

# Global Warming and Terrestrial Ecosystems

We applaud Shaver et al. (2000) for an excellent article stressing the complexity of ecosystem responses to direct and indirect effects of global warming, as well as the range of time scales over which to expect responses. Furthermore, the individual case studies summarized in the article show how diverse the initial responses to experimental warming may be across ecosystems, and hint at a variety of causal mechanisms. For example, Shaver and colleagues relate short-term loss of soil carbon in some ecosystems, such as the Toolik Lake site studied by Shaver and Chapin, to increasing heterotrophic respiration under warming. In contrast, shifts in vegetation composition and litter quality are proposed as the causal mechanism for carbon loss in a subalpine meadow studied by Harte and colleagues.

Readers should be aware, however, that the evidence is mixed for a vegetation shift in the subalpine meadow. Whereas Harte and Shaw (1995) concluded that warming had induced a shift in species composition from forbs toward shrubs, a more complete analysis of spatial and temporal patterns (Price and Waser 2000) showed that shrub cover was higher in warmed plots, just by chance, even before heaters were turned on in 1991. No subsequent vegetation shift in warmed relative to control plots could be detected through 1994, essentially the same period considered by Harte and Shaw. As an explanation for this lack of response, we suggested that more rapid drying of soils in warmed plots compensated for earlier snowmelt, causing the effective growing season length to be unaffected by warming. This raises the likelihood (also mentioned by Shaver et al.) that correlated changes in precipitation will have greater effects than an increase in temperature itself in arid ecosystems (including some montane ecosystems). If these interpretations are correct, any present-day difference in soil carbon between warmed and control plots at Harte's site may simply reflect the preexisting differences among plots in shrub cover and litter

type. Alternatively, if there has been a true differential loss of carbon in warmed plots, some mechanism other than shift in vegetation type apparently must be responsible.

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## Response from Shaver:

Price and Waser strongly support the conceptual approach to interpretation of responses to global warming that we describe in our paper. Their overall favorable comments are much appreciated. Because their criticisms are narrowly focused on just one of the specific examples we used, and because their dismissal of that particular example does not seem to affect their overall evaluation of our paper, as a group we can only be pleased.

In fairness, though, a response to their specific criticisms is also appropriate. For that, we direct readers to the accompanying letter by John Harte.

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## Response from Harte:

Price and Waser's overall enthusiasm for our article is gratifying. But on the narrower issue they raise, ample evidence

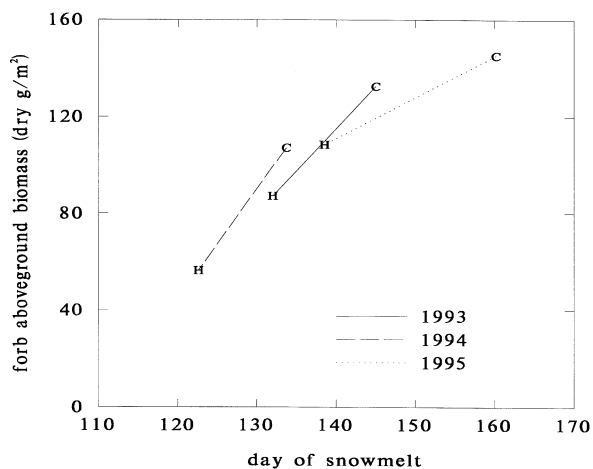
contradicts their suggestion that some mechanism other than a decline in forb production is needed to explain an observed decrease in soil organic matter in our meadow-warming experiment. This study, now in its tenth year, concerns warming and drying soil and causing earlier snowmelt (Harte et al. 1995). Numerous effects on the phenology, growth, and physiological state of the vegetation in the plots have been observed. For example, forbs in heated plots show significant reductions in aboveground biomass (AGB) (Harte and Shaw 1995), net primary productivity (Saleska et al. 1999), and shoot elongation rates (de Valpine and Harte 2001), as well as physiological responses indicative of stress under drying (Loik and Harte 1996, 1997, Loik et al. 2000). Sagebrush (*Artemisia tridentata*) in heated plots shows enhanced aboveground biomass, shoot elongation rates, and seedling success (Harte and Shaw 1995) and physiological responses indicative of increased vigor under heating (Loik and Harte 1996, 1997, Loik et al. 2000, Shaw et al. 2000).

Price and Waser suggest that observed vegetation treatment differences may simply reflect putative differences in vegetation cover prior to the onset of heating. To test their suggestion, we exploit the fact that snowmelt date is unambiguously advanced by the heating treatment and that before the onset of heating, meltdate did not differ between the two treatment groups. A plot of total forb AGB in each treatment group against date of snowmelt for the years 1993–1995 (Figure 1) shows that the heating effect and the interannual variability within just the control plots

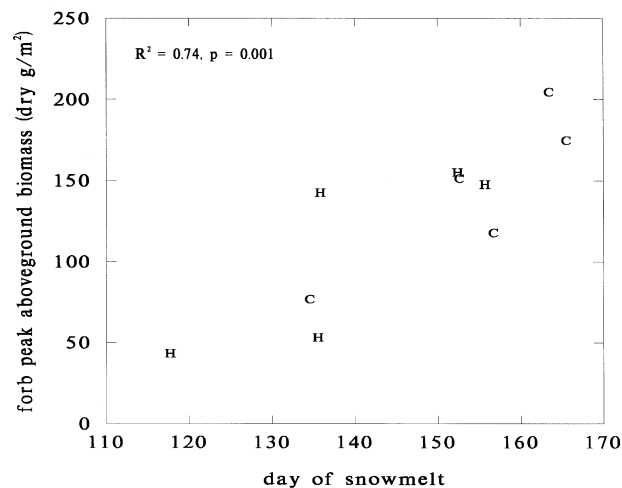
## Letters to the Editor

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**Figure 1.** Forb aboveground peak biomass in the control (C) and heated (H) plots, as estimated by areal coverage measurements described in Harte and Shaw (1995). SEM ( $n = 5$ ) values for these measurements averaged  $18 \text{ g/m}^2$ , with the largest SEM,  $24.6 \text{ g/m}^2$ , in the heated plots in 1995.



**Figure 2.** Forb aboveground peak biomass in each of the control (C) and heated (H) plots in 1995. Within-year, between-plot regressions of forb AGB against meltdate are highly significant in 1994 and 1995 ( $p = 0.017$  and  $.001$ ;  $r^2 = 0.53$  and  $0.74$ , respectively) and marginally significant in 1993 ( $p = 0.10$ ;  $r^2 = 0.30$ ).

depend in a similar manner upon day of snowmelt. Warming-induced early snowmelt thus appears to be the major cause of the observed decline in forb AGB in the heated plots. Further confirmation of this conclusion is provided by examining plot-to-plot variation in forb AGB versus date of snowmelt; Figure 2 indicates that the within-control-plot relation between meltdate and AGB explains the between-treatment-group pattern of dependence of AGB on meltdate. A plot of *A. tridentata* AGB against soil moisture by treatment and year shows a similar pattern; the dependence of control-plot sagebrush AGB on soil moisture explains a significant fraction of the treatment effect.

In contrast to these results, Price and Waser (2000) did not report a treatment effect on aboveground forb or sagebrush biomass. We suggest that this is because they carried out their censuses in a narrow (25 cm) belt transect located near an edge of the 3-m-wide plots, where the effect of the heat treatment was only slightly felt. In contrast, we conducted our aboveground biomass measurements in  $75 \text{ cm} \times 75 \text{ cm}$  quadrats centered under each heater, which is where the soil microclimate probes are located

and where the effect of the heaters is most intense. Indeed, visual inspection of the heated plots during the time of peak flowering shows clearly that the density of forb flowers in the heated plots is now greatest along the periphery, where Price and Waser conducted their census. Price and Waser's suggestion that soil drying may have compensated for earlier meltdate, thereby leaving effective growing season unaffected, fails to account, even qualitatively, for the observations that shrub AGB is enhanced, and forb AGB reduced, by drying and by earlier meltdate.

We conclude that a heating-induced, meltdate-mediated, depression of forb production occurred and remains the most likely explanation for the observed loss of soil carbon in the heated plots.

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