

Effects of water addition on above- and below-ground carbon processes across a montane elevational gradient

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Abstract

Local temperature increases and more frequent extreme rainfall events are predicted effects of climate change at high latitudes (IPCC 2007). Precipitation regimes are also shifting, but science is less able to predict these patterns (IPCC 2007). Water balance is critical as it ultimately drives primary production. Yet, there is a lack of understanding about the relative importance of how water influences carbon dynamics in plant communities (Hodkinson et al. 1999, Niu et al. 2007). To be able to use species-specific responses to anticipate the impacts of climate change in montane regions, it is necessary to know how both species and entire communities respond to climate change. We tested the hypothesis that water is a limiting factor for both decomposition of organic matter and for net carbon assimilation in montane and subalpine plant communities. For this study increased water supply resulted in only biologically significant increase in community carbon uptake as predicted and failed to affect soil respiration at the community level. A slight treatment effect of increased below-ground respiration in the watered plots was also shown, especially over time and for the two higher elevations.

The ability of communities to act as carbon sinks depends in part on water availability. Thus, it is important that further studies explore carbon dynamics and

effects of moisture on plant communities for anticipating the impacts of changing precipitation regimes as an outcome of climate disruption.

Introduction

High latitudes and elevations are expected to experience disproportionate temperature increases and more frequent extreme rainfall events in the coming decades due to climate change (IPCC 2007). Shifting precipitation regimes and more frequent extreme rainfall events are more difficult to predict than factors like temperature as local and global climate becomes increasingly variable (IPCC 2007). Nonetheless it is expected that precipitation regimes will be altered everywhere on earth, followed by altered carbon budgets of ecosystems (Saleska et al. 1999).

Both water and temperature are limiting factors for plant growth and productivity (Illeris et al. 2004; Niu et al. 2007). Nutrients and soil type and quality can also be limiting as they influence carbon balance (Espeleta 2002) but it is temperature and water availability that ultimately determine water balance in a system (Saleska et al. 1999). Water balance is critical as it ultimately drives primary production. Yet, there is a lack of understanding about the relative importance of how water influences species composition and dynamism in plant communities (Hodkinson et al. 1999, Niu et al. 2007). Many experiments focus on the role of temperature on plant traits and nutrients cycling but a quantitative understanding of both water and temperature's influence on carbon cycling is needed to anticipate the impacts of climate change on plant communities. The carbon balance of terrestrial plants is mainly a function of (i) carbon fixation through photosynthesis, (ii) carbon release via respiration from autotrophs, and (iii) heterotrophic

(microbial and fungal) decomposition of soil organic matter (SOM). The response of these processes to climate change will determine terrestrial carbon balances.

Changes of the earth's surface temperature and precipitation regimes could stimulate positive feedback to global climate change due to decreased carbon sequestration and water and temperature limitations of terrestrial plants (Niu et al. 2007). Understanding how changing water availability, through local increase or reduction, influences carbon use at the community level provides some basis for anticipating community responses to climate change.

There is evidence that increased water availability influences both species-level alpine plant photosynthesis and growth rates and heterotrophic respiration/decomposition rates. For example, Enquist et al. (1994) found that increasing water supply in alpine plant communities on Pikes Peak, CO raised photosynthetic rates for the alpine forb *Bistorta vivipara*. Photosynthetic rates were higher in watered plots than in controls even during a wetter than average growing season (Enquist et al. 1994). Several arctic tundra studies demonstrate that water availability increases photosynthetic rates and alters respiration rates, but respiration responses have been inconsistent, possibly due to some combination of varying temperatures, humidity and anaerobic soil conditions among studies (Nobrega et al. 2008, Illeris et al. 2004, Sjögersten et al. 2006). Similarly, microbial respiration is dependant on soil moisture in conjunction with soil quality, temperature and aeration (Fisk et al. 1998, Schjønning et al. 2003, Skopp et al. 1990).

While many studies have examined the effects of changing temperature, nutrients, CO₂ and H₂O fluxes at the species level, our ability to link these species-level responses to ecosystem functioning is questionable (Enquist et al. 1994, Totland et al. 1998, Silvola

1990, Williams et al. 1996). To be able to use species-specific responses to anticipate the impacts of climate change in montane regions, it is necessary to know how both species and entire communities respond to climate change.

We tested the hypothesis that water is a limiting factor for both decomposition of organic matter and for net C assimilation in montane and subalpine plant communities. This hypothesis encompasses three prominent hypotheses for alpine ecosystem carbon balance: (i) increased water supply increases rates of heterotrophic respiration, (ii) increased water supply increases net assimilation, and (iii) below-ground heterotrophs will respond quicker than above-ground autotrophs to an increased water supply. I predicted that microbe communities, having short generation times, will respond quickly to additional water, in which case microbe respiration will increase and carbon content of the soil will decrease. Conversely, if added water influences plant processes more than microbes we should see higher photosynthetic and possibly higher plant respiration rates.

This study examines how water influences the main components of the Net Ecosystem Exchange of Carbon (NEE) where $NEE = \text{carbon assimilated by plants} - \text{plant respiration} - \text{heterotrophic respiration}$. Potts et al. emphasizes that measuring both above- and below-ground activity is necessary for understanding ecosystem functional responses to multiple environmental factors (Potts et al. 2006). Measurements were made on watered and non-watered plots of plant communities over an elevational gradient. Flux differences among sites suggest additional importance of elevation on the response of communities to added water. Although other factors are at work besides elevation in making each community along the gradient unique, it should be noted that more than 50% of plant species are present at all three sites.

To assess whether water is a significant limiting factor for soil heterotrophs we measured rates of decomposition (soil carbon content) and rates of soil respiration. We will simultaneously assess whether water is a limiting factor of net assimilation for montane and alpine plant communities by measuring plant cover in the plots and net CO₂ fluxes. Subsequently, by measuring both soil heterotrophic and plant responses to added water we were then able to assess whether responses are equally expressed between heterotrophs and plants to address the third hypothesis that below-ground heterotrophs will respond quicker than above-ground autotrophs to an increased water supply.

Methods

The three studies sites in Washington Gulch, north of Crested Butte, CO are arranged on south/southwest aspects on an elevational gradient from about 2,600m to 3,350m between lower Mt. Crested Butte and the abandoned Painter Boy mine on Mount Baldy.

Five 1.2 x 1.2m plots were chosen for water treatment along side five control plots of the same dimensions at three sites. Plots were selected to capture the plant community variation at each site. The water treatment plots received 16.9 liters of water each week (1 cm depth). This is close to the average weekly precipitation for June-August for the years 1990-2007 (excluding 1990 data due to disorganized formatting) (RMBL weather records). This amount aims to simulate what would be a wetter than average summer for this area.

Treatment plots were watered once each week for four weeks between June 24 and August 14, 2008. Watering was started at each site based on phenology; beginning

when flowering species approached peak flowering. Carbon flux measurements were done on both the watered and control plots three times during the summer, the first measurements being done before the first watering. Measurements were taken approximately four days after a watering event. Net assimilation was measured with a Li-cor 7500 CO₂ and H₂O analyzer during the photosynthetic peak of the day, between 11:00 and 13:00 hours, when there was no cloud cover. To measure respiration and assimilation for a given plant community, a 1.2 m³ tent permeable to photosynthetically active radiation (PAR) was placed on a plot over the Li-7500. The Li-7500 was fitted with fans to circulate air in the closed system. The tent material allows passage of approximately 70% PAR through, so net assimilation measurements are likely conservative. The Li-7500 measured CO₂ and H₂O flux on each plot for 90 seconds. It has been shown that the pressure gradient caused by changing concentrations of CO₂ and H₂O in the closed system begins to affect stomatal conductance after about 90 seconds (Huxman et al. 2004a, Potts et al. 2006). This length of time also mitigates the effect of increasing temperature on the plants under the tent.

Soil respiration was measured three times at each site with a Licor-6400. The soil chamber on the Li-6400 rests on a PVC ring set in the ground to prevent atmospheric air leakage into the chamber. Two measurements were taken for each plot.

In the laboratory, soil carbon content and soil moisture was measured by burning soil samples from the plots. Two soil samples were collected from the top 10 cm of soil at each plot. These top 10 cm should contain most roots and microbes (Cable et al. 2004).

Biomass of shrubs, herbs, grass, soil and rock were calculated by measuring percent area cover of each plant type and plant height measurements. Additionally plant leaf

surface temperatures were measured during daytime and nighttime flux measurements as well as soil and ambient air temperatures, to take into account the effect of temperature on respiration and assimilation.

Results

The growing season for Washington Gulch was drier and warmer than average. The adjacent valley to the East received 8.2 cm for the duration of the experiment (June 24 to Aug 12). The average summer rainfall (June-August) for the years 1990-2007 is 17.99 cm, approximately twice the amount received this summer (data provided by Billy Barr, RMBL weather station). Since flux measurements were started at peak flowering phenology at each site the low site measurements were conducted during the driest part of the summer while the high site received substantially more precipitation.

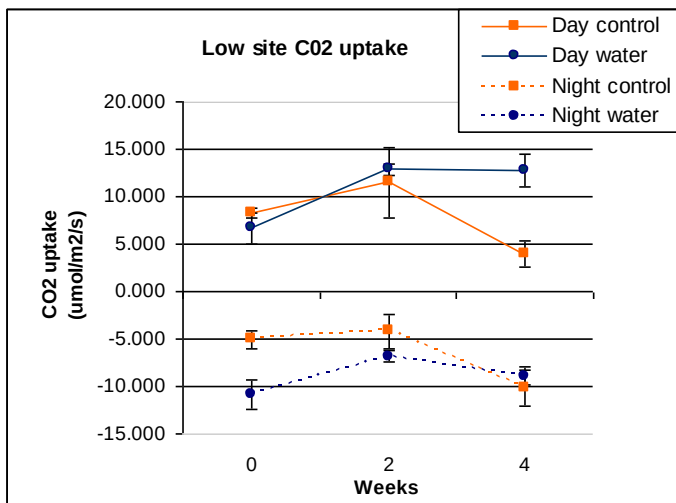
More than 50 percent of plant species occurred at all three sites. The low elevation site was dominated by sage brush (*Artemisia aggregata*), while both the middle and high sites were dominated by *Veratrum Californicum* and *Ribes montigenum*. Many species of the family Asteraceae were present at all three sites.

Community Flux

Daytime community CO₂ flux (NEE_{day}) measurements were similar for watered and control plots for the three measurement periods spanning four weeks. By the third measuring period the watered plots had greater CO₂ uptake than control plots for the low and middle elevation sites although the differences were not significant. The high site had significantly greater CO₂ uptake than the lower sites for both watered and control plots for the first two measurement periods. Nighttime community respiration rates

experienced almost no change over the summer for both watered and control plots at all three elevations. The greatest differences between watered and control plots for nighttime community flux measurements occurred during the first measurement period before water addition began. This was true for the two lower sites. Respiration rates for watered and control plots converged for the second and final measurements at these sites (see Figure 1 a-b).

a



b

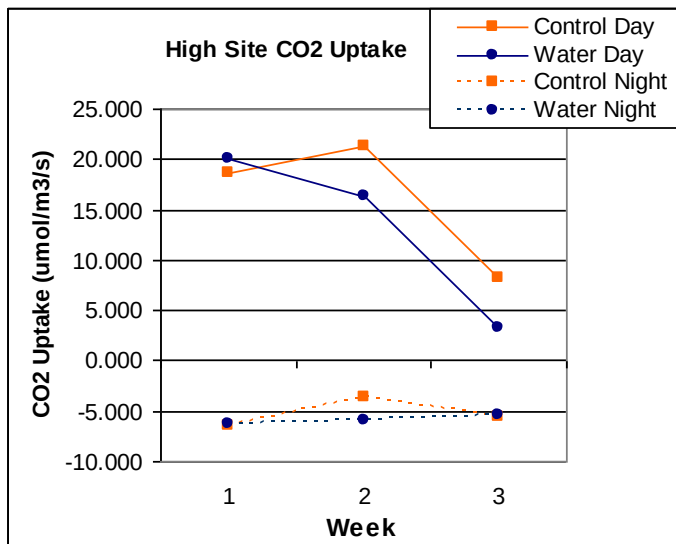


Figure 1. a-b Community CO₂ fluxes represented as CO₂ uptake by plant communities at the lowest elevation site. Times 1-3 refer to the three sets of flux measurements taken on (1) 24 June 2008, (2) 7 July 2008, and (3) 22 July 2008. Low site community fluxes are displayed in figure **a** and high site fluxes are shown in **b**.

Soil respiration

No significant difference between night and day soil efflux was found for any combination of elevation and treatment. Treatment effects varied between sites. The low site saw a significant increase in respiration over time for both treatments (control treatment: $p=0.003$, water treatment= 0.002). Middle site soil respiration decreased significantly and then increased for the three treatment periods for the control plots ($p=0.002$) but the watered plots' respiration did not change ($p=0.656$). There was no significant difference between measurements for either water or control plots over time at the high site (control treatment: $p=0.957$, water treatment= 0.110).

There was found to be no treatment effect on soil temperature. There was also no strong correlation between soil temperature and respiration rate for either treatment. However above-ground flux rates (proportion of NEE) sometimes showed a significant negative correlation to soil temperature. Soil temperature analysis for the high elevation site is not included here.

Above- and Below-ground Components of NEE

The above-ground contribution (leaf respiration and assimilation) and below-ground contribution (roots and heterotroph activity) to NEE were separated by subtracting soil respiration rates from community flux rates per plot given the equation (Huxman, Travis, personal communication):

$$\text{Above-ground flux rate (umol/m}^2\text{/s)} = \text{NEE}_{\text{plot}} - (\% \text{ soil cover}_{\text{plot}} \times \text{average soil respiration}_{\text{plot}})$$

$$\text{Below-ground flux rate (umol/m}^2\text{/s)} = (\% \text{ soil cover}_{\text{plot}} \times \text{average soil respiration}_{\text{plot}})$$

Here soil respiration is scaled for the proportion of bare ground in the plots to account for the barrier for CO₂ created by canopy architecture (Potts et al. 2006). Above-ground processes make up over 90% NEE during the day (10:00am-12:00pm) and over 70% of NEE at night (10:00pm-12:00am). There was no difference in the contribution of above-ground processes to NEE for daytime measurements between treatments (See Figure 2). This was true for above-ground processes at all three elevations.

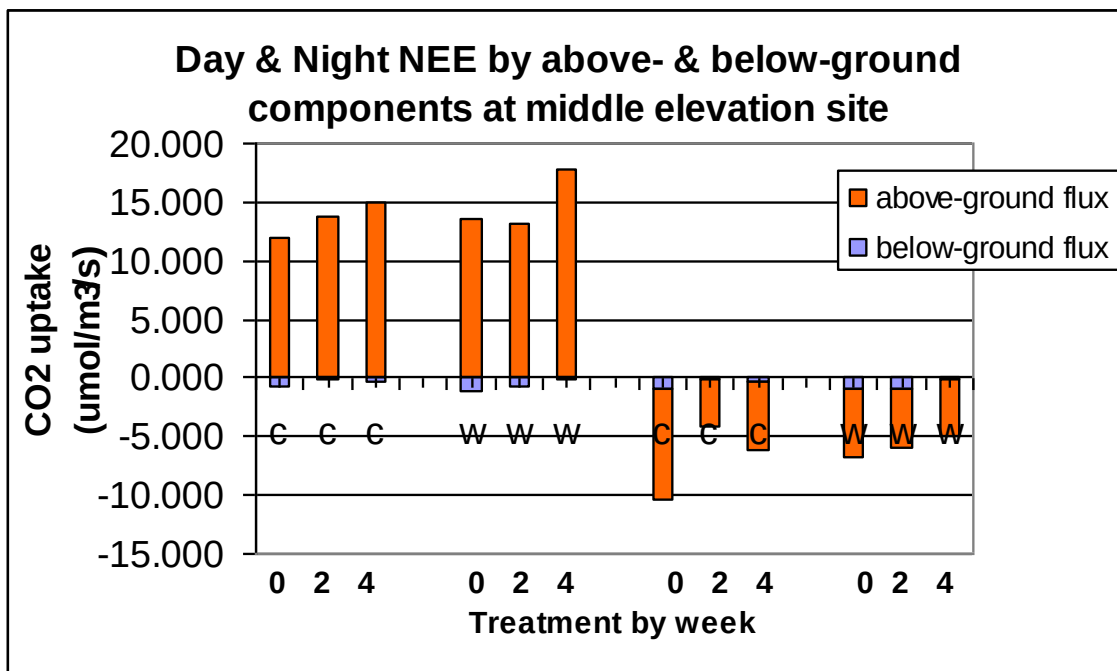


Figure 2. NEE exchange represented by CO₂ uptake for all three measurement periods indicated by weeks 0,2,4 on the x-axis. Control plot averages are marked with 'c' and water plot average are marked with 'w'. Above-ground flux includes daytime assimilation and respiration by above-ground autotrophs and below-ground flux includes respiration by roots and heterotrophs. The first set of control and water measurements (with positive above-ground flux) are daytime NEE and the following set is nighttime NEE.

The high and middle sites had a higher contribution of nighttime NEE by below-ground processes for the watered plots. The high site increased below-ground respiration over the measurement period (See figures 3 a-b). The low site did not change above- and below-ground contributions over time.

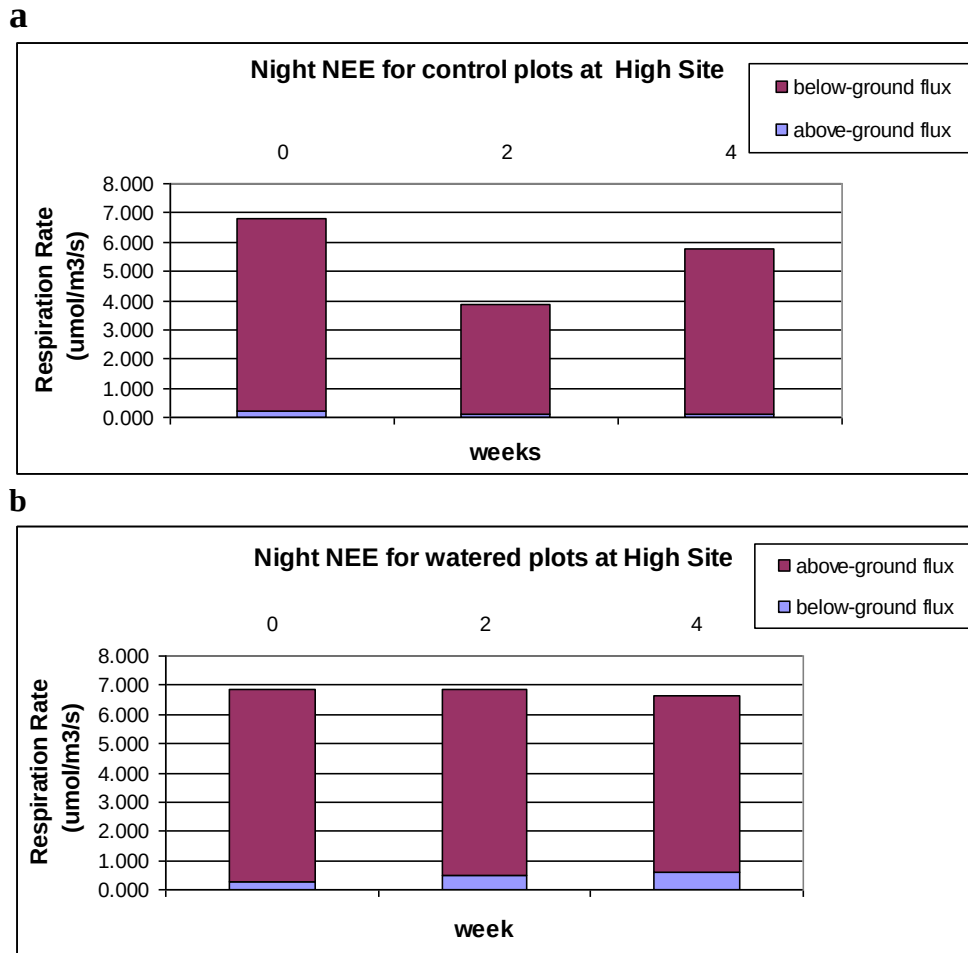


Figure 3 a. control plots and **b** watered plots nighttime NEE separated into relative contributions of above-ground and below-ground CO₂ fluxes. Week of measurement is on the x-axis.

Discussion

For this study, increased water supply resulted in only biologically significant increase in community carbon uptake as predicted and failed to affect soil respiration at the community level. Additionally, most of the time soil temperature had no effect on flux rates except for above-ground flux which was significantly negatively correlated to temperature about 50% of the time. There also seems to be a treatment effect of increased below-ground respiration in the watered plots, especially over time and for the two higher elevations. This disproportional increase in below-ground flux supports the

hypothesis that below-ground heterotrophs respond faster than above-ground plants to increased water supply. The decrease in daytime assimilation for watered plots between the second and final measurement periods at the high site also suggest increased below-ground activity (negative flux) contributing to lower NEE.

Many other ecosystem properties and functions could help explain the variety of results found in this study. Namely, it is likely that initial community response to water addition was not measured because the treatment effect had lessened by the time flux measurements were taken, four days following the watering events. It is also possible that species-specific responses masked the treatment effect because of different species composition of the plots. Soil quality and drainage would also be influential factors here. Interestingly, the systematic watering schedule may have altered the watered communities' normal carbon dynamics by stimulating a change in microbe community composition. Bacteria respond well to cycling moisture levels while fungi are generally negatively impacted (Clein et al. 1994).

The fact that many of the community responses to added water in this study were insignificant also hints at the possible explanation that water is not limiting productivity in this system. More analysis is needed to understand the underlying mechanisms at work here. Many other studies provide evidence that water is limiting to plant assimilation and NEE in different types of ecosystems (Jasoni et al. 2005, Niu et al. 2008, Huxman et al. 2004, Saleska et al. 1999). Thus, the ability of plant montane plant communities to act as carbon sinks depends, in part, on water availability. It is important that further studies explore carbon dynamics and the effects of moisture on montane plant

communities in order to better anticipate the impacts of shifting precipitation regimes and concurrent abiotic and biotic changes brought about by climate disruption.

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