

Shifts in plant dominance control carbon-cycle responses to experimental warming and widespread drought

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Abstract

Global climate change is predicted to increase the intensity and frequency of future drought, which in turn may be expected to induce a range of biogeochemical climate feedbacks. A combination of model simulations and observational studies of a recent wide-scale drought, suggested that the drought induced substantial terrestrial ecosystem carbon loss, but hypothesized mechanisms could not be evaluated via comparison to a control. Here, we investigated carbon-cycle responses to climate changes by combining results from a controlled 15-year ecosystem warming experiment in montane grassland with observational data from before and during the recent drought. We found that both experimental warming and real-world drought induced substantial soil carbon loss in our study system, and that the same mechanism, a drying-induced shift in plant species composition and an associated decline in community productivity, provides a common explanation for these declines in soil carbon.

Keywords: carbon, climate, drought, vegetation, feedback

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1. Introduction

Global climate change is expected to have substantial hydrological impacts, and is specifically anticipated to increase the intensity and frequency of drought in many continental interiors [1, 2]. Some reports suggest that these impacts are already being observed, and that current climate change contributed to the pattern of sea-surface temperatures that drove the widespread drought in the US, Europe, and Southwest and Central Asia in 1998–2002 [3]. Model simulations [4] and observational studies [5, 6] suggest that this wide-scale drought induced substantial terrestrial ecosystem

carbon loss. Here, we tested whether ecosystem-scale mechanisms previously deduced from a controlled climate manipulation experiment were also consistent with observed effects of the real-world drought on the same experiment. We are thus able to directly evaluate causal mechanisms underlying simulated and observed carbon cycle effects.

2. Field site and methods

Our long-term ecosystem warming experiment was conducted on the western slope of the Colorado Rockies (38°57' N; 106°59' W; 2920 m elev.), where in 1990 we established ten 3 m × 10 m plots, each spanning in the long direction an elevational, microclimate, and vegetational gradient from a dry ridgeline down to the edge of a willow bog [7]. Our focus here is on the upper drier zone of each plot, which is

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⁵ TS used the model in Saleska *et al* [8] to derive predicted soil carbon levels over time.

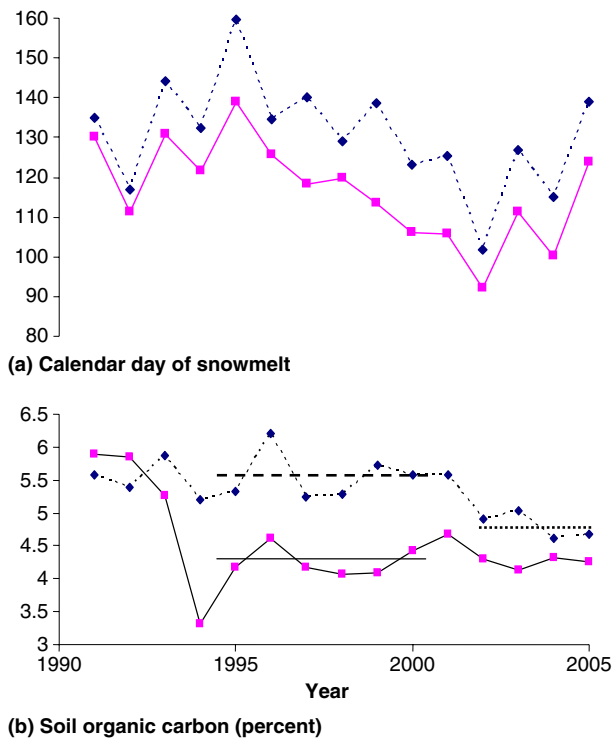


Figure 1. Calendar day of snowmelt (a) and per cent soil organic carbon (SOC) (b) in control (dotted line) and heated (solid line) plots from 1991 to 2005. Heating treatment (pre-drought) reduces the SOC (dashed versus solid horizontal lines, 1995–2000) by 1.25 ± 1.09 per cent units (95% confidence interval, two-sample t -test, $n = 10$ plots). The control plot SOC after drought onset (2002–2005, horizontal dotted line) is $0.85 \pm 0.45\%$ units less (95% confidence interval, paired t -test, $n = 5$ plots) than the pre-drought average (1995–2000, horizontal dashed line). Each treatment data point is an average over five replicate plots.

most typical of the meadow habitat throughout the montane West. In that zone, the dominant vegetation consists of a woody shrub (*Artemisia tridentata*, or sagebrush), a bunch grass (*Festuca thurberi*), and, within each plot, ~25 species of forbs (including *Erigeron speciosus*, *Delphinium nelsonii*, and *Helianthella quinquerivis*). Five of the plots have been continuously heated since the beginning of 1991 with overhead heaters that provide on each plot a nearly uniform infrared radiation flux of 22 W m^{-2} . The top 10 cm of the soil are warmed by approximately 2°C and dried by approximately 15% (gravimetric) during the growing season [7, 8]. Each spring the heaters advance snowmelt by approximately two weeks relative to the timing of snowmelt in the control plots (figure 1(a)). Interannual variation in snowmelt date in this region is a direct index of coincident variation in wintertime snowfall ($r = 0.9$, $n = 30$ years: 1975–2005), which accounts for 80% of annual precipitation.

The Southwestern US experienced severe, protracted drought and anomalously high temperatures in the years spanning the beginning of the millennium which started in 2001 [6]. By 2002, moderate to severe drought conditions expanded to over 50% of the continental US, and severe drought persisted in the interior Western US through 2004 [9].

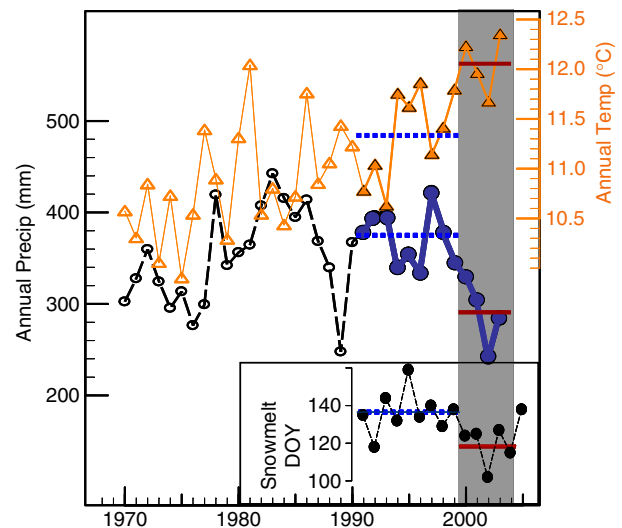


Figure 2. Annual mean precipitation (mm) and average of minimum and maximum temperatures ($^\circ\text{C}$) for all stations in Southwest North America (CO, UT, NM, AZ) [6], with data highlighted (bold points and line) for the years of the warming experiment, and with recent drought years (2000–2004) indicated by vertical shaded band. Mean precipitation during drought (solid horizontal line at 288 mm, 2000–2003) is $\sim 20\%$ lower than before drought (dotted line at 372 mm, 1991–1999). Inset: snowmelt day of year (DOY) for warming experiment control plots. Drought snowmelt (solid horizontal line, 2000–2004) arrives 18 ± 2 days earlier (95% confidence interval, paired t -test, $n = 5$ plots) than before drought (dotted blue horizontal line, 1991–1999).

This drought induced widespread climatic changes that in the experimental warming meadow were, using snowmelt date as an index, comparable to those caused by the heating manipulation (figure 2).

3. Results

During the first ten years of the warming experiment, before the drought, soil organic (SOC, g carbon g^{-1} dry soil) levels in the control plots did not vary, whereas SOC levels in the heated plots declined to a level $\sim 22\%$ below that of the control plots (figure 1(b)), corresponding to a $\sim 200 \text{ g(C) m}^{-2}$ loss of carbon from the top 10 cm of soil [10] (see the supplementary methods available at stacks.iop.org/ERL/1/014001). During those same years, monitoring of aboveground vegetation biomass in each of the three plant growth forms (forb, shrub, and grass) revealed an increase in the aboveground biomass of sagebrush [11, 12], and an approximately compensating decline in that of forbs, especially the shallow-rooted ones [11, 13, 14] (figure 2); biomass in grasses showed no response to warming. Then, during the drought years from 2001 to 2005, SOC levels in the control plots also declined below the levels observed in the first ten years of the experiment (figure 1(b)).

Our previous work [10] demonstrated that the loss of SOC in the heated plots in the first five years of the experiment was caused by a decline in carbon inputs from vegetation community production, a consequence of two distinct effects of soil drying: a direct physiological drought-stress response

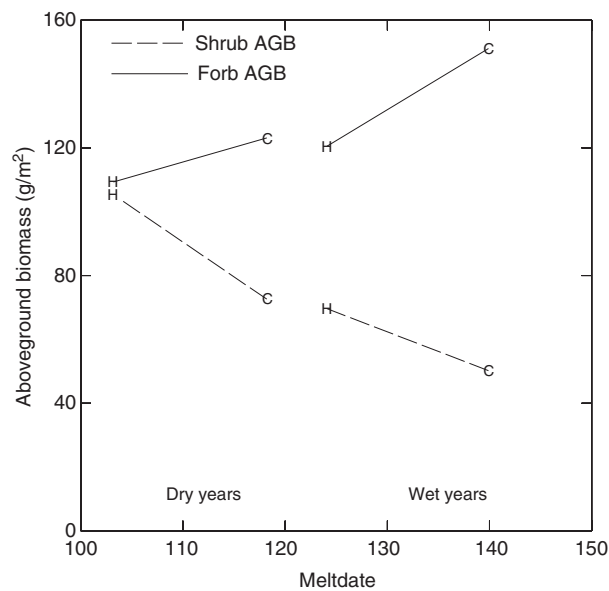


Figure 3. Peak aboveground biomass of forbs (solid line) and shrubs (dashed line) in heated (H) and control (C) plots, as a function of snowmelt date. Biomass data are for the drought years 2000–2004 and pre-drought years 1993–1999. Drought effects are significant for both snowmelt date (see figure 2) and aboveground biomass ($p < 0.05$ in all cases; see the supplementary data available at stacks.iop.org/ERL/1/014001).

to decreased soil moisture [8], and an indirect effect of the shift in species composition, reported above, from forbs to shrubs. Shrubs are more drought tolerant, but less productive than forbs, so forb biomass decline resulted in a decline in forb production approximately twice as large as the increase in sagebrush production [10]. A widely hypothesized alternative explanation for heated-plot SOC decline—a warming-induced increase in soil microbial decomposition and associated carbon loss [15, 16]—was not observed here because of the opposing and, it turned out, canceling effects on decomposition of higher soil temperatures and reduced soil moisture [10].

Could the large-scale 2000–2004 drought anomaly (figure 2) explain the observed drop in control plot SOC during the years 2001–2005? This climate anomaly, similar in character to the artificial warming experiment, although covering a far larger spatial extent, provides a test of whether predictions based on an artificial manipulation are also realized in response to a real-world climate change. Observations on control plots show that, during the years 2000–2004, the large-scale climate anomaly did indeed largely reproduce effects of the experimental warming: the decline in SOC in the control plots following the onset of drought was 15% relative to control-plot SOC in previous, non-drought, years of the study, and this coincides with a shift in species composition from forb to shrub in the control plots (figure 3). Thus with respect to both SOC and aboveground biomass (AGB) of vegetation, the control plots responded to the drought in the same way that the heated plots responded to the heaters during the wetter period.

If the mechanisms of SOC loss following drought are the same as those we previously deduced from the warming

experiment, then we should expect that the relative magnitude of the decline in SOC and its proximate causes, the decline in vegetation productivity, should be consistent between experiment and drought. The ratio of the experiment's effect on SOC (in the relatively wet years 1995–1999) to the effect of the drought on control-plot SOC in the comparable 2002–2005 drought years is

$$\frac{[(SOC_{H,wet} - SOC_{C,wet})/SOC_{C,wet}]}{[(SOC_{C,drought} - SOC_{C,wet})/SOC_{C,wet}]} = \frac{-22\%}{-15\%} = 1.46 \quad (1)$$

where C and H refer to control and heated plots, and wet and drought refer to the two intervals of years with contrasting climate conditions. SOC levels in the heated plots did not decline between the second half of the wet period and the dry period.

From the measured changes in vegetation AGB we can estimate the ratio of the differences in vegetation production corresponding to the numerator and denominator on the left side of equation (1). The experimental heating effect on AGB during the pre-drought years (heated minus control AGB, averaged over 1993–1999) was $-15.3 \text{ g(C) m}^{-2}$ for forbs and $+9.7 \text{ g(C) m}^{-2}$ for shrubs. The drought's effect on control-plot AGB (the 2000–2004 average minus 1993–1999 average for controls plots was $-13.9 \text{ g(C) m}^{-2}$ (forbs) and $+11.2 \text{ g(C) m}^{-2}$ (shrubs) (figure 3)). The annual biomass production per unit of forb AGB was found in previous work to be ~ 2.25 greater than that from a unit of shrub AGB [10]. Hence, the ratio of the experiment effect to the drought effect (following equation (1)) on productivity is $[9.7 - 2.25(15.3)]/[11.2 - 2.25(13.9)] = 1.23$, within experimental uncertainty of the observed ratio of effects on SOC (equation (1)).

Further evidence that this mechanism is correct comes from a comparison of SOC levels in the heated plots during the same wet and dry periods. The ratio analogous to that in equation (1) indicates negligible change:

$$\frac{[(SOC_{H,drought} - SOC_{H,wet})/SOC_{H,wet}]}{[(SOC_{C,drought} - SOC_{C,wet})/SOC_{C,wet}]} = \frac{-1.5\%}{-15\%} = 0.1. \quad (2)$$

Between these two periods, heated-plot forb AGB declined by 5.6 g(C) m^{-2} and shrub AGB increased by 17.6 g(C) m^{-2} ; therefore we find that, for plant productivity, the ratio of the drought effect on heated plots to its effect on control plots is $\sim [17.6 - 2.25(5.6)]/[11.2 - 2.25(13.9)] = -0.2$, in accord with small observed value for the corresponding ratio of the drought effect on SOC (equation (2)).

4. Discussion and conclusions

We conclude that the observed effects of the warming manipulation on SOC in the heated plots and the effects of a widespread drought on SOC in the control plots are consistently explained by the shift in primary production that in turn is associated with shifting species composition in the plant community. By identifying the common mechanism using the combination of a controlled experiment and time-series observations during climate changes, we strengthen

the inference of a carbon dioxide release during drought, and thus of a possible positive feedback response to climate change. If anthropogenic global warming makes such droughts more common, as anticipated by some model studies [1] and as implied by long-term reconstructions revealing extended mega-droughts in North America during the medieval warm period [9], this work provides empirical confirmation of predictions of significant short-term positive feedbacks to warming.

What effects can be anticipated over time periods longer than that of the experimental warming and the recent drought? Although shifts in species composition from forbs to shrubs reduced carbon inputs to the soil in the short term, they will also reduce the decomposability of bulk litter due to the greater recalcitrance, as measured directly by species-specific litter decomposition rates in the field, or indirectly by species-specific measures of litter chemistry such as lignin:nitrogen ratio of shrub litter compared to forb litter [17]. Our semi-empirical mass balance model (see the supplementary methods available at stacks.iop.org/ERL/1/014001) used to quantify the combined effect of changes in annual production and litter quality shows that a change in litter quantity exerts its influence rapidly, whereas a change in litter quality exerts a longer-term control on SOC.

Thus in the absence of further shifts in vegetation composition, we should expect at least partial recovery of SOC levels due to the effect on SOC residence time of poorer litter quality. This prediction can be tested at the local scale by continued observations locally, and at the large scale by, for example, the global atmospheric CO₂ dataset [18], which we expect to show a negative growth rate anomaly following the recently identified positive anomaly due to drought [4].

Plant species shifts induced by climate change can thus mediate feedbacks to climate change differently on different time scales. These results have significant implications for modeling of carbon-cycle responses to global change effects, and for the prediction of the magnitude of future climate change, since most current coupled global climate-carbon-cycle models [19, 20] do not simulate shifts in species composition.

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