Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming

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[1] We integrated two methods, experimental heating and observations across natural climate gradients, to elucidate both short- and long-term climatic controls on ecosystem carbon storage and to investigate carbon-cycle feedbacks to climate in montane meadows. A 10-year heating experiment warmed and dried heated plot soils and substantially decreased (by $\sim 200 \pm 150$ g C m^{-2}) the amount of carbon stored in soil organic matter, a positive feedback to warming. In situ CO_2 flux measurements, laboratory soil incubations, and a heating-induced shift in vegetation community composition from high- to low-productivity species indicate that a decline in community productivity and resultant decrease in soil inputs from plant litter caused most of the soil carbon decrease. An alternative widely hypothesized mechanism for soil carbon decrease under warming is stimulation of soil respiration, but we observed no increase in seasonally integrated soil respiration in our experiment (soil drying inhibited microbial decomposition even as soil warming stimulated it). To extend our analysis from the short-term transient response represented by the heating experiment to the presumed long-term approximate steady state represented by natural climate gradients, we tested a hypothesized relation between vegetation community composition (which controls both litter input rate and average litter quality) and soil carbon along the climate gradient. The gradient analysis implies that the experimentally induced decline in soil carbon is transient and will eventually reverse as lower quality litter inputs from the increasingly dominant low-productivity species reduce soil respiration losses. This work shows that ecological processes can control both short- and long-term responses to climate change, confirming some model-based predictions about the importance of vegetation shifts, but challenging the widely held hypothesis that the effect of temperature change on respiration will dominate soil carbon changes.   *INDEX TERMS:* 1610 Global Change: Atmosphere (0315, 0325); 1620 Global Change: Climate dynamics (3309); 1615 Global Change: Biogeochemical processes (4805); 1866 Hydrology: Soil moisture; 1851 Hydrology: Plant ecology

1. Introduction

[2] Climate change can alter the terrestrial ecosystem carbon balance of plants and soil, resulting in feedback that could either enhance or retard the anthropogenic buildup of atmospheric CO_2 [*Lashof et al.*, 1997; *Melillo et al.*, 1996]. Such feedback is especially likely in montane and high-latitude ecosystems where soils are carbon rich [*Schlesinger*,

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1997; *Whittaker*, 1975], vegetation is sensitive to climatic variables such as snowmelt date and length of growing season [*Goulden et al.*, 1998; *Harte and Shaw*, 1995; *Körner*, 1992; *Price and Waser*, 1998], and climate change is expected to be large due to snow cover feedback [*Groisman et al.*, 1994].

[3] A dominant paradigm for the response of the soil carbon component of terrestrial ecosystems, based on a combination of observation [*Raich and Schlesinger*, 1992; *Peterjohn et al.*, 1994; *Trumbore et al.*, 1996] and modeling [*Jenkinson et al.*, 1991; *Townsend et al.*, 1992; *Schimel et al.*, 1994; *Kirschbaum*, 1995; *Parton et al.*, 1995; *Cao and Woodward*, 1998] studies, has been that climate change will increase soil temperature, hence will increase organic matter decomposition rates, and will therefore lead to soil carbon loss (but see *Luo et al.* [2001] for an alternative view). However, as most of these studies acknowledge, and as Hans Jenny implied long ago [*Jenny*, 1941], the actual response of soils depends on many factors in addition to temperature-mediated loss rates, in particular, on the plant communities that provide the carbon inputs to soils.

[4] Whole-ecosystem carbon feedbacks to climate are thus less well understood, especially when it comes to predicting the net biogeochemical implications of how ecological interactions can mediate plant community responses to climate change. For example, ecological interactions can cause climate change to induce shifts in species composition, which can result in long-term whole-ecosystem responses that are markedly different from short-term transient responses [*Chapin et al.*, 1995; *McKane et al.*, 1997; *Shaver et al.*, 2001; *Smith and Shugart*, 1993]. With a few recent exceptions [e.g., *Foley et al.*, 1998; *Moorcroft et al.*, 2001], most large-scale regional or global modeling studies of ecosystem–climate interactions [*Potter et al.*, 1993; *Cao and Woodward*, 1998] do not include such ecological interactions in their simulations, though a growing number of field experiments [*Chapin et al.*, 1995; *Bazzaz et al.*, 1995; *Verville et al.*, 1998] and conceptual or small-scale models [*Herbert et al.*, 1999] show that the combined net effect of shifts in competitive balance between species in response to environmental changes can substantially modify or reverse the effects expected with static vegetation composition.

[5] In sum, understanding carbon-cycle feedbacks to climate in terrestrial ecosystems requires a better understanding of climate–ecology interactions in a wider range of ecosystems. Field studies in this area typically rely on either experimental climate manipulations [*Luo et al.*, 2001; *Weltzin et al.*, 2000; *Saleska et al.*, 1999; *Hobbie and Chapin*, 1998; *Peterjohn et al.*, 1994] or natural climate gradients [*Austin*, 2002; *Schuur et al.*, 2001; *Trumbore et al.*, 1996; *Townsend et al.*, 1995; *Tate*, 1992] to investigate effects of climate change, but whole-ecosystem studies that combine these methods to distinguish transient and long-term feedback responses and that include biogeochemical effects of species composition shifts are lacking.

[6] To investigate the role of these effects on ecosystem carbon responses to climate change in montane meadow ecosystems of the Colorado Rocky Mountains, we integrated (1) results from a whole-system warming manipu-

lation (which elucidate short- to medium-term responses), with (2) analysis of ambient ecological trends along a natural climate gradient (which elucidates long-term climate–ecosystem equilibria) and (3) combined these into a simple conceptual model of how vegetation community composition and climate control soil carbon balance across a range of timescales.

2. Site Description and Experimental Design

[7] The study sites are ungrazed montane meadows near the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado (38°57′N, 106°59′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: mixed conifer forest consisting of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies bifolia*), quaking aspen forest (*Populus tremuloides*), and open meadow. RMBL is in the southern Rockies, at the boundary between high-elevation montane meadow and lower elevation Great Basin Sagebrush desert scrub. Annual precipitation averages ~750 mm, with over 80% falling as snow.

[8] The study sites support a diverse assemblage of angiosperm species, with ~100 species in the study plots, ~90% of which are perennial. The relatively high biodiversity of the study sites is a result of both their location on the boundary between life zones and the steep glaciated topography (which causes dramatic physical and vegetational changes on small spatial scales). The study sites are dominated by long-lived herbaceous perennials and a few woody species. Most plant biomass is associated with a few species, including the woody shrubs *Artemisia tridentata spp. vaseyana* (sagebrush) and *Pentaphylloides floribunda*, herbaceous forbs *Erigeron speciosus* (fleabane), *Helianthella quinquenervis* (sunflower), *Dephinium nuttallianum* (larkspur), *Potentilla gracilus*, and graminoids *Festuca thurberi* (fescue) and *Poa spp.* (bluegrass) [*Harte and Shaw*, 1995; *De Valpine and Harte*, 2001]. The study site soils are well-drained Cryoborolls formed on deep, rocky, noncalcareous, glacial till and, aside from a surface layer of litter, lack developed soil horizons above 50 cm.

2.1. Warming Experiment

[9] In 1991, at the first of four study sites (elevation: 2920 m), we initiated a warming treatment in a meadow (the "warming meadow") to investigate short-term ecosystem responses to climate change (Figure 1) [*Harte et al.*, 1995]. At the onset of heating (January 1991), two electric radiant heaters per treatment plot were suspended 2.6 m above the ground to subject five of ten 3×10 m experimental plots to 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 ~12 W m^{-2} because of feedback enhancement (e.g., by water vapor) of the initial forcing [*Ramanathan et al.*,
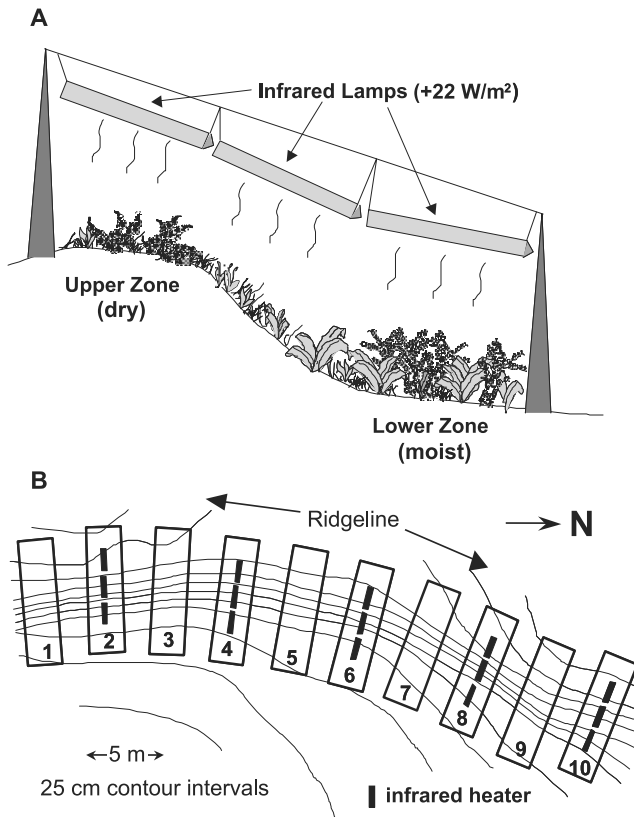
Figure 1. Design of warming meadow experiment. (a) Heated plot profile. (b) Arrangement of heated and control plots.

1987]. 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 $2 \times CO_2$ atmosphere [Harte et al., 1995; Saleska et al., 1999].

[10] Two zones comprise each plot: an upper "dry zone" along a semi-arid ridgeline and a lower "moist zone" near a wet swale (Figure 1). We confine this analysis to the dry zone, which is more typical of montane meadow habitat generally.

[11] We log soil temperature and moisture data every 2 hours, year round, at 5, 12, and 25 cm depths. The heating treatment has negligible effect on air temperature and humidity above the plots, but it dries and warms the soil and advances snowmelt considerably (Table 1).

2.2. Elevational Gradient Experiment

[12] To investigate the long-term dependence of carbon cycling on climate, we established 10 plots in 1996 at each of three additional sites along an elevational transect (2710 m, 2920 m, and 3170 m) that brackets the warming meadow (2920 m) (Figure 2). The elevational sites are typical of warming-meadow habitat (including similar slope) and span a climatic gradient comparable (in terms of differences in snowmelt date and soil temperature) to that induced by the experimental effect of heating (Table 1) [Dunne et al.,

2002]. Beginning in 1996 a climate manipulation (snow removal) was also begun on randomly selected plots at each of the elevational sites [Dunne et al., 2002]. We confine the analysis of this paper to baseline measurements obtained prior to onset of microclimate treatment effects on soil carbon.

3. Methods and Materials

3.1. Carbon Stocks (Warming Meadow and Elevation Sites)

[13] In order to characterize the effect of heating on carbon storage, we measured the stocks of carbon in aboveground vegetation, aboveground litter, soil organic matter, and fine roots.

3.1.1. Aboveground Carbon Stocks: Vegetation and Litter

[14] Plants were divided into three growth forms: forbs, shrubs, and graminoids. Aboveground biomass (AGB, in g C m^{-2}) was estimated for each growth form separately from frequent (once per ~10 days) areal coverage measurements in 75×75 cm quadrats in each plot using methods described by Harte and Shaw [1995] and calibrated at each site separately [Dunne, 2000].

[15] Aboveground litter stocks were measured by harvesting senesced litter from 0.25 m^2 warming-meadow quadrats in June 1995 and 1996, oven dried, weighed, and returned

Table 1. Site Microclimate Characteristics

	Warming Meadow (2920 m)		Elevational Gradient		
	Control	Heated	Lower (2710 m)	Middle (2920 m)	Upper (3170 m)
Soil Temperature, Annual Mean °C[a]					
1994	5.6	6.5			
1995	4.4	5.3			
1996	4.7	5.2			
1997	5.4	6.4	6.6	5.5	5.2
Soil Moisture (Growing Season Mean g H$_2$O/g Dry Soil), %[a]					
1994	17.3	15.7			
1995	24.1	21.4			
1996	19.5	18.4			
1997	20.5	20.4	22.0	21.5	23.7
Date of Snowmelt, Julian Day[b]					
1994	133	122			
1995	160	139			
1996	135	125	124	135	135
1997	141	117	120	140	138
June–August Precipitation, cm[c]					
1994		2.9			
1995		7.1			
1996		6.3			
1997		9.0 (6.8[d])	9.5[d]	12.0[d]	10.7[d]

[a] Average of measurements taken every 2 hours over two depths (12 and 25 cm), day and night, over whole year (temperature) or over period from end of snowmelt to end of August (soil moisture). Warming meadow heaters have negligible effect on air temperature above plots.

[b] Date on which 12-cm soil temperature reaches 1°C.

[c] Averages ~75 cm, over 80% as snow.
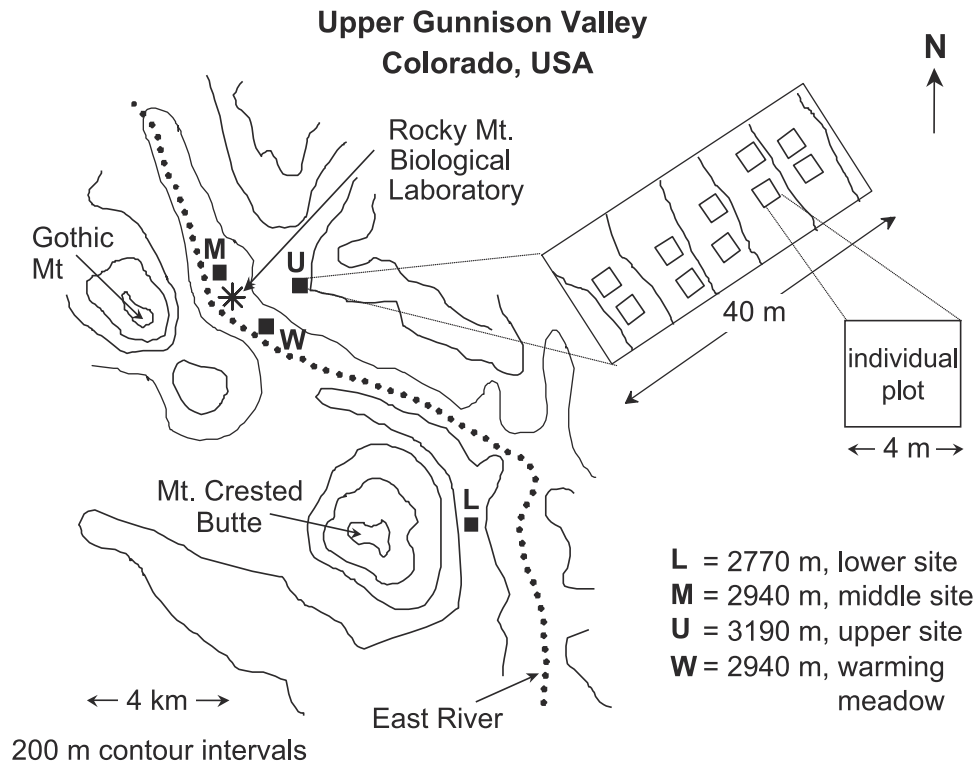
[d] July–August precipitation only.

Figure 2. Map of locations of three elevational sites and warming meadow. Inset shows detail of upper site.

to plots. A similar harvest was done on the elevational transect in June 1997, from quadrats (12 random locations per plot, total $N = 360$) on which AGB and soil organic matter measurements (see section 3.1.2) were also made. These litter harvests undercount graminoid litter, a substantial fraction of which remains as standing blades long after senescence.

3.1.2. Belowground Carbon Stocks: Soil and Roots

[16] We measured soil organic matter as percent carbon by weight of dry soil and then used soil density measurements to extrapolate to carbon on a per unit area basis.

3.1.2.1. Percent Carbon

[17] Soil organic carbon (SOC) and fine roots were sampled with a stainless steel soil corer (30 cm long, 1.7 cm in diameter). We cleared away obvious surface litter and took soil samples from the same location as AGB measurements (soil cores were either inside of or within ~20 cm of the AGB sampling quadrat). Rocks in the soil made it difficult to obtain samples of consistent depth, so we allowed core depths to vary from sample to sample (typically 8–15 cm) so long as the core was at least 8 cm. As expected, SOC content declined with depth, but there was no difference in core depth between treatments. Coarse roots (>2 mm) were obtained by passing soil cores through a sieve. Fine roots (<2 mm) were hand picked from the remaining soil. Root carbon was estimated as 50% of mass loss on combustion (LOC) at 430°C. SOC was also estimated by LOC at 430°C of the 2-mm soil fraction. LOC results for SOC were tightly correlated with total C determined by combustion/gas chromatography (Europa Scien-

tific): %C (gas chromatography) = 0.535 (±0.015, 95% confidence) × (% mass lost), $r^2 = 0.94$, ($N = 40$ samples). Warming meadow soil cores were taken every summer from 1991 through 1999. Except for 1991–1993, the standard sampling intensity of warming meadow soil was four cores per plot ($N = 20$ per treatment) and twice per growing season (in mid-June and mid-August). (In 1991–1993, sampling intensity was one core per plot, $N = 5$ per treatment.) Transect meadow soil cores (four per plot) were taken in June and August every summer from 1997 to 1999.

[18] We examined the correlation between SOC samples from the June 1999 warming meadow coring as a function of distance from one another in a spatial statistical analysis using a semi-variogram plot [*Cressie,* 1993, p. 69]. This analysis showed that although variation among very near cores (~10cm) is reduced due to spatial autocorrelation, variation among within-plot soil cores that are the standard sampling distance apart (~1 m) is no less than variation across warming meadow plots (5–40 m apart). This analysis indicates that within-plot cores (≥1 m apart) can be treated as independent samples without risk of pseudoreplication.We therefore tested for the effects of heating on warming meadow soil organic matter (SOM) using a standard two-sample t test (N equals 4 cores per plot times 5 plots per treatment, or 20 per treatment).

3.1.2.2. Soil Density and Areal Carbon Content

[19] Site specific bulk density of <2-mm soil was measured at the sites by drying and weighing all soil and rock material excavated from volumes of 1–7 L and 10–15 cm depth at random locations between plots. Overall site-specific soil
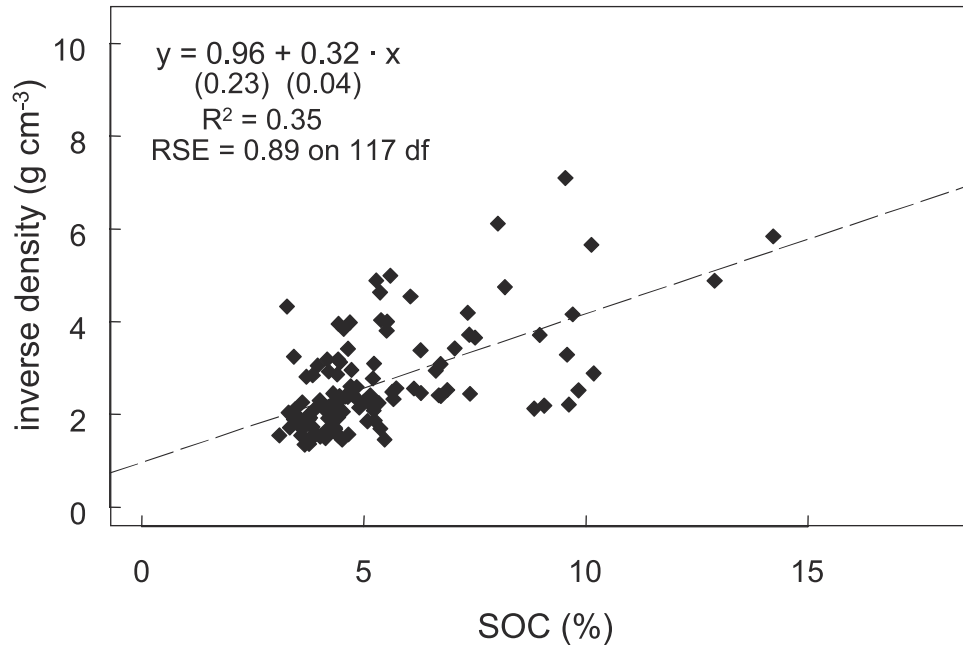
Figure 3. Inverse soil density, in grams soil (<2-mm soil) cm^{-3} versus soil %C (in <2-mm fraction, warming meadow soils, summer 2000), including regression line and statistics (values in parentheses are standard errors on corresponding regression coefficients).

densities, D_{site} (in g cm^{-3}) of <2-mm soil in the top 10 cm were calculated from bulk density (<2-mm soil) $\times (1 - f_{\text{rock}})$, where f_{rock} is the fraction of the ground surface area occupied by large rocks. Values of soil density were 0.459 for the warming meadow and 0.672, 0.509, and 0.451 for the lower, middle, and upper elevational sites, respectively.

[20] Areal SOC (g C m^{-2} in the top 10 cm) was derived by combining the %SOC core data both with the site-specific mean soil densities and with estimates of relative density of individual cores. We included relative core density because in our high-organic and highly heterogeneous soils, individual core densities are significantly anti-correlated with individual core %SOC (Figure 3). Thus an appropriate estimate for areal SOC (C_{ai}, g C m^{-2} in the top 10 cm) in the ith core is

$$C_{\text{a}i} = (C)_i \, (D_{site}/\overline{d_{site}}) \, d_i \times 10\,\text{cm} \times 10,000\,\text{cm}^2\,\text{m}^{-2}, \quad (1)$$

where C_i is carbon fraction by weight (g C per g soil) in the ith core, d_i is the density of <2-mm soil in the ith core, and $\overline{(d_{site})}$ is the mean core density across all cores at the site. A site-specific density correction factor, $D_{site}/\overline{(d_{site})}$, is also included because individual cores are a biased estimator of site-wide density because of the presence of many stones and rocks too large to be sampled by soil cores.

[21] In some years (1997–1999), SOC was measured only on core subsamples and hence we have no direct density information on those cores. In this case, plot-averaged areal soil carbon to 10 cm depth for an individual core was estimated as

$$C_{\text{a}i} = C_i \left(D_{site}/\overline{d(C_{site})} \right) \times d(C_i) \times 10\,\text{cm} \times 10,000\,\text{cm}^2\,\text{m}^{-2}, \quad (2)$$

where the function $d(C_i)$ as an indirect estimate of the density of the ith core and $\overline{(d(C)_{site})}$ is the mean across

all core density estimates at the site. Here, $d(C)$ is a site-specific function of the form $d(C) = 1/(a + b \cdot (C))$, where a and b are derived from regressions with data when individual core densities were measured (Figure 3, from the warming meadow site in 2000, is representative of the relationship seen at all sites). As in equation (1), $D_{site}/\overline{(d(C)_{site})}$ is a site-specific density correction factor to force the average density across all cores at a site to equal the best estimate of density for that site.

[22] We note in passing that the functional form for $d(C)$ is motivated by conceptualizing soil as a two-component mixture of organic and mineral components: $V_{\text{core}} = M_c \, \delta_c^{-1} + M_{\text{min}} \, \delta_{\text{min}}^{-1}$ where M_c is the mass of the organic carbon component and M_{min} is the mass of the mineral component, each having its own characteristic density δ_x and collectively occupying core volume V_{core}. Dividing this equation through by M_{tot}, the total mass of the core, gives

$$\delta_{\text{tot}}^{-1} = f_c\delta_c^{-1} + f_{\text{min}}\delta_{\text{min}}^{-1} = f_c\delta_c^{-1} + (1 - f_c)\delta_{\text{min}}^{-1}$$
$$= \delta_{\text{min}}^{-1} + (\delta_c^{-1} - \delta_{\text{min}}^{-1})f_c, \quad (3)$$

where f are the mass fraction of each component. The far right-hand side of equation (3) is identical to the form used for $d(C)$ if we let $a = \delta_{\text{min}}^{-1}$ and $b = (\delta_c^{-1} - \delta_{\text{min}}^{-1})/100$. Warming meadow soil data (Figure 3) show that inverse density is in fact significantly linearly related to %C as predicted by equation (3), although the unexplained variation suggests that soil is probably not as simple as a two-component model.

3.2. Soil Fractionation Experiment (Warming Meadow)

[23] In order to test the plausibility of observed patterns in bulk SOC response to heating, we used a physical–chem-

ical separation technique followed by ^{14}C analysis [*Trumbore et al.*, 1996; *Trumbore and Zheng*, 1996] to separate soils from the warming meadow into fractions with different turnover times.

[24] The method isolates a low-density fraction, LF (primarily relatively undecomposed or partially decomposed vascular plant material of recent origin), then uses hydrolysis by acids and bases to separate the high-density fraction (HF) into a nonhydrolyzable residue, Res (typically older mineral-associated organic matter adsorbed onto clay particles), and a hydrolyzable component (Hyd) of intermediate age. Measurement of ^{14}C in such fractions shows separation of SOM carbon by age class with some consistency across soil types [*Trumbore and Zheng*, 1996], though because the method is not universally successful (e.g., *Townsend et al.* [1995] were not able to distinguish different age fractions in allophanic soils at Hawaiian sites), ^{14}C measurements are critical in confirming the success or failure of the technique.

3.2.1. Soil Fractionation Experiment: Sampling and Laboratory Analysis

[25] On 12 and 13 June 1997 (near the time of the regular June bulk soil sampling), multiple soil cores (4–8 cores of ∼1.75 cm diameter) were taken from each plot in the warming meadow following the same methods employed in the regular soil sampling (section 3.1.2), except samples were bulked by plot for two depths separately (0–10 and 10–20 cm). Samples were oven dried for 24 hours and passed through a 2-mm sieve, and tweezers were used to separate obvious roots and root fragments.

[26] Density separation into LF and HF was achieved using sodium polytungstate solution (adjusted to a density of 2 g mL^{-1}). A portion of the HF was then treated by washing in acid (0.5 M HCl), then base (0.1 M NaOH + 0.1 M Na$_4$ P$_2$O$_7$), and, finally, weak acid (0.05 M HCl), leaving a nonhydrolyzable residue (Res). This fractionation method is very similar to the method used by *Trumbore et al.* [1996], with the exception that we excluded a final washing in very strong acid (6 M HCl). The methodological study of *Trumbore and Zheng* [1996] showed that the addition of a strong acid washing step following the base washing step made little difference in the degree of ^{14}C separation in the soils they studied.

3.2.2. Soil Fractionation Experiment: Elemental and Isotopic Measurements

[27] The three soil fraction samples (LF, HF, Res) from each plot's 0- to 10-cm interval were sent to University of Arizona's Accelerator Mass Spectrometer (AMS) lab, which combusted samples to CO$_2$ and then reduced the CO$_2$ to a graphite target whose ^{14}C content was measured by accelerator mass spectrometry [*Vogel*, 1992]. Bulk samples from the 10- to 20-cm interval were also sent to the AMS lab. The AMS measured ^{14}C; ^{13}C and %C are also determined separately at the University of Arizona AMS facility. Splits of the samples sent to the AMS lab were also run on University of California Berkeley's Europa 20/20 continuous flow mass spectrometer, along with additional samples of the bulk soil from which the fractions were taken. This gave independent measurements of %C, ^{13}C, %N, and [15]N.

[28] Carbon isotope (^{13}C and ^{14}C) content of the measured samples is reported as $\delta^{13}C$ and $\Delta^{14}C$ values, where

$\delta^{13}C$ is the fractional deviation of the isotopic ratio of the sample ($^{13}R_{sample} = {}^{13}C_{sample}/{}^{12}C_{sample}$) from the same ratio in the international standard Peedee belemnite (PDB) carbonate [*Craig*, 1957]: $\delta^{13}C = ({}^{13}R_{sample}/{}^{13}R_{standard} - 1)$, reported in parts per thousand (per mil, ‰). $\Delta^{14}C$ is derived from $\delta^{14}C$ (defined analogously to $\delta^{13}C$, with NBS oxalic acid as the standard) by correcting to constant ^{13}C content ($\delta^{13}C = -25‰$) to account for the isotopic fractionation due to photosynthesis [*Stuiver and Pollach*, 1977]: $\Delta^{14}C = \delta^{14}C - 2(\delta^{13}C + 25)\left(1 + \frac{\delta^{14}C}{1000}\right)$.

[29] Turnover times in each soil fraction were estimated from the $\Delta^{14}C$ according to the method of *Trumbore et al.* [1996], which assumes that each fraction is a homogeneous, single pool in steady state for carbon 12 and that each year's inputs have the same ^{14}C content as that year's Northern Hemisphere atmospheric CO$_2$ (adjusted for photosynthetic fractionation). The Northern Hemisphere atmospheric $\Delta^{14}C$ data used as inputs to this simple model were from *Burcholadze et al.* [1989], as updated by Susan Trumbore (personal communication, 1998).

3.3. Field CO$_2$ Fluxes and Relative Vegetation Productivity (Warming Meadow)

[30] In order to characterize the effects of heating on carbon fluxes, we measured whole-system and soil respiration fluxes of CO$_2$ in the warming meadow. A large (75 × 75 × 42 cm) clear chamber, together with a Li-Cor 6200 portable infrared gas analyzer system, was used to measure whole-system (plants plus soil) CO$_2$ fluxes on each warming meadow plot 5–6 times per measurement day, approximately once every 10 days throughout the 1993 and 1994 growing seasons and less frequently in 1995 (see *Saleska et al.* [1999] for details on methods). Soil respiration (microbial decomposition plus plant roots) was measured separately in 1994 and 1995 on the same days as whole-system fluxes, using a small (∼10 cm diameter) soil chamber placed on PVC rings (10 cm diameter) that had been previously installed by pushing them several centimeters into the soil in small bare patches between vegetation. This method may result in a small underestimate of absolute value of total belowground soil respiration because the sample area is biased away from the root zone directly under larger plants, but our primary focus here is on relative differences induced by heating.

[31] We conducted two kinds of statistical analysis of the flux data set: integration of CO$_2$ fluxes over time (to look at treatment effects on accumulated fluxes of net ecosystem exchange and soil respiration) and multiple regression analysis (net CO$_2$ flux versus explanatory variables) to investigate how environmental variables and vegetation characteristics jointly influence carbon uptake. In particular, we obtained estimates of the relative productivities of the different growth forms from the regression coefficients on the associated aboveground biomasses (see section 4).

3.4. Laboratory Soil Incubations (Warming Meadow and Elevation Sites)

[32] In order to characterize the effect of climatic variations on decomposition rates of montane meadow soils in a way that both excluded root respiration and allowed us to

distinguish between the potentially confounding effects of temperature and moisture, we conducted two short-term controlled incubation experiments similar to that of *Nadelhoffer et al.* [1991]. One was done in 1994 with soils from each plot in the warming meadow, and one was done in 1996 with soils from the two treatments at the warming meadow and at each of the three elevational sites. Soil samples were collected from the top 15 cm of soil. In 1994, 15-g (sun dried and sieved to 2 mm) of warming-meadow soil from each plot were rehydrated with deionized water and incubated in small-mouthed 100 mL glass jars in a full temperature–moisture factorial ($T = 0, 10, 13, 18,$ and $30°C$; $M = 2, 10, 20, 30,$ and 40 g H_2O per 100 g soil). There were 250 jars in 1994: 5 temperatures × 5 moistures × 10 plots. In 1996, 10-g (sun dried and sieved to 2 mm) soil samples were incubated at a full factorial ($T = 1, 10, 20,$ and $30°C$; $M = 5, 20, 35,$ and 50 g H_2 per 100 g dry soil). There were 184 jars in 1996: 4 temperatures × 4 moistures × 4 sites × 2 jars from each site (each jar was drawn from pooled soil samples from five plots, including heated and control plots at the warming meadow), plus 56 duplicate jars at a subset of the full factorial.

[33] In both years, jars were covered with ∼0.025-mm-thick polyethylene film (Handiwrap) to approximately maintain field moisture conditions but to allow some CO_2 and O_2 to exchange with the ambient air. All jars were allowed to equilibrate undisturbed for several days. After the equilibration period all of the jars were capped with airtight rubber septa and aluminum foil crimps, and headspace CO_2 was measured at three time points (using a gastight syringe and Li-Cor 6200 infrared gas analyzer in closed loop configuration) as it built up over the following 55-hour measurement period. (Three time points were used in order to assess the linearity of CO_2 build-up; there was no detectable deviation from linearity in all but a few cases, which showed a slight falloff in CO_2 buildup in high-respiration treatments.) Regression of CO_2 versus time through the three points gave a single estimate, for each jar, of average CO_2 evolution rate over the measurement period, from which decomposition rates (in μg C g^{-1} soil s^{-1}) were estimated (in cases where detectable falloff in CO_2 buildup was observed, just the first two points were used to estimate CO_2 evolution rate). Following the measurement period the actual soil moisture content of each jar was measured, and most jars were within 5% of the desired moisture.

[34] We used multiple regression analysis of the soil incubation data to model SOC decomposition rates as a simple function, $R = k(T,M)$ SOC, where SOC is soil organic carbon in percent carbon and the first-order rate constant k is a simple function of soil temperature T and moisture M. We then drove this decomposition function with measured microclimate field data from heated and control plots integrated over the growing seasons (end of March to mid-September) of 1991 and 1994 to estimate the relative cumulative heterotrophic respiration (ΣR) in heated and control plots. This method may be a poor one for estimating absolute heterotrophic decomposition in the field due to disturbance from extracting soils, but we used it here only to estimate the treatment ratio $\Sigma R_{heated}/\Sigma R_{control}$.

Assuming that disturbance introduces errors in both treatments equally, the treatment ratio will be little affected, since such errors will tend to cancel.

3.5. Field Litter Incubations and Litter Chemistry (Warming Meadow)

[35] We characterized the decomposability of litter from different meadow species by two different methods: field litter incubations, and measurement of lignin/nitrogen ratios Decomposition of senesced leaf litter from warming-meadow plants, *Artemisia tridentata* (the dominant shrub), *Festuca thurberi* (the dominant graminoid), *Delphinium nuttallianum* (the dominant early-season forb), and *Erigeron speciosus* (a dominant late-season forb that is also the main contributor to AGB [*De Valpine and Harte*, 2001]), was measured over 1-year periods using the litter-bag field incubation method [*Berg et al.*, 1993] in 1991, 1992, and 1994 [*Shaw and Harte*, 2001]. The shrub litter was collected as attached, senesced leaves. The forb litter included only browned leaves that had recently fallen to the ground. The graminoid litter was collected as standing dead blades of unknown age, but <18 months. Collected litter was dried, weighed, and placed in nylon mesh bags, which were returned to the field for an incubation period of up to $a \approx 1$ year (half of the litter bags were collected after the first 2–3 months). At the end of the incubation period, litter bags were collected, gently scraped to remove surface debris, dried at $50°C$, and weighed. Decay rates, k, for each species were obtained by fitting $\ln(m_t) = -k \cdot t + c$, where m_t is the fraction of initial mass remaining at time t and c is a constant. Subsamples of each initial litter type from each year were also analyzed for %lignin (acid-insoluble C fraction according to the method of *Iiyama and Wallis* [1990] and for total C and N, using a Carlo-Erba 1500 Nitrogen Analyzer (see *Shaw and Harte* [2001] for a detailed discussion of methods), giving lignin/nitrogen ratios for litter from each species.

3.6. Decomposition-Weighted Productivity Conceptual Model of Soil Carbon

[36] Three key factors controlling SOC levels can potentially vary over space or through time: (1) the bulk quantity of litter inputs (i.e., net productivity of the plant community), (2) the bulk quality, or decomposability, of litter, and (3) soil microclimate (which influences SOC decomposition rates). If these factors are indeed the principal controls on SOC, then SOC levels should be proportional to a "decomposition-weighted productivity" (DWP) variable defined by

$$\text{SOC} \propto \text{DWP} = \sum_{\substack{i=\text{forb,} \\ \text{shrub,} \\ \text{gram}}} \frac{p_i AGB_i}{k_i \mu_{\text{site}}}, \qquad (4)$$

where AGB_i is aboveground biomass (g C m^{-2}) for each of the three plant growth forms (forb, shrub, and graminoid) and p_i, k_i, and μ_{site} are parameters that quantify, respectively, factors one, two, and three, as identified above.

[37] Equation (4) derives from the solution to a simple three-box model with a box for each type of plant-derived

Table 2. Carbon Budget for Warming Meadow and Elevational Gradient[a]

| | Warming Meadow (2920 m) | | Elevational Gradient | | |
	Control	Heated	Lower (2710 m)	Middle (2920 m)	Upper (3170 m)
Carbon Stocks, g C m^{-2}					
Peak aboveground biomass (AGB)[b]	105 ± 3	104 ± 10	125 ± 6	76 ± 3	49 ± 2
Forbs	60 ± 8	47 ± 9	65 ± 4	47 ± 3	17 ± 1
Shrubs	22 ± 6	34 ± 18	36 ± 4	5 ± 2	13 ± 2
Graminoids	22 ± 5	24 ± 5	23 ± 3	25 ± 2	18 ± 1
Soil organic matter[c]	2340 ± 128	2127 ± 72	2525 ± 73	2343 ± 52	1848 ± 26
Fine roots[c]	150 ± 40	120 ± 50	130 ± 15	98 ± 40	130 ± 20
Aboveground litter[d]	96 ± 10	88 ± 10	79 ± 7	16 ± 4	16 ± 2
Integrated Growing-Season CO_2 Fluxes to Atmosphere, g C m^{-2}[e]					
Net whole system					
1993 (days 168–228)	−27 ± 50	65 ± 60		NA	
1994 (days 158–218)	45 ± 30	65 ± 10		NA	
Soil respiration					
1994 (days 158–218)	153 ± 7	133 ± 4		NA	
1995 (days 175–235)	233 ± 7	224 ± 14		NA	
Above and Belowground Inputs to Litter Pool, g C m^{-2}[f]					
Inferred annual range	260–330	220–280	255–335	175–235	180–200

[a] Given as mean values across years plus or minus standard error ($N = 5$ for warming meadow treatments, $N = 10$ for elevational gradient sites).

[b] Averages, for each growth form, over the period of peak AGB (typically between calendar days 190 and 230) over the years 1994–1997 (for warming meadow) and 1997 (for elevational transect). Averaging across years for purposes of constructing a carbon budget dilutes the statistical significance of heating on shrubs revealed by individual year analysis discussed by *Harte and Shaw* [1995].

[c] Carbon pool in 0- to 10-cm interval. Average June and August soil organic carbon (SOC) over years 1996–1998 (all sites) converted to C per area by taking the density- and depth-adjusted average across cores. Averaging across measurement times and adjusting to area with density dilutes the statistical significance apparent from many of the individual corings (Figure 4).

[d] Mid-June standing litter stock averaged over 1995–1996 (warming meadow) and in 1997 (elevational transect).

[e] CO_2 fluxes integrated over comparable 60-day periods during main part of growing season in 1993–1995 (1993–1994 values reanalyzed from data of *Saleska et al.* [1999]). Soil respiration includes both SOC decomposition and root respiration.

[f] Inferred range. Lower bound inferred from sum of belowground input (assumed equal to fine-root inventory) and peak AGB (most likely an underestimate). Upper bound also accounts for AGB turnover by weighting according to growth form productivity (Table 5, normalized to 1 for shrub). Because not all components of carbon budget are known (e.g., litter turnover), actual C inputs to SOC are highly uncertain.

SOC (i = graminoid, shrub, forb) subject to mass balance constraint:

$$\frac{d(\mathrm{SOC}_i)}{dt} = P_i B_i - K_{\mathrm{SOC}-i}\mathrm{SOC}_i, \qquad (5)$$

where inputs are the product of B_i (total plant biomass) and P_i (plant productivity per unit biomass) and outputs are the product of $K_{\mathrm{SOC}-i}$ (a first-order decomposition rate) and SOC_i. Assuming that $P_i B_i \propto p_i\, \mathrm{AGB}_i$ (relative aboveground production among growth forms is proportional to relative total plant production among growth forms) and $K_{\mathrm{SOC}-i} \propto K_{\mathrm{litter}-i} \propto k_i\, \mu_{\mathrm{site}}$ (SOC decomposition is proportional to the decomposition of the litter from which it derives, and litter decomposition, k_i, at one site can be extrapolated to other sites via climate factor μ), then steady state $\mathrm{SOC}_i = \beta \frac{p_i \mathrm{AGB}_i}{k_i \mu_{site}}$ (where β is a proportionality constant), which can be summed across growth forms to give equation (4).

[38] To test equation (4) (the SOC-DWP model), we estimated DWP for each plot at each site and compared it to SOC both within and across sites of the elevational gradient (excluding warming meadow heated plots). DWP was calculated by combining AGB_i with the growth-form specific parameters p_i (productivity) and k_i (decomposition), estimated from the multiple regressions on whole-system CO_2 flux and from the litter decomposition experiment,

respectively. We took the average of measurements on *D. nuttallianum* and *E. speciosus* as representative of forb litter characteristics. By combining several different estimates of litter quality (lignin/nitrogen ratio as well as litter-bag decomposition rate) and plant productivity, we arrived at three separate estimates of the p_i/k_i ratio and hence of DWP.

[39] We derived the DWP site-specific microclimate factor μ_{site} from the laboratory soil incubation analysis, by integrating $k(T, M)$, the microclimate part of the respiration function R, over the annual cycle of field-measured microclimate data at each site, averaging across 1997 and 1998, and normalizing to one for the warming meadow (site of the litter incubation study).

[40] We do not expect all of the assumptions made here to be strictly correct. For example, one does not expect soil decomposition rates (K_{SOC}) generally to be proportional to litter decomposition rates (K_{litter}), especially if K_{litter} is estimated by litter-bag studies (since labile material dominates decay rate estimates, while the material that becomes SOC is more recalcitrant). In our case, however, since we focus on the top 10 cm of soil, much of what comes through a 2-mm sieve is still identifiable plant litter that has been physically broken up but not yet much decomposed, making the assumption more plausible. In addition, as stated above, we estimate relative K_{litter} among growth forms not only by litter-bag decomposition but also by intrinsic litter chem-
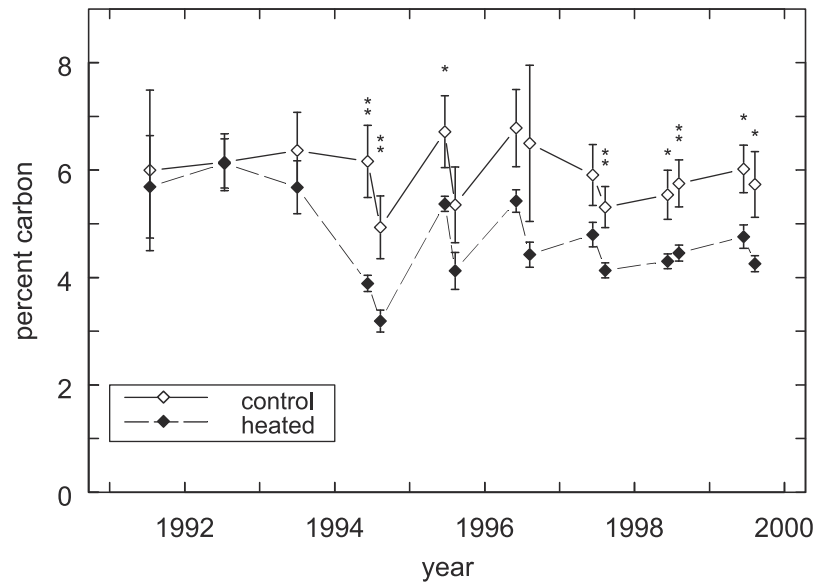
Figure 4. Control and heated plot soil carbon means (±1 standard error, $n = 5$ per treatment in 1991–1993; $n = 20$ per treatment in 1994–2000) versus year in top 8–15 cm of warming meadow soils. In 1994, sampling frequency was increased to twice per growing season (mid-June and mid-August), revealing seasonal variation in soil carbon in most years. A single asterisk denotes $p < 0.05$; two asterisks denote $p < 0.01$ (two-sample t test, $n = 20$ per treatment). Because of negative correlation between %C and soil density (Figure 3), the apparent magnitude of the treatment effect is smaller when converted to g C per unit area (Table 2).

istry (lignin/nitrogen), which should be less susceptible to this issue.

[41] In any case, part of our goal is narrowly utilitarian: to discover whether simple measurements of plant community characteristics do in fact consistently predict SOC. If they do, they can be used for that purpose, even if the relations are based on simplifying assumptions.

4. Results
4.1. Carbon Stocks (Warming Meadow and Elevation Sites)
4.1.1. Carbon in the Warming Meadow
[42] Heating had no effect on total aboveground plant biomass (AGB) (Table 2). However, as previously reported by *Harte and Shaw* [1995], by the third and fourth years of the heating experiment we observed a shift in vegetation community composition from forbs to shrubs in heated plots. This observation is corroborated for years 5–8 by *Dunne* [2000]. Thus, although warming did not affect total carbon stored in AGB, it did result in a significant increase in peak shrub AGB and a compensating decrease in peak forb AGB of ∼13 g C m^{-2} (Table 2).

[43] Heating induced a dramatic decline in SOC (in %C) in the top of the soil profile (core depths ranged between 8 and 15 cm) of the warming meadow (Figure 4). The heating-induced decline was often statistically different from zero at the 95 or 99% confidence level ($p < 0.05$ or $p < 0.01$, two-sample t test, $N = 20$) (Figure 4). When adjusted to carbon per unit area in the top 10 cm and averaged over multiple years (Table 2), the heated plot decline in SOC is ∼200 g C m^{-2}. It is not possible to

calculate an uncertainty on this decline in units of g C m^{-2} directly from the data, because averaging over multiple years and multiplying by density dilutes statistical significance, but on the basis of coefficients of variation for the decline in %C at individual measurement times, we impute a plausible 95% confidence uncertainty of ∼70–80% of the treatment effect, i.e., ∼150 g C m^{-2}.

[44] Since it is not balanced by increases in carbon in fine root biomass, litter, or AGB (Table 2), the decline in SOC is a decline in total system stored carbon and hence is a positive feedback to warming. Also evident in Figure 4 is a general tendency for percent organic C to be slightly higher in late spring than in late summer, possibly reflecting decomposition losses over the course of the growing season that are not balanced by litter inputs until the following fall and winter.

4.1.2. Carbon in the Elevation Sites
[45] Carbon in soil and biomass exhibited clear patterns across elevational sites, generally declining with increasing elevation (Table 2). The trend in SOC with mean annual temperature at the elevational sites is the opposite of that at the warming meadow: SOC increased with temperature coming down in elevation, but decreased with temperature going from control to heated plots.

4.2. Soil Fractionation Experiment (Warming Meadow)
[46] The soil fractionation experiment provided a test of the plausibility of the observed SOC decline in the heated plots of the warming meadow (Figure 4), since in order for the decline in SOC to be plausible over the time span of the

Table 3. Soil Fractionation Analysis, June 1997 Coring[a]

	Depth	Treatment	Bulk	LF	Hyd	Res
Weight, % of bulk	0–10	C	100	22.5 (5.1)	6.6 (0.6)	71.0 (4.9)
		H	100	17.8 (3.2)	6.5 (0.4)	75.7 (2.9)
	10–20	C	100	9.2 (2.5)	90.8 (2.5)	90.8 (2.5)
		H	100	8.8 (2.2)	91.2 (2.2)[b]	91.2 (2.2)[b]
Carbon, %C in each fraction	0–10	C	5.8 (0.8)	16.4 (1.2)	20.0 (1.2)	1.1 (0.1)
		H	5.0 (0.2)	15.5 (0.8)	21.1 (2.5)	1.4 (0.3)
	10–20	C	4.4 (0.4)	18.5 (0.9)	3.04 (0.1)	3.04 (0.1)
		H	4.2 (0.3)	17.7 (1.1)	2.85 (0.1)[b]	2.85 (0.1)[b]
Carbon, kg C m^{-2}	0–10	C	2.32 (0.31)	1.50 (0.35)	0.53 (0.07)	0.31 (0.04)
		H	2.00 (0.09)	1.07 (0.13)	0.54 (0.09)	0.40 (0.08)
	10–20	C	1.78 (0.17)	0.68 (0.17)	1.10 (0.03)	1.10 (0.03)
		H	1.66 (0.13)	0.62 (0.17)	1.04 (0.05)[b]	1.04 (0.05)[b]
C:N ratio	0–10	C	11.6 (0.2)	14.2 (0.3)	13.2 (1.5)	8.9 (0.5)
		H	11.7 (0.2)	14.4 (0.3)	12.5 (0.5)	8.5 (0.4)
	10–20	C	11.6 (0.3)	15.5 (0.7)	10.8 (0.1)	10.8 (0.1)
		H	11.8 (0.4)	15.7 (0.5)	10.9 (0.2)[b]	10.9 (0.2)[b]
$\delta^{13}C$, ‰	0–10	C	−25.6 (0.1)	−25.9 (0.1)	−24.7 (0.2)	−25.5 (0.2)
		H	−25.5 (0.1)	−25.9 (0.1)	−24.5 (0.2)	−25.6 (0.2)
	10–20	C	−24.9 (0.1)		NA[c]	
		H	−25.3 (0.2)			
$\Delta^{14}C$, ‰	0–10	C	+43 (11)	+108 (11)	−34 (16)	−82 (24)
		H	+35 (13)	+105 (8)	+22 (35)	−75 (29)
	10–20	C	6 (19)		NA[c]	
		H	10 (12)			
^{14}C-derived turnover time, years[d]	0–10	pooled	NA	3.3 (0.6) (short)	451 (78)	913 (145)
				92 (6) (long)[e]		

[a] Characteristics of bulk SOC (<2 mm) and its fractions, for samples collected from control (C) and heated (H) plot soils, from 0- to 10- and 10- to 20-cm-depth increments. LF is low-density (<2.0 g cm^{-3}) organic matter, and Hyd and Res are the hydrolyzable (in acids and bases) and residue fractions, respectively, of the high-density organic matter (>2.0 g cm^{-3}). Mean of measurements (standard errors, $N = 5$) is given in parentheses.

[b] High-density portion of 10- to 20-cm soil samples not hydrolyzed. Measurements are of the Hyd plus Res fractions combined.

[c] Isotopes in the 10- to 20-cm samples measured in bulk soil only.

[d] Turnover times derived directly from measured $\Delta^{14}C$ according to method of *Trumbore et al.* [1996].

[e] Contains high $\Delta^{14}C$ values, for which there are two possible turnover times, corresponding to rising and descending limbs of response to bomb ^{14}C spike. On the basis of estimated inflow rates (~300 g C m^{-2} yr^{-1} (Table 2)) and LF pool size (1000–1500 g C m^{-2}) the shorter turnover time is more plausible.

experiment, it must come from soil carbon pools with relatively short turnover times.

[47] The regular June 1997 coring indicated an average carbon content of 5.9% (control) and 4.8% (heated), a difference of 1.1% ($p = 0.025$, two-sample t test, $N = 20$ samples per treatment) (Figure 4). The soil cores for the fractionation experiment analyzed here were taken separately a week earlier and were consistent with the regular intensive coring (showing 5.8 and 5.1% carbon for control and heated plots, respectively (Table 3)), although the heating effect on bulk carbon content was not significant for the fractionation experiment samples ($p = 0.35$, paired t test, $N = 5$), in part because the sample size was smaller.

[48] There were no detectable heating-induced differences in the isotopic carbon content of SOC. With the two treatments lumped together (giving $N = 10$), the fractionation method achieved reasonably good statistical separation of the three fractions isotopically (Figure 5b and Table 3): The lowest statistical resolution was achieved on the ^{14}C difference between hydrolyzable (Hyd) and residue (Res) fractions ($p = 0.053$, paired t test, $N = 10$) and on the ^{13}C difference between LF and Res (paired $p = 0.076$, $N = 10$); all other isotopic differences among fractions, and between bulk soil composition at the two depths, were statistically well resolved (paired $p < 0.006$ in all cases).

[49] The ^{14}C is highest in the low-density SOC and gets progressively lower in the hydrolyzed and residue fractions, confirming the trend from shorter to longer turnover time for SOC in LF, Hyd, and Res soil fractions. (Since the prebomb atmosphere had $\Delta^{14}C \approx 0$, and since new plant matter carries the ^{14}C signal of the CO_2 from which it was formed, negative $\Delta^{14}C$ values indicate that on average the ^{14}C has resided in SOC long enough to have undergone radioactive decay, while positive $\Delta^{14}C$ values indicate that the soil must be cycling rapidly enough to have incorporated significant amounts of the elevated ^{14}C from atmospheric nuclear bomb tests).

[50] The C:N ratios are consistent with the ^{14}C data, with high C:N (typical of "fresh" organic matter from plants) correlating with high (fast turnover) $\Delta^{14}C$: Average C:N in 0- to 10-cm SOC fractions is 14.3 (LF), 12.8 (Hyd), and 8.7 (Res), while the corresponding $\Delta^{14}C$ values are +106, −6, and −78 (Table 3).

4.3. Field CO_2 Fluxes and Relative Vegetation Productivity (Warming Meadow)

[51] Measurements of net whole-system CO_2 exchange in the warming meadow are discussed in detail by *Saleska et al.* [1999]; the relevant results for this analysis are that (1) during the moderately dry growing season of 1993, CO_2 efflux integrated over the main part of the growing season was 133 g C m^{-2} greater ($p < 0.10$, two-sample t test, $N = 10$
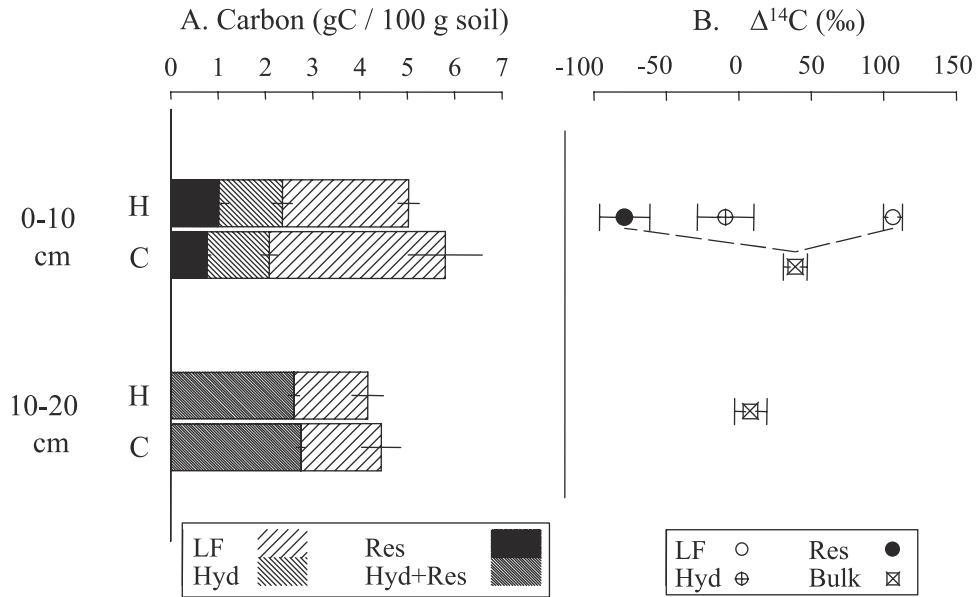
Figure 5. Soil fractionation analysis, June 1997 coring. (a) Soil carbon by depth interval, treatment (H, heated; C, control), and soil fraction (LF, light fraction; Hyd, hydrolyzable component of heavy fraction; Res, residue after hydrolysis of heavy fraction), with error lines indicating ± 1 standard error ($n = 5$) (rightmost error line on each bar indicates error on bulk soil). (b) Soil $\Delta^{14}C$, by soil fraction (including bulk soil) and depth interval, with error bars indicating ± 1 standard error on combined treatments (heated and control plots pooled, $n = 10$; there were no isotopic differences between treatments).

plots) from heated plots than from control plots (Table 2); and (2) although soil respiration in 1994–1995 was briefly elevated in heated plots early in the season (due to earlier snowmelt), this early season effect was canceled or reversed by reductions later in the season, and hence the net effect of heating on field-measured integrated soil respiration in these years was near zero (Table 2).

[52] We also applied regression analysis to the flux data. The most explanatory simple model (Table 4) of CO_2 flux was

$$CO_{2flux} = a_0 + a_1(\text{day of year}) + a_2 PAR + a_3 M_{soil}$$
$$+ a_4 M_{soil}^2 + \sum_{\substack{i=\text{Forb,} \\ \text{Shrub,} \\ \text{Gram}}} p_i AGB_i, \qquad (6)$$

where CO_{2flux} is the average of daytime uptake for each plot and measurement day in the dry zone and a_i are fitted regression coefficients on environmental factors (day of year, photosynthetically active radiation (PAR), and a quadratic in gravimetric soil moisture M_{soil}). The fitted p_i (coefficients on AGB_i in units of day^{-1}) are, in essence, "relative productivity" coefficients for each of the three major plant growth forms in the experimental plots (forb, shrub, and graminoid); they account for relative differences in uptake between growth forms that are not already accounted for by the relative differences in AGB.

[53] Since the AGB of the plant growth forms are in the same units (g C m^{-2}), their respective regression coefficients, p_i, can be compared directly. Among the three growth forms the p_i fit for equation (6) (Table 4) show that a given biomass of forb contributes more strongly to CO_2

uptake than does the same biomass of graminoid, which in turn contributes more than the same biomass of shrub.

4.4. Laboratory Soil Incubations (Warming Meadow and Elevation Sites)

4.4.1. Warming Meadow

[54] The decomposition rates, R (in g C g^{-1} soil yr^{-1}), of soil in the incubated jars from the 1994 warming meadow experiment ranged from ~ 0.00 (for cold, dry soil) to 0.03 (for warm, wet soil) and were well represented ($r^2 = 0.81$, $N = 250$) (see Table 5) by a first-order model of the form $R = k(T, M)SOC$, where SOC is soil organic carbon in grams C gram^{-1} soil and the first-order rate constant k (in year^{-1}) is a function of soil microclimate that is exponential in soil temperature (T, in °C) and Michaelis–Menten in soil moisture (M, g H$_2$O g^{-1} soil):

$$k(T, M) = \alpha \exp(\beta T) M / (M + \mu), \qquad (7)$$

where the Michaelis–Menten saturation parameter $\mu = SOC m_0$ (this accounts for the dependence of water-holding capacity on soil organic matter variations). This function saturates but never declines with increasing soil moisture, consistent with the incubation data. Such a function is appropriate here because, although decomposition can in general be expected to decline at high soil moistures when decomposition becomes anaerobic [e.g., *Flanagan and Veum*, 1974; *Schuur et al.*, 2001], our sites are dry (growing season soil moisture rarely exceeds 30% gravimetric), and aerobic conditions prevail in the soil environment [*Torn and Harte*, 1996].

Table 4. Linear Multiple Regression Results For Average Daytime CO_2 Uptake (Warming Meadow)[a]

	1993[b]			1994[c]		
Coefficient (Variable)	Coefficient Estimate	Standard Error	p Value	Coefficient Estimate	Standard Error	p Value
a_0 (Intercept)	2.39	3.87	NS	−7.81	3.22	**
a_1 (day of year)	−0.090	0.012	***	−0.089	0.012	****
a_2 (PAR)	0.003	0.001	**	3.477	0.526	****
a_3 (**moisture**)	**0.608**	0.132	***	**0.234**	0.122	*
a_4 (**moisture²**)	**−0.011**	0.003	**	**−0.007**	0.003	**
p_1 (**FORB**)	**0.061**	0.009	***	**0.047**	0.007	****
p_2 (**SHRUB**)	**0.025**	0.004	***	**0.022**	0.006	***
p_3 (GRAM)	0.040	0.011	**	0.023	0.008	**

[a] Based on model $CO_{2flux} = a_0 + a_1(day\ of\ year) + a_2PAR + a_3M_{soil} + a_4M_{soil}^2 + \sum_{i=Forb, Shrub, Gram} p_iAGB_i$. Variables in bold are significantly affected by heating and, taken together, account for treatment effect on CO_2 fluxes (that is, the addition of these variables in the model eliminates the significance that treatment as a categorical variable would otherwise have). A single asterisk denotes $p < 0.10$, two asterisks denote $p < 0.05$, three asterisks denote $p < 0.001$, and four asterisks denote $p < 0.0001$. Source for data is *Saleska et al.* [1999, Table 2].
[b] Model statistics: $R^2 = 0.704$; RSE = 2.3 (82 degrees of freedom).
[c] Model statistics: $R^2 = 0.605$; RSE = 2.1 (82 degrees of freedom).

[55] Because R in equation (7) increases with both T and M, we expect the effects of heating (higher T, lower M) on soil decomposition to at least partially cancel. Indeed, integrating R over different (1991 and 1994) seasonal cycles of measured heated and control plot temperature, moisture, and SOC yielded simulated decomposition ratios, $\Sigma R_{heated}/\Sigma R_{control}$, ranging (depending on year and choice of parameters within confidence intervals) from 0.8 to 0.94, indicating that if anything, decomposition should have been lower in the heated plots. Because the effect of lower levels of measured SOC in the heated plots itself tends to lower simulated decomposition rates (due to first-order kinetics), we repeated the analysis holding SOC constant across treatments. This gave $\Sigma R_{heated}/\Sigma R_{control} = 0.96–1.05$, suggesting that even before the heating treatment reduced heated plot SOC, the combined microclimate effects (warming and drying) had little effect on SOC decomposition rates.

4.4.2. Elevation Gradient

[56] The results of the 1996 incubation experiment conducted on soils from both warming meadow and elevational sites were well represented by a model similar to that in section 4.4.1 except for one difference: Soil texture differed across the elevational sites and hence so did field water-holding capacity. With M defined slightly differently (as fraction field water-holding capacity) and the regression

Table 5. Nonlinear Regression Models of Soil Respiration Rates During Temperature- and Moisture-Controlled Laboratory Incubation Experiments

	Model Statistics			Parameter Estimates (Standard Error)		
Soil Respiration Model[a]	R^2	Degree of Freedom	RSE, g C g^{-1} soil yr^{-1}	α, year^{-1}	β, °C^{-1}	μ[b]
1994 Experiment (Warming Meadow)						
Treatments combined	0.81	247	0.0026	0.18 (0.02)	0.046 (0.002)	6.14 (1.00)
Treatments separated[c]						
Control	0.82	244	0.0025	0.14 (0.02)	0.046 (0.003)	4.32 (0.51)
Heated				0.20 (0.03)	0.045 (0.003)	6.08 (0.93)
1996 Experiment (All Sites)						
Warming	0.94	37	0.0017	0.15 (0.04)	0.066 (0.004)	1.08 (0.37)
Lower	0.93	45	0.0010	0.20 (0.04)	0.054 (0.003)	1.04 (0.27)
Middle	0.88	45	0.0016	0.19 (0.05)	0.054 (0.004)	1.27 (0.49)
Upper	0.96	44	0.0013	0.20 (0.03)	0.062 (0.003)	1.13 (0.26)
All sites together	0.90	180	0.0018	0.18 (0.02)	0.059 (0.002)	1.13 (0.21)

[a] SOC $\alpha \exp(\beta \cdot T) \frac{M}{(M+\mu)}$. This is a first-order decomposition model of the form (SOC) k, where SOC is soil organic carbon in fraction carbon and the first-order rate constant k (year^{-1}) is a function of soil microclimate exponential in soil temperature (T, in °C) and a function of Michaelis–Menten in soil moisture (M, g H_2O g^{-1} soil for the 1994 incubation or fraction field water-holding capacity for the 1996 incubation).
[b] For 1994, $\mu = SOCm_0$, and the fitted parameter values for m_0 (in units of g H_2O g^{-1} SOC) are shown. For 1996, μ = fraction field water capacity, and the fitted parameter values for μ are shown.
[c] Control and heated plots for 1994 experiment parameterized separately within a single model of form $R = (\alpha + \partial\alpha)$ (SOC) $\exp[(\beta + \partial\beta) T] M/[M + (\mu + \partial\mu)SOC]$, where each parameter ($\alpha$, β, or μ) is for control plots alone and ∂ of that parameter is the incremental effect of heating on the control parameter. Thus a single set of summary statistics (R^2 and residual standard error (RSE)) applies to the separate parameterization model. None of the model parameters were statistically significantly affected by heating when considered separately. Joint confidence region for heating effect on parameters α and μ taken together, however, was significantly different from zero ($p < 0.001$, F test).

Table 6. Species-Specific Results From Litter-Bag Incubation Study in Warming Meadow, Average Across Years (1991, 1992, 1994), and Treatments[a]

Species (Growth Form)	Initial Litter Chemistry					Litter Decomposition, k (days^{-1})
	N, %	C, %	C:N	L, %	L:N	
Artemisia (shrub)	0.92	48.45	52.81	15.82	17.29	0.0016
Delphinium (forb)	2.84	42.27	15.48	9.04	3.31	0.0113
Erigeron (forb)	2.28	44.91	20.16	38.96	17.39	0.0036
Festuca (graminoid)	0.958	41.41	43.26	35.44	37.08	0.0012

[a] From *Shaw and Harte* [2001, Tables 2 and 4].

coefficient μ fitted directly (also in these units), the same form for $k(T, M)$ (equation (7)) worked equally well. The fitted models (Table 5) from the 1996 incubation were then used to characterize the effect of variations in microclimate across the elevation gradient on soil decomposition (see section 4.6).

4.5. Field Litter Incubations and Litter Chemistry (Warming Meadow)

[57] Results from the litter decomposition experiments in the warming meadow (Table 6) show that on average, litter from the graminoid *F. thurberi* was the most recalcitrant (turnover time of 833 days) and the two forbs, *E. speciosus* and *D. nuttallianum*, were the least recalcitrant (turnover time of 287 and 95 days, respectively), with the shrub *A. tridentata* in between (672 days), but falling closer to *F. thurberi*. Measurements of the lignin/N ratio for each litter type are consistent with this ranking (Table 6).

[58] Differences in litter mass loss among growth form were consistently highly statistically significant, but there was generally little or no statistically significant effect of heating on litter decomposition within species [*Shaw and Harte*, 2001].

4.6. Test of Decomposition-Weighted Productivity Model

[59] The test of equation (4) (the SOC-DWP model) uses AGB (peak values from 1997) and SOC (%C adjusted to g

C m^{-2} using equation (2), averaged across 1997–1998) from the elevational gradient, relative p_i/k_i estimated by three methods (Table 7), and estimated μ_{site} from laboratory soil incubations and field soil microclimate measurements, which gave μ_{site} = 0.84, 0.95, and 0.79 (all normalized to one for the warming meadow site) for the lower, middle, and upper sites, respectively. The three different estimates of p_i/k_i (from Table 7) provide a sensitivity analysis on the robustness of the SOC-DWP model.

[60] These measurements determine a fixed, empirical estimate of DWP for each plot independently of SOC, with no adjustable parameters. If the DWP-SOC conceptualization is right, DWP should be proportional to SOC across plots.

[61] Regression of SOC against DWP for the 30 plots along the gradient and the five warming meadow control plots quantifies this proportionality; the results show good, consistent fits both within each site separately and across all sites combined (Figure 6a), independent of method used to estimate p/k (regression across all sites consistently gives $r^2 \approx 0.8$) (Table 7). For each p/k estimation method, the regression at each site independently is statistically consistent with the regressions at the other sites; that is, the regression line estimated at site i falls within the 95% confidence limits of the regression line estimated at site j for all ij pairs of sites, providing a first-order cross-validation of the SOC-DWP model.

[62] The heated plot SOC-DWP regression (Figure 6b), by contrast, is poor ($r^2 = 0.02–0.05$), with its fitted line differ-

Table 7. Estimates of Growth-Form Vegetation Parameters Used to Calculate Decomposition-Weighted Productivity (DWP)[a]

Growth Form	Productivity p, days^{-1c}	Recalcitrance (1/k)		Method of Estimating p/k (Varying Units)[b]		
		τ, days[d]	Lignin/N[e]	1 (0.84) $p\tau$	2 (0.79) p(L:N)	3 (0.84) Litter Regression[f]
Forb	0.054	190	10	10.1	0.56	0.18
Shrub	0.024	672	17	15.4	0.41	0.39
Graminoid	0.032	833	37	26.1	1.17	0.67

[a] DWP: Soil carbon predictor variable defined in equation (4): productivity (p_i), litter recalcitrance ($1/k_i$), and combined p_i/k_i ratio, shown according to plant growth form and by different methods. Also included is goodness-of-fit statistic (r^2) from SOC-DWP regression for each method of estimating p/k.

[b] Goodness-of-fit statistic (r^2) for SOC-DWP regression is given in parentheses after method number.

[c] Productivity estimated from multiple regression analysis of average daily CO_2 uptake versus aboveground biomass by growth form, averaged across 1993–1994 data (see Table 4).

[d] Inverse of first-order litter decay constant determined from averages of three separate 1-year litter-bag incubations in warming meadow plots (see Table 6).

[e] Lignin/N ratios in senesced warming meadow litter, averaged over three separate years (see Table 6).

[f] Model: $L = b_0 + b_1 \times AGB_{Forb} + b_2 \times AGB_{Shrub}$ ($r^2 = 0.308$, $N = 360$), where L is bulk litter (principally from forbs and shrubs) harvested from transect sites, gives forb (b_1) and shrub (b_2) p/k. Graminoid p/k assumes shrub and graminoid productivity (per unit of AGB) are equal and that their recalcitrances are the average of their Lignin/N and τ values. Since litter pool size reflects the balance of inputs and outputs, this method provides an estimate of average p/k across the elevational transect.
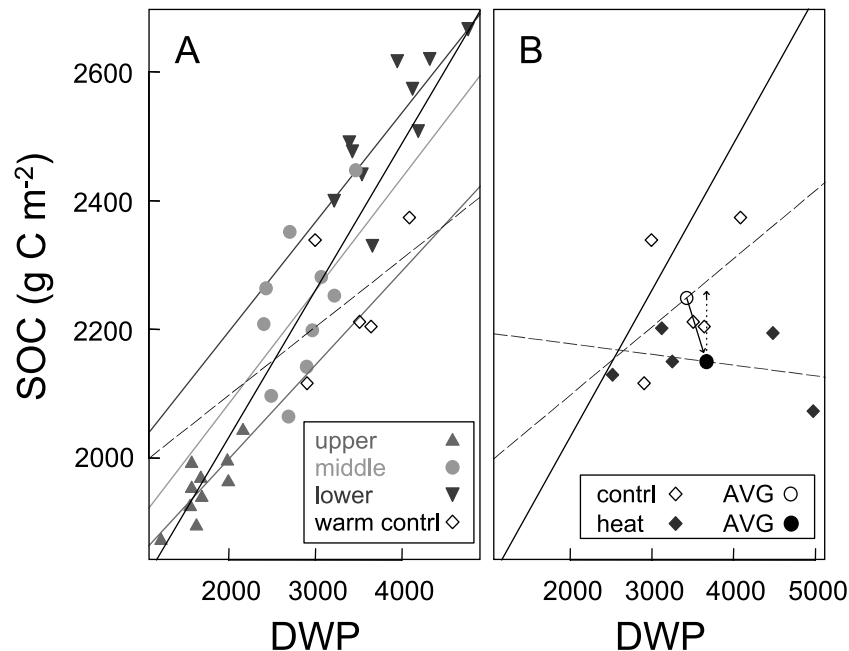
Figure 6. (a) Observed soil organic compound (SOC) (1997–1998 average, in g C m^{-2}) versus 1997 decomposition-weighted productivity (DWP) (the soil carbon predictor variable defined in equation (4), using the first p/k estimate (Table 7)), including least squares regression lines for each site separately (colored lines) and for all sites combined (black line, $r^2 = 0.84$). (b) Observed SOC versus DWP, same as in Figure 6a, but for warming meadow control (open diamonds) and heated (solid diamonds) plots only. Observed transient shift (solid arrow) from control-plot mean (open circles) to heated plot mean (solid circles) and anticipated steady state recovery (dotted arrow) of heated plot mean are also shown. See color vesion of this figure at back of this figure.

ing significantly from all other fits due to a shift to lower SOC and slightly higher DWP (solid arrow in Figure 6b), presumably because the transient response to the warming manipulation violates the steady state assumption underlying equation (4).

5. Discussion

[63] The observed decrease in heated plot SOC of ∼200 g C m^{-2} (an ∼8.5% reduction relative to warming meadow control plots) suggests that ecosystem warming of a magnitude anticipated with a doubling in atmospheric CO_2 can induce large and rapid losses of soil carbon, representing a strong positive feedback to warming. This result is surprising, as it has been suggested that statistical power in most field experiments is insufficient to detect plausible changes in bulk soil C after only a few years [*Hungate et al.*, 1996].

[64] Our result thus raises at least three questions: (1) Is it plausible and consistent with our understanding of soil turnover rates at this site? (2) What mechanisms are responsible for the observed decline? (3) What will be the long-term response?

[65] Regarding the first question, the decline in SOC is consistent with both the magnitude of observed net CO_2 flux measurements and with soil carbon dynamics as revealed by the soil fractionation experiment. First, since the net CO_2 efflux from heated plots was 100+ g C m^{-2} greater than from controls in the first year that flux measurements were

made (1993), the observed decline of ∼200 g C m^{-2} after several years of heating treatment is plausible, at least in terms of overall carbon balance. Second, the soil fractionation data (Table 3 and Figure 5) suggest that the observed decline in heated plot surface soil carbon (Figure 4) is due entirely to a drop in the high-turnover carbon contained in the LF. The LF ^{14}C data are consistent with a short (∼3 year) turnover time for this pool, and the high LF C:N indicate that it consists of relatively fresh plant material. The much smaller effect on deeper (10–20 cm) soil carbon (whether in the bulk soil or in the separate fractions) suggests that the heating effect on soil carbon diminishes quickly with depth.

[66] We note that although the drop in surficial LF SOC is large (heated plot LF SOC has one third less C than controls (due to both a drop in the proportion by weight of LF in the soil and a drop in the carbon content of LF SOC) (Table 3)), the statistical significance is low because of high variation and low sample number. The significant differences between heated and control plot soil carbon that are regularly detected as part of the more intensive bulk soil time series data (Figure 4), however, suggest that the lack of statistical significance here (Figure 5a and Table 3) is due to the high variability in soil properties and consequent low statistical resolving power rather than to an absence of real difference.

[67] Regarding the second question, the mechanism for the SOC decline, the observed SOC decrease could have

resulted from a decrease in C input to the soil (due to reduced plant production or reduced transfer of litter C to SOC) or from an increase in C output (due to increased SOC decomposition). Most ecosystem models assume temperature increases will increase decomposition rates and hence SOC loss [*Cao and Woodward*, 1998; *Kirschbaum*, 1995; *Parton et al.*, 1995; *Schimel et al.*, 1994; *Trumbore et al.*, 1996], but three lines of evidence in this case, the field measurements of CO_2 flux, the laboratory soil incubations, and vegetation biomass censusing, point to a decrease in input as the primary cause.

[68] The first line of evidence is that field measurements of CO_2 flux from soil (Table 2) showed that heating had either a negative effect or no net effect on integrated soil respiration in 1994 and 1995. (More recently, *Luo et al.* [2001] observed a similar null effect of experimental warming in a tallgrass prairie, though they attributed their lack of response to acclimation rather than to a tradeoff between the opposing effects of heating and drying on microbial metabolism.) Further, partitioning the 1994 heating effect on average daily CO_2 efflux to the atmosphere into aboveground and belowground components gave the regression $\Delta\text{flux}_{\text{aboveground}} = -2.0\Delta\text{flux}_{\text{belowground}}$ ($r^2 = 0.76$, $p = 0.002$, $N = 8$ measurement days) [*Saleska et al.*, 1999]. This suggests that belowground flux effects (whether caused by changes in root respiration or SOC decomposition) are reversed by the larger changes in plant-driven fluxes aboveground and hence that changes in the plant community (as opposed to the soil microbial community) are dominating the shift in ecosystem carbon balance.

[69] A question remains, however: Could CO_2 efflux from the soil have been elevated in the first few years of the experiment and then declined by the time our soil flux measurements were made (similar to observations of *Peterjohn et al.* [1994] in a forest soil warming experiment)? Laboratory soil incubations, the second line of evidence, address this question.

[70] The laboratory soil incubations indeed show that decomposition depends significantly on SOC and that heated plot soils are probably respiring less now because they have less carbon. However, as reported in section 4, holding soil carbon constant across treatments to simulate the treatment effect in the early years gave a seasonally integrated soil decomposition treatment ratio, $\Sigma R_{\text{heated}}/\Sigma R_{\text{control}}$, ranging from 0.96 to 1.05, indistinguishable from 1. Conservatively assuming that (1) $\Sigma R_{\text{heated}}/\Sigma R_{\text{control}} = 1.05$, and (2) field SOC decomposition is not more than 350 g C m^{-2} yr^{-1} (double the soil respiration CO_2 flux in Table 2 to account for the full annual cycle, less a lower bound 10% for root respiration), then a plausible upper bound on the SOC decomposition heating effect in the early years is $\sim$15 g C m^{-2} yr^{-1}, enough to account for only a fraction of the observed decline in heated plot soil C of 200 g C m^{-2} over several years.

[71] The first two lines of evidence thus effectively rule out an increase in respiratory losses as the primary cause of the SOC decline. The third line of evidence, the observed shift in vegetation community composition from forbs to shrubs, suggests that a decrease in litter inputs is an alternative mechanism that can account for the SOC decline. The vegetation shift is a shift from high-productivity to low-productivity growth forms. This productivity difference is evident from forb phenology: The $\sim$30 species of perennial forbs grow and senesce throughout the growing season, with the occurrence of peak AGB of the different species spread out in time [*De Valpine and Harte*, 2001]. High turnover of forb biomass means that the seasonal peak of total forb AGB underrepresents seasonal aboveground forb production. Aboveground production of *Artemesia tridentata*, the main shrub species, or of the graminoids, by contrast, should be well represented by their peak in new growth AGB.

[72] The difference in relative productivity among growth forms, quantitatively estimated by the p_i from CO_2 flux regressions (Table 4), was able to account for 86 g C m^{-2} less heated plot uptake over just a 2-month period in 1993 [*Saleska et al.*, 1999]. Another estimate is given by averaging across 1994–1997 estimates of annual plant inputs (Table 2), which suggests that reductions in those years may have been on the order of 50 g C m^{-2} yr^{-1}, although the uncertainty here is high. In addition, the shift in vegetation composition to shrubs in heated plots also implies a greater fraction of woody matter, a consequent slowing of litter pool turnover, and a transition period during which litter-to-SOM transfers are even less than plant production inputs to litter. These estimates are sufficiently large to show that observed shifts in vegetation can quantitatively account for the magnitude of ecosystem carbon loss.

[73] Other studies have shown that reduced litter inputs can lead to very large drops in SOC (28% decline after 45 years in shortgrass steppe [*Kelly et al.*, 1996]; 27% loss after 40 years in the Rothamsted experiments [*Jenkinson and Rayner*, 1977]). However, these studies were very different: They involved near-complete cutoff of litter input imposed by external means (direct manipulation [*Jenkinson and Rayner*, 1977] or western harvester ants [*Kelly et al.*, 1996]), as opposed to smaller changes over shorter times caused by internal community ecological dynamics.

[74] The underlying ecological cause of the vegetation shift is addressed in more detail elsewhere [*Harte and Shaw*, 1995; *De Valpine and Harte*, 2001], but we note that it is likely due to a shift in the competitive balance among species of varying tolerance to drought stress. For example, heater drying lowered the leaf water potential in heated plot plant species [*Loik and Harte*, 1997] and increased photosynthetic rates and water use efficiency for *A. tridentata* [*Shaw et al.*, 2000].

[75] While warming meadow results imply that shifts in species composition have reduced C inputs to SOC in the short term, shifts in vegetation community composition can also influence SOC over the long term by reducing the decomposability of bulk litter and SOM in heated plots due to the greater recalcitrance of shrub litter compared to forb litter (Table 6).

[76] This brings us to the third question: What will be the likely long-term response to warming? To address this question, we developed the DWP model as a first-order

means for integrating the net effect of the trade-off between decreased productivity and increased recalcitrance into a long-term prediction for steady state. For example, if we assume that the heating treatment continues, then our model predicts the eventual steady state level of SOC in the heated plots, under the further assumptions that the microclimate conditions (Table 1), the mix of vegetation growth forms in those plots (Table 2), the respiration parameters (Table 5), and the parameters k and p (Table 7) remain roughly constant in time. In particular, the reproducibility of the SOC-DWP correlation across all sites (Figure 6a) suggests that heated plot SOC should recover to approximately previous levels, as the effect of decreased litter decomposability is realized and heated plot soils achieve a new steady state (dotted arrows in Figure 6b). This prediction suggests that heated plot SOC will recover from its current depressed value, reaching in steady state a level approximately equal to that before the heating began.

[77] The picture developed here has some broad features in common with findings that have emerged for the effects of climate change on carbon storage in Arctic tundra ecosystems [*Shaver et al.*, 1992]. For example, *Herbert et al.* [1999] used a model calibrated to tussock vegetation at Toolik Lake, Alaska [*Chapin et al.*, 1995; *McKane et al.*, 1997] to examine the potential importance of species interactions for short- and long- term biogeochemical responses to climate change. In one scenario, *Herbert et al.* [1999] modeled the effects of warming on a community consisting of two species: one with high productivity but low nutrient-use efficiency (NUE) (analogous to the forbs in our community), and one with low productivity but high NUE (analogous to our shrubs). The pattern of overall response to elevated temperature was similar to our prediction here: shifting species dominance and initial decline in SOC, ultimately followed by recovery; however, the mechanism was quite different. In the modeled tundra community a temperature increase stimulated microbial metabolism, causing both an initial SOC loss due to increased soil respiration and higher N availability due to increased N mineralization. The consequent release from N limitation favored the low-NUE, high-productivity plant species ("forb") more than the high-NUE species ("shrub") and in the long run, increased litter inputs from the more dominant high-productivity species (forbs) restores some of the initial SOC decline.

[78] This is almost the mirror image of the patterns and mechanisms observed and predicted in the montane meadow, and a key difference is probably found in the degree of water limitation in the montane meadow compared to the moist tundra ecosystem, combined with the related fact that our experimental manipulation included soil drying, while the modeling exercise of *Herbert et al.* [1999] had no changes in soil moisture.

[79] The similarities (in overall pattern) and differences (in the details) between these studies highlight even more sharply the fundamental problem of predicting biogeochemical responses to climate variations: both confirm that ecological interactions can importantly affect biogeochemical responses, but their differences illustrate that these interactions are highly site and ecosystem dependent, mak-

ing generalizable predictions at regional and global levels harder.

6. Conclusion

[80] This analysis gives a unified picture, partitioned into short- and long-term components, of how vegetation community composition, interacting with climate, controls SOC. This picture suggests that (1) extrapolation from experimental manipulations can yield poor predictions for the long term, but that (2) by integrating experimental manipulations with patterns across natural gradients, we can forecast with greater confidence the likely carbon trends expected under anthropogenic climate warming. In particular, for water-limited systems where high-productivity forbs are likely to be replaced by less-productive but more drought-tolerant shrubs under a warmer and drier climate, we anticipate a decline in SOC that follows a pattern of initial overshoot followed by long-term partial recovery.

[81] This work calls into question the common assumption of many ecosystem models that the principal effect of warming on soil carbon will be enhanced loss due to elevated soil respiration. We have shown how soil drying and carbon loss that accompanies warming can confound the temperature sensitivity of soils and how ecological interactions, including shifts in vegetation community composition brought about by heating-induced drought stress, can dominate long- and short-term effects of warming on soil carbon balance.

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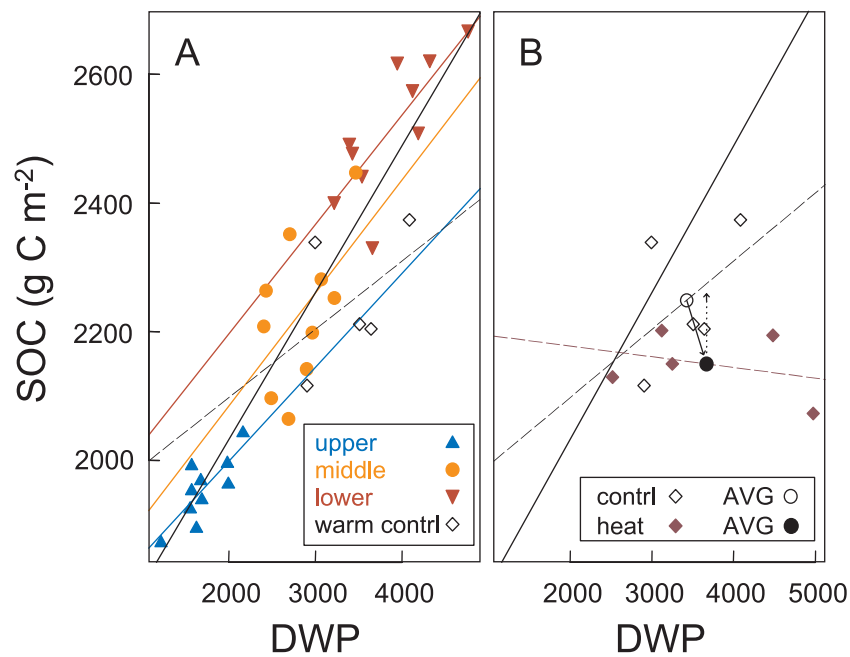
Figure 6. (a) Observed soil organic compound (SOC) (1997–1998 average, in g C m^{-2}) versus 1997 decomposition-weighted productivity (DWP) (the soil carbon predictor variable defined in equation (4), using the first p/k estimate (Table 7)), including least squares regression lines for each site separately (colored lines) and for all sites combined (black line, $r^2 = 0.84$). (b) Observed SOC versus DWP, same as in Figure 6a, but for warming meadow control (open diamonds) and heated (solid diamonds) plots only. Observed transient shift (solid arrow) from control-plot mean (open circles) to heated plot mean (solid circles) and anticipated steady state recovery (dotted arrow) of heated plot mean are also shown.