

Effects of water addition on above- and below-ground carbon processes in montane meadows

Teal Potter

August 2009

AUR program

Rocky Mountain Biological Laboratory

Mentors: Brain Enquist and Christine Lamanna



Effects of water addition on above- and below-ground carbon processes in montane meadows

Abstract

The carbon balance of a system is particularly sensitive to water availability because carbon availability drives both the mechanisms of photosynthesis and decomposition (Huxman et al. 2004 b, Ignace et al. 2007). 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. Soil microbes, (bacteria, fungi) first respond within hours of an irrigation event, while above-ground autotrophs generally do not increase photosynthetic activity until days later (Huxman et al. 2004b). Studying community function at both the species-level and community level over different time scales is needed to reveal the mechanisms controlling carbon balance and the potential impacts of a changing climate on montane systems.

I tested the hypotheses that (1) water is a limiting factor for decomposition of organic matter and for net carbon assimilation in montane plant communities over the course of a growing season and that (2) changes in the rates of carbon uptake and release after a water pulse will differ on a fine temporal scale for three components of a subalpine plant community: below-ground processes, shallow-rooted plant species, and deep rooted plant species. Results from this study suggest that water is one limiting factor to carbon inputs and plant photosynthesis. Below-ground processes respond to added water on a shorter time scale than do above-ground plant processes. More studies like this run concurrently with accurate precipitation modeling will provide greater predictive power for understanding system responses to a changing climate.

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). How precipitation regimes will shift is less predictable.

Nonetheless it is expected that precipitation regimes will be altered everywhere on earth, followed by altered carbon budgets of ecosystems (Saleska et al. 1999). Learning about carbon dynamics is important because carbon feedback can be large, especially at high elevations which may be especially sensitive to climatic changes (Huxman and Turpinseed 2004).

Carbon balance is particularly sensitive to water availability because water drives both the mechanisms of plant photosynthesis and respiration as well as microbial decomposition (Huxman et al. 2004 b, Ignace et al. 2007). Each of these components of ecosystem carbon balance may respond differently to climate events such as rainfall. In the Sonoran Desert of the U.S., a small water pulse generally leads to a net carbon loss as the main response is from microbes in subsurface soil. On the other hand, a large pulse leads to carbon sequestration as plants are able to make use of the water at greater soil depths and also as the surface soil dries, thereby reducing microbe activity (Huxman et al. 2004a). Therefore, it is important to understand how rainfall events affect carbon flux from different ecosystem components, in order to predict how whole systems will respond to climate change.

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 (De Valpine and Harte 2001, Enquist et al.

1994, Totland et al. 1998, Silvola 1990, Williams et al. 1996). A long-term warming experiment in Colorado found that shallow-rooted species were adversely affected by decreased soil moisture, which was a direct consequence of warming (Harte et al. 1995, de Valpine and Harte 2001). Species of similar rooting depths are known to share other functional response traits and therefore may be expected to respond similarly to local abiotic changes like water availability (Cross and Harte 2007). Nevertheless, further research is needed to reveal if the same traits that lead to similar responses to a shifting local climate are also responsible for community-driving processes such as nutrient cycling (Lavorel 2002).

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. To address this question, I conducted two water addition experiments in the high elevation rocky mountains. First, I tested the hypothesis that water is a limiting factor for both decomposition of organic matter and for net C assimilation in montane plant communities over the course of a growing season. Above- and below-ground CO₂ fluxes were measured at three sites spanning an elevational gradient. Additionally, we conducted a water pulse experiment to examine carbon exchange by three community components to understand community function on a finer temporal scale. I tested the hypothesis that below-ground processes, shallow-rooted species (2) and deep-rooted species (2) would increase photosynthesis and respiration activities at different times following a water pulse. For both experiments I predicted that microbe communities, having short generation times, would respond quickly to additional water, in which case microbe respiration will increase and carbon content of the soil will

decrease. For the pulse experiment, I expected to see increased below-ground respiration to be followed by increased rates of photosynthesis and respiration from shallow-rooted plants and then deep-rooted plants. These hypotheses encompass 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 microbes respond quicker than above-ground plants to an increased water supply. Conversely, if added water influences plant processes more than microbes we should see higher photosynthetic and possibly higher plant respiration rates.

Methods

Water addition experiment

The three study sites in Washington Gulch, northwest of Crested Butte, CO were selected to span an elevation gradient from about 2,600m to 3,350m between lower Mt. Crested Butte and the abandoned Painter Boy mine on Mount Baldy. The sites were sloping meadows with varying aspects; the high, middle and low elevation sites have south, west and northeast aspects respectively. Five 1.3 x 1.3m plots were chosen to receive a water treatment alongside five control plots of the same dimensions at the three sites. Plots were selected to represent the plant community composition present at each site. The water treatment plots received 16.9 liters of water each week (1 cm depth). This amount was the average weekly precipitation for June-August for the years 1991-2007 (RMBL weather records). This amount aims to simulate a wetter than average summer for this region.

Treatment plots were watered once each week for four weeks between June 24 and August 14, 2008. Watering commenced as phenology approached peak flowering at each site. Carbon flux measurements were done on both watered and control plots three times during the summer, the first measurements being completed for base-line data, before watering began. Measurements were taken approximately four days after a watering event. Net carbon assimilation was measured with a Li-cor 7500 CO₂ and H₂O analyzer during the photosynthetic peak of the day, between 1100 and 1300 hours, when cloud cover was absent. To measure respiration and assimilation for a given plant community, a 1.3 m³ tent permeable to photosynthetically active radiation (PAR) was placed on a plot over the Li-7500 sensor on its tripod. The Li-7500 was fitted with fans to circulate air in the closed system. The translucent tent allowed approximately 70% PAR to pass inside. Therefore net assimilation measurements are conservative yet consistent. 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 estimated by measuring percent area cover of each category and with plant height measurements and applying a model to calculate biomass.

Water pulse experiment

The two subalpine meadows used for the pulse experiment are the lower elevation and mid-elevation sites from the water addition experiment. Five 1.3m x 1.3m plots were selected, each chosen to represent the meadows' common species as well as containing individuals of the four target species. The two shallow-rooted species at both sites were an aster, *Erigeron speciosus*, and a legume, *Lathyrus leucanthu*. The two tap-rooted species used at the low elevation site were a shrub *Artemisia tridentate*, and *Lupinus argenteus*. Another aster, *Helianthella quinquenervis* replaced *A. Tridentate* at the high site due to switching of the abundances of these species between the two sites. The root length distinctions were based on Harte's classification of a short-rooted plant having fibrous roots less than 10cm (Cross and Harte 2007).

The day before adding the water pulse (day -1), base-line measurements were taken for leaf-level photosynthesis (0930) and nighttime respiration (2130) using a Licor-6400 (Li Cor, Lincoln, Nebraska) infrared gas analyzer with leaf chamber attachment. Daytime and nighttime soil respiration was also measured on two collars per plot simultaneously. Soil temperature, ambient air temperature and leaf surface temperatures were recorded, as well as 10 cm soil cores for gravimetric determination of percent soil water content and percent soil organic carbon to compare against carbon flux data.

A 16.9 liter pulse was added to each plot with a watering can the following morning (0930). Water addition was staggered among the plots to allow for soil respiration measurements to be taken immediately after each pulse. Leaf-level photosynthesis and soil respiration were measured on the plots immediately following water addition (0930), and two rounds two hours and four hours after the water addition (1130, 1430). One set of leaf-level and soil respiration measurements were taken at 2130 on day zero and day one. Two sets were taken at 0930 and 1430 on day one and one set on the morning of day two (0930). Eight plants were chosen at random for leaf readings within the five plots.

Results

Water addition experiment

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 showed 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. Surprisingly, 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 (Fig. 1 a-b).

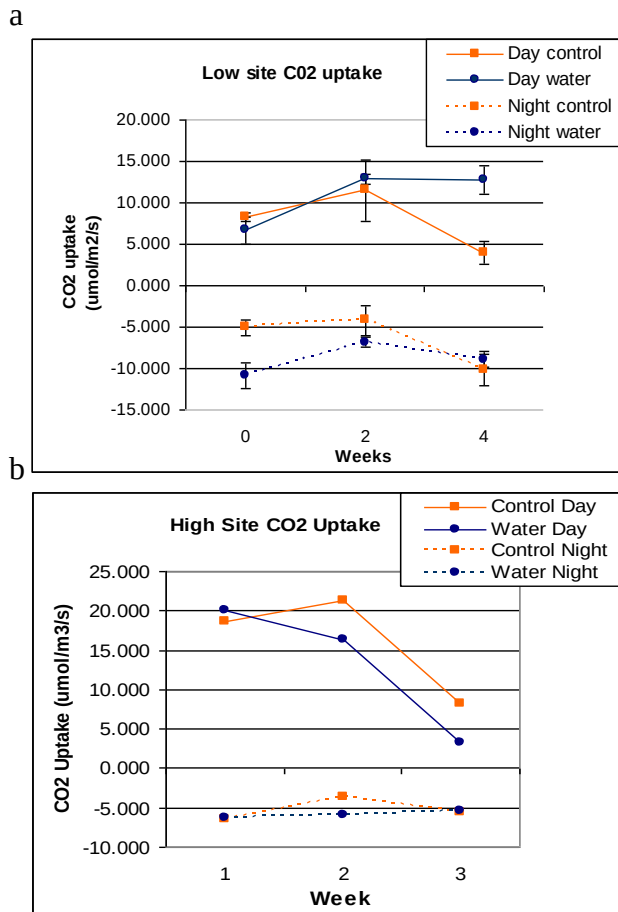


Figure 1. a-b Community CO₂ fluxes represented as CO₂ uptake by plant communities at the lowest elevation site. Times 1-3 refer to the three sets of flux measurements taken on (1) 24 June 2008, (2) 7 July 2008, and (3) 22 July 2008. Low site community fluxes are displayed in figure **a** and high site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

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):

$$\text{Above-ground flux rate (umol/m}^3\text{/s)} = \text{NEE}_{\text{plot}} - (\% \text{ soil cover}_{\text{plot}} \times \text{average soil respiration}_{\text{plot}})$$

$$\text{Below-ground flux rate (umol/m}^3\text{/s)} = (\% \text{ soil cover}_{\text{plot}} \times \text{average soil respiration}_{\text{plot}})$$

Here soil respiration is scaled for the proportion of bare ground in the plots to account for the barrier for CO_2 created by canopy architecture (Potts et al. 2006). Above-ground processes make up over 90% NEE during the day (1000-1200) and over 70% of NEE at night (1000-1200). There was no difference in the contribution of above-ground processes to NEE for daytime measurements between treatments (Fig. 2). This was true for above-ground processes at all three elevations.

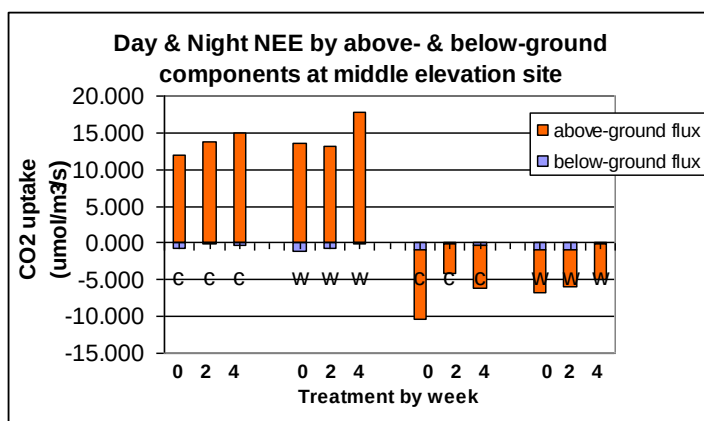


Figure 2. NEE exchange represented by CO₂ uptake for all three measurement periods indicated by weeks 0,2,4 on the x-axis. Control plot averages are marked with ‘c’ and water plot average are marked with ‘w’. Above-ground flux includes daytime assimilation and respiration by above-ground autotrophs and 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.

Water pulse Experiment

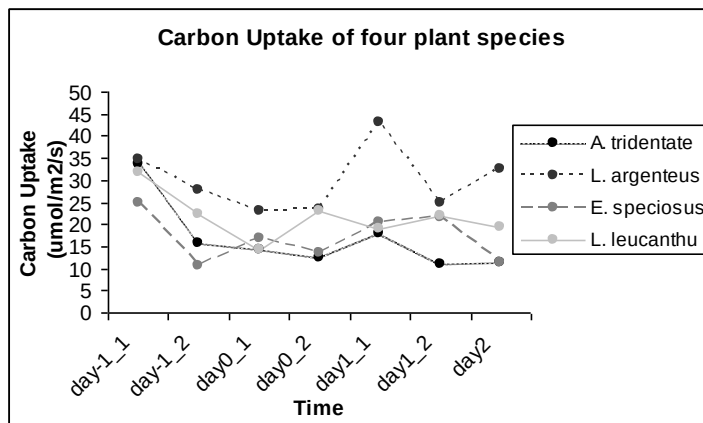
Leaf-level

Each of the four target species at the low elevation site showed different flux activity following the pulse. All species decreased photosynthetic activity during the day of baseline measurements prior to watering. These decreases were significant for the two shallow-rooted species using a one-way ANOVA statistical test and student t test ($p < .001$, *E. speciosus*: $F_{9,67}=18.17$, *L. leucanthu*: $F_{9,69}=19.6$). Shallow-rooted *L. argenteus* produced the only significant increase in CO₂ uptake 24 hours following the pulse. ($p < .001$, $F_{9,65}=34.85$)(Fig. 3a). A comparison of shallow and taproot species daytime assimilation rates revealed that on average, shallow-rooted species began elevating rates of C assimilation immediately following application of the water pulse (see Figure 3b. day0_1). Rates for shallow-rooted species steadily increased until

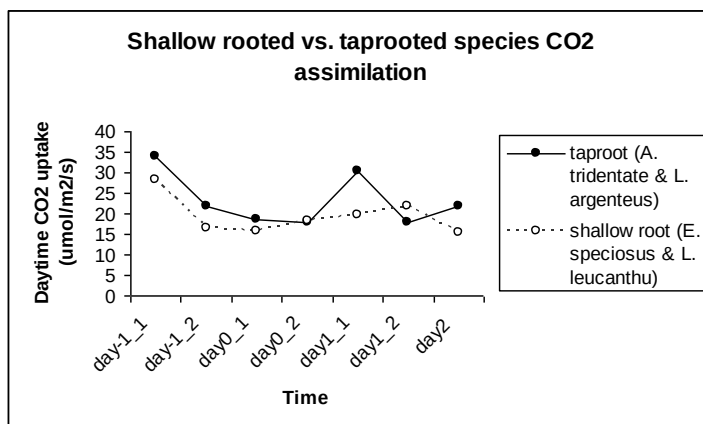
dropping off on day 2 of the experiment compared to the taproot species which showed sharper increases in rate in the mornings one day and two days following the water pulse (Fig 3b).

Nighttime respiration increased for both taproot species following the water pulse, with *A. tridentate* showing a greater increase the first night and *L. argenteus* having the greater increase the second night. Both shallow-rooted species increased respiration the night after the pulse and decreased respiration the following night (Fig. 3c).

a



b



C

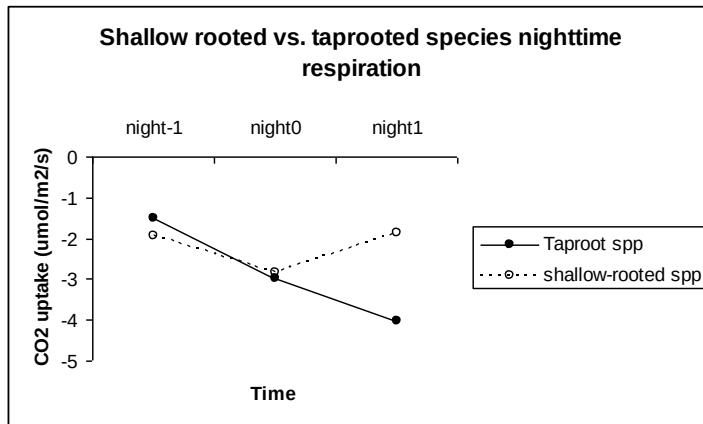


Figure 3 CO₂ uptake by leaves of target species in $\mu\text{mol}/\text{m}^2/\text{s}$ where day-1_1 on the x axis refers to the first set of pre-pulse measurements taken at 9:30, day0_2 refers to the second set of post-pulse measurements on day 0 (pulse day) and so on.

Soil Respiration:

Soil respiration efflux increased from pre-pulse measurement to the first measurement period following the precipitation pulse ($p < .001$, $F_{6,206} = 7.76$) (Fig. 4). A slight increase in respiration rate was also observed between the first and second measurement taken on each plot immediately following application of the pulses. Daytime soil respiration then gradually declined for the remainder of the experiment, to near baseline averages.

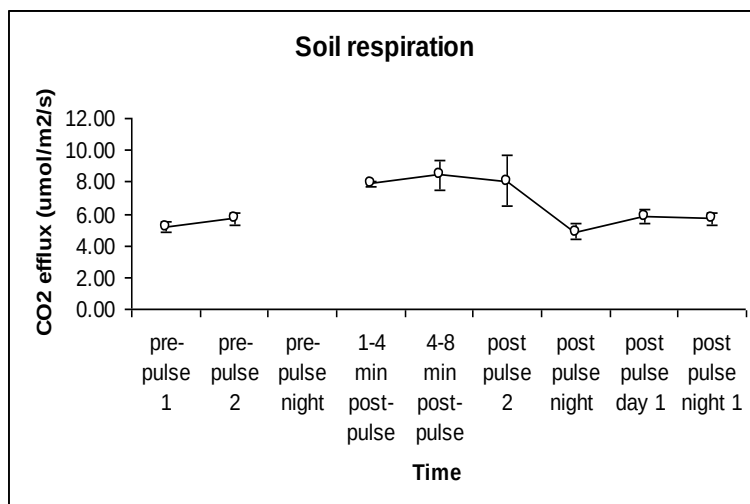


Figure 4 Daytime and nighttime soil respiration. Nighttime respiration is indicated with filled circles. X axis titles followed by '1' indicate measurements taken at 9:30, '2' was taken at 15:00 and 'night' at 21:00. Note that time increments on the x axis are not equal. Variance is shown with standard error bars.

Discussion

Results of this study indicated that water is a factor controlling carbon dynamics of montane meadow communities; however inconsistent patterns indicate that other factors are controlling carbon dynamics within these communities. Water addition over the summer appeared to have slightly extended the growing season across the elevational gradient. On a smaller temporal scale, water pulses resulted in changes in CO₂ flux, but at differing times for different components of the meadow community.

Supplemental water, added over the growing season, led to slightly increased CO₂ uptake at the two lower elevations, but decreased uptake at the high elevation site. This was the net effect of increased daytime photosynthesis and relatively unchanged plant and soil respiration in the watered plots. This suggests that while the meadows may

be water-limited, other factors such as temperature are influencing carbon flux, particularly early in the growing season and at the higher elevations.

The peak in soil respiration during the first measurement period following water application in the pulse experiment infers that below-ground processes are responding almost immediately (1-8 minutes following pulse). This may explain why respiration was unchanged four days following watering during the water addition experiment.

The three components of the system, measured in the water pulse experiment, increased C flux at different times. Soil responded first, followed by shallow-rooted and then deep-rooted species as predicted. This trend was stronger when shallow-rooted species and deep-rooted species fluxes were averaged separately as opposed to looking at each species individually. This supposes direct relationships among rooting depth, infiltration timing and timing of water integration by plants in this system. The observed variation in carbon uptake between species questions the accuracy of using species-level physiology alone to explain community or ecosystem function. It is also possible that responses of the abundant target species in this study were influenced by unstudied interactions with other species.

While these findings suggest direct responses to supplemental water, inconsistent trends in these data imply that many other factors besides water availability are at work in this system. It has been shown that temperature, for example, has a stronger influence than water availability on rates of nighttime soil respiration (Lamanna and Potter unpublished data). In another system, during a cold desert spring, photoperiod and/or temperature were shown to control physiological activity (Schwinning and Osvaldo 2004).

Many 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). And the ability of montane plant communities to act as carbon sinks depends, in part, on water availability as I have shown here over two ecological scales and two time scales. 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.

Acknowledgements

Fieldwork assistance, teaching, and guidance from Brian Chaszar, Brian Enquist and Christine Lamanna were greatly appreciated. I would like to thank billy barr for making available RMBL weather records. Additional thanks go to the REU program at the Rocky Mountain Biological Laboratory, Gothic, CO and the local coordinators of this program, Laura Burkle (2008) and Nathan Sanders (2009).

References

- Beckmann G, Klopries B (1991) CO₂ increase – Questions beyond climatic-change. *Energy* 16:1317-1330.
- Cable J and Huxman T (2004) Precipitation pulse size effects on Sonoran Desert soil microbial crusts. *Oecologia* 141: 317-324.
- Cross M, Harte J (2007) Compensatory responses to loss of warming-sensitive plant species. *Ecology* 88:740-748.
- De Valpine, P. and J. Harte. 2001. Plant responses to experimental warming in a montane meadow. *Ecology* 82:637–648.

- Enquist BJ and JJ Ebersole (1994) Effects of Added Water on Photosynthesis of *Bistorta vivipara*: The Importance of Water Relations and Leaf Nitrogen in Two Alpine Communities, Pikes Peak, Colorado, U.S.A. *Arctic and Alpine Research*, 26 (1): 29-34.
- Huxman T, Smith M, Fay P, Knapp A, Shaw M, Loik M, Smith S, Tissue D, Zak J, Weltzin J, Pockman W, Sala O, Haddad B, Harte J, Koch G, Schwinning S, Small E, Williams D (2004) Convergence across biomes to a common rain-use efficiency. *Nature* 429:651-654.
- Huxman T, Snyder K, Tissue D, Leffler J, Ogle K, Posckman W, Sandquist D, Potts D, Schwinning S (2004) precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141: 254-268.
- Huxman T, A Turnipseed, J Sparks, P Harley, R Monson (2003) Temperature as a control over ecosystem CO₂ fluxes in a high-elevation, subalpine forest. *Oecologia* 134:537-546.
- Markham A (1996) Potential impacts of climate change on ecosystems: A review of implications for policymakers and conservation biologists. *Climate Research* 6:179-191.
- Niu S, M Wu, Y Han, J Xia, L Li, SWan (2008) Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytologist* 177 (1): 209–219.
- Reynolds J, Kemp P, Ogle K, Fernandez R (2004) Modifying the “pulse-reserve” paradigm for deserts of North America: Precipitation pulses, soil water and plant responses. *Oecologia*. 141:194-210.
- Saleska S, J Harte, M Torn (1999) The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Global Change Biology* 5: 125-141.
- Schwinning S and S Osvaldo (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia*: 141:2
- Silvola J (1990) Combined effects of varying water content and CO₂ concentration on photosynthesis in *Spagnum fuscum*. *Ecography* 13 (3): 224–228.
- Sponseller R (2007) Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem. *Global Change Biology* 13: 426-436.
- Totland Ø, J Nylén (1998) Assessment of the effects of environmental change on the performance and density of *Bistorta vivipara*: the use of multivariate analysis and experimental manipulation. *Journal of Ecology* 86 (6): 989–998.

Williams TG and BF Lawrence (2004) Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}\text{CO}_2$ and $\text{C}^{18}\text{O}^{16}\text{O}$ in *Pleurozium* and *Sphagnum*. Oecologia. 108: 38-46.