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Response of sagebrush carbon metabolism to experimental precipitation pulses

Bhaskar Mitra [a, *], D. Scott Mackay [a], Brent E. Ewers [b, c], Elise Pendall [b, c, d]

[a] Department of Geography, State University of New York at Buffalo, 105 Wilkeson Quadrangle, Buffalo, NY 14261, USA
[b] Department of Botany, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA
[c] Program in Ecology, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA
[d] Hawkesbury Institute for the Environment, University of Western Sydney, Australia

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ABSTRACT

Effects of future large summer storm events due to climate change on vegetation carbon metabolism across western United States remains poorly understood. Canopy carbon metabolism of sagebrush (*Artemisia tridentata*) was evaluated for 7 days during the two driest months (July and August) by irrigating sagebrush plots with 20 mm precipitation pulses. Due to its dimorphic rooting system, we hypothesized sustained response to large precipitation events. Photosynthesis (A_n) and stomatal conductance (g_s) peaked within 2–3 days of irrigation and returned to pre-irrigation values by day 7. Predawn water potential (Ψ_{pd}) peaked within 1 day and returned to its pre-pulse value by day 3 while potential quantum efficiency for light adapted leaves (F_v'/F_m') as well as intrinsic water use efficiency (WUE_i) was unresponsive. Unlike leaves, fine roots in the top 30 cm of soil were not a carbon sink. Heterotrophic respiration (R_h) was the dominant contributor to total soil respiration (R_s), and peaked within 24 h before it dropped to pre-pulse value by day 3. Different environmental drivers regulated R_s and R_h, highlighting different kinetics of carbon production. Our study suggests ephemeral response of cold desert vegetation to future large summer storm events with important implications for the overall carbon storage capacity.

1. Introduction

The Great Basin of western United States contains a large area of shrub cover (~60 million hectares, Anderson and Inouye, 2001), which stores a significant amount of carbon, especially belowground (de Graaff et al., 2014). Snow remains the predominant form of precipitation across these regions while summer rainfall events are sporadic. Soil moisture recharge during the snow season not only favors the growth and development of woody species, but also allows it to sustain physiological activities during the summer (Ehleringer et al., 1991; Schenk and Jackson, 2002; Ogle and Reynolds, 2004). Most summer rain pulses across these regions are $\leq$ 5 mm (Loik et al., 2004) and they initiate microbial activity and photosynthetic response from shallow rooted plant species (Schwinning and Sala, 2004). Climate models predict dominant precipitation dynamics across these regions to shift from a winter to fall/spring regime, while summer precipitation is expected to show a reduction in storm frequency with a greater amount of rain per event under future scenarios of climate change (IPCC, 2007) with potentially significant impacts on the overall carbon sequestration capacity across these regions.

Our overarching question is whether large summer storms (>15 mm, Schwinning et al., 2003) can trigger lasting physiological responses in the plant-soil system? The focus on the response of vegetation to large events is necessary for three reasons: 1) It will trigger physiological responses from both aboveground and belowground plant process; 2) Responses to a large event can help us design experiments to analyze productivity of vegetation to smaller rainfall events (Snyder et al., 2004); 3) From the perspective of climate change, a few large rainfall events in the future could be the difference between ‘wet’ and ‘dry’ years (Schwinning et al., 2003). Predicting vegetation responses to large summer storm events across semi-arid ecosystems in general remains complex because threshold-type responses are modulated by plant architecture, soil texture, and soil nutrient conditions (Huxman et al., 2004a; Potts et al., 2006a, b).

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* Corresponding author.
E-mail address: bhaskar.mitra6@gmail.com (B. Mitra).

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List of symbols

ABA	Abscisic acid concentration
ATP	Adenosine triphosphate
T_a	Air temperature
C_a	Ambient carbon dioxide concentration
A_n	Assimilated carbon (or Photosynthesis)
A_i	Assimilated carbon in the irrigated plots
A_{ni}	Assimilated carbon in the non-irrigated plots
R_a	Autotrophic Respiration
$A_i - A_{ni}$	ΔA_n
BIC	Bayes information criteria
CO_2	Carbon dioxide concentration
DOY	Day of year
R_h	Heterotrophic Respiration
$\delta^{13}C$	Isotope ratio measurements
$\delta^{13}C_{leaf}$	Isotope measurement of leaf-respired CO_2
$\delta^{13}C_{il}$	Isotope measurement of leaf-respired CO_2 in irrigated plot
$\delta^{13}C_{nil}$	Isotope measurement of leaf-respired CO_2 in non-irrigated plot
$\delta^{13}C_{il} - \delta^{13}C_{nil}$	$\Delta\delta^{13}C_l$
$\delta^{13}C_{root}$	Isotope measurement of root-respired CO_2
$\delta^{13}C_{ir}$	Isotope measurement of root-respired CO_2 in irrigated plot
$\delta^{13}C_{nir}$	Isotope measurement of root-respired CO_2 in non-irrigated plot
$\delta^{13}C_{ir} - \delta^{13}C_{nir}$	$\Delta\delta^{13}C_r$
$\delta^{13}C_{trench}$	Isotope measurement of root-respired CO_2 from trench plots
T_l	Leaf temperature
Ψ_{pd}	Predawn Water Potential
PAR	Photosynthetically active radiation
Φ_{PSII}	Quantum yield
F_v'/F_m'	Quantum efficiency for light adapted leaves
RH	Relative Humidity
RuBP	Ribulose-1,5-bisphosphate
R_s	Soil Respiration
θ_s	Soil moisture in the respiration plots
θ_h	Soil moisture in the trench plots
g_s	Stomatal conductance
T_s	Temperature of the respiration plots
T_h	Temperature of the trench plots
TREES	Terrestrial Regional Ecosystem Exchange Simulator
D	Vapor pressure deficit
V-PDB	Vienna Pee Dee Belemnite
WUE_i	Water Use Efficiency

Extensive analyses at plant scale (e.g., Lauenroth et al., 1987; Cui and Caldwell, 1997; Dougherty et al., 1996; Golluscio et al., 1998; BassiriRad et al., 1999; Gebauer and Ehleringer, 2000; Schwinning et al., 2002) have provided insight with regard to the response of vegetation across semi-arid ecosystem to large summer experimental pulses. These studies have either used a combination of isotope analysis, sap flow, gas exchange measurements, soil water content or respiration to analyze the impact of simulated rainfall events on vegetation productivity. But simultaneous measurements of the three key processes – carbon assimilation, allocation and respiration – that regulate productivity at plant scale remain scarce. Measuring these processes together is important because the timing of photosynthesis and respiration responses to large precipitation pulses during summer has implications for the carbon storage capacity of dryland ecosystems as well as overall impact on plant community dynamics. Recent assessment of carbon exchange across cold-desert shrub ecosystems has found high intensity summer storm events lead to disproportionate increase in ecosystem respiration compared to photosynthesis, while small storm events facilitate the carbon sink behavior of the biome (Xie et al., 2015), both of which may be modulated by the spring moisture received by deep roots (Kwon et al., 2008). Ecological manipulation experiments that analyze the vulnerability of these key processes to large precipitation pulses can provide additional mechanistic insights into arid land carbon metabolism (Jentsch et al., 2007; Chen et al., 2009).

A_n is a robust metric to quantify carbon assimilation as it encompasses a broad range of a plant's physiological activities. For pulse-driven ecosystems, however, extensive periods of dry conditions during summer may impair the carbon uptake capacity of the plant in response to large precipitation (Flexas and Medrano, 2002; Flexas et al., 2006; Grassi and Magnani, 2005). Therefore, apart from A_n, a mosaic of metrics, including Ψ_{pd}, g_s, and quantum efficiency for light-acclimated leaves (F_v'/F_m') need to be analyzed to provide a comprehensive understanding of the role of *a priori* drought stress in regulating the carbon assimilation capacity of the vegetation including stomatal and non-stomatal regulation of A_n (Davis and Mooney, 1986; Maxwell and Johnson, 2000; Yan et al., 2000; Maestre et al., 2005). Another important metric to quantify change in vegetation productivity in response to variation in precipitation pulses is intrinsic water use efficiency (WUE_i). WUE_i is a function of plant genetics as well as the environment (Garten and Taylor, 1992; Zhang et al., 1993; Lauteri et al., 1997). While the metric can be measured at several scales, WUE_i, measured at leaf level and defined as the ratio of A_n/g_s, is of particular interest to quantify the physiological acclimation to changes in water stress and is strongly induced by stomatal control (Bierhuizen and Slatyer, 1965; Galmes et al., 2011; Zegada-Lizarazu and Berliner, 2011).

For dryland vegetation to benefit from a precipitation pulse either it must have active roots, or it must quickly reestablish root activity (BassiriRad et al., 1999). Previous studies on shrubs in the Great Basin have found a decline in root activity during the late summer (Holthausen and Caldwell, 1980; Carbone and Trumbore, 2007). For non-forest ecosystems in general, dynamics of fine root biomass (<2 mm in diameter) in the upper 30 cm of soil is critical in modulating the overall productivity (Barbosa et al., 2012). An improved understanding of fine root turnover remains a hindrance for predicting vegetation productivity in a changing climate (Norby and Jackson, 2000). Hence, linking carbon allocation to fine roots will be key to understanding the response of vegetation to large precipitation pulses. A strong link between photosynthesis and root activity has already been established for grassland (Craine et al., 1998; Johnson et al., 2002) and forest ecosystems (Hogberg et al., 2001; Irvine et al., 2005; Liu et al., 2006), but semi-arid shrublands remain understudied.

Total soil respiration (R_s), another critical component of the carbon balance, originates from roots (R_a, autotrophic) and microbes (R_h, heterotrophic). Separate analysis of the response of R_h, as well as its sensitivity to moisture and temperature is crucial as this provides information about the response of microbial decomposition processes to an altered precipitation regime. R_h should be analyzed separately because it has different responses to