO_2 *uptake*' is the average of daytime uptake for each plot and measurement day in the dry zone, and the a_i are fitted regression coefficients on environmental factors (day of year, photosynthetically active radiation, and a quadratic in soil moisture), and the b_i are the regression coefficients on above-ground biomass of each of the three major plant growth forms in the experimental plots (forb, shrub, and graminoid, as measured by Harte & Shaw 1995).

The results of the model fits for dry-zone CO_2 fluxes in the 1993 and 1994 growing seasons are shown in Table 2. This model explains 65–75% of the variance in CO_2 fluxes, and confirms positive dependence of CO_2 uptake on PAR and standing above-ground biomass. The dependence of CO_2 uptake on soil moisture is quadratic, with an initially positive slope that rises to an optimum at moderately high moisture levels. Among the plant growth forms, the regression coefficients show that forb biomass contributes most strongly to CO_2 uptake, followed by graminoid biomass, followed by shrub biomass (Table 2).

Discussion

Our results suggest that heater-induced drought stress to plants brought about by a reduction in soil moisture is more important for understanding the treatment effect on carbon balance than is the direct warming effect on soil temperature. This 'drought stress hypothesis' posits that the effect of moisture in reducing plant photosynthetic inputs is larger than the temperature effect predicted to increase soil respiration outputs. It is supported by four lines of evidence.

First, the patterns of whole-system carbon uptake reported here are consistent with drought stress. The substantial reduction (≈100 g carbon m^{-2}) in net seasonal carbon uptake in heated relative to control plots in the dry zone in 1993 was due to a reduction in daytime carbon uptake, rather than to a change in night-time respiration. We observed no similar effect of heating on moist zone 1993 carbon fluxes, although moist zone fluxes in general were greater than dry zone fluxes. Further, as illustrated in Fig. 6, mid-day CO_2 uptake was usually suppressed relative to morning or late-afternoon in the dry zone, an indicator of plant drought stress that was less frequently observed in the moist zone. In the dry 1994 growing season, carbon uptake was substantially reduced throughout the growing season in both heated and control plots compared to the wetter 1993 season, and the late-season treatment effect was also much less than for the comparable time period in 1993. Where water is less limiting to plants (e.g.

Table 2 Linear regression models of average daytime CO_2 uptake (dry zone)

Variable	1993			1994		
	Coefficient	SE	P-value	Coefficient	SE	*P*-value
(Intercept)	2.39	3.87	NS	− 7.81	3.22	*
day of year	− 0.090	0.012	***	− 0.089	0.012	***
PAR	0.003	0.001	**	0.002	0.001	*
moisture (g H_2O/100 g soil)	**0.608**	0.132	***	**0.234**	0.122	†
moisture^2	**− 0.011**	0.003	**	**− 0.007**	0.003	*
GRAM (g biomass m^{-2})	0.040	0.011	**	0.023	0.008	*
FORB	**0.061**	0.009	***	**0.047**	0.007	***
SHRUB	**0.025**	0.004	***	**0.022**	0.006	**
Model Statistics:	R^2 = 0.74			R^2 = 0.65		
	RSE = 2.3 (82 d.f.)			RSE = 2.1 (82 d.f.)		

Variables in **bold** are significantly affected by heating, and, taken together, account for the treatment effect on CO_2 fluxes (i.e. the addition of these variables in the model eliminates the significance that treatment as a categorical variable would otherwise have).
†$P < 0.10$, * $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$

the moist zone), the small amount of heater-induced drying did not significantly affect carbon uptake in 1993, but in the drought summer of 1994, the effect of heating on soil water content in the moist zone was larger, and average carbon uptake appeared to be substantially lower in heated plots (though it was not statistically significant).

Second, the observed reductions in carbon uptake cannot be due to increases in soil respiration, since in 1994, soil respiration effects on carbon balance were in the opposite direction from whole-system effects. Indeed, soil respiration was actually *reduced* by the heating treatment during most of the growing season, suggesting either that the concurrent reduction in above-ground plant activity was also manifested in reduced root respiration, or that soil drying hindered microbial respiration more than soil warming enhanced it. Either way, the implication is that plant responses to heating dominated soil microbial responses.

Third, heater-induced drying caused lower leaf water potentials in plant species in the heated plots of the dry zone in 1994 (Loik & Harte 1997), potentially altering the competitive balance among plant species of varying tolerance to drought stress. Harte & Shaw (1995) observed a shift in species composition, reporting 30–40 g m^{-2} decreases in the above-ground biomass of drought-intolerant forbs in dry zone heated plots in 1993 and 1994, accompanied by comparable increases in the above-ground biomass of a drought-tolerant shrub, *Artemisia tridentata*.

Finally, our regression analysis (Table 2) quantifies the relation between the shifts in species composition observed by Harte & Shaw (1995) and the changes in carbon uptake reported here. This analysis shows an association that suggests a causal link: shifts from more productive forbs to less productive shrubs should result in significantly reduced CO_2 uptake. Specifically, for each gram of AGB shifted from forb plants to shrub, it predicts that uptake would be reduced by the difference in the relevant coefficients in Table 2 (i.e. 0.061–0.025 = 0.036 gC m^{-2} d^{-1} less uptake in 1993, and 0.047–0.022 = 0.025 gC m^{-2} d^{-1} less uptake in 1994). These differences are large enough for the shift in species composition alone to account for a substantial amount of observed differences in carbon uptake: the ≈40 g m^{-2} shift observed in 1993, for example, if sustained for 2 months of the growing season, accounts for 86 gC m^{-2} less uptake in heated plots, a substantial fraction of the actually observed reduction of 147 gC m^{-2} (Fig. 7f).

The dependence of CO_2 uptake on a negative parabola in soil moisture with an initially rising slope (Table 2) suggests that at low to moderate levels of soil moisture, net plant assimilation is water-limited, and hence, that in addition to the species composition effect, there is also a direct physiological response that decreases carbon uptake with decreased soil moisture.

Another explanation for the differences in carbon uptake should be considered, however. The earlier snowmelt in the heated plots may change the timing, but not the integrated annual budget, of CO_2 fluxes. A phase shift alone could cause an apparent but artifactual change in integrated carbon uptake if fluxes from only part of the annual cycle are considered. Our dataset cannot conclusively resolve this question, since fluxes for the whole year were not measured. Although there was an effect of snowmelt on the timing of carbon fluxes, as observed in 1994, two lines of evidence suggest that this is not the only effect of heating.

First, although heating caused photosynthetic uptake to start earlier in the spring, it also caused the snow-free period to last longer, and there is no reason to expect a compensating cutoff in late-season respiratory losses in

heated plots. The period of time from the end of the growing season to snowfall, when the ecosystem is a net source of carbon to the atmosphere, could last longer in heated plots.

Second, the time-series of flux data suggest that a phase shift alone cannot explain the difference in carbon uptake, at least in 1993. To compare carbon fluxes between treatments at the same period of the growing season, i.e. the same time since snowmelt, we compared each day of heated plot measurements to control plot measurements taken 10 days later, since heating advanced snowmelt by ≈10 days. With heated plots shifted back into phase with controls, they still exhibited about the same magnitude of carbon loss in 1993 (although the statistical significance is reduced: $P = 0.16$ for average whole-day losses as opposed to $P = 0.09$, and $P = 0.06$ for daytime losses as opposed to $P = 0.04$); in 1994, by contrast, the phase shift did remove the early and late-season heating effects shown in Fig. 9(c) and Fig. 10. We conclude from this that in 1994, the principal effect of heating was a forward shift in the timing of heated plot uptake, while in 1993, the effect was *both* a forward shift in timing and an absolute reduction in late season uptake.

However, the anomalously dry 1994 conditions suppressed carbon uptake in all plots. Thus the magnitude of plant response to the further stress of heating was likely limited in 1994 compared to what it might be in an average rainfall year, and we should expect that heating would therefore cause less of a reduction in late season uptake than in an average year. The enhancement of early season CO_2 uptake (before the carbon flux 'crossover'), by contrast, is unlikely to have been similarly affected by the 1994 drought, since soil moisture during the few weeks after snowmelt is controlled more by the amount of meltwater than by rainfall (the majority of which falls in late July and August). Thus, one would expect that in an average year, the late-season heating-induced reduction in CO_2 uptake would be large compared to the early season enhancement caused by earlier snowmelt. For example, if early season fluxes in 1993 were similar to the early season in 1994, the net effect of heating on the 1993 growing season carbon budget for daytime fluxes would be: +24 gC m^{-2} (precrossover, based on Fig. 9c) −147 gC m^{-2} (post-crossover, based on Fig. 7f) = −123 gC m^{-2}.

Conclusions

Experimental warming of this montane ecosystem substantially affected both the timing and magnitude of carbon fluxes. On balance, the direction of these effects was to reduce overall ecosystem carbon storage. The main mechanism behind these effects was the influence of water limitation in reducing net plant carbon assimilation, and not a temperature-driven increase in carbon outputs through soil respiration.

The results of this transient experiment are consistent with the hypothesis that there may be positive feedback generated by ecosystems and climatic change. Without flux measurements for the entire annual cycle we cannot construct a definitive carbon budget, but the mechanisms elucidated here, including moisture stress and associated shifts in species composition, suggest that carbon transfer to the atmosphere is likely, at least in the short term. The long-term effects of the processes observed here could be quite different, however, since a shift in species composition would alter the quality of litter inputs to the soil. For example, if litter from the drought-tolerant shrubs decomposes more slowly than that of the drought-intolerant forbs they replace, the stock of soil carbon would increase, ameliorating or possibly reversing the effect of reduced plant productivity. In addition, the overall response of ecosystems to climatic change will depend on many other environmental factors as well. For example, changes in precipitation regime could swamp the comparatively small changes in soil moisture that were induced by our heaters, and increases in atmospheric CO_2 should increase plant water-use efficiency (Rawson 1992; Korner & Bazzaz 1996), possibly ameliorating the drought stress-induced changes that we report here. Nevertheless, this study highlights ecological processes that may be important in controlling how ecosystem carbon balance is affected by climatic change, and in particular the sensitivity of ecosystems to soil moisture conditions.

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