CONCEPTS & SYNTHESIS
EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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INTEGRATING EXPERIMENTAL AND GRADIENT METHODS IN ECOLOGICAL CLIMATE CHANGE RESEARCH

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Abstract. Field-based research on the responses of ecosystems to anthropogenic climate change has primarily used either natural gradient or experimental methods. Taken separately, each approach faces methodological, spatial, and temporal limitations that potentially constrain the generality of results and predictions. Integration of the two approaches within a single study can overcome some of those limitations and provide ways to distinguish among consistent, dynamic, and context-dependent ecosystem responses to global warming. A simple conceptual model and two case studies that focus on climate change impacts on flowering phenology and carbon cycling in a subalpine meadow ecosystem illustrate the utility of this type of integration.

Key words: climate change; ecosystem-warming experiment; gradient analysis; integrative research; methodology; plant flowering phenology; soil carbon cycling; spatial and temporal scale; subalpine meadow.

INTRODUCTION

By the end of the 21st century, atmospheric concentrations of carbon dioxide are expected to more than double over preindustrial levels, due primarily to anthropogenic fossil fuel emissions and development activities (Houghton et al. 2001). A consensus of scientists predicts that a global average surface warming of 1.4–5.8°C will occur by AD 2100 as a result of increased greenhouse gas levels (Houghton et al. 2001). Potentially profound changes in CO_2 levels, temperature, moisture, light, and disturbance due to climate change will likely alter ecosystem structure and function, which can in turn produce positive or negative feedbacks to climate via changes in vegetation dynamics and processes such as nutrient and carbon cycling (e.g., Woodwell and Mackenzie 1995, Lashof et al. 1997).

Current predictions of global climate change are based on general circulation models (GCMs) that are only beginning to incorporate the key climate–ecosystem interactions (Cox et al. 2000). To quantify effects of climate change on ecosystems as well as feedbacks, a detailed and mechanistic understanding of climate–ecosystem interactions on the scale of experimental plots is needed, along with reliable methods for obtaining larger scale, more general information about such interactions. In general, scientists doing field-based research have pursued these two goals separately, primarily focusing on either natural climate gradients or climate manipulations. In the first half of the article, we summarize both types of research, discuss some of their limitations, and review the rationale for combining the two approaches within focused research programs. This type of integration, while hinted at in a few recent studies, has yet to be systematically implemented in multisite fieldwork and analysis. In the second half, we characterize a simple conceptual model for integrating gradient and experimental approaches and describe our research design for investigating interactions between climate change and a subalpine meadow ecosystem. We use two case studies from our project, one drawn from community ecology and one from ecosystem ecology, to illustrate the utility of an integrated experiment/gradient research and analysis strategy.

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Natural Climate Gradients

A widely used approach for acquiring large spatial scale understanding of ecosystem responses to climate change is to identify relationships between ecosystem variables and climatic conditions across sites or studies within a watershed, landscape, or region, or across the globe (Koch et al. 1995). Biogeochemistry studies have particularly benefited from this approach. Within single studies, temperature (Burke et al. 1991, Tate 1992, Wieder and Yavitt 1994, Townsend et al. 1995) and moisture (Mosier et al. 1993, Schurr et al. 2001, Austin 2002) gradients have been used to describe ecosystem carbon dynamics. At very large spatial scales, general relationships between climate and soil CO_2 emissions (Jenkinson et al. 1991, Raich and Schlesinger 1992, Lloyd and Taylor 1994, Raich and Potter 1995) have been postulated via comparative, synthetic analysis of data from multiple studies. These types of spatial gradient analyses have been important for predicting the presence, magnitude, and dynamics of ecosystem-mediated carbon-cycle feedbacks to climate.

Spatial climate gradients have also been used to postulate climate change impacts on diverse organismal traits such as tree growth (Callaway et al. 1994, Villalba et al. 1994), leaf phenology (Kramer 1995), beetle life-cycle strategies (Butterfield 1996), plant nutritional status (Korner 1989), and plant species distribution and biomass (Walker et al. 1993, Stanton et al. 1994). At larger spatial scales, climate–vegetation distribution classifications (Holdridge 1947, Box 1981) have been used to predict major shifts in species' ranges and biome boundaries due to global warming (Emmanuel et al. 1985, Davis and Zabinski 1992, Monserud et al. 1993), shifts which may precipitate significant albedo and carbon-cycle feedbacks to climate (e.g., Lashof 1989, Foley et al. 1994).

The value of predictions from gradient analyses depends on the assumption that ecosystems will track changing climate over time in the same way that ecosystems now vary with climate variability over space. In general, long-term adaptation to local climatic conditions, fine-scale environmental heterogeneity, covarying abiotic factors, non-monotonic changes, and differences in time constants may confound the straightforward use of spatial gradients to predict responses to global warming (Peters et al. 1991, Bazzaz and Wayne 1994, Villalba et al. 1994, Vitousek 1994). For example, the ''space-for-time'' substitutions implied by spatial gradient research can be misleading where historical attributes of sites have unexpected or unique effects on ecosystem structure and function (Pickett 1989) or where biotic interactions are strong and also poorly correlated with climate. The rapid pace of anthropogenic climate change may outstrip possible rates of change in species distributions (Davis 1989, Webb and Bartlein 1992), soil characteristics (Pennington 1986), and other ecosystem properties, resulting in a future decoupling of climate–ecosystem relationships that held along previously slowly changing spatial gradients.

In addition to spatial gradients, researchers have used temporal gradients to infer relationships between ecosystem and climate variables. A rich body of paleoecological research documents effects of historical climate change over very long time sequences and large spatial scales (e.g., Webb 1987, Cooperative Holocene Mapping Project [COHMAP] 1988, Davis 1989, Graham 1992, FAUNMAP 1996). Many studies have used multidecadal data sets (e.g., Inouye and McGuire 1991, Walker et al. 1994, Fitter et al. 1995, Sparks and Carey 1995, Crick and Sparks 1999, Inouye et al. 2000, McLaughlin et al. 2002) or site resampling (e.g., Grabherr et al. 1994, Barry et al. 1995, Parmesan 1996, Bradley et al. 1999, Brown et al. 1999, Parmesan et al. 1999, Thomas and Lennon 1999) to document ecological responses to recent climate change. These types of temporal gradient studies have been used to predict ecosystem responses and feedbacks to future climate change. As with spatial gradient studies, ecosystem responses to temporal climate gradients may be poor predictors of future responses due to differences among historic, current, and future rates, magnitudes, and types of climate change and ecosystem response. Paleoecological studies face additional challenges, including low data resolution, limited data availability and reliability, and weak biotic and geologic parallels to future conditions (Overpeck et al. 1991, Adams and Woodward 1992, Webb 1992, Roy et al. 1996).

Climate Change Experiments

Compared to gradient studies, experiments provide a more controlled, mechanistic approach to forecasting ecosystem responses to climate change, and can identify the most important contingent factors that influence those responses. We focus on field-based climate manipulations, rather than microcosms or CO_2 manipulations, because of the potential for strong analogy with natural climate gradient studies. Researchers have used climate manipulations in a variety of mostly mid- to high-latitude terrestrial ecosystems including arctic tussock tundra (Chapin and Shaver 1985, Chapin et al. 1995, Hobbie and Chapin 1998), subarctic heath (Wookey et al. 1993, Parsons et al. 1994, Jonasson et al. 1999), Antarctic fellfield (Kennedy 1995*b*), subalpine meadow (Harte and Shaw 1995, Harte et al. 1995*b*, Saleska et al. 1999), grassland (Nijs et al. 1996, Ineson et al. 1998, Grime et al. 2000, Luo et al. 2001, Rillig et al. 2002), boreal forest (Van Cleve et al. 1990, Beerling and Woodward 1994), temperate forest (Peterjohn et al. 1994, Farnsworth et al. 1995, Melillo et al. 2002), and tropical forest (Nepstad et al. 2002).

In these and other experimental studies, researchers manipulate climate warming factors (e.g., infrared radiation, soil and air temperature) and sometimes additional global change factors (e.g., precipitation, nu-

trients, light levels) and monitor ecosystem responses. The two primary tools for simulating warming are (1) passive greenhouses and (2) active heating devices including soil and aerial arrays, with particular methods reviewed and critiqued elsewhere (Kennedy 1995*a*, Marion et al. 1997, Shen and Harte 2000). Experimentalists face a dual challenge specific to climate change research. First, researchers must decide which climate change projections to use as their target. Climate change associated with a doubled carbon dioxide atmosphere is often used as the approximate goal, but there can be large variation and uncertainty in what models predict for global versus regional and local climate change. Second, researchers must attempt to simulate the desired change(s) in climate while minimizing confounding changes in other factors. All warming manipulations fail to simulate some aspects of climate change, as well as altering other environmental conditions in unexpected or unwanted ways. A further complication concerns alteration of disturbance regimes (e.g., fires, hurricanes) or extreme events (e.g., drought, deluge) by climate change. Such shifts may prove more important in determining ecosystem effects from and feedbacks to climate than the usual experimental focus on average changes in microclimate variables.

As with other types of ecosystem experiments, potential generality of results is limited by a variety of issues: the manipulation of very few factors, the difficulty of establishing good controls, and the expense and time required to implement adequate plot size and replication. Ecosystem variability and complexity, as well as unintentional experimental effects, may confound unambiguous interpretation of results and identification of mechanisms. The role of historical factors, edge effects, large or mobile organisms, and exclusion of rare, emergent, or large-scale processes precludes scaling up by simply assuming that information learned on experimental plots at one or a few sites will apply in straightforward manner to apparently similar habitat across a landscape.

The short duration of most experiments can also lead to incomplete or inaccurate predictions of climate change effects. Initial ecosystem responses to experimental climate change may differ from responses observed when the manipulation is sustained over longer periods. For example, changes in plant biomass in response to the first three years of an open-top chamber greenhouse warming experiment in tussock tundra was dominated by direct growth responses of individuals initially present in the plots (Chapin et al. 1995). Such short-term biomass changes were poor predictors of changes over nine years, perhaps because of delayed responses of the plant community to longer-term resource feedbacks, growth, mortality, and competition. Similarly, in other high-latitude warming experiments using open-top chambers, tundra plants exhibited increased vegetative growth in the first three years of manipulation, but during the fourth year displayed more variable, individualistic responses that shifted toward changes in reproductive effort and success (Arft et al. 1999). Thus, experimentalists must be alert to the possibility that short-term mechanisms regulating rapid ecosystem responses may differ from longer-term mechanisms and feedbacks regulating slowly changing responses (Magnuson 1990, Shaver et al. 2000).

Integrating Climate Gradients and Experiments

The task of extrapolating experimental results of ecosystem responses and feedbacks to climate change from the scale of plots to that of landscapes or larger is widely accepted as one of the central challenges facing global change science (Rosswall 1988, Lubchenco et al. 1991, Walker et al. 1993, Rastetter 1996). One approach synthesizes results across multiple experimental and/or natural gradient studies, using either qualitative assessment (Shaver et al. 2000) or quantitative meta-analysis (Arft et al. 1999, Rustad et al. 2001, Parmesan and Yohe 2003, Root et al. 2003). Another approach integrates monitoring along natural climate gradients with field experimentation, especially where manipulations can be conducted along a climatic gradient. While this strategy has been repeatedly called for (Vitousek and Matson 1991, Pacala and Hurtt 1993, Vitousek 1994, Koch et al. 1995, Root and Schneider 1995, Shaver et al. 2000), we know of no prior research project that explicitly integrates both types of research in a single ecosystem-level study using multiple sites across a landscape.

A few studies have compared responses to experimental and natural climate variation within a single site. Over the course of a nine-year warming experiment in arctic tundra, researchers observed large declines in biomass of a dominant sedge both within long-term experimental plots (warming plus increased nutrients) and within control plots during a 10-year period of regional warming (Chapin et al. 1995). While the results suggest a possible congruity between experimental effects and natural temporal change for that species, five other plant species studied did not display consistent responses. Similarly, in an alpine study that looked at responses of snow bed plant species to experimental and small-scale spatial changes in growing-season length (Galen and Stanton 1995), the responses of five of six species monitored to three-year experimental changes in snow depth were not predictable from their distributions along a natural snow depth gradient. During the first four years of a subalpine meadow warming experiment (Harte et al. 1995*a*), soil mesofauna biomass responded similarly to experimental and natural interannual changes in soil temperature and moisture, but responded differently to small-scale spatial variation in microclimate within the experimental site. At the same site, some aspects of reproductive plant phenology were consistent in their response to

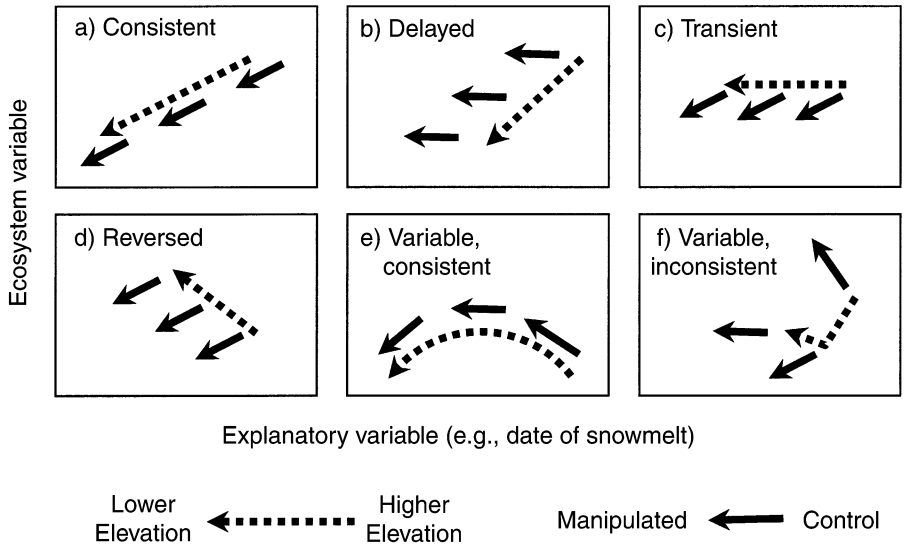


FIG. 1. Idealized graphs showing six scenarios of the response of an ecosystem variable to an explanatory climate variable as a result of a climate change experiment replicated at three elevational sites (solid arrows) and resulting from climate variability across an elevational climate gradient (dashed arrows).

within-site spatial and experimental variation in snowmelt date, while other aspects were not (Price and Waser 1998). These studies suggest that results from either experiments or natural gradients must be carefully interpreted, since they often fail to reinforce each other and thus may reflect only a part of the potential dynamics of an ecosystem in response to climate.

The combination of gradient analyses and experiments in climate change research may be particularly useful because of the way these two approaches bracket temporal rates associated with anthropogenic climate change. Manipulations tend to be brief, running typically from one to 10 years, and experimental changes are usually introduced instantaneously at a single or very few levels of effect. Only very plastic ecosystem properties will noticeably respond to such short-term perturbations. Natural climate gradients, on the other hand, allow study of ecosystem adjustments to longer-term climate trends across sites in which temporal climate change can be assumed to be erratic, with average trends shifting slowly over the course of centuries. In comparison, significant anthropogenic climate change is taking place over the course of decades, with the rates of changes in average effects intermediate to the two extremes represented by experiments and natural gradients. Both short and longer-term ecosystem responses need to be understood to predict impacts of and feedbacks to climate change.

A Simple Conceptual Model

Fig. 1, modified from Harte (1998), shows six idealized cases that illustrate some possible relationships that can be observed between ecosystem responses to natural climate gradients versus experimental climate change. We use a simple, heuristic format to facilitate comparisons between ecosystem response to natural landscape-scale spatial climate variation from higher to lower elevation sites (dashed arrows) and response to a climate manipulation that is replicated across three sites along an elevational gradient (solid arrows). The direction of the arrows, which show the response of an ecosystem variable to an explanatory climate variable, denotes the expected direction of change in the explanatory variable under anthropogenic climate change. For these idealized cases, we use date of snowmelt as the example climate variable, and the arrows thus point left to show trends towards earlier snowmelt date. Had we used temperature as the example, the arrow directions would have been reversed to represent predicted trends toward warmer temperatures.

Case a illustrates the most straightforward ''consistent'' scenario in which manipulations at three sites along an elevational gradient induce the same sign and magnitude of change in the ecosystem variable, and those responses are matched by the change observed across the natural climate gradient. This set of responses suggests that both short and longer-term responses will be similar, perhaps as a result of strong control by the explanatory variable regardless of spatial or temporal scale. This scenario represents the situation where ''space for time'' type substitutions appear warranted, i.e., where monitoring along a natural spatial gradient accurately represents responses to manipulated climate within sites, and vice versa.

Cases b, c, and d illustrate dynamic scenarios where the manipulations induce similar ecosystem responses regardless of what site they occur at, but the response to the manipulations does not match the trend across the natural spatial gradient. In case b, experimental climate change does not affect the ecosystem property,

but there is a strong trend across the spatial gradient. We refer to this as a ''delayed'' ecosystem response because it suggests that short-term, plot-level climate change has little impact on the ecosystem property, but responses manifest at larger spatial scales over the longer term. Case c shows the reverse situation, where the manipulations induce a particular ecosystem response, but this effect appears ''transient'' because there is no trend across the spatial gradient. Case d shows a combination of the previous two cases, where the ecosystem property response to experimental climate change is ''reversed'' compared to its response to spatial gradient variability. Cases b, c, and d demonstrate situations where incorporating experimental and natural gradient research is crucial for identifying changes in ecosystem responses, and mechanisms underlying those dynamic responses, that may change over different spatial or temporal scales.

Cases e and f illustrate ''variable'' scenarios where the response of the ecosystem property to experimental climate change varies dramatically from site to site. In case e, manipulation effects vary in sign among sites, but considered together are consistent with nonlinear spatial gradient trends. Case f portrays variable ecosystem responses across manipulations and different parts of the spatial gradient. This is obviously the most conceptually limiting situation, since results are inconsistent and context-dependent in ways not captured by simple ecosystem–climate relationships. If unrecognized by the researcher, cases b–f can lead to spurious over-generalization of results derived from a particular experiment, gradient analysis, or site. However, when recognized, cases b–f can lead researchers to develop more general or sophisticated assessments of ecosystem–climate relationships, and steer them away from unfruitful ones. For example, the nonconsistent trends of cases b, c, d, and f could indicate that explanatory variables may differ between gradients and experiments or among sites (e.g., variability in a particular ecosystem property is associated with snowmelt date under a manipulation but with growing season soil moisture along a spatial gradient).

We stress that these scenarios are highly simplified and are meant to provide an initial overview that can motivate, and complement, more detailed, comprehensive, statistical analyses. Additional trends resulting from multiple kinds of manipulations, interannual variation, and spatial variation at smaller or larger spatial scales can be incorporated (see *Case study 1: Plant flowering phenology*). Also, other types of scenarios can be postulated, for example experimental and natural trends that display the same sign but differ in magnitude. The explanatory variable does not need to be limited to a simple climatic variable, but may be defined in a more complex way (see *Case study 2: Soil carbon dynamics*).

For the remainder of the article, we describe our integrated, multimethod, and multisite research design and give two case studies of experiment/gradient integration from our study, one drawn from community ecology (plant phenology), and one drawn from ecosystem ecology (soil carbon dynamics). The plant phenology study provides an example of a consistent response (Fig. 1a) to climate change, where the ecological dynamics studied are context independent, regardless of ecological scale or field methodology. The soil carbon dynamics study provides an example of a reversed response (Fig. 1d), where an experimentally induced response differs from a trend observed along a spatial gradients. In this case, using either method alone would yield a limited understanding of ecological dynamics, and could lead to incorrect predictions.

Research Design

Since 1991, a year-round ecosystem-warming experiment has been used to explore the impacts of climate change on a Colorado Rocky Mountain subalpine meadow, as well as potential ecosystem-mediated climate feedbacks (Harte and Shaw 1995, Harte et al. 1995*a*, *b*, Loik and Harte 1996, 1997, Torn and Harte 1996, Price and Waser 1998, Saleska et al. 1999, Shaw et al. 2000, Shaw and Harte 2001*a*, *b*, de Valpine and Harte 2001). We extended the scope of the original climate change experiment in 1995 by establishing nearby subalpine meadow sites in a common watershed along an elevational climate gradient, and by initiating an annual snowmelt manipulation at the new sites. The goal of the expanded study was to explore interactions between climate change and subalpine meadow ecosystems through a systematic combination of experimental and natural gradient research approaches within a single study. Our research design provides two types of experimental climate change (warming via infrared radiators, early snowmelt via spring snow removal) and three types of natural climate variability (small-scale within-site spatial variability, landscape-scale among-site spatial variability, interannual variability) against which to evaluate ecosystem responses. By comparing responses of subalpine meadow properties to natural and manipulated climate change, we demonstrate one of many possible ways to integrate multiple field methods in climate change research, and we explore the utility of this type of integration for interpreting and generalizing research results.

The study sites are located at and near the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, USA. Our research focuses on ungrazed, dry meadows whose dominant shrub is mountain big sagebrush, *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Boivin. Snowfall provides ~80% of total annual precipitation, and snowmelt occurs in mid to late spring. In 1990, 10 ''warming meadow'' plots (3×10 m) were established along a moraine ridgeline (Fig. 2a). Three electric infrared radiators, suspended 2 m above each of five treatment plots (Fig. 2b), provide 22 W/m^2 additional heat flux to simulate soil warming predicted from

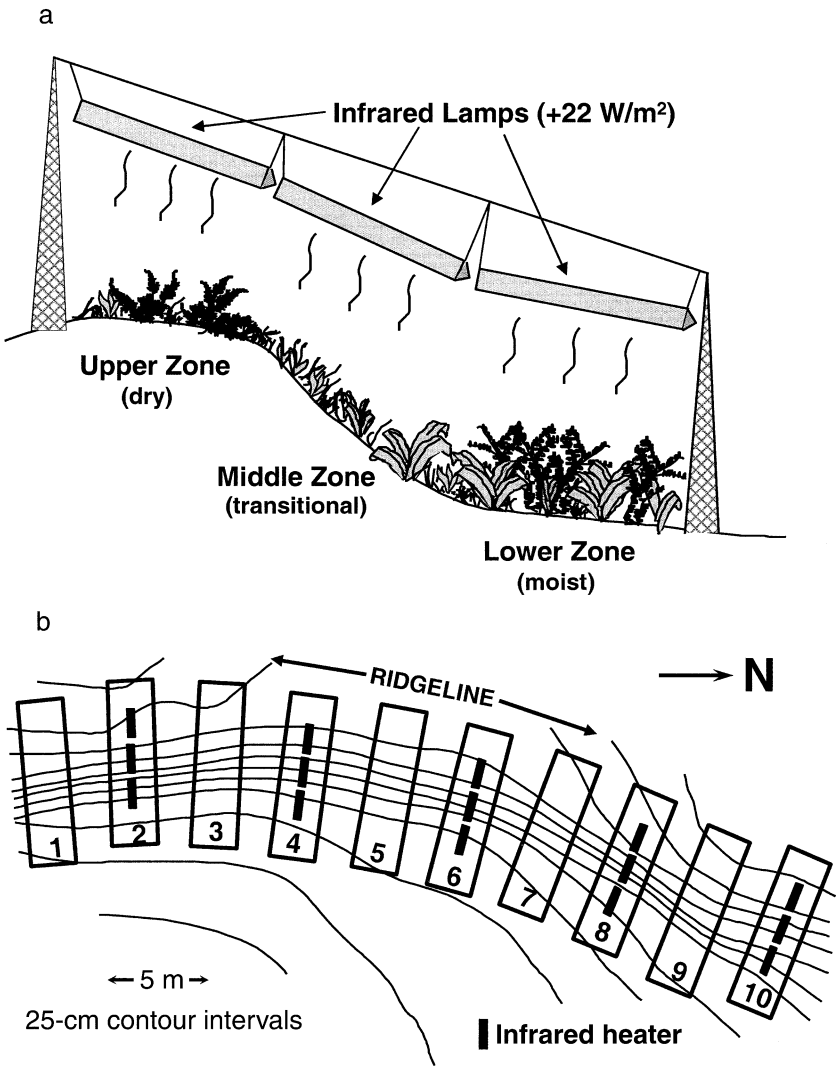


FIG. 2. (a) Lengthwise cross-section of a single experimental warming plot and (b) layout of 10 study plots at the warming meadow. Current research is focused on the upper dry zone along the ridgeline of each plot.

direct plus major feedback effects of doubled atmospheric CO_2 (Harte and Shaw 1995, Saleska et al. 2002). The radiators advance snowmelt by ~2 wk and significantly warm and dry the soil during the growing season. In 1995, we established three additional subalpine meadow ''elevational sites'' (''lower,'' ''middle,'' and ''upper'') spanning 420 m elevation, with five pairs of control and treatment plots (4 × 4 m) at each site (Fig. 3). In the early spring from 1996 through 1998, snow was partially removed via shoveling from each treatment plot, resulting in ~1 week earlier snowmelt but no significant changes to growing season soil temperature or moisture. Detailed methods and microclimate results are reported elsewhere (Harte et al. 1995*b*, Saleska et al. 2002, Dunne et al. 2003).

CASE STUDY 1: PLANT FLOWERING PHENOLOGY

Global warming in high elevation and latitude regions is likely to alter snow regimes, including reductions in snowpack levels and shorter periods of winter snow coverage (e.g., Brown et al. 1994, Whetton et al. 1996). Many researchers have reported strong relationships between snowpack timing and structure and various aspects of plant performance including distribution, growth, productivity, flowering phenology, and reproductive success (see Dunne et al. 2003 for overview). Thus, climate change has the potential to greatly affect vegetation in ecosystems with seasonal snowpack.

We investigated the relationship of flowering phenology, specifically the timing and duration of flowering, of 11 subalpine meadow plant species to variation in microclimate associated with experimental climate change and natural climate gradients (Dunne et al. 2003). Although here we compare experimental and gradient trends between snowmelt date and timing of flowering for one early-flowering species, *Delphinium*

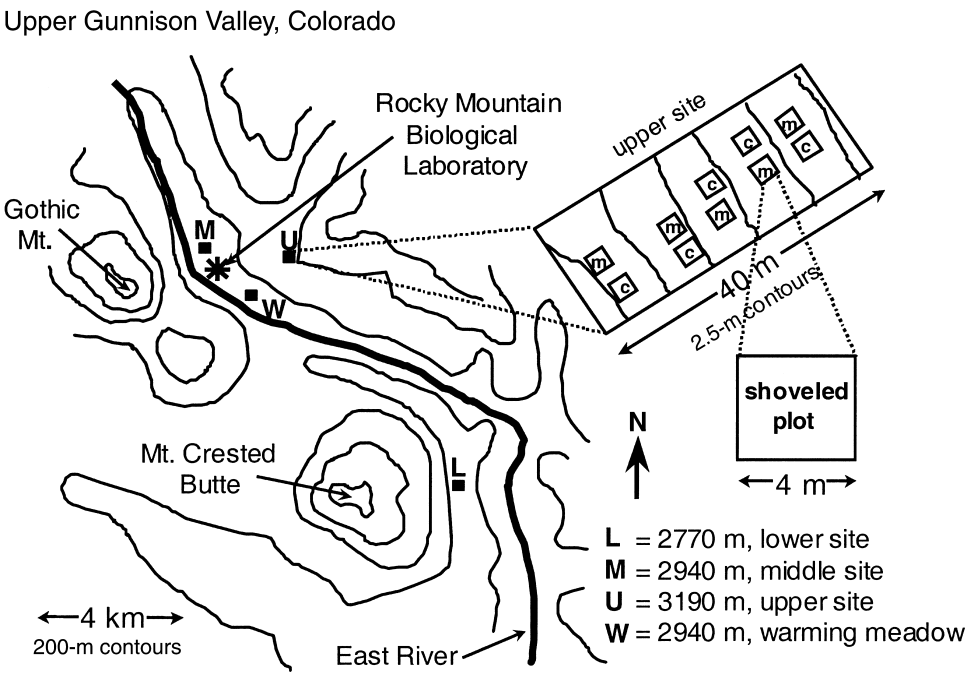


FIG. 3. Map showing the location of three elevational sites and the warming meadow. The inset shows plot layout of a representative elevational site (c = control plot, m = manipulated plot).

nuttallianum Pritz. ex Walp. (larkspur), the results are generally representative for the other species, especially so for early flowering species. In this ecosystem, snowmelt date is a highly significant explanatory variable for timing of flowering in most species (Price and Waser 1998, Dunne et al. 2003). Climate factors, particularly snowmelt date and warmer soil temperatures, explain most of the variability (>80% across eight species) in timing of flowering at our sites (Dunne et al. 2003).

In order to compare simplified trends in phenological response to different types of climate variability, we averaged over each set of control and experimental plots ($n = 5$) at the four sites in different years and plotted the means against average snowmelt date for those plots. We use the average values as a heuristic to look at experimental and natural gradient trends in the context of our simple conceptual model (Fig. 1). We do not describe previously reported detailed statistical analyses (Dunne et al. 2003), and instead focus on a simplified visual representation of overall trends.

In Fig. 4a, we show the effects of the warming manipulation and the snow removal manipulations in different years at the four sites. The experimental trends are similar across sites, between different manipulations, and in different years, and they closely match the overall trend (dotted line). Fig. 4b shows landscape-scale natural spatial gradient trends from higher to lower elevation control plots. There is little separation in either snowmelt date or flowering time from the upper to middle sites, rendering them minimally useful for identifying trends. However, the trends from either of the two higher elevation sites to the lower site in all three years closely match each other as well as the overall trend. Smaller scale spatial trends across individual control plots in different years within the warming meadow site, where there is a strong snowmelt gradient due to changing aspect, are also similar to the overall trend (data not shown, Dunne et al. 2003). Fig. 4c shows interannual trends within all four sites that are similar to the overall trend.

Taken together, these trends demonstrate that regardless of how variation in snowmelt date was induced or monitored, we found a ''consistent'' (Fig. 1a) strong response of timing of flowering to the timing of snowmelt. This, along with more detailed statistical analyses, suggests that snowmelt date has strong, primary control over timing of flowering in *D. nuttallianum* (and other species) that does not vary at different spatial or temporal scales. In this case, we can predict with confidence that to the degree that anthropogenic climate change advances snowmelt date, it will also advance flowering time in a way that is quantifiable from experimental *or* natural gradient data. More sophisticated analyses at finer resolution and across multiple climate variables reinforce these results (Dunne et al. 2003). However, until we directly compared experimental and gradient results, we could not have known that our results would be robust across methods that reflect short term responses (experiments) as well as those that reflect longer term dynamics (gradients).

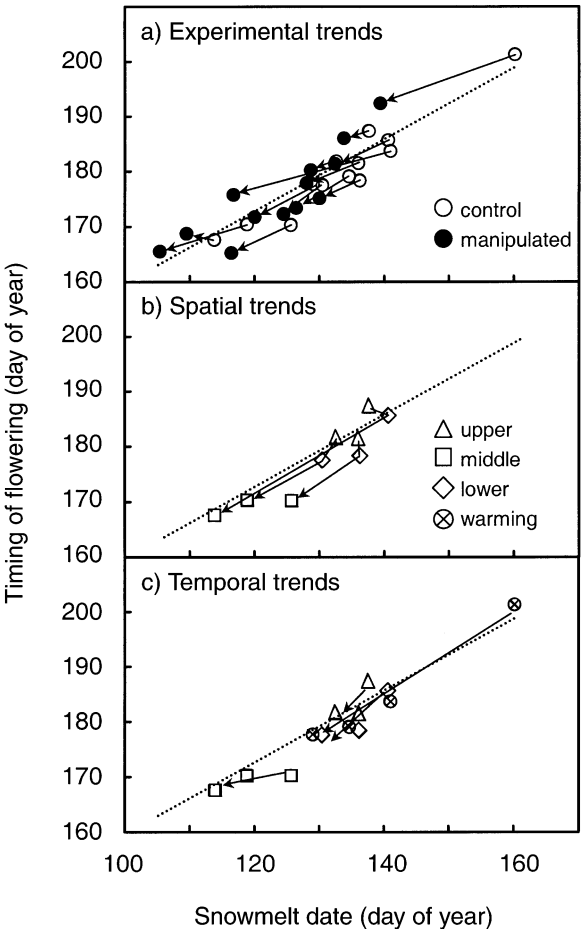


FIG. 4. Experimental, spatial, and temporal trends in the average timing of flowering over each set of control and treatment plots ($n = 5$) of *Delphinium nuttallianum* as a function of snowmelt date. The dotted line shows the overall trend. Spatial and temporal trends are based on control-plot data only. The warming meadow is excluded from spatial trends.

CASE STUDY 2: SOIL CARBON DYNAMICS

Climate change is likely to alter the carbon balance of many terrestrial ecosystems, potentially producing positive and negative feedbacks to anthropogenic buildup of CO_2 in the atmosphere (for reviews see Woodwell and Mackenzie 1995, Lashof et al. 1997, Cao and Woodward 1998). Many ecosystem models assume, with supporting evidence from field and lab studies, that increased temperatures will lead to increased respiration, producing a positive feedback release of carbon from ecosystems (e.g., Tate 1992, Schimel et al. 1994, Kirschbaum 1995, Parton et al. 1995, Trumbore et al. 1996, Cao and Woodward 1998).

In our investigation of short-term soil carbon responses of subalpine meadow to experimental ecosystem warming over a nine-year period, heating induced a dramatic decline in soil organic carbon (SOC) in the top 8–15 cm of soil (Fig. 5). The average decline corresponds to a loss of ~200 g C/m², or an 8.5% decrease, in the top 10 cm of soil in the warmed plots compared to the control plots (Saleska et al. 2002). Since it is not balanced by increases in carbon in fine root biomass, litter, or total aboveground biomass (AGB), it represents a positive feedback to warming. While this pattern of soil carbon loss due to warming is consistent with findings in other ecosystems, laboratory soil incubations and field measurements of CO_2 fluxes indicate that increased respiration is not responsible for the observed drop in SOC in this system (Saleska et al. 2002). Instead, monitoring of aboveground biomass suggests that drier soil induced a shift in plant community composition, with shrubs favored at the expense of forbs in the heated plots (Harte and Shaw 1995, Dunne 2000, de Valpine and Harte 2001). Because forbs, which are not woody, are more productive and have higher turnover rates than the less-productive, slower turnover shrubs, the observed shift in community composition results in less total litter added to the soil, resulting in lower soil carbon storage (Saleska et al. 2002).

When SOC at the warming meadow and the elevational sites is plotted against various climatic factors (snowmelt date, soil temperature, soil moisture), the relationships display nonsignificant overall trends and highly variable subtrends across sites, manipulations, spatial scales, and years (i.e., Fig. 1f, data not shown).

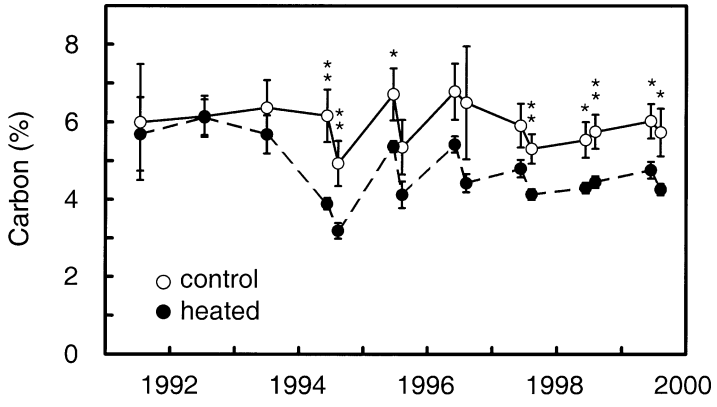


FIG. 5. Control and heated plot soil carbon means (±1 SE; $n = 5$ per treatment in 1991–1993, $n = 20$ per treatment in 1994–2000) vs. year in the top 8–15 cm of warming meadow soils. In 1994, sampling frequency was increased to twice per growing season (mid-June and mid-August), revealing seasonal variation in soil carbon in most years. Reproduced with permission from Saleska et al. (2002).

* $P < 0.05$; ** $P < 0.01$ (two-sample t test, $n = 20$ per treatment).

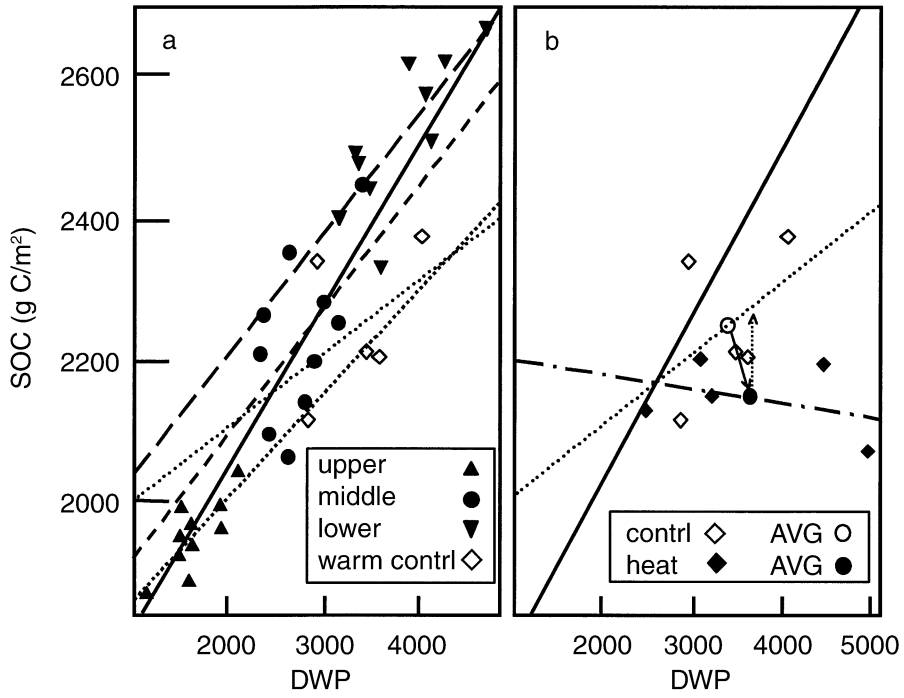


FIG. 6. (a) Observed soil organic compound (SOC) (1997–1998 average, in g C/m^2) vs. 1997 decomposition-weighted productivity (DWP; the soil carbon predictor variable defined in Eq. 1), including least-squares regression lines for each site separately (long dashed line, lower site; medium dashed line, middle site; short dashed line, upper site; dotted line, warming meadow), and for all sites combined (solid line, $r^2 = 0.84$). (b) Observed SOC vs. DWP; same as in (a), but for warming meadow control (open diamonds with dotted line) and heated (solid diamonds with dash-dot line) plots only, with the regression for all plots combined shown as in (a) (solid line). The observed transient shift (solid arrow) from control-plot mean to heated-plot mean and anticipated steady-state recovery (dotted arrow) of heated plot mean are also shown. Reproduced and modified with permission from Saleska et al. (2002).

In particular, the correlation of SOC with mean annual soil temperature had opposite sign depending on whether the temperature variation was due to gradient or experiment (Saleska et al. 2002). Thus, a simple prediction of SOC response to temperature, based on either manipulation or gradient analysis alone, would have been wrong if generalized from only one method. This suggests that a more sophisticated description of mechanisms underlying soil carbon cycling is needed.

While multiple lines of evidence paint a compelling picture of vegetation-mediated mechanisms of short-term carbon loss due to warming in this ecosystem, plant species can differ not only in quantity of litter production but also in quality, and thus decomposability, of litter produced. The influence of litter quality on SOC levels, given changes in climate and resulting changes in vegetation composition, is likely to be expressed over longer time periods than changes in quantity of litter inputs. In this system, while a shift to shrubs adds less litter and thus less carbon to the soil, shrub litter is lower quality and more highly recalcitrant than forb litter, which will tend to slow the release of soil carbon (Shaw and Harte 2001*a*, Saleska et al. 2002).

To examine the net effect of these various controlling factors within the framework of the combined experiment and gradient study, we formulated a simple model of SOC levels that incorporates three controlling factors: (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. The measurement of these factors, conducted in field and laboratory settings, is described in detail in Saleska et al. (2002). 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

$$\text{SOC} \propto \text{DWP} = \sum_{i=\text{forb,shrub,gram}} \frac{p_i \times \text{AGB}_i}{k_i \mu_{\text{site}}} \qquad (1)$$

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, the three factors identified above. Each parameter was quantified for each site to generate a plot-specific SOC level (Saleska et al. 2002).

Among the 30 elevational site plots and five warming meadow control plots, regression of observed SOC levels against the predictive DWP variable produced a strong relationship across all plots ($r^2 \approx 0.8$; Saleska et al. 2002). Additionally, regressions within each site

are largely consistent with each other and the overall trend (Fig. 6a). In contrast, a regression of SOC against DWP across the heated plots at the warming meadow is poor ($r^2 < 0.06$, Saleska et al. 2002), presumably because the longer-term influence of changes in litter quality is not expressed in the observed short-term response to warming (Fig. 6b).

By incorporating an understanding of ecosystem responses to experimental heating and along natural spatial gradients, we predict that dramatic, short-term soil carbon losses will be followed by long-term recovery of soil carbon levels in this ecosystem (i.e., a version of the ''reversed'' scenario of Fig. 1d; Fig. 6b). This may occur in any ecosystem where drought tolerant, low-productivity, and low-turnover species with recalcitrant litter are likely to replace drought intolerant, high-productivity, and high-turnover species with higher quality litter. The SOC–DWP relationship may be useful for postulating differences or similarities between short- and longer-term effects of climate change in different ecosystem types. In this water-limited subalpine meadow ecosystem, an exclusive focus on either an experimental or gradient approach would have yielded an incomplete understanding and misleading prediction of soil carbon response to climate change.

Conclusion

The potential complexity of terrestrial ecosystem responses to anthropogenic climate change requires that scientists develop understanding of those responses that is both mechanistic and general, facilitating robust predictions about climate-ecosystem interactions. In particular, it is important to distinguish among ecosystem responses that are consistent and readily generalizable, responses that shift at different temporal or spatial scales, and responses that are highly context dependent. The varied field methodology that exists for examining ecosystem response to changing climate, including both experimental and natural gradient approaches, provides a unique opportunity for inter-method comparison and synthesis. Both community-oriented research (e.g., reproductive phenology) and ecosystem oriented research (e.g., soil carbon dynamics) can benefit from this type of integrative approach. Our work provides an explicit and comprehensive integration of ecosystem-level climate change experiments with natural spatial and temporal climate gradient research methods across multiple sites within a single research program.

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