

PRECIPITATION EFFECTS ON SOIL CARBON CYCLING IN THE SONORAN  
DESERT

by

Jessica Marie Cable

---

A Dissertation Submitted to the Faculty of the  
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

2006

THE UNIVERSITY OF ARIZONA  
GRADUATE COLLEGE

As members of the Dissertation Committee, we certify that we have read the dissertation prepared by Jessica Marie Cable entitled "Precipitation Effects on Soil Carbon Cycling in the Sonoran Desert" and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

\_\_\_\_\_  
Travis E. Huxman Date: 4-7-2006

\_\_\_\_\_  
Brian J. Enquist Date: 4-7-2006

\_\_\_\_\_  
Robert Robichaux Date: 4-7-2006

\_\_\_\_\_  
Alfredo Huete Date: 4-7-2006

\_\_\_\_\_  
Russell L. Scott Date: 4-7-2006

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

\_\_\_\_\_  
Dissertation Director: Travis E. Huxman Date: 4-7-2006

### STATEMENT BY AUTHOR

This dissertation has been submitted in partial fulfillment of requirements for an advanced degree at The University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library.

Brief quotations from this dissertation are allowable without special permission, provided that accurate acknowledgement of source is made. Requests for permission for extended quotation from or reproductions of this manuscript in whole or in part may be granted by the copyright holder.

Signed: Jessica M. Cable

## ACKNOWLEDGEMENTS

I am grateful to the following people that supported my research and professional development: my husband, Bill Cable; my parents, Jane Young and Dr. David T. Young; my faithful hound, Pete; members of my dissertation committee, collaborators, and peers; Dr. Kiona Ogle, Dr. David Williams, Dr. David Tissue, Dr. Scott Saleska, Joost Van Heran, Enrico Yopez-Gonzalez, and Dr. Keirith Snyder.

The following organizations and institutions provided material and financial support during my doctoral research: The Institute for the Study of Planet Earth; The University of Arizona Department of Ecology and Evolutionary Biology; the United States Department of Agriculture – Agricultural Research Center; SAHRA (Sustainability of semi-Arid Hydrology and Riparian Areas); NCEAS - PrecipNet (National Center for Ecological Analysis and Synthesis); CATTs, NSF GK-12 science outreach fellowship; BASIN (Biosphere-Atmosphere Stable Isotope Network); International Arid Lands Consortium; and NSF Division of Environmental Biology.

## DEDICATION

I am grateful to my husband Bill, who through late nights, warm meals, and unmatched technical expertise, has supported and encouraged me. I could not have done this without you, and I would split this PhD with you if it were permitted.

## TABLE OF CONTENTS

LIST OF FIGURES.....	9
LIST OF TABLES.....	11
ABSTRACT.....	12
INTRODUCTION.....	14
PRESENT STUDY.....	21
REFERENCES.....	33
APPENDIX A: PRECIPITATION PULSE SIZE EFFECTS ON SONORAN DESERT SOIL MICROBIAL CRUSTS.....	
Abstract.....	43
Introduction.....	44
Materials and methods .....	45
Results.....	48
Discussion.....	57
Acknowledgements.....	59
References.....	63
Figure legends.....	64
Figures.....	71
APPENDIX B: SOIL RESPIRATION RESPONSE TO PRECIPITATION: THE EFFECTS OF GRASS AND SOIL SURFACE ON SOIL MOISTURE.....	
Abstract.....	73
.....	78
Abstract.....	79

TABLE OF CONTENTS - *continued*

Introduction.....	80
Methods.....	84
Results.....	88
Discussion.....	93
Acknowledgements.....	102
Literature cited.....	103
Tables.....	114
Figure legends.....	116
Figures.....	119
APPENDIX C: EFFECTS OF PRECIPITATION PULSE SEQUENCING ON PLANT AND SOIL RESPONSE TO PRECIPITATION PULSE SIZE IN THE SONORAN DESERT.....	
Abstract.....	125
Introduction.....	126
Methods.....	127
Results.....	130
Discussion.....	133
Acknowledgements.....	137
Literature cited.....	143
Figure legends.....	144
Figures.....	153
	156

TABLE OF CONTENTS - *continued*

APPENDIX D: PRECIPITATION EFFECTS ON SOIL RESPIRATOIN IN SEMI-ARID ECOSYSTEMS: THE ROLE OF WOODY PLANT ENCROACHMENT.....	164
Abstract.....	165
Introduction.....	166
Methods.....	169
Results.....	172
Discussion.....	175
Acknowledgements.....	179
Literature cited.....	180
Tables.....	188
Figure legends.....	189
Figures.....	191
APPENDIX E: PERMISSION FROM JOURNAL.....	195
Journal cover page.....	197

## LIST OF FIGURES

## APPENDIX A: PRECIPITATION PULSE SIZE EFFECTS ON SONORAN DESERT

## SOIL MICROBIAL CRUSTS

FIGURE 1, Crust CO <sub>2</sub> flux response to water application.....	73
FIGURE 2, Keeling plot intercepts for different watering treatments.....	74
FIGURE 3, Carbon pool isotope values.....	75
FIGURE 4, Percent carbon contributed to CO <sub>2</sub> flux from crust and soil.....	76
FIGURE 5, Precipitation size distribution across 3 deserts.....	77

## APPENDIX B: SOIL RESPIRATION RESPONSE TO PRECIPITATION: THE EFFECTS OF GRASS AND SOIL SURFACE ON SOIL MOISTURE

FIGURE 1, Effects of a large pulse after prolonged drought on respiration, soil moisture, and soil temperature.....	119
FIGURE 2, Effects of pulse size and initial soil moisture on respiration, soil temperature, soil moisture, and soil temperature and moisture effects on respiration.....	120
FIGURE 3, Effects of pulse history and a large pulse after prolonged drought on respiration, soil moisture, and soil temperature.....	121
FIGURE 4, Effects of pulse size, initial soil moisture, and pulse history on respiration, soil temperature, soil moisture, and soil temperature and moisture effects on respiration.....	122
FIGURE 5, Relationship between initial respiration rate and respiration responsiveness to rainfall.....	123

LIST OF FIGURES - *continued*

FIGURE 6, Relationship between cumulative carbon loss and mean soil moisture.....	124
APPENDIX C: EFFECTS OF PRECIPITATION PULSE SEQUENCING ON PLANT AND SOIL RESPONSE TO PRECIPITATION PULSE SIZE IN THE SONORAN DESERT	
FIGURE 1, Soil moisture over time.....	156
FIGURE 2, Soil respiration at 4am over time.....	157
FIGURE 3, Effect of soil moisture and temperature on soil respiration.....	158
FIGURE 4, Leaf water potential over time.....	159
FIGURE 5, Leaf respiration over time.....	160
FIGURE 6, Photosynthesis at 2pm over time.....	161
FIGURE 7, Peak day photosynthesis at 2pm comparison.....	162
FIGURE 8, Rhizosphere respiration over time.....	163
APPENDIX D: PRECIPITATION EFFECTS ON SOIL RESPIRATOIN IN SEMI-ARID ECOSYSTEMS: THE ROLE OF WOODY PLANT ENCROACHMENT	
FIGURE 1, Summer precipitation, soil moisture, and respiration from five microsites.....	191
FIGURE 2, Relationship between respiration and soil moisture.....	192
FIGURE 3, In situ CO <sub>2</sub> measurements and incubations of soil at 35°C.....	193
FIGURE 4, Q <sub>10</sub> for respiration in dry and wet soil.....	194

## LIST OF TABLES

APPENDIX C: EFFECTS OF PRECIPITATION PULSE SEQUENCING ON PLANT  
AND SOIL RESPONSE TO PRECIPITATION PULSE SIZE IN THE SONORAN  
DESERT

TABLE 1, Statistical analyses of Experiments in June 2002 and 2003.....114

TABLE 2, Statistical analyses of Experiments in August 2002 and 2003.....115

APPENDIX B: SOIL RESPIRATION RESPONSE TO PRECIPITATION: THE  
EFFECTS OF GRASS AND SOIL SURFACE ON SOIL MOISTURETABLE 1, Statistical analysis of the relationship between soil moisture and  
respiration.....188

## ABSTRACT

Biological activity in desert soils is driven by water availability. The nature of individual precipitation events is critical to understanding soil moisture availability. Rain falls as discrete events (pulses) that vary in size and sequencing, resulting in soil “wet-dry cycles”. Soil organisms are responsive to wet-dry cycles with rapid changes in activity. How soil activity is driven by changes in water content associated with individual pulses is poorly understood. The effects of precipitation on soil processes likely depend on ecosystem structure, which influences the soil environment. The goal of this dissertation was to determine how soil carbon cycling responds to precipitation in the context of ecosystem structure (plant composition, geomorphology) and climate.

I used differences in stable carbon isotopic composition of soil organisms and plants to understand how positioning in the soil profile influences biological responses to different sized pulses. I evaluated how soil texture and grass species composition affect soil process response to rainfall in different seasons. I manipulated rainfall sequence to understand the interaction between closely spaced rainfall events of different sizes on soil processes. I evaluated the role of plant functional types in influencing soil microclimate and litter deposition and the response of soil processes to seasonal rainfall.

Chamber measurements of soil and plant CO<sub>2</sub> flux were used to understand their response to rainfall. I found that surface organisms are more responsive to small rainfall events due to the relationship between pulse size and infiltration. While soil texture and season of rainfall are important, the best predictor of the response of soil respiration to rainfall was initial activity levels. Grass species was not important. Grass roots and soil

microbes differ in response to sequences of precipitation. Grasses responded less to subsequent large events if they were already 'activated' by a recent rainfall event. The effect of plant functional type was size dependent with differences occurring only with large shrubs. This work suggests that large scale simulations of soil carbon cycling in deserts should carefully consider wet-dry transitions in the context of plant functional type and initial soil condition in order to predict the responses to global change.

## INTRODUCTION

### *Water limited regions and precipitation patterns*

Rising atmospheric CO<sub>2</sub> concentrations have consequences for the climate system, due to the effect on global temperatures (Stouffer et al. 1994, Keeling et al. 1995, Sellers et al. 1996, Petit et al. 1999). In the past century, mean global air temperature has increased 0.5°C and it is expected to continue rising (Stouffer et al. 1994, Easterling et al. 2000, Moraes et al. 2005), likely resulting in amplification of the global water cycle, changing regional patterns of precipitation and extreme events (Keeling et al. 1995, Liang et al. 1995, Easterling et al. 2000, Dai et al. 2001, Houghton 2005). Effects of altered precipitation on terrestrial ecosystems appear to be biome-specific, with arid and semi-arid regions being quite responsive (Yu and Neil 1993, Giorgi et al. 1994, Smith et al. 2000, Huxman et al. 2004c). Predictions of rainfall change on an annual or seasonal time-scale are not sufficient to determine the impacts on ecosystem processes in arid and semi-arid ecosystems (Weltzin et al. 2003, Loik et al. 2004). It is more important to determine how precipitation may change on nested time scales (e.g. – daily and seasonal) and at fairly small spatial scales in order to predict the response of terrestrial ecosystems (Yu and Neil 1993, Liang et al. 1995, Meehl et al. 2000, Weltzin et al. 2003, Loik et al. 2004).

In arid and semi-arid regions, rainfall occurs as discrete events or “pulses” because the timing of storms relative to evaporative demand results in significant periods of low water availability in soils (Noy-Meir 1973, Weltzin et al. 2003). In the upper

Sonoran Desert, 50 to 60% of rainfall occurs in the summer as part of the North American Monsoon (Adams and Comrie 1997). High air temperatures and low atmospheric water vapor contents during this period cause soil to rapidly dry between storms, resulting in elevated soil moisture only in the immediate days following a rain event, limiting the access of organisms to resources that may be available in the soil or maintaining them in periods of dormancy (Noy-Meir 1973, Weltzin et al. 2003, Huxman et al. 2004b). Pulses of precipitation vary in magnitude and timing, altering the depth of water infiltration and the duration of high soil moisture (Weltzin et al. 2003, Schwinning and Sala 2004). Variation in soil moisture often results in a non-linear response of ecosystem processes, such as CO<sub>2</sub> exchange, due to the differential activation of organisms distributed throughout the soil profile (Huxman et al. 2004b, Schwinning et al. 2004). Combining our understanding of the spatial distribution of organisms in an ecosystem with the time-depth distribution of soil moisture that derives from rainfall events provides an important paradigm for understanding the controls over ecosystem function in arid and semi-arid ecosystems.

The spatial distribution of plants species or functional types may determine how they influence ecosystem processes in response to a pulse of precipitation, due to differences in photosynthetic capacity, phenology, canopy structure, and litter deposition dynamics (Fierer et al. 2003, Huxman et al. 2004a, Huxman et al. 2004b, Scott et al. 2006, Ignace et al. *in prep*). For example, the ratio of woody to herbaceous plants affects the spatial pattern of soil resources and energy, as a result of differential soil shading and litter accumulation under shrub canopies (Garcia-Moya and McKell 1969, Schlesinger et

al. 1996, Paruelo and Lauentroth 1996, Schlesinger and Pilmanis 1998, Cross and Schlesinger 1999). The spatial pattern of these features likely influences the potential activity of microbial components of the soil systems, which in turn would affect decomposition, nitrogen mineralization / immobilization and soil carbon cycling. These effects on ecosystem processes occur in addition to the direct effects plants have on ecosystem processes by their own physiological processes.

Variation in ecosystem processes across a landscape may be influenced by soil properties because soils in water limited landscapes influence many biological and physical processes (McAuliffe 1994). Through altering water infiltration and retention, soil texture can impact the response of different ecosystem components to a pulse of precipitation (Huxman et al. 2004a). For example, fine textured soil has higher potential for microbial activity due to higher moisture retention capacity and organic matter content (Austin et al. 2004), but infiltration rates on these soil types are relatively slow, affecting the potential amplitude of soil moisture peaks following rain and the characteristics of wet-dry cycles. Soil texture additionally affects aspects of ecosystem structure, including the establishment, composition, and activity of plants (Noy-Meir 1973, McAuliffe 1994, 1999, 2003, Parker 1995, Smith et al. 1995, Hamerlynck *et al.* 2002, Huxman et al. 2004a, Thomas and Dougill 2006).

#### *Carbon cycling, soils and precipitation change*

One of the most important contributors to variation in the global annual CO<sub>2</sub> cycle is the effect of short-term changes in climate on ecosystem carbon cycling (Houghton

2000). The response of ecosystem processes, such as the biological exchange of CO<sub>2</sub>, to precipitation is important to quantify because of the climatic sensitivity of photosynthesis and respiration and the potential of ecosystems to feedback to climate (Grogan et al. 2001, Huxman et al. 2004a, Li et al. 2004, Loik et al. 2004, Scott et al. 2006). As a major contributor to ecosystem CO<sub>2</sub> exchange, soil respiration is the efflux of CO<sub>2</sub> from the activity of microbes (defined as free-living heterotrophic micro-organisms) and the rhizosphere (defined here as the activity of plant roots and their closely associated microorganisms). In non-water limited ecosystems, soil respiration is modeled as a temperature response from first order kinetics (Lloyd and Taylor 1994). However where soils are ephemerally wet, water inputs may be an overriding driver of biological activity in soils (Borken et al. 1999, Davidson et al. 2000, Austin et al. 2004).

The rapid increase of CO<sub>2</sub> from soils following the application of water has been documented, and attributed to changes in microbial biomass, rapid upregulation of physiological processes associated with carbon and nitrogen cycling, and differences in the sensitivity of microbial species to water status (Rochette et al. 1991, Schimel et al. 1999, Franzluebbers et al. 2000, Fierer and Schimel 2003, Austin et al. 2004, Huxman et al. 2004a Saetre and Stark 2005). Through soil-water films, soil moisture controls availability of nutrients and labile carbon, which may alter the role of soil texture and the response of respiration to temperature (Skopp et al. 1990, Davidson et al. 2006). Soil moisture indirectly affects substrate supply through promoting plant production of labile carbon from plant litter, fine roots, and root exudates (Raich and Schlesinger 1992, Raich et al. 2002, Townsend et al. 1997, Trumbore 2000, Janssens et al. 2001) and by altering

the delivery of resources in the soil solution to different microsites (Heffernan and Sponseller 2004, Agehara and Warncke 2005). However how the direct and indirect effects of moisture interact with temperature following rainfall is poorly understood (Lloyd and Taylor 1994, Borke et al. 1999, Conant et al. 1998, Conant et al. 2004).

Although much of the CO<sub>2</sub> efflux from soils after a rain event is hypothesized to be from microbial activity, autotrophic / rhizosphere respiration can be nearly 50% of total soil respiration (Bowden et al. 1993, Andrews et al. 1999, Tang and Baldocchi 2005). Nearly 12% of recent photosynthate is respired in the rhizosphere (Nguyen 2003), representing a major allocation sink for plant carbon. In contrast to heterotrophic microbial activity, rhizosphere activity is indirectly controlled by factors that influence photosynthesis, such as light, temperature, moisture, and nutrients (Son et al. 2004, Irvine et al. 2005). The direct effect of water is likely through nutrient availability and relaxation of plant water stress (Huang and Fu 2000, DaCosta et al. 2004, Peek et al. 2005, Irvine et al. 2005). The responses of both rhizosphere and heterotrophic activity to precipitation depend on the location in the soil profile, where small rain events may activate only surface organisms, but larger rainfall events influence organisms deeper in the soil profile (Huxman et al. 2004b). Partitioning the responses of heterotrophic microbes and rhizosphere to precipitation would aid in our mechanistic understanding of how water controls biological activity in large portions of the terrestrial globe.

The effects of water on respiration have been primarily explored in laboratory settings (Orchard and Cook 1983, Fierer and Schimel 2003, Conant et al. 1998, Conant et al. 2004). This work has been instrumental in evaluating microbial population dynamics,

nutrient mineralization, and the effects of multiple wet-dry cycles on these processes. *In situ* measurements of the response to rainfall are increasing (e.g. Amundson et al. 1989, Liu et al. 2002), but there is a surprising lack of data from many biome types, including those in arid and semi-arid regions. Many questions persist, such as: what is the response of rhizosphere respiration to a pulse, what is the impact of single vs. multiple rainfall events on soil respiration, and how does ecosystem structure affect soil carbon cycling processes following rainfall?

This dissertation contributes to an understanding how soils contribute to ecosystem function in response to rainfall in semi-arid regions. The contributions of CO<sub>2</sub> to whole ecosystem exchange from both the rhizosphere and heterotrophic microbes are quantified by using flux-chamber based and isotopic techniques. By measuring the precipitation response of soils across plant communities, soil types, microclimate gradients, and across seasons, this dissertation evaluates how complexities of the environment affect carbon cycling in soils at different temporal scales. A primary goal of this research is to generate data to be used in predictive modeling exercises of soil respiration in water limited ecosystems and to determine how potential climate changes affect carbon cycling through altered precipitation regimes.

Short-term threshold processes, such as the rewetting of dry soil associated with individual rainfall events, represent a major challenge for the current suite of equilibrium models used to understanding how climate change and variability influence ecosystem processes (Groffman & Tiedje 1988; Davidson et al., 1993; Cabrera et al., 2005; Weltzin et al., 2003). Many of these models evaluate soil respiration as primarily a function of

temperature (Lloyd and Taylor 1994, Frank et al. 2002), and a few use moisture indices to incorporate the effects of soil moisture (Bunnell and Tait 1974, O'Connell 1990, Pumpanen et al. 2003), substrate chemistry (Bunnell et al. 1977, Schimel and Weintraub 2003), and oxygen availability (Bunnell and Tait 1974). The models rarely consider the co-variation of water, temperature and temperature extremes or the importance of antecedent conditions and rainfall sequencing. Most models are also limited to microbial respiration from decomposition (but see Pumpanen et al. 2003), but rhizosphere respiration is an important contributor to ecosystem CO<sub>2</sub> efflux. These models perform poorly in environments with dynamic wet-dry soil cycles with conditions ranging from saturated and anoxic to dry (Bunnell and Tait 1974, O'Connell 1990). Additionally, the temperature relationship commonly used in models (Lloyd and Taylor 1994, Pumpanen et al. 2003) does not adjust with high or low temperatures, so the predictions may break down in extreme temperature environments, such as arid and semi-arid ecosystems. Thus, there is a significant need for concurrent measurements of soil moisture, soil temperature, and soil respiration, and the role of precipitation pulse variation (eg- size, history, sequence, and antecedent conditions) to properly develop models of soil respiration in arid and semi-arid ecosystems.

## PRESENT STUDY

The methods, results and conclusions of this research program are presented in manuscript form, appended to this dissertation. The following is a description and summary of the most important findings in these documents.

### **PRECIPITATION PULSE SIZE EFFECTS ON SONORAN DESERT SOIL MICROBIAL CRUSTS**

(This work has been published: Cable JM and Huxman TE (2004) Precipitation pulse size effects on Sonoran Desert soil microbial crusts. *Oecologia* 141(2): 317-324; and has been included in this dissertation in Appendix A with kind permission of Springer Science and Business Media.)

Arid and semi-arid regions have large areas of unvegetated space due to the spatial and temporal heterogeneity of soil water and constraints on plant establishment (Noy Meir 1973, Ehleringer 1985, Smith and Nowak 1990, Smith et al.1997). These large expanses of unvegetated space are not devoid of autotrophic activity due to the presence of microbial crust communities (Belnap 2003). These assemblages of lichen, algae, moss, fungi, cyanobacteria, and bacteria can occupy up to 70% of intercanopy space, and are found on the surface of all deserts around the world (Belnap 2001). Their activity is directly linked to periods following rain events when soil surface moisture is high (Lange 2001), but they are quiescent during dry inter-rainfall periods (Lange et al. 1986). These groups of organisms appear to have an important role in the stability of ecosystem structure in arid landscapes but the role of crusts in ecosystem carbon cycling

is unclear (Belnap 2003). Due to their extensive coverage and frequency with which they experience precipitation, crusts may have a significant influence on ecosystem level production.

The objective of this study was to determine how the stratification of organisms in the soil affects the response of soils to precipitation pulse size. Because rainfall event size affects water infiltration depth (larger events infiltrate to greater depths), crusts and sub-surface microbial communities and plants may differentially respond to precipitation events of different sizes. Crusts may be activated by essentially any rainfall event, while relatively large pulses are required to activate plants and soil microbes (Huxman et al. 2004b). The questions addressed in this study are: what are the photosynthetic and respiratory responses of crusts to a precipitation pulse? What is the contribution of soil microbial crusts to the efflux of CO<sub>2</sub> from soils, relative to the respiration derived from other soil micro-organisms and plant roots? How does this relative contribution change as a function of precipitation pulse size?

This work was carried out in pots and *in situ* in the Sonoran Desert. Following a single water application, diurnal measurements of gas exchange were made to characterize CO<sub>2</sub> exchange response through time. Following water application simulating two pulse sizes, respired CO<sub>2</sub> was collected and Keeling plots and mixing model analyses were done to determine the dominant contributor to ecosystem respiration. The Keeling plot technique has been used in several studies to partition respiration into its sources (Rochette et al. 1999, Bowling et al. 2001).

I found that at ambient conditions, CO<sub>2</sub> effluxes from soils were small and crusts contributed more than the two remaining belowground components to total flux. However, this approximated 50% from the crust and remaining soil components. I hypothesized that small events would activate only surface organisms and large events would activate deeper organisms. I found that following a 2 mm pulse, crusts dominated the respiratory CO<sub>2</sub> efflux, while following a 25.4 mm pulse, heterotrophic soil microbial communities and roots dominated the efflux. The small pulse did not infiltrate to depth and evaporated quickly only activating the crust and leaving the plant roots and soil microbes dormant. The large event infiltrated to depth and activated each component. As such, the contribution of different ecosystem components to ecosystem carbon cycling is pulse size dependent due to the different locations of these components into the soil profile.

The majority of rainfall events in the Sonoran, Chihuahuan, and Mojave Deserts are small pulse events (<2mm). Therefore, the contribution of crusts to ecosystem CO<sub>2</sub> exchange and productivity may be large (Jasoni et al., 2005). In pulse driven ecosystems, the size of the rainfall events appear to be important in determining which components are active and to what degree. Soil respiration, that is respiration from soil microbes, roots, and crusts if present, represents one of the largest components of the local carbon cycle contributing to the global carbon budget (Rustad et al. 2000). Soil moisture is a controller of soil respiration so a change in precipitation regimes, as predicted from climate change models, in a pulse driven ecosystem may alter respiratory responses from the soil as a whole (Rustad et al. 2000; Easterling et al. 2000). However, as suggested in

this study, a change in precipitation patterns such as a trend toward more frequent events of large or small pulses may alter the respiratory contribution from different components of the ecosystem, thereby altering the carbon budget of desert ecosystems and the relative importance of crusts.

### **SOIL CO<sub>2</sub> EFFLUX RESPONSE TO PRECIPITATION: THE EFFECTS OF GRASS AND SOIL SURFACE ON RESPIRATION**

(The methods, results, and conclusions of this study are presented in the paper appended to this dissertation in Appendix B. The following is a summary of the most important findings in this document. This paper will be submitted to *Plant and Soil* for publication.)

Pulses of precipitation characterize rainfall in deserts (Noy-Meir 1973). The response of ecosystem processes, such as soil respiration from microbes and autotrophs, to pulses is controlled primarily by soil moisture (Orchard and Cook 1983; Liu et al., 2002; Fierer and Schimel 2003; Conant et al., 2004). Temporal and spatial variation in soil moisture is driven by characteristics of rainfall, such as seasonal timing, frequency, magnitude, and inter-annual variation, along with ecosystem factors, such as soil texture and plant species (Austin et al., 2004; Huxman et al., 2004). The magnitude and duration of soil respiratory activity is influenced by a number of features that impact the “biological effectiveness” of a pulse, including: seasonal precipitation affects initial soil moisture; inter-annual variation in pulses (pulse history) influencing soil resources; soil texture alters water infiltration and retention; and plants alters soil microclimate.

The objective of this study was to evaluate how soil CO<sub>2</sub> efflux in a semi-arid grassland responds to individual precipitation pulses, in the context initial soil moisture and pulse history. Four experiments were carried out over two years to address the role of plant species and soil texture in how respiration responds to a pulse at a rainfall manipulation experiment (English et al. 2005). In the four experiments the following questions were addressed: (1) what is the effect of a large pulse after a prolonged period of drought? (2) What is the effect of pulse size with different initial soil moisture conditions? (3) How does pulse history influence the effect of a large pulse following prolonged drought? (4) How does pulse history influence how pulse size with different antecedent moisture conditions affects soil respiration?

This work was carried out at the Santa Rita Experimental Range in southeastern Arizona, beneath rainout manipulation shelters with plots of native and non-native grass species located on two contrasting soil surfaces. Over two years, plots received equivalent rainfall, except in the monsoon when plots received either above or below mean summer rainfall. Efflux of soil CO<sub>2</sub>, soil moisture and temperature were measured before and for several days after a targeted pulse event prior to and during the monsoon.

We found that a pulse translates into less biological activity when initial soil moisture is high, but following a long period of very dry soil, a pulse induces large soil CO<sub>2</sub> efflux. Due to the upregulation and substrate use of the soil organisms, we found that respiration response to a pulse is stronger after the dry fore-summer that resulted in low cellular activity, whereas in the monsoon, organism activity may be restricted by substrate limitation (Fierer and Schimel 2002). An interesting finding from this study is

that higher soil temperature was associated with lower respiration rates, differing from previous research (Lloyd and Taylor 1994; Conant et al., 2004; Xu et al., 2004). Due to the covariation of soil moisture and temperature, microbes rapidly use substrates at high soil temperatures (Eliasson et al., 2005, Leifeld and Fuhrer 2005), but due to low soil moisture, diffusion of solutes may become the rate limiting step (Skopp et al. 1990). Thus, substrate availability may be inversely related to temperature (Davidson et al. 2006), resulting in the inverse soil respiration-temperature relationship. Soil texture had the most significant effect on how a single pulse, pulse history, and initial soil moisture interacted to affect soil respiration. I found that the primary effect of pulse history was likely a reduction of substrates for microbial response to increased water availability of any kind. If more rain falls during the monsoon, as induced with the water treatment differences, more carbon will be lost from fine textured soils.

Arid and semiarid regions are increasing in area globally (Schlesinger et al., 1990) and current predictions of climate change and current land-use practices suggest that trend will continue (Abahussain et al., 2002; Lin and Tang 2002; Geist and Lambin 2004). For many of these regions, global circulation models predict changes in the frequency, magnitude and seasonality of precipitation (IPCC 2001). For example, the frequency of relatively large precipitation events is expected to increase in the Southwestern United States (Easterling et al. 2000; IPCC 2001); currently small events (<5mm) are most common (Sala et al. 1982), and changes in the event size distribution of rainfall events appears important at controlling features such as site water balance (Loik et al., 2004). Shift in features such as the seasonal distribution of precipitation, or inter-

annual variability in total sums, may have consequences for a number of ecosystem processes (Sala et al., 1982; Sala et al., 1992; Schlesinger 1997; Golluscio et al., 1998; Conant et al., 1998; Borken et al., 1999; Reynolds et al., 2000; Weltzin and Tissue 2003; Weltzin and McPherson 2003; Huxman et al., 2004). Because rainfall indirectly and directly influences soil CO<sub>2</sub> efflux (through characteristics such as substrate supply rate, soil temperature, microbial and plant physiological status, the diffusivity of CO<sub>2</sub>—Davidson et al., 2006), a greater mechanistic understanding is the key to predicting the carbon cycling consequences of changes in precipitation for arid and semiarid regions.

### **EFFECTS OF PRECIPITATION PULSE SEQUENCING ON PLANT AND SOIL CO<sub>2</sub> RESPONSE TO PULSE SIZE IN THE SONORAN DESERT**

(The methods, results, and conclusions of this study are presented in the paper appended to this dissertation in Appendix C. The following is a summary of the most important findings in this document. This paper is in preparation for submission to *Oecologia*.)

Episodic inputs of precipitation are important for the biological activity in desert ecosystems (Noy-Meir 1973). The sequence and event size distribution of precipitation are likely both important for different ecosystem components, but their interaction is not as well understood (Austin et al. 2004, Huxman et al. 2004b). Plants and soil organisms may respond differently to features of precipitation, such as event size, due to differences in their patterns of physiological upregulation, nutrient requirements / availability, and location in the soil profile. Individual rainfall events isolated in time often result in a large efflux of CO<sub>2</sub> from the soil due primarily to a rapid increase in microbial activity

from nutrient mineralization (Fierer and Schimel 2003, Austin et al. 2004). A slower response from plants generally occurs due to limited leaf area display and upregulation of photosynthetic activity (Sala et al. 1982, Flanagan et al. 2002, Schwinning et al. 2002, Huxman et al. 2004a). Multiple, clustered rain events can alter the response of different components, by influencing antecedent soil moisture conditions and the physiological state of ecosystem components (Reynolds et al. 2004).

The objective of this study was to determine how a short sequence of rainfall events influences the responsiveness of soil microbes and plants to different sized rainfall events. Specifically, we ask: what is the response of whole plant vs. soil CO<sub>2</sub> exchange to rainfall events of different sizes (target pulses), when the system has experienced a recent rainfall event? Although surface soils may dry between even short sequences of rainfall events, the history of soil moisture change may affect the responsiveness of both the plant and soil microbial activity to subsequent rain events. This study was conducted at the Santa Rita Experimental Range in southeastern Arizona on plots of a native grass species. Initially plots received either a large or no pulse, followed a week later by either no water, a small or large target pulse. Measurements of plant and soil CO<sub>2</sub> exchange were measured prior to and after the second series of pulses.

I hypothesized that a preconditioning pulse event would prime leaf-level plant activity, which would affect responsiveness to different sized target pulses. This is due to the requirement for an initial rainfall event to upregulate leaf processes and initiate the development of canopy leaf area (Huxman et al., 2004). However, I found that when plants were activated by a preconditioning rainfall event, it elevated plant water status

and increased the photosynthetic responsiveness to our smallest target rainfall treatment. This is consistent with other studies that have shown sequences of mid-season small rainfall events allow for continued responsiveness to precipitation of any kind (Sala and Lauenroth 1982). In contrast to the plant response, I hypothesized that a preconditioning pulse would result in a reduction in soil respiration responsiveness to target pulses due to the effects of wet-dry cycle dynamics on microbes (Fierer and Schimel 2003). However, I found that precondition did not affect how soil CO<sub>2</sub> efflux responded to target pulses of different sizes.

An interesting finding in our study was that there was greater respiratory carbon loss from leaves when antecedent plant water status was high, but rhizosphere respiration showed the opposite trend. Perhaps the lower rhizosphere respiration rates in plants that received a precondition pulse are due to a shift in allocation of carbon to support growth of the canopy (Albaugh et al. 1998), where the initial watering event of a season primarily initiates root development. Greater leaf respiration with a preconditioning pulse is consistent with this hypothesis. As such, whole plant carbon dynamics following our target pulses may be similar from both preconditioning treatments due to the differential response of shoots versus roots. This suggests that patterns of allocation significantly affect the interaction between rainfall event size distribution and sequencing in these plants.

I found that the preconditioning treatment ‘activated’ the plants, causing them to respond more to the small target rainfall events, but there was no effect of preconditioning on the response of soil CO<sub>2</sub> efflux to the target pulses. The frequency of

large precipitation events for the Southwestern United States is predicted to increase in the future (IPCC 2001, Easterling et al. 2000). Depending upon how changes in frequency are overlaid with this prediction, plants and soil may differently contribute to ecosystem carbon exchange in arid and semi-arid ecosystems with shifts in precipitation. Even a small shift in seasonal precipitation could have significant consequences by differentially influencing components of net ecosystem production, or feedbacks on ecosystem structure by nutrient cycling (Sala et al., 1982; Sala et al., 1992; Schlesinger 1997; Golluscio et al., 1998; Conant et al., 1998, Borke et al. 1999; Reynolds et al., 2000; Weltzin and Tissue 2003; Weltzin and McPherson 2003; Huxman et al., 2004a). Arid and semiarid regions are predicted to increase in area and soil carbon dynamics are predicted to change from vegetation shifts, so deserts may play large roles in global biogeochemical cycles with shifts in precipitation (Schlesinger et al. 1990).

### **PRECIPITATION PULSE EFFECTS ON SOIL RESPIRATION IN SEMI-ARID ECOSYSTEMS: THE ROLE OF WOODY PLANT ENCROACHMENT**

(The methods, results, and conclusions of this study are presented in the paper appended to this dissertation in Appendix D. The following is a summary of the most important findings in this document. This paper will be submitted to *Global Change Biology* for publication.)

Variation in the timing and magnitude of rainfall influences the temporal availability of soil moisture (Noy-Meir 1973). Vegetation composition interacts with these features of precipitation and alters the spatial dynamics of soil water (Loik et al.,

2004) – the fraction of woody versus herbaceous cover influences precipitation interception, infiltration into the profile, and soil water evaporation. Combined with differential litter inputs from these two functional types, it is likely that there are important spatial and temporal variations in soil resource pools and microclimate that can influence the activity of organisms in soils. As such, the increasing abundance and density of shrubs in the desert southwest at the expense of grasses may significantly affect soil biogeochemical processes, such as carbon cycling (Schlesinger et al. 1996; Jackson et al., 2002; Huxman et al., 2005).

The objective of this study was to determine how plant functional type affects the response of soils to precipitation. We focused on a mixed grass-shrub site on an upper-alluvial terrace of the San Pedro River, where we were additionally evaluating CO<sub>2</sub> and water exchanges at the ecosystem scale. Thus, in this study I asked: how variation in soil moisture, temperature, and nutrients resulting from woody-versus-grass canopy cover influences the response of soil CO<sub>2</sub> efflux to summer rainfall. Throughout the summer period, I measured soil CO<sub>2</sub> efflux, soil temperature and moisture in microsites created by the canopy distributions of large and medium sized shrubs (mesquite), bunchgrasses (sacaton), and open spaces.

Based on differences in resource pool size, we hypothesized that respiration in open spaces would have the lowest response to rainfall and as compared to the largest response from under the canopy of the nitrogen-fixing shrub, *Prosopis velutina* (mesquite). We hypothesized that grasses would have an intermediate response. We found that respiration near the trunk of large mesquite had the highest respiration rates,

even well into the monsoon. This flux was likely due to high fine root activity. Efflux rates near the canopy edge of very large mesquite and beneath grasses were equivalent. There were large microsite effects, but the most unexpected was that medium-sized mesquite had soil CO<sub>2</sub> efflux responses to rainfall that were similar to that of bare-ground, open spaces. Potts et al. (*in prep*) found that photosynthesis is higher for medium mesquite than sacaton grasses, and when combined with data from this experiment, showing low soil respiration rates indicates that this size class may represent patches that accumulate carbon at a greater rate, relative to other patch types. In general, soil temperature was not as important as soil moisture in driving respiration across all microsites. Similar interactions of soil temperature and moisture have been found in other studies, where in dry periods, moisture is more constraining and respiration is less responsive to increases in temperature (Amundson et al. 1989, Conant et al. 1998, Rustad et al. 2001, Conant et al. 2004, Tang and Baldocchi 2005).

Arid and semi-arid regions of the southwestern US are undergoing landscape scale changes in ecosystem structure and regional climate. In combination with continued woody plant expansion, precipitation patterns are predicted to shift in the southwestern US to a greater frequency of large events (Easterling et al. 2000; IPCC 2001). The response of ecosystem processes to such shifts will be affected by the change in soil carbon (Hibbard et al. 2001, Scott et al. 2006). Thus, gaining a mechanistic understanding of the changes in soil carbon processes with vegetation change will be important in determining how precipitation change will affect ecosystem function in arid and semi-arid regions.

## REFERENCES

- Abahussain A A, Abdu A S, Al-Zubari W K, El-Deen N A, and Abdul-Raheem M 2002 Desertification in the Arab Region: analysis of current status and trends. *Journal of Arid Environments* 51, 521-545.
- Adams DK and Comrie AC 1997 The North American Monsoon. *Bulletin of the American Meteorological Society* 78, 2197-2213.
- Agehara S and Warncke DD 2005 Soil moisture and temperature effects on nitrogen release from organic nitrogen sources. *Soil Science Society of America Journal* 69 (6), 1844-1855.
- Albaugh TJ, Allen HL, Dougherty PM, Kress LW, and King JS 1998 Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *Forest Science* 44, 317-328.
- Amundson R G, Chadwick O A, Sowers J M, and Doner H E 1989 Soil evolution along an altitudinal transect in the eastern Mojave desert of Nevada, USA. *Geoderma* 43, 349-371.
- Andrews JA, Harrison KG, Matamala R, and Schlesinger WH 1999 Separation of root respiration from total soil respiration using carbon-13 labeling during Free-Air Carbon Dioxide Enrichment (FACE). *Soil Science Society of America Journal* 63, 1429-1435.
- Austin A T, Yahdjian L, Stark J M, Belnap J, Porporato A, Norton U, Ravetta D A, Schaeffer S M 2004 Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141, 221-235.
- Belnap J 2001 Microbes and microfauna associated with biological soil crusts. In: Belnap and Lange (eds) *Ecological Studies. Biological Soil Crusts: Structure, function, and management*. Springer-Verlag GmbH & Co. New York, pp 167-176.
- Belnap J 2003 The world at your feet: desert biological soil crusts. *Frontiers in Ecology* 1:181-189.
- Borken W, Xu Y-J, Brumme R, and Lamersdorf N 1999 A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: Drought and rewetting effects. *Soil Science Society of America Journal* 63, 1848-1855.
- Bowden RD, Nadelhoffer KJ, Boone RD, Melillo JM, and Garrison JB 1993 Contributions of aboveground litter, and root respiration to total soil respiration in

a temperate mixed hardwood forest. *Canadian Journal of Forest Research – Revue Canadienne de Recherche Forestiere* 23, 1402-1407.

- Bowling DR, Tans PP, Monson RK 2001 Partitioning net ecosystem carbon exchange with isotopic fluxes of CO<sub>2</sub>. *Global Change Biology* 7:127-145.
- Bunnell FL and Tait DEN 1974 Mathematical simulation models of decomposition processes. In: *Soil Organisms and Decomposition in Tundra*, Holding AJ, Heal OW, MacLean SF, and Flanagan PW, Tundra Biome Steering Committee, Stockholm, 207-244p.
- Bunnell FL, Tait DEN, Flanagan PW, and Van Cleve K 1977 Microbial respiration and substrate weight loss – I. *Soil Biology and Biochemistry* 9:33-40.
- Conant R T, Klopatek J M, Malin R C, and Klopatek C C 1998 Carbon pools and fluxes along an environmental gradient in northern Arizona. *Biogeochemistry* 43, 43-61.
- Conant R T, Dalla-Betta P, Klopatek C C, and Klopatek J A 2004 Controls on soil respiration in semiarid soils. *Soil Biology and Biochemistry* 36, 945-951.
- Cross AF and Schlesinger WH 1999 Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. *Plant Ecology* 145:11-25.
- DaCosta M, Wang ZL, and Huang BR 2004 Physiological adaptation of Kentucky bluegrass to localized soil drying. *Crop Science* 44, 1307-1314.
- Dai A, Wigley TML, Boville BA, Kiehl JT, and Buja LE 2001 Climates of the twentieth and twenty-first centuries simulated by the NCAR climate system model. *Journal of Climate* 485-519.
- Davidson E A, Verchot L V, Cattanio J H, Ackerman I L, and Carvalho J E M 2000 Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* 48, 53-69.
- Davidson EA, Janssens IA, and Luo YQ 2006 On the variability of respiration in terrestrial ecosystems: moving beyond Q(10). *Global Change Biology* 12, 154-164.
- Easterling D R, Meehl G A, Parmesan C, Changnon S A, Karl T R, and Mearns L O 2000 Climate extremes: Observations, modeling, and impacts. *Science* 289, 2068-2074.
- Ehleringer J (1985) Annuals and perennials of warm deserts. In: Chabot BF, Mooney HA (eds) *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York, pp 162-180.

- Eliasson P E, McMurtrie R E, Pepper D A, Stromgren M, Linder S, and Agren G I 2005 The response of heterotrophic CO<sub>2</sub> flux to soil warming. *Global Change Biology* 11, 167-181.
- English NB, Weltzin JF, Fravolini A, Thomas L, and Williams DG 2005 The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. *Journal of Arid Environments* 63(1), 324-343.
- Evans RD, Johansen JR 1999 Microbiotic crusts and ecosystem processes. *Critical Review in Plant Science* 18(2):183-225.
- Fierer N and Schimel J P 2002 Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology and Biochemistry* 34, 777-787.
- Fierer N and Schimel J P 2003 Mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Science Society of America Journal* 67, 798-805.
- Flanagan LB, Wever LA, and Carlson PJ 2002 Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology* 8, 599-615.
- Frank AB, Liebig MA, and Hanson JD 2002 Soil carbon dioxide fluxes in northern semiarid grasslands. *Soil Biology and Biochemistry* 34(9):1235-1241.
- Franzluebbers A J, Haney R L, Honeycutt C W, Schomberg H H, and Hons F M 2000 Flush of carbon dioxide following rewetting of dried soil relates to active organic pools. *Soil Science Society of America Journal* 64, 613-623.
- Garcia-Moya E and McKell CM 1969 Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51(1):81-88.
- Geist H J and Lambin E F 2004 Dynamic causal patterns of desertification. *Bioscience* 54, 817-829.
- Giorgi F, Brodeur CS, and Bates GT 1994 Regional climate-change over the United-States produced with a nested regional climate model. *Journal of Climate* 7, 375-399.
- Golluscio R A, Sala O E, and Laurenroth W K 1998 Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia* 115, 17-25.

- Hamerlynck E P, McAuliffe J R, McDonald E V, and Smith S D 2002 Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. *Ecology* 83, 768-779.
- Heffernan JB and Sponseller RA 2004 Nutrient mobilization and processing in Sonoran desert riparian soils following artificial re-wetting. *Biogeochemistry* 70 (1), 117-134.
- Hibbard KA, Archer S, Schimel DS, and Valentine DW 2001 Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82, 1999-2011.
- Houghton RA 2000 Interannual variability in the global carbon cycle. *Journal of Geophysical Research- Atmospheres* 105(D15), 20121-20130.
- Houghton J 2005 Global warming. *Reports on Progress in Physics* 68, 1343-1403.
- Huang BR and Fu JM 2000 Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying. *Plant and Soil* 227 (1-2): 17-26.
- Huxman T E, Cable J M, Ignace D D, Eilts J A, English N B, Weltzin J, and Williams D G 2004a Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141, 295-305.
- Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, and Schwinning S 2004b Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141, 254-268.
- Huxman TE, Smith MD, Fay PA, Knapp AK, Shaw MR, Loik ME, Smith SD, Tissue DT, Zak JC, Weltzin JF, Pockman WT, Sala OE, Haddad BM, Harte J, Koch GW, Schwinning S, Small EE, and Williams DG 2004c Convergence across biomes to a common rain-use efficiency. *Nature* 429(6992), 651-654.
- Ignace D D, Huxman T E, Weltzin J F, and Williams D G *In preparation* Functional response of native and non-native grasses to precipitation manipulation in the Sonoran Desert.
- IPCC, Climate Change 2001 The Scientific Basis. Cambridge University Press, Cambridge.

- Irvine J, Law BE, and Kurpius MR 2005 Coupling of canopy gas exchange with root and rhizosphere respiration in a semi-arid forest. *Biogeochemistry* 73, 271-282.
- Jasoni RL, Smith SD, and Arnone JA 2005 Net ecosystem CO<sub>2</sub> exchange in Mojave Desert shrublands during the eighth year of exposure to elevated CO<sub>2</sub>. *Global Change Biology* 11(5), 749-756.
- Janssens I A, Lankreijer H, Matteucci G, Kowalski A S, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grunwald L, Montagnani L, Dore S, Rebmann C, Moors J, Grelle A, Rannik U, Morgenstern K, Oltchev S, Clement R, Gudmundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen O, Vesala T, Granier A, Schulze E D, Lindroth A, Dolman A J, Jarvis P G, Ceulemans R, and Valentini R 2001 Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7, 269-278.
- Keeling CD, Whorf TP, Wahlen M, and Vanderpligt J 1995 Interannual extremes in the rate of rise of atmospheric carbon-dioxide since 1980. *Nature* 375, 666-670.
- Lange OL, Kilian E, Ziegler H 1986 Water vapor uptake and photosynthesis of lichens: Performance differences in species with green and blue-green algae as photobionts. *Oecologia* 71:104-110
- Lange OL 2001 Photosynthesis of soil-crust biota. In: Belnap and Lange (eds) *Ecological Studies. Biological Soil Crusts: Structure, function, and management*. Springer-Verlag GmbH & Co. New York, pp 217-240.
- Leifeld J and Fuhrer J 2005 The temperature response of CO<sub>2</sub> production from bulk soils and soil fractions is related to soil organic matter quality. *Biogeochemistry* 75, 433-453.
- Liang XZ, Wang WC, and Dudek MP 1995 Interannual variability of regional climate and its change due to the greenhouse-effect. *Global and Planetary Change* 10, 217-238.
- Lin N F and Tang J 2002 Geological environment and causes for desertification in arid-semiarid regions in China. *Environmental Geology* 41, 806-815.
- Liu X Z, Wan S Q, Su B, Hui D F, and Luo Y Q 2002 Response of soil CO<sub>2</sub> efflux to water manipulation in a tallgrass prairie ecosystem. *Plant and Soil* 240, 213-223.
- Lloyd J and Taylor JA 1994 On the temperature dependence of soil respiration. *Functional Ecology* 8:315-323.

- Loik ME, Breshears DD, Lauenroth WK, and BeInap J 2004 A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141:269-281.
- McAuliffe J R 1994 Landscape evolution, soil formation and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs* 64, 111-148.
- McAuliffe J R 1999 The Sonoran Desert: landscape complexity and ecological diversity. *In Ecology of Sonoran Desert Plants and Communities* Eds R Robichaux. pp 87-104. University of Arizona Press, Tucson, AZ.
- McAuliffe J R 2003 The interface between precipitation and vegetation *In Changing Precipitation Regimes and Terrestrial Ecosystems: a North American Perspective* Eds J F Weltzin and G R McPherson. University of Arizona Press, Tucson, AZ.
- Meehl GA, Zwiers F, Evans J, Knutson T, Mearns L, and Whetton P 2000 Trends in extreme weather and climate events: Issues related to modeling extremes in projections of future climate change. *Bulletin of the American Meteorological Society* 81, 427-436.
- Moraes EC, Franchito SH, and Rao VB 2005 Evaluation of surface air temperature change due to the greenhouse gases increase with a statistical-dynamical model. *Journal of Geophysical Research-Atmospheres*, 110 (D24): Art. No. D24109.
- Nguyen C 2003 Rhizodeposition of organic C by plants: mechanisms and controls. *Agronomie* 23, 375-396.
- Noy-Meir I 1973 Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25-51.
- O'Connell AM 1990 Microbial decomposition (respiration) of litter in Eucalypt forests of southwestern Australia: an empirical model based on laboratory incubations. *Soil Biology and Biochemistry* 22(2):153-160.
- Orchard V A and Cook F J 1983 Relationship between soil respiration and soil-moisture. *Soil Biology and Biochemistry* 15, 447-453.
- Parker K C 1995 Effects of complex geomorphic history on soil and vegetation patterns on arid alluvial fans. *Journal of Arid Environments* 30, 19-39.
- Paruelo JM and Lauenroth WK 1996 Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecological Applications* 6(4):1212-1224.

- Peek MS, Leffler AJ, Ivans CY, Ryel RJ, and Caldwell MM 2005 Fine root distribution and persistence under field conditions of three co-occurring Great Basin species of different life form. *New Phytologist* 165 (1): 171-180.
- Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola JM, Basile I, Bender M, Chappellaz J, Davis M, Delaygue G, Delmotte M, Kotlyakov VM, Legrand M, Lipenkov VY, Lorius C, Pepin L, Ritz C, Saltzman E, and Stievenard M 1999 Climate and atmospheric history of the past 420,000 years from the Vostoc ice core, Antarctica. *Nature* 399, 429-436.
- Potts DL, Scott RL, Williams DG, Goodrich, D, and Huxman TE *in prep* Sensitivity of *Prosopis velutina* to summer rainfall and consequences for seasonal patterns of ecosystem carbon exchange.
- Pumpanen J, Ilvesniemi H, and Hari P 2003 A process-based model for predicting soil carbon dioxide efflux and concentration. *Soil Science Society of America Journal* 67:402-413.
- Raich J W, Potter C S, and Bhagawati D 2002 Interannual variability in global soil respiration, 1980-94. *Global Change Biology* 8, 800-812.
- Raich J W and Schlesinger W H 1992 The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81-99.
- Reynolds J F, Kemp P R, and Tenhunen J D 2000 Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: A modeling analysis. *Plant Ecology* 150, 145-159.
- Rochette P, Desjardins R L, and Pattey E 1991 Spatial and temporal variability of soil respiration in agricultural fields. *Canadian Journal of Soil Science* 71, 189-196.
- Rochette P, Flanagan LB, Gregorich EG 1999 Separating soil respiration into plant and soil components using analyses of the natural abundance of Carbon-13. *Soil Sci. Soc. Am. J.* 63, 1207-1213.
- Rustad LE, Huntington TG, Boone RD 2000 Controls on soil respiration: Implications for climate change. *Biogeochemistry* 48, 1-6.
- Rustad L E, Campbell J L, Marion G M, Norby R J, Mitchell M J, Hartley A E, Cornelissen J H C, and Gurevitch J 2001 A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126, 543-562.

- Saetre P and Stark JM 2005 Microbial dynamics and carbon and nitrogen cycling following re-wetting of soils beneath two semi-arid plant species. *Oecologia* 142, 247-260.
- Sala OE and Lauenroth WK 1982 Small rainfall events: An ecological role in semiarid regions. *Oecologia* 53, 301-304.
- Sala O E, Lauenroth W K, and Parton W J 1982 Plant recovery following prolonged drought in a shortgrass steppe. *Agricultural Meteorology* 27, 49-58.
- Sala O E, Lauenroth W K, and Parton W J 1992 Long-term soil water dynamics in the shortgrass steppe. *Ecology* 73, 1175-1181.
- Schimel J P, Gullledge J M, Clein-Curley J S, Lindstrom J E, and Braddock J F 1999 Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. *Soil Biology and Biochemistry* 31, 831-838.
- Schimel JP and Weintraub MN 2003 The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biology and Biochemistry* 35:549-563.
- Schlesinger W H, Reynolds J F, Cunningham G L, Huenneke L F, Jarrell W M, Virginia R A, and Whitford W G 1990 Biological feedbacks in global desertification. *Science* 247, 1043-1048.
- Schlesinger WH, Raikes JA, Hartley AE, and Cross AF 1996 On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77(2):364-374.
- Schlesinger W H 1997 *Biogeochemistry: An analysis of global change*. Academic Press, New York. 588pp.
- Schlesinger WH and Pilmanis AM 1998 Plant-soil interactions in deserts. *Biogeochemistry* 42:169-187.
- Schwinnig S, Davis K, Richardson L, and Ehleringer JR 2002 Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia* 130, 345-355.
- Schwinnig S and Sala OE 2004 Hierarchy of responses to resource pulses in and and semi-arid ecosystems. *Oecologia* 141, 211-220.
- Schwinnig S, Sala OE, Loik ME, and Ehleringer JR 2004 Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141, 191-193.

- Sellers PJ, Bounoua L, Collatz GJ, Randall DA, Dazlich DA, Los SO, Berry JA, Fung I, Tucker CJ, Field CB, and Jensen TG 1996 Comparison of radiative and physiological effects of doubled atmospheric CO<sub>2</sub> on climate. *Science* 271, 1402-1406.
- Scott RL, Huxman TE, Williams DG, and Goodrich DC 2006 Ecohydrological impacts of woody-plant encroachment: seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment. *Global Change Biology* 12, 311-324.
- Skopp J, Jawson M D, and Doran J W 1990 Steady-state aerobic microbial activity as a function of soil-water content. *Soil Science Society of America Journal* 54, 1619-1625.
- Smith SD, Nowak RS 1990 Ecophysiology of plants in the intermountain lowlands. In: Osmond CB, Pitelka LF, Hidy M (eds) *Plant Biology of the Basin and Range*. Springer-Verlag, New York, pp 179-241
- Smith S D, Herr C A, Leary K L, and Piorkowski J M 1995 Soil-plant water relations in a Mojave desert mixed shrub community- A comparison of 3 geomorphic surfaces. *Journal of Arid Environments* 29, 339-351.
- Smith SD, Monson RK, Anderson JE 1997 *Physiological Ecology of North American Desert Plants*. Springer-Verlag, Berlin.
- Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seemann JR, and Nowak RS 2000 Elevated CO<sub>2</sub> increases productivity and invasive species success in an arid ecosystem. *Nature* 408, 79-82.
- Son Y, Jun YC, Lee YY, Kim RH, and Yang SY 2004 Soil carbon dioxide evolution, litter decomposition, and nitrogen availability four years after thinning in a Japanese larch plantation. *Communications in Soil Science and Plant Analysis* 35, 1111-1122.
- Stouffer RJ, Manabe S, and Vinnikov KY 1994 Model assessment of the role of natural variability in recent global warming. *Nature* 367, 634-636.
- Tang J W and Baldocchi D D 2005 Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. *Biogeochemistry* 73, 183-207.

- Tang J, Baldocchi D D, and Xu L 2005 Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology* 11, 1298-1304.
- Thomas AD and Dougill AJ 2006 Distribution and characteristics of cyanobacterial soil crusts in the Molopo Basin, South Africa. *Journal of Arid Environments* 64, 270-283.
- Townsend A R, Vitousek P M, Desmarais D J, and Tharpe A 1997 Soil carbon pool structure and temperature sensitivity inferred using CO<sub>2</sub> and <sup>13</sup>CO<sub>2</sub> incubation fluxes from five Hawaiian soils. *Biogeochemistry* 38, 1-17.
- Trumbore S 2000 Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications* 10, 399-411.
- Turnbull MH, Whitehead D, Tissue DT, Schuster WSF, Brown KJ, and Griffin KL 2001 Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. *Tree Physiology* 21, 571-578.
- Ullman I, Budel B 2001 Ecological determinants of species composition of biological soil crusts on a landscape scale. In: Belnap and Lange (eds) *Ecological Studies. Biological Soil Crusts: Structure, function, and management*. Springer-Verlag GmbH & Co. New York, pp 203-216
- Weltzin J F and McPherson G R 2003 Predicting the response of terrestrial ecosystems to potential changes in precipitation regimes. In: *Changing Precipitation Regimes and Terrestrial Ecosystems*. Eds J F Weltzin and G R McPherson. pp 3-8. University of Arizona Press, Tucson.
- Weltzin J F and Tissue D T 2003 Resource pulses in arid environments – patterns of rain, patterns of life. *New Phytologist* 157, 171-173.
- Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin GH, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, and Zak JC 2003 Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53, 941-952.
- Xu L K, Baldocchi D D, and Tang J W 2004 How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochemical Cycles* 18, Art. No. GB4002.
- Yu B and Neil DT 1993 Long-term variations in regional rainfall in the south-west of western-Australia and the difference between average and high-intensity rainfalls. *International Journal of Climatology* 13, 77-88.

APPENDIX A

PRECIPITATION PULSE SIZE EFFECTS ON SONORAN DESERT SOIL

MICROBIAL CRUSTS

Jessica M. Cable and Travis E. Huxman

**Abstract**

Deserts are characterized by low productivity and substantial unvegetated space, which is often covered by soil microbial crust communities. Microbial crusts are important for nitrogen fixation, soil stabilization and water infiltration, but their role in ecosystem production is not well understood. This study addresses the following questions: what are the CO<sub>2</sub> exchange responses of crusts to pulses of water, does the contribution of crusts to ecosystem flux differ from the soil respiratory flux, and is this contribution pulse size dependent? Following water application to crusts and soils, CO<sub>2</sub> exchange was measured and respiration was partitioned through mixing model analysis of Keeling plots across treatments. Following small precipitation pulse sizes, crusts contributed 80% of soil-level CO<sub>2</sub> fluxes to the atmosphere. However, following a large pulse event, roots and soil microbes contributed nearly 100% of the soil-level flux. Rainfall events in southern Arizona are dominated by small pulse sizes, suggesting that crusts may frequently contribute to ecosystem production. Carbon cycle studies of arid land systems should consider crusts as important contributors because of their dynamic responses to different pulse sizes as compared to the remaining ecosystem components.

*Key words: soil CO<sub>2</sub> flux; gas exchange; isotope analysis; Keeling plot; soil respiration*

## **Introduction**

Large areas of unvegetated space characterize water-limited regions of the southwestern U.S. This is a result of constraints on plant performance by spatial and temporal heterogeneity of soil water content and near-surface microenvironmental constraints on plant establishment (Noy-Meir 1973; Ehleringer 1985; Smith and Nowak 1990; Smith et al. 1997). However, these large expanses of unvegetated space are not devoid of autotrophic activity, due to the presence of a diversity of microbotic organisms, which are differentially affected by the biotic and abiotic factors that constrain plant function (Belnap 2003). Such assemblages, soil microbial crust communities, consist of lichen, algae, moss, fungi, cyanobacteria and bacteria that can occupy up to 70% of intercanopy space and are found in all deserts around the world (Belnap 2001). Their distribution and composition is limited across a landscape by soil texture, pH, and water content (Ullmann and Budel 2001), and their activity is directly tied to periods following rain events where soil surface water availability is high (Lange 2001). These groups of organisms appear to have an important role in the stability of ecosystem structure in arid landscapes (Belnap 2003).

A greater appreciation is developing for the role that microbial systems play in shaping ecosystem structure and function (Thompson et al. 2001). As such, soil microbial crusts have several important identified roles in desert ecosystems. These include their contribution to nitrogen input, water infiltration, and influence over patterns of erosion (Evans and Johansen 1999; Belnap 2003). However, studies of crust ecophysiology are

limited in scope by crust-physiognomic type, geographical region, and climate conditions (Lange 2001). This has to some degree constrained our ability to evaluate specific aspects of crust functioning, like their growth and seasonal performance. Consequently, an area that is in its infancy, with respect to the effect of soil microbial crust on ecosystem characteristics, is the role they play in ecosystem carbon cycling (Belnap 2003).

Arid and semi-arid regions are characterized by episodic precipitation inputs that interact with season to influence the type and functioning of autotrophic life on the landscape (Schlesinger et al. 1990; Noy-Meir 1973; Smith et al. 1997). Precipitation occurs in isolated events or pulses, and is accompanied by large interpulse periods with little or no rainfall (Noy-Meir 1973). This episodic nature of precipitation input results in co-varying characteristics of other nutrients, such as nitrogen, with periods of soil water availability (Noy-Meir 1973). Pulse driven ecosystems, such as deserts, are important to understand in light of current climate change because of their high degree of responsiveness to global change (Smith et al. 2000). The activity of crusts has this pulse driven characteristic. Cyanobacteria and cyanolichens begin exchanging CO<sub>2</sub> in the presence of liquid water whereas phycolichens and chlorophyta require water vapor, but each is quiescent during dry interpulse periods (Lange et al. 1986).

The photosynthetic and respiratory activity of microbial crusts is an important missing component of desert carbon cycling (Belnap 2003). Due to their extensive coverage of

unvegetated space in deserts and frequency with which they experience precipitation inputs, crusts may have a significant influence on ecosystem level production. However, crusts may be differentially responsive to precipitation events as compared to plants, and this results from the importance of pulse size on soil infiltration. Relatively large precipitation pulses influence plant roots and soil microbes because water infiltrates deeper into the soil profile, but both large and small pulses may impact crust activity. For the arid, southwestern U.S., several global change scenarios predict alterations in the frequency, intensity and seasonality of precipitation, each of which could impact the functioning of desert soil microbial crusts (Schlesinger et al. 1990). The questions addressed in this study are: what are the photosynthetic and respiratory responses of crusts to a precipitation pulse? What is the contribution of soil microbial crusts to the efflux of CO<sub>2</sub> from soils, relative to respiration derived from other soil micro-organisms and plant roots? How does this relative contribution change as a function of precipitation pulse size?

Here we report on work carried out in the Sonoran Desert *in situ* and in pots. Following a single water application, diurnal measurements of gas exchange were made to characterize the CO<sub>2</sub> exchange response through time. Following water application simulating two pulse sizes, respired CO<sub>2</sub> was collected and Keeling plots and mixing model analyses were done to determine the dominant contributor to ecosystem respiration. The Keeling plot technique has been used in several studies to partition respiration into its sources (Rochette et al. 1999; Bowling et al. 2001).

## Materials and Methods

### Study sites and species composition

Data were collected from two experiments: an *in situ* experiment at Saguaro National Park West approximately 10 miles west of Tucson, AZ, and a pot experiment on crusts collected from Tumamoc Hill in Tucson, AZ. The dominant vegetation cover at Saguaro National Park West consists of the C<sub>3</sub> woody plants paloverde (*Cercidium microphyllum*), creosotebush (*Larrea tridentata*), and triangle leaf bursage (*Ambrosia deltoides*). For the *in situ* experiments, five crust samples from each plot were collected and analyzed for lichen, moss, and cyanobacteria species composition by microscopic technique using an extensive collection of field samples (USGS-Southwestern Biological Science Center, Jayne Belnap's laboratory, Moab, UT). The dominant cyanobacteria genera in the crust were *Microcoleus*, *Scytonema*, *Nostoc* and the dominant lichen genera and species were *Catapyrenium*, *Peltula*, *Collema tenax*, and *Collema coccophorum*.

At Saguaro National Park, ground devoid of crusts were considered bare plots (hereafter referred to as soil plots) and ground covered with crusts were considered crust plots. The different  $\delta^{13}\text{C}$  values of the crust organisms and the bulk soil from the top 5cm from the bare plots suggest that bare plots did not have cyanobacteria (see Results of ecosystem carbon pools). Soil plots had plant roots and soil micro-organisms as contributors to respiratory gas efflux, whereas crust plots had microbial soil crusts, soil micro-organisms and plant roots as contributors.

Seasonally, the temperature (average minimum and average maximum) for both sites ranges from 16°C to 21°C in the winter and 38°C to 45°C in the summer, and the average annual precipitation is less than 30.5 cm. Pot studies occurred during late August, 2002, and *in situ* measurement of crust CO<sub>2</sub> exchange occurred during late March, 2003. For the August measurements, there was no precipitation for the three days prior to measurement. Pots were stored in a greenhouse for the day prior to measurement. The high temperatures for the three days before and the day of the measurements in August were 40.6, 40.3, 40.6, 37.2°C, and the low temperatures were 15.7, 15.7, 16.8, and 20.2°C (AZMET database). At Saguaro National Park, cumulative rainfall was 0.41cm on the two days prior to measurements. The high temperatures for the three days prior to and the day of the measurements were 14.5, 15.4, 18, and 21.8°C, and the low temperatures were 6.3, 6.6, 5.8, and 4.3°C (AZMET database).

The frequency of different size rainfall events were compared for the Sonoran, Mojave and Chihuahuan deserts from 1996 to 1999. Precipitation data for the Sonoran Desert were provided by the AZMET database. Precipitation data for the Mojave Desert were provided by the Nevada Desert FACE Facility. Precipitation data for the Chihuahuan Desert were provided by the Jornada Long-Term Ecological Research (LTER) project.

### **Pot experiment of photosynthesis and respiration**

Crusts were collected from Tumamoc Hill near Tucson, AZ. For each crust sample, the ground was dampened and the top 5mm of the ground surface was collected with a spatula. The soil from beneath the collected sample was harvested and placed in pots, and the crust samples were replaced on the soil in the pots. Six pots of crust were collected (3 for wet crust replicates and 3 for dry crust replicates). PVC rings (hereafter collars) 11.4cm in diameter and 17.8cm long were installed to a depth of 12.7cm into each pot. A 25.4mm water pulse was applied randomly to 3 of the crust pots. Paired light and dark measurements of gas exchange were made on each collar with a Li-6400 portable photosynthesis system (Li Cor Inc., Lincoln, NE) with a clear chamber with approximately a 1L volume. The block temperature was maintained between 33°C and 34°C. Measurements were made at a CO<sub>2</sub> concentration of 370 ppm. Paired light and dark measurements of gas exchange were made in random order on the collars. First, measurements were made in the light by placing the chamber on the collars and allowing the chamber to equilibrate with the crust. Approximately 10 measurements were made for each collar at 1 min intervals, standardizing the IRGAs of the open path system between each measurement using the 'Match' procedure. Then measurements were made in the dark by placing a box on the collar for 15 minutes allowing the crusts to dark-adapt prior to measurement. The chamber was placed under the box on the collars and measurements were made in the dark, using the same measurement technique as in the light, and maintaining similar temperature conditions of the crust and soil. Collar

specific differences between the dark and light measurements are considered gross photosynthetic activity of the crust community.

**(1) In situ experiment: CO<sub>2</sub> collection and isotope analysis**

Eighteen PVC collars were installed on soil and crust plots at Saguaro National Park West near Tucson, AZ, within 1m of the base of paloverde trees, the dominant C<sub>3</sub> woody plant. This was done to maintain consistent microclimate conditions of the collars. Watering treatment was applied at random in late March over an area of 0.0625m<sup>2</sup> in two pulse sizes, 2mm and 25.4mm, and a control (0mm) to 9 crust and 9 soil plots (three replicates of each treatment). Water was applied with a gardening water wand to achieve a sprinkling effect and watering was conducted such that runoff was not allowed to occur. Care was taken to apply water slowly to allow for maximum potential infiltration.

To determine the contribution of crusts to soil-level CO<sub>2</sub> flux, natural variation of the stable isotope <sup>13</sup>C in vegetation, soil, and microbial crusts, along with respired gas, was used to partition respiration from the two dominant sources, soil (sub-surface soil microbes and roots) and crusts. We assume there is no isotopic fractionation of <sup>13</sup>C from CO<sub>2</sub> during mitochondrial or microbial respiration (Lin and Ehleringer 1997; Ehleringer et al. 2000). However, it has been suggested there may be fractionation during microbial respiration, and this is an area of active research (Schweizer et al. 1999). The inverse of the concentration of the CO<sub>2</sub> in the respired air and the isotopic signature of carbon were regressed in a Keeling plot. This is a linear relationship wherein the intercept represents

the source of the respired CO<sub>2</sub> (Keeling 1961). The intercepts can be related to the pools of carbon in the soil and crusts with the use of a mixing model (Phillips and Gregg 2001). We experimentally isolated the combined contribution of soil sub-surface microbes and roots in order to compare crust respiration to belowground respiration as a whole.

Opaque PVC chambers (lids) 3 liters in volume with a septum port (Ultra torr fitting (Swagelok) with a rubber septum (Labco Inc. UK)) in the top were placed on the collars. To assure proper mixing of air within the lid, a 4.5V microfan was placed inside the lid midway up the wall to avoid excessive disruption the boundary layer above the soil surface. The fan drew air from the center of the lid air space and directed the airflow to the top of the lid. Respired CO<sub>2</sub> from soil and crust plots were collected over the period of a day. Respired air was allowed to build up and 15mL was drawn out with a 20mL LUER LOK syringe (BD Syringe) with a 22-gauge needle, and 5 samples were collected successively from a single plot over a period of 30 to 50 minutes. We removed only 0.5% of the total volume with each withdrawal from a chamber with slight leaks, while allowing sufficient time for CO<sub>2</sub> efflux from the plots was enough to replace the CO<sub>2</sub> removed from the lids. Careful sampling from a slightly leaky chamber would relieve the pressure differential occurring between the inside and outside of the lids (Davidson et al. 2002).

A time series of samples from each collar was determined once. On dry plots, samples were withdrawn every 10 minutes for 50 minutes and on wet plots, samples were

withdrawn every 6 minutes for 30 minutes, due to differences in CO<sub>2</sub> respiration rates. Atmospheric air was collected three times throughout the day. The gas samples were injected into 12mL Exetainer evacuated vials (Labco Inc, UK). The vials were overpressurized by 3mL to avoid contamination of samples with atmospheric air. Vials of reference gas of a known CO<sub>2</sub> concentration and  $\delta^{13}\text{C}$  value were collected throughout the measurement time to correct sample values for any drift in isotope values or concentration due to vial effects, as in Tu et al. (2001). The gas samples were stored for 1 to 5 days prior to analysis. Reference gas samples were collected during the storage time to correct for any drift that may occur. No effects on the concentration or  $\delta^{13}\text{C}$  values from vial storage or overpressurization were observed so no corrections were applied to the data (one way ANOVA for area vs. date  $F_{3,4} = 54.54$ , two sided  $p = 0.10$ ; one way ANOVA for  $\delta^{13}\text{C}$  vs. date  $F_{3,4} = 121.58$ , two sided  $p = 0.07$ ). Drift did not occur while the samples were run due to the mass spectrometer ( $t$ -test comparing peak areas and  $\delta^{13}\text{C}$  of standard gasses run at the beginning and the end of a run  $t_{3 \text{ area}} = -2.808$ , two sided  $p = 0.07$ ;  $t_{3 \delta^{13}\text{C}} = 1.017$ , two sided  $p = 0.38$ ). Just prior to analysis, depressurization of gas samples was done by quickly poking an open top LUER LOK needle through the septum and covering the top of the needle as it was withdrawn. Samples were analyzed for CO<sub>2</sub> concentration and  $\delta^{13}\text{C}$  on a Finnigan Delta-S mass spectrometer interfaced with a Gas Bench II at the University of Arizona. Two CO<sub>2</sub> standard gasses of known  $\delta^{13}\text{C}$  values and concentrations were run at the beginning and end of the run.

The  $\delta$  notation is a symbol used to describe the isotopic composition of a gas or material relative to an internationally accepted standard such as PDB in the following equation:

$$\delta^{13}\text{C} = 1000 * ((R_{\text{sample}}/R_{\text{standard}}) - 1) \quad (1)$$

where  $R_{\text{sample}}$  is the  $^{13}\text{C}/^{12}\text{C}$  ratio of the sample,  $R_{\text{standard}}$  is the  $^{13}\text{C}/^{12}\text{C}$  ratio of the standard material, and the  $\delta$  value is expressed as a per mil (‰) because it is multiplied by 1000 (Dawson et al. 2002). In this study,  $\delta^{13}\text{C}$  values are reported to the PDB internationally accepted standard.

#### *Testing for vial effects*

To further ensure that vial usage, overpressurization and storage did not influence our results, we carefully evaluated our techniques. For four separate sampling dates, vials with a standard  $\text{CO}_2$  gas were collected on three consecutive days and overpressurized. If overpressurization or storage causes gas to diffuse out of the vials and cause isotopic fractionation, the samples should become more enriched through time. No effects were seen for either  $\text{CO}_2$  concentration or  $\delta^{13}\text{C}$  values. Additionally, comparisons were made of 4 vials containing a known reference gas that were stored for 7 days against 3 vials stored for 2 days. The  $\delta^{13}\text{C}$  values did not differ between the 7 day and the 2 day vials (-27.12‰ +/- 0.0467‰ vs. -27.23‰ +/- 0.0843‰ respectively). Finally, to ensure that the septa of the Exetainer vials are not offgassing  $\text{CO}_2$  and contaminating the samples, we analyzed the septa material for  $\delta^{13}\text{C}$  and found the mean value was -27.6‰ +/- 0.13‰. We filled six vials with pure  $\text{N}_2$  gas and ran 3 samples after 24 hours and the remaining 3 after 5 days of storage. These vials were taken in the field and experienced the same

temperature and pressure fluctuations other samples experienced. They were analyzed on the Finnigan Delta-S mass spectrometer interfaced with a Gas Bench II. We found that there was no CO<sub>2</sub> in the vials. This is not an exhaustive test of possible effects from vial storage and overpressurization and further research needs to be done.

## **(2) In situ experiment: collection of ecosystem carbon pools**

At Saguaro National Park, samples of plant leaves and roots were collected within a 1m radius of the collars. Fine roots were collected from the top 10-15cm of the soil within 20cm of the plant base. Soil was collected from the top 5cm because the majority of soil respiration is from the labile carbon pool (Townsend et al. 1997; Janssens et al. 2001).

Crusts were collected from the top 5mm ground surface. We separated the lichen samples from the soil as best we could without damaging the integrity of the lichen. For non-lichen samples, the top 5mm of the soil was collected and soil was gently dusted off the bottom. Samples were dried at C for 24 hours. Soil and crust samples were ground, acidified with 1M HCl (Fisher Scientific), rinsed with deionized water over glass filter paper, and dried at 60°C for 24 hours. Crust samples were processed as a whole; they were not separated into different species prior to processing. All samples were analyzed for  $\delta^{13}\text{C}$  on a Finnigan Delta-S mass spectrometer online with an elemental analyzer at the University of Arizona.

The  $\delta^{13}\text{C}$  values of the respired air were compared to the  $\delta^{13}\text{C}$  of the pools in a mixing model using two end members, crust and soil (Phillips and Gregg 2001). For the soil

plots, the two pools (end members) were the soil and plant root tissue. For the crust plots, the two pools were the  $\delta^{13}\text{C}$  of the respired  $\text{CO}_2$  from the soil plots (e.g. combined soil and root) and the crust tissue samples. The  $\delta^{13}\text{C}$  of the soil and plant pools from the crust plot could not simply be averaged and used as a general belowground pool because the average should be weighted (both are not contributing equally to ecosystem flux). The  $\delta^{13}\text{C}$  of the respired air from the soil plots represents this weighted average.

### **Statistical Analyses**

The time-course of respiration and net  $\text{CO}_2$  exchange was analyzed with multiple regressions because the  $\text{CO}_2$  fluxes of the dark and light measurements were compared over time. Gross photosynthesis (or photosynthetic  $\text{CO}_2$  fixation) over time was analyzed with a linear regression. The gas collection data were analyzed with linear regressions of  $\delta^{13}\text{C}$  on  $1/[\text{CO}_2]$ . The intercepts from the regression analyses were compared between crusts, soil and roots across the watering treatments and control with a multi-way ANOVA. The pool  $\delta^{13}\text{C}$  values for plant roots, soil and crusts were analyzed with a one-way ANOVA. The percent carbon contributed from crust, soil and root across the watering treatments and control were compared qualitatively by examining standard errors (calculated from mixing model from Phillips and Gregg (2001)) because the data were repeated measures. The statistical package JMP-IN (version 4.0.1 Academic, SAS Institute, Inc.) was used for data analysis.

## Results

### Pot experiment of respiration and photosynthesis

There was a positive relationship between time since water application and gross photosynthetic CO<sub>2</sub> fixation (linear regression  $t_4 = 3.35$ , two sided  $p < 0.05$ , fig. 1a).

Relative to the maximum value measured, gross photosynthesis responded quickly (<100 minutes) to water application. Respiration and net CO<sub>2</sub> fixation differed following water application (multiple regression  $t_{32} = 4.62$ , two sided  $p < 0.05$ , fig. 1b). Respiration increased through time while net CO<sub>2</sub> exchange remained nearly unchanged and slightly positive (CO<sub>2</sub> efflux from soil and crusts). Negative values represent CO<sub>2</sub> efflux and positive values represent CO<sub>2</sub> influx.

#### (1) In situ experiment: CO<sub>2</sub> collection and isotope analysis

The intercepts from the Keeling plots of soil and crust for the watering treatments differed from each other, and the intercept depended on the watering treatment (multi-way ANOVA  $F_{2,9} = 4.06$ , two sided  $p = 0.055$ , fig. 2). In particular, the intercept of  $-21.9\% \pm 1.39$  (standard error) from crusts receiving the 2mm water treatment was greater than all other treatments of crust and soil (linear contrast  $t_{14} = 2.69$ , two sided  $p < 0.05$ ). The intercepts of  $-24.8\% \pm 1.01$  and  $-24.6\% \pm 2.66$  from the crust and soil receiving 25.4mm of water were less than the intercepts of the other plots (linear contrast  $t_{14} = 2.79$ , two sided  $p < 0.05$ ). Only the crust and soil receiving the 2mm water treatment differed from each other when comparing within treatment contrasts (linear

contrast  $t_{14} = 2.288$ , two sided  $p < 0.05$ ). The intercept values reflect the addition of a 4.4‰ diffusion fractionation to account for the differential movement of the lighter isotope out of the soil (Amundson et al. 1998). The diffusion fractionation was applied to the intercepts because we assume the CO<sub>2</sub> moving out of the crust and soil was via diffusion and not mass flow. The standard fractionation applied to diffusion of the lighter isotope out of the soil is 4.4‰ (Amundson et al. 1998).

## **(2) In situ experiment: collection of ecosystem carbon pools**

The mean  $\delta^{13}\text{C}$  pool values of soil, crust and plant roots differed significantly (one-way ANOVA  $F_{2,13} = 14.015$ , two sided  $p = 0.0006$ ,  $n_{\text{roots}} = 9$ ,  $n_{\text{soil}} = 5$ ,  $n_{\text{crust}} = 5$ , fig. 3). In particular, the crust pool of  $-21.5\text{‰} \pm 0.66$  was greater than the soil and root pool (linear contrast  $t_{15} = 4.44$ , two sided  $p = 0.0007$ ). The soil pool of  $-23.9\text{‰} \pm 0.21$  was greater than the root pool of  $-25.3\text{‰} \pm 0.41$  (linear contrast  $t_{15} = 2.51$ , two sided  $p = 0.026$ ).

## **Comparison of pools and Keeling plots**

Keeling plot values were compared to the pool values using a mass balance approach in a mixing model from Phillips and Gregg (2001). The soil Keeling plot intercept from the 25.4mm treatment was used as the pool value for the soil and roots to compare to the crusts. Crusts contributed greater amounts of carbon to the CO<sub>2</sub> efflux under control conditions than the soil and root component (fig. 4). A 2mm precipitated pulse essentially stimulated only crust respiratory activity, and created a large discrepancy in

the relative contributions of crust, soil and roots. Application of 25.4mm of water resulted in substantial contributions of carbon to the CO<sub>2</sub> efflux from soil and roots relative to crusts. The standard errors from each treatment for soil and crust did not overlap the means, indicating that the mean percentage of carbon contribution from each source differed from each other.

### **Discussion**

Microbial soil crusts are important components of desert ecosystems owing to their contributions to the nitrogen cycle and water infiltration (Evans and Johansen 1999; Belnap 2003). However, little is known about crust contribution to the carbon cycle, making this important to understand. Because the isotopic composition of ecosystem carbon pools differed from each other in the current study (fig. 3), CO<sub>2</sub> fluxes could be partitioned using Keeling plots and a mixing model. At ambient conditions (control), CO<sub>2</sub> fluxes from soils were small and microbial soil crusts contributed more than the remaining belowground ecosystem components to the total flux (fig. 4); however, this approximated 50% from the crust and soil. In contrast, following the 2mm pulse, the crusts dominated the respiratory CO<sub>2</sub> efflux and following the 25.4mm pulse, soil and roots dominated the response (fig. 4). The small pulse evaporated quickly and primarily activated the crust instead of the plant roots and soil microbes because it did not move as far through the soil profile as did the 25.4mm pulse. These results suggest that following small pulse events, crusts are the sole contributors to ecosystem carbon cycling and their contribution to CO<sub>2</sub> efflux is pulse size dependent.

Gross photosynthesis increased through time following water application, so there is a clear time course of carbon fixation and CO<sub>2</sub> exchange is responsive to watering (fig. 1). Initially after water application, the crusts upregulate photosynthetic enzymes and repair damaged cells (Smith and Mollesworth 1973). Crust ecophysiology has not been previously characterized in the region where the gas collection for this study was conducted. The  $\delta^{13}\text{C}$  values of the crusts from Saguaro National Park West are intermediate with values reported in the literature for lichen and cyanobacteria. The reported values for lichen are less than -23‰ and cyanobacteria is approximately 12‰ (Evans and Belnap 1999), and for this study the value for crusts were about -21‰, so most likely some crust was a mix of lichens and cyanobacteria but dominated by lichens. Photosynthetic rates were slightly lower than those reported for crusts on the Colorado Plateau (Lange 2001).

Much of the early work on crust contribution to ecosystem nitrogen levels, soil stabilization, and their influence on vascular plant establishment was completed in the Sonoran Desert (McIlvanie 1942; Mayland et al. 1966). Comparisons of crust function across the hot deserts (Sonoran, Chihuahuan, Mojave) have focused on species composition, crust structure, nitrogen fixation capacities and capabilities, fluxes of N<sub>2</sub>O, influences on desert hydrology, influences on soil micro-organisms, and disturbance effects (Guilbault and Matthias 1998; Rosentreter and Belnap 2001; Belnap 2001; Evans and Lange 2001; Warren 2001). Examinations of patterns of crust CO<sub>2</sub> exchange and

levels of production have focused primarily on lichens, with some work done on cyanobacteria and moss (Lange 2001). However, properties of crust CO<sub>2</sub> exchange and productivity and their contribution to ecosystem production have not been examined in the Sonoran Desert, and a comparison between the hot deserts has not been completed. Rainfall events in the three hot deserts are dominated by pulse events smaller than 2mm (fig. 5). As reported here, small pulse events cause crusts to dominate ecosystem CO<sub>2</sub> exchange. Therefore, in the hot deserts, crusts are potentially the sole contributors to ecosystem carbon cycling following the majority of rain events.

Non-vascular plants play significant roles in ecosystem processes in other biome types. In extreme environments, such as Antarctica, communities such as algal and cyanobacterial-mats and cryptoendolithic communities have been shown to be important in influencing glacier surface albedo, nitrogen fixation and soil input, and soil carbon inputs through organic matter deposition (Friedmann et al. 1993; Burkins et al. 2000; Tekeuchi et al. 2001; Fernandez-Valiente et al. 2001). Effects of global change in the short term on Antarctic ecosystems will depend on the ecophysiological responses of the cryptogamic communities (Kennedy 1995). Although Antarctica is a continent dominated by non-vascular plants, Boreal forests have more plant life-form diversity. However, the contribution of the non-vascular understorey vegetation such as mosses to ecosystem productivity is extensive. Moss store a large amount of carbon, can contribute 25% to net primary productivity (NPP), offset carbon loss from soil respiration, and increase nitrogen input through symbioses with cyanobacteria (Rapalee et al. 1998;

Moren and Lindroth 2000; Grant et al. 2001; DeLuca et al. 2002). Contributions of moss to NPP and net ecosystem production are highly influenced by frequency of precipitation input, whereas the dominant spruce tree species are unresponsive to changes in frequency (Frolking 1997). Therefore, the influence of non-vascular plants on ecosystem processes is significant for many biome types, including the deserts of the southwestern U.S.

The majority of rainfall events in the Sonoran, Chihuahuan, and Mojave Deserts are small pulse events (<2mm) (fig. 5, AZMET, Jornada LTER, Nevada FACE). Therefore, the contribution of crusts to ecosystem CO<sub>2</sub> exchange and productivity is potentially large. In pulse driven ecosystems, the size of the rainfall events appear to be important in determining which components are active and to what degree. Soil respiration, that is respiration from soil microbes, roots, and crusts if present, represents one of the largest components of the local carbon cycle contributing to the global carbon budget (Rustad et al. 2000). Soil moisture is a controller of soil respiration so a change in precipitation regimes, as predicted from climate change models, in a pulse driven ecosystem may alter respiratory responses from the soil as a whole (Rustad et al. 2000; Easterling et al. 2000). However, as suggested in this study, a change in precipitation patterns such as a trend toward more frequent events of large or small pulses may alter the respiratory contribution from different components of the ecosystem, thereby altering the carbon budget of desert ecosystems and the relative importance of crusts.

Although not addressed in this study, it will be important to consider frequency of different sized pulse events, and the duration of high soil water availability following pulses of different sizes. The respiratory response from plant roots and soil microbes may be limited to large pulse events, but the overall annual magnitude of their contribution could be large due to the soil remaining wet for a longer period of time. The top 5cm of soil dries quickly so crusts would dry out faster than lower soil layers. However, the frequency of small pulse events is greater than large pulse events and crusts respond to any water present. Therefore, crust contribution may be comparable to the other components of the ecosystem and should be considered in carbon cycle studies of arid land systems because of their dynamic responses to different pulse sizes.

### **Acknowledgements**

The authors thank Danielle Ignace for help in data collection, Bill Cable for help with gas collection, Dr. David Dettman for mass spec assistance, and Dr. Alfredo Huete for discussion and critique. We are especially grateful for the assistance provided by Dr. Jayne Belnap and Bernadette Graham in analyzing samples for crust identification and chlorophyll content. The authors acknowledge support from the University of Arizona and the USDA Forest Service through an International Arid Lands Consortium grant (02R-06).

## References

- Amundson R, Stern L, Baisden T, Wang Y (1998) The isotopic composition of soil and soil-respired CO<sub>2</sub>. *Geoderma* 82:83-114
- Belnap J (2001) Microbes and microfauna associated with biological soil crusts. In: Belnap and Lange (eds) *Ecological Studies. Biological Soil Crusts: Structure, function, and management*. Springer-Verlag GmbH & Co. New York, pp 167-176
- Belnap J (2003) The world at your feet: desert biological soil crusts. *Frontiers in Ecology* 1:181-189
- Bowling DR, Tans PP, Monson RK (2001) Partitioning net ecosystem carbon exchange with isotopic fluxes of CO<sub>2</sub>. *Global Change Biology* 7:127-145
- Burkins MB, Virginia RA, Chamberlain CP, Wall DH (2000) Origin and distribution of soil organic matter in Taylor Valley, Antarctica. *Ecology* 81(9):2377-2391
- Davidson EA, Savage K, Verchot LV, Navarro R (2002) Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agricultural and Forest Meteorology* 113:21-37
- Dawson TE, Mambelli S, Plamboek AH, Templer PH, Tu KP (2002) Stable isotopes in plant ecology. *Annual Reviews in Ecology and Systematics* 33:507-559
- DeLuca TH, Zackrisson O, Nilsson MC, Sellstedt A (2002) Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature* 419(6910):917-920

- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: Observations, modeling, and impacts. *Science* 289(5487): 2068-2074
- Ehleringer J (1985) Annuals and perennials of warm deserts. In: Chabot BF, Mooney HA (eds) *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York, pp 162-180
- Ehleringer JR, Buchmann N, Flanagan LB (2000) Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications* 10(2):412-422
- Evans RD, Belnap J (1999) Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology* 80(1):150-160
- Evans RD, Johansen JR (1999) Microbiotic crusts and ecosystem processes. *Critical Review in Plant Science* 18(2):183-225
- Evans DR, Lange OL (2001) Biological soil crusts and ecosystem nitrogen and carbon dynamics. In: Belnap and Lange (eds) *Ecological Studies. Biological Soil Crusts: Structure, function, and management*. Springer-Verlag GmbH & Co. New York, pp 263-280
- Fernandez-Valiente E, Quesada A, Howard-Williams C, Hawes I (2001) N-2-fixation in cyanobacterial mats from ponds on the McMurdo Ice Shelf, Antarctica. *Microbial Ecology* 42(3):338-349
- Friedmann EI, Kappen L, Meyer MA, Nienow JA (1993) Long-term productivity in the cryptoendolithic microbial community of the Ross Desert, Antarctica. *Microbial Ecology* 25(1):51-69

- Frolking S (1997) Sensitivity of spruce/moss boreal forest net ecosystem productivity to seasonal anomalies in weather. *Journal of Geophysical Research-Atmospheres* 102(D24):29053-29064
- Grant RF, Goulden ML, Wofsy SC, Berry JA (2001) Carbon and energy exchange by a black spruce-moss ecosystem under changing climate: Testing the mathematical model ecosys with data from the BOREAS experiment. *Journal of Geophysical Research-Atmospheres* 106(D24):33605-33621
- Guilbault MR, Matthias AD (1998) Emissions of N<sub>2</sub>O from Sonoran desert and effluent-irrigated grass ecosystems. *Journal of Arid Environments* 38:87-98
- Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grunwald L, Montagnani L, Dore S, Rebmann C, Moors J, Grelle A, Rannik U, Morgenstern K, Oltchev S, Clement R, Gudmundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen O, Vesala T, Granier A, Schulze ED, Lindroth A, Dolman AJ, Jarvis PG, Ceulemans R, Valentini R (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7:269-278.
- Keeling CD (1961) A mechanism for cyclic enrichment of carbon-12 by terrestrial plants. *Geochimica et Cosmochimica Acta* 24(3-4):299-313
- Kennedy AD (1995) Antarctic terrestrial ecosystem response to global environmental-change. *Annual Review of Ecology and Systematics* 26:683-704

- Lange OL, Kilian E, Ziegler H (1986) Water vapor uptake and photosynthesis of lichens: Performance differences in species with green and blue-green algae as photobionts. *Oecologia* 71:104-110
- Lange OL (2001) Photosynthesis of soil-crust biota. In: Belnap and Lange (eds) *Ecological Studies. Biological Soil Crusts: Structure, function, and management.* Springer-Verlag GmbH & Co. New York, pp 217-240
- Lin G, Ehleringer JR (1997) Carbon isotopic fractionation does not occur during dark respiration in C<sub>3</sub> and C<sub>4</sub> plants. *Plant Physiology* 114:391-394.
- Mayland HF, McIntosh TH, Fuller WH (1966) Fixation of isotopic nitrogen in a semi-arid soil by algal crust organisms. *Soil Science Society of America Proceedings* 30:56-60
- McIlvanie SK (1942) Grass seedling establishment and productivity – overgrazed vs. protected range soils. *Ecology* 23:228-231
- Moren AS, Lindroth A (2000) CO<sub>2</sub> exchange at the floor of a boreal forest. *Agricultural and Forest Meteorology* 101(1): 1-14
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25-51
- Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. *Oecologia* 127:171-179

- Rapalee G, Trumbore SE, Davidson EA, Harden JW, Veldhuis H (1998) Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape. *Global Biogeochemical Cycles* 12(4):687-701
- Rochette P, Flanagan LB, Gregorich EG (1999) Separating soil respiration into plant and soil components using analyses of the natural abundance of Carbon-13. *Soil Sci. Soc. Am. J.* 63:1207-1213
- Rosentreter R, Belnap J (2001) Biological soil crusts of North America. In: Belnap, J. and O.L. Lange (eds) *Biological Soil Crusts: Structure, function and management*. Springer-Verlag GmbH & Co. New York, pp 31-50
- Rustad LE, Huntington TG, Boone RD (2000) Controls on soil respiration: Implications for climate change. *Biogeochemistry* 48:1-6
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247:1043-1048
- Schweizer M, fear J, Cadisch G (1999) Isotopic ( $^{13}\text{C}$ ) fractionation during plant residue decomposition and its implications for soil organic matter studies. *Rapid Communications in Mass Spectrometry* 13:1284-1290
- Smith DC, Molesworth S (1973) Lichen physiology. XIII. Effects of rewetting dry lichens. *New Phytologist* 72:525-533
- Smith SD, Nowak RS (1990) Ecophysiology of plants in the intermountain lowlands. In: Osmond CB, Pitelka LF, Hidy M (eds) *Plant Biology of the Basin and Range*. Springer-Verlag, New York, pp 179-241

- Smith SD, Monson RK, Anderson JE (1997) *Physiological Ecology of North American Desert Plants*. Springer-Verlag, Berlin
- Smith S, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seeman JR, Nowak RS (2000) Elevated CO<sub>2</sub> increases productivity and invasive success in an arid ecosystem. *Nature* 408:79-82
- Takeuchi N, Kohshima S, Seko K (2001) Structure, formation, and darkening process of albedo-reducing material (cryoconite) on a Himalayan glacier: A granular algal mat growing on the glacier. *Arctic, Antarctic and Alpine Research* 33(2):115-122
- Thompson JN, Reichman OJ, Morin PJ, Polis GA, Power ME, Sterner RW, Couch CA, Gough L, Holt R, Hooper DU, Keesing F, Lovell CR, Milne BT, Molles MC, Roberts DW, Strauss SY (2001) Frontiers of ecology. *BioScience* 51(1):15-24
- Townsend AR, Vitousek PM, Desmarais DJ, Tharpe A (1997) Soil carbon pool structure and temperature sensitivity inferred using CO<sub>2</sub> and <sup>13</sup>CO<sub>2</sub> incubation fluxes from five Hawaiian soils. *Biogeochemistry* 38:1-17
- Tu KP, Brooks PD, Dawson TE (2001). Using septum-capped vials with continuous-flow isotope ratio mass spectrometric analysis of atmospheric CO<sub>2</sub> for Keeling plot applications. *Rapid Communications in Mass Spectrometry* 15:952-956
- Ullman I, Budel B (2001) Ecological determinants of species composition of biological soil crusts on a landscape scale. In: Belnap and Lange (eds) *Ecological Studies. Biological Soil Crusts: Structure, function, and management*. Springer-Verlag GmbH & Co. New York, pp 203-216

Warren SD (2001) Synopsis: Influence of biological soil crusts on arid land hydrology and soil stability. In: Belnap and Lange (eds) Ecological Studies. Biological Soil Crusts: Structure, function, and management. Springer-Verlag GmbH & Co. New York, pp 349-362

### Figure Legends

Figure 1. CO<sub>2</sub> fluxes of crusts following water application in pots. The top panel (a) is time course of gross photosynthesis following water application standardized to the maximum rate measured for each pot. Error bars are the standard errors. The bottom panel (b) is the change in respiration and net CO<sub>2</sub> exchange following water application. The difference between respiration and net CO<sub>2</sub> exchange is gross photosynthesis. In panel b, negative values represent CO<sub>2</sub> efflux and positive values represent CO<sub>2</sub> influx.

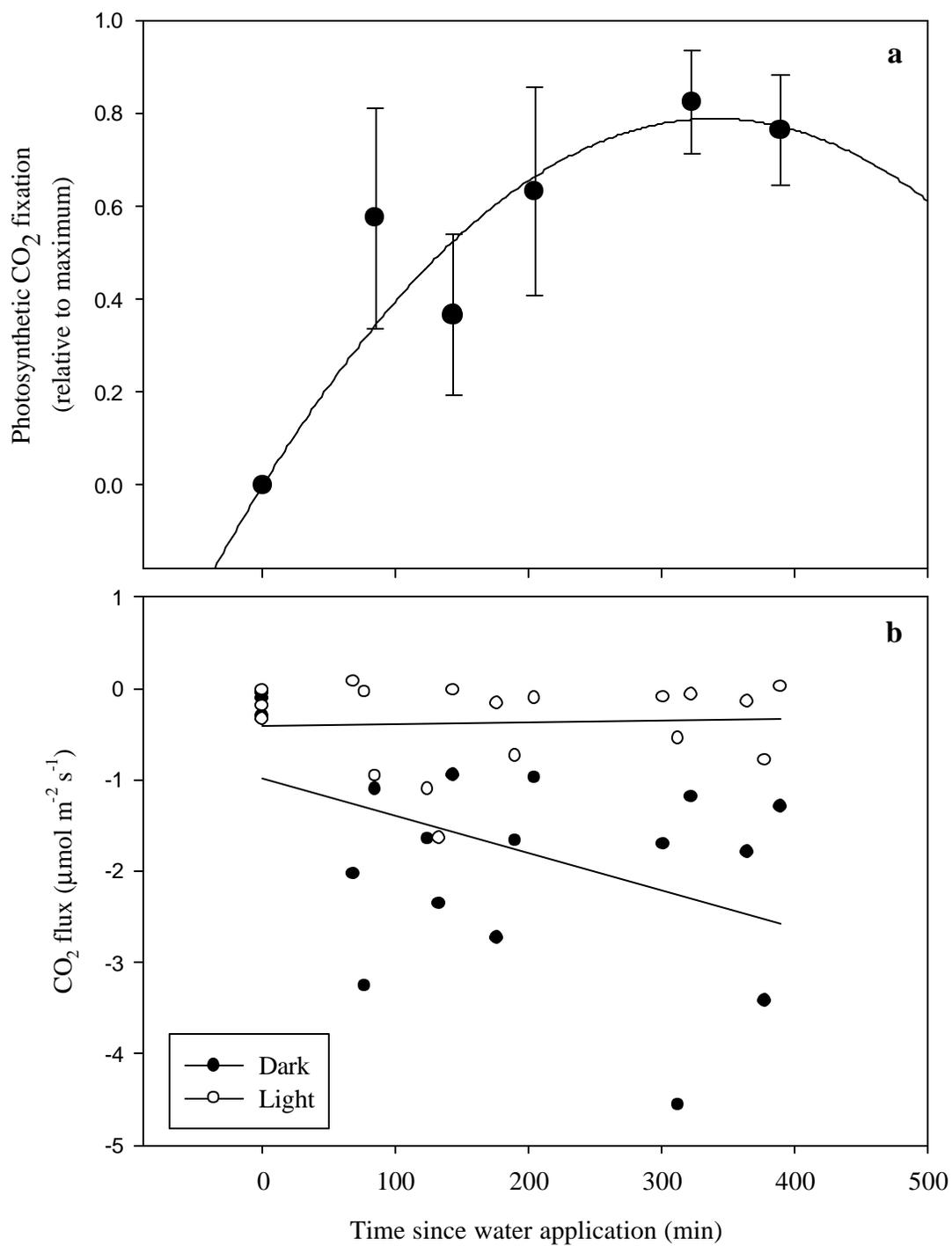
Figure 2. Keeling Plot intercepts of crust and soil for three watering treatments following an adjustment of 4.4 per mil due to diffusion fractionation (Amundson et al 1998). The error bars are one standard error. Different letters indicate statistical differences between measurements.

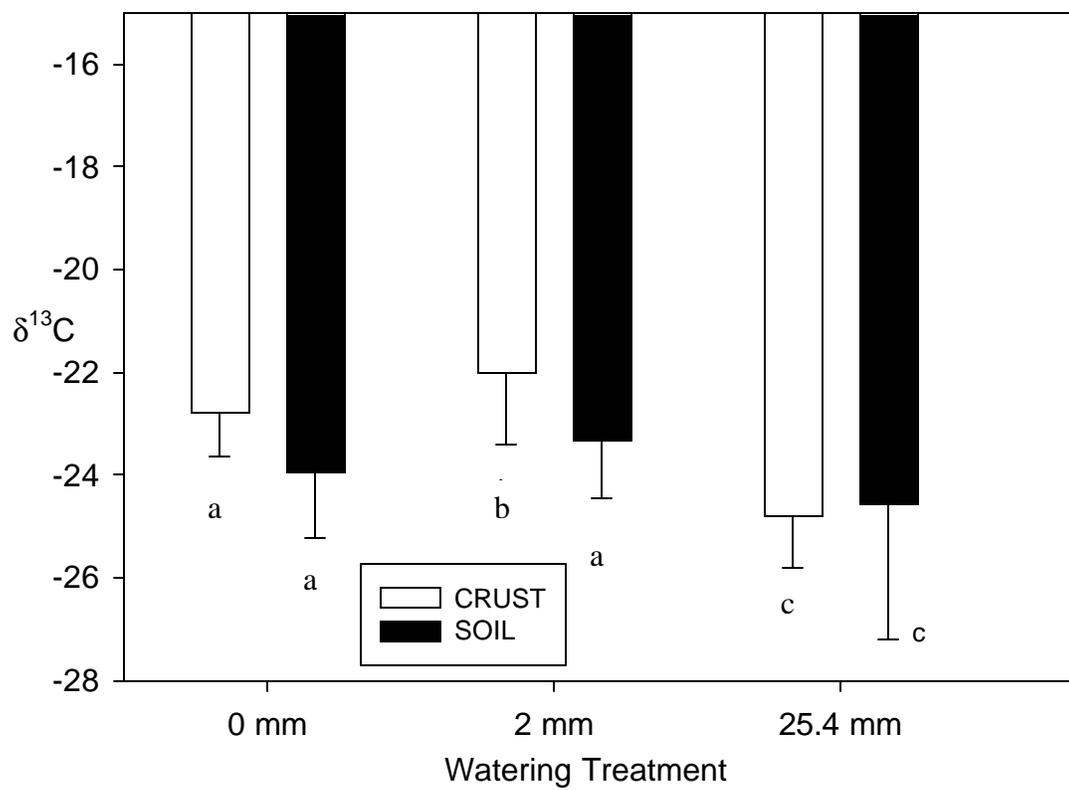
Figure 3. Pool  $\delta^{13}\text{C}$  values from C<sub>3</sub> roots, soil, and crust at Saguaro National Park in southern Arizona. Error bars are one standard error. Different letters indicate statistical differences between means.

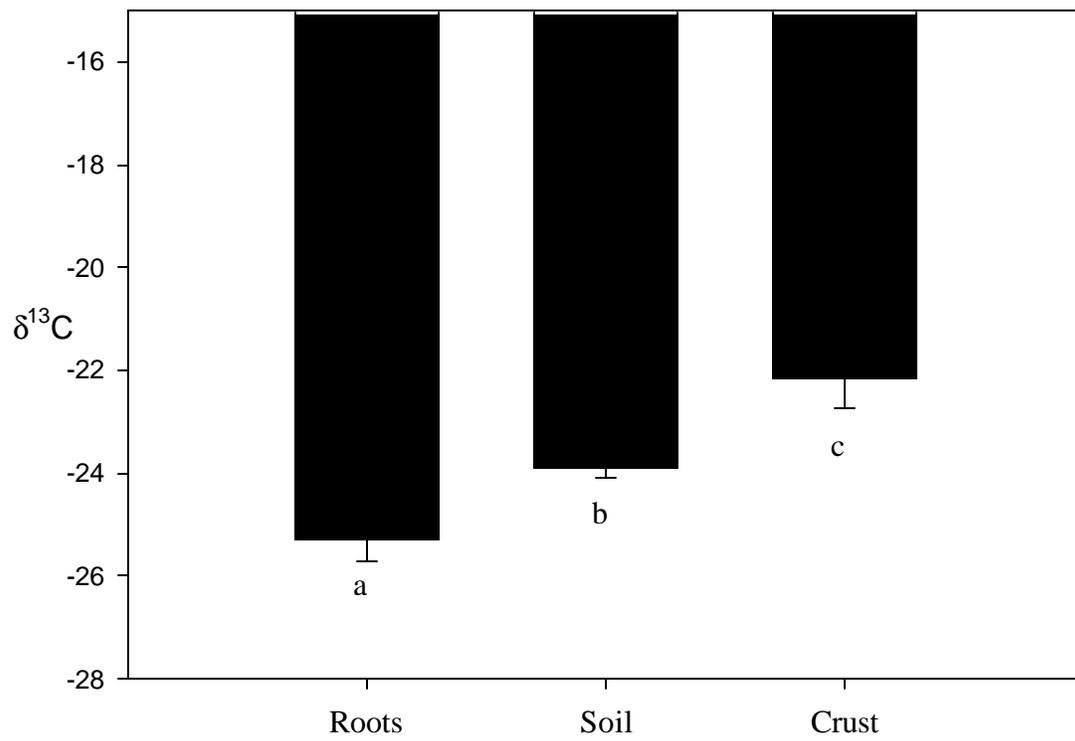
Figure 4. Percent of carbon contributed to total CO<sub>2</sub> flux from crust and soil after the three watering treatments. Error bars are one standard error. Different letters indicate statistical differences between measurements.

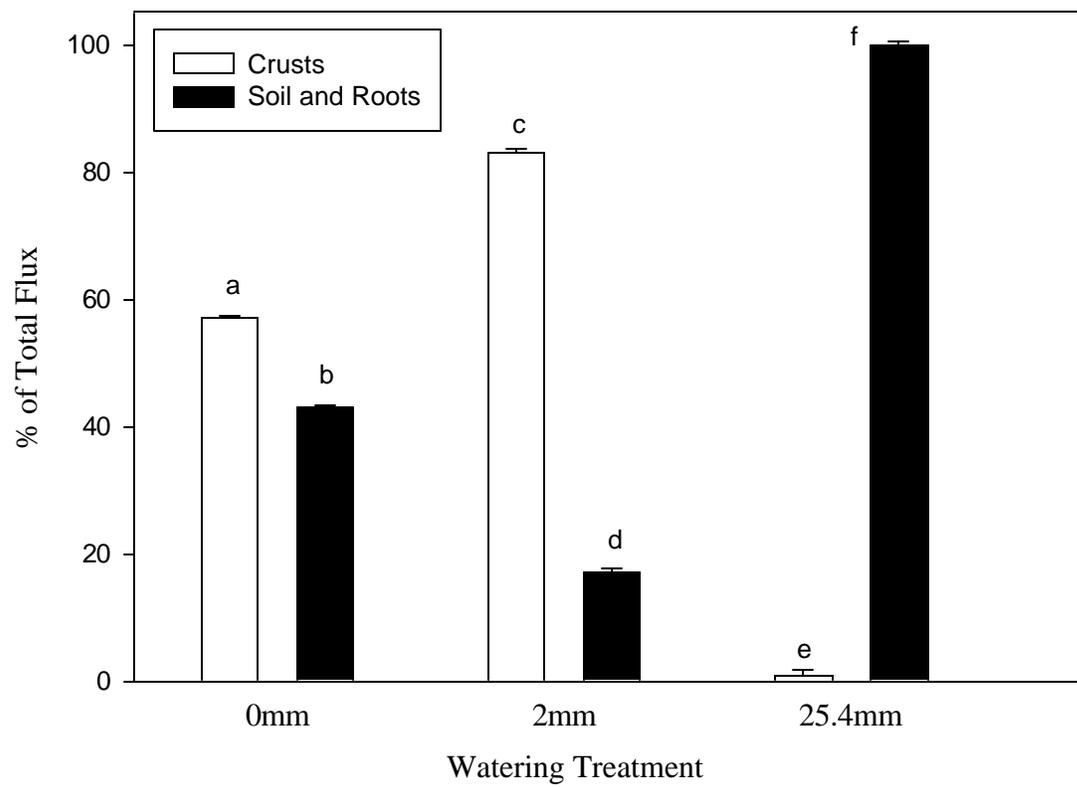
Figure 5. Number of rainfall events of pulse sizes corresponding to the 2mm bins for the Mojave, Sonoran, and Chihuahuan Deserts. Precipitation data is from 1996 to 1999. The first bin is  $\leq 2$ . Precipitation data for the Sonoran Desert were provided by the AZMET database. Precipitation data for the Mojave Desert were provided by the Nevada Desert FACE Facility. Precipitation data for the Chihuahuan Desert were provided by the Jornada Long-Term Ecological Research (LTER) project.

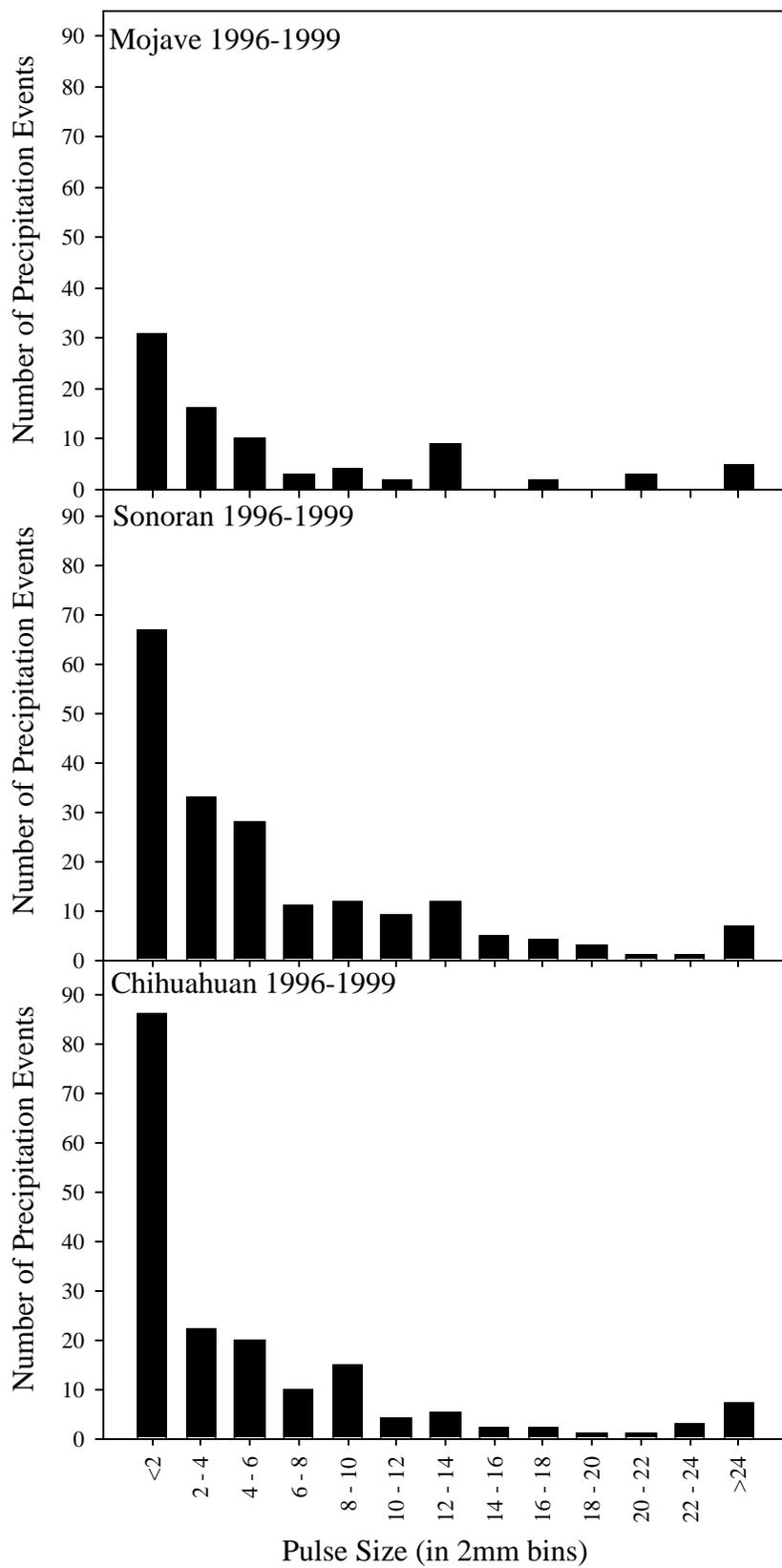
Figures











## APPENDIX B

SOIL RESPIRATION RESPONSE TO PRECIPITATION: THE EFFECTS OF GRASS  
AND SOIL SURFACE ON SOIL MOISTURE

Jessica M. Cable, Travis E. Huxman, Jake Weltzin, David G. Williams

**Abstract**

Soil respiration is controlled by soil moisture in arid and semi-arid ecosystems. However, it is unclear how the respiration response to precipitation is affected by soil texture and vegetation community, and if the response will depend on precipitation pulse size, antecedent soil moisture conditions, and pulse history. To test these effects of precipitation and ecosystem structure, four experiments were conducted on plots of two grass species on two soil surfaces. In 2002 and 2003, we added equivalent amounts of precipitation in the dry fore-summer, and in the monsoon, we simulated dry and wet monsoon conditions. Soil texture significantly affected respiration response to pulses, where the fine textured soil had higher respiration rates, and amplified pulse size effects. The effect of pulse history in the dry fore-summer was to reduce the role of the plant species compared to the previous year, when the non-native plants had higher respiration rates on the fine-textured soil. The effect of pulse history on how a large pulse of water with high antecedent soil moisture occurred in a soil surface effect, where the coarse textured soil responded slightly more to the pulse than the previous year. The effect of pulse history on how a small pulse with low antecedent soil moisture affected respiration was through reducing the difference in respiration rates between the soil surfaces. Rates of CO<sub>2</sub> efflux from soils were higher with cooler, wetter conditions, and were most influenced by water addition when initial soil moisture was low. Cumulative carbon loss was greatest with higher soil moisture. Under future climate change scenarios, larger rain events are possible, which may result in greater carbon loss from desert soils.

Key Words: desert grassland, *Eragrostis lehmanniana*, grass, *Heteropogon contortus*, season, soil texture

## **Introduction**

The climate of the southwestern US is characterized by low annual precipitation that occurs in discrete, ephemeral “pulses” varying in frequency and magnitude (Noy-Meir 1973, Schlesinger et al., 1990). These pulses result in soil wet-dry cycles, which in turn influence the response of biological activity to environmental variables (Noy-Meir 1973). Roots and plant-associated and free-living microorganisms respond rapidly to increased soil moisture (Orchard and Cook 1983, Fierer and Schimel 2003, Liu and Li 2005, Tang and Baldocchi 2005). Ecosystem characteristics (such as plant species composition or soil texture) and climatic factors (such as ambient temperature) influence this response in part by changing biological potential, soil moisture, nutrient availability, and soil microclimate.

Soil respiration is an important part of the carbon cycle, and is thought to be controlled primarily by temperature (Lloyd and Taylor 1994). This is based on the assumption that enzymatic rates control soil physiological processes to a greater extent than resource supply rates (Skopp et al., 1990; Craine et al., 1998). However, transitions between low and high water status can override temperature as a control on soil respiration (Giardina and Ryan 2000; Rustad 2001; Melillo et al., 2002). In arid and semiarid ecosystems, soil moisture has a strong influence on soil respiration (Amundson

et al., 1989; Borken et al., 1999; Davidson et al., 2000; Conant et al., 2004). Soil moisture promotes plant production of labile carbon substrates for heterotrophic respiration (Raich and Schlesinger 1992; Townsend et al., 1997; Trumbore 2000; Janssens et al., 2001; Raich et al., 2002; Hibbard et al., 2005). Also, rapid increases in soil moisture enhance microbial community size and activity (Schimel et al., 1999; Fierer et al., 2003). However, rhizosphere respiration (roots and associated microbes) may be nearly 45% of total soil respiration (Silvola et al., 1996; Tang and Baldocchi 2005), which is controlled by temperature, light availability, and soil moisture (Craine et al., 1998). Although it is clear that soil moisture influences respiration (Orchard and Cook 1983), little is known about the dynamics of the response of soil respiration to individual precipitation events *in situ* (but see Amundson et al., 1989; Liu et al., 2002). These dynamics are likely mediated by the interaction of variables that affect soil moisture availability, such as plant species and soil texture, and the covariation of other drivers such as nutrient availability and soil microclimate.

Plant species differ in their effects on the response of respiration to precipitation.

For example, invasive grass species can influence respiration by altering nutrient cycling, soil microclimate, and soil community composition (D'Antonio and Vitousek 1992; Mack et al., 2001; Zak et al. 2003). In arid and semi-arid ecosystems, the most significant influence of plants may be the alteration of soil moisture through canopy interception, transpiration, macropore-facilitated percolation, and microclimate alteration (Raich and Tufekcioglu 2000; Huxman et al., 2004; Loik et al. 2004). Plant effects on

soil moisture likely interact with other ecosystem characteristics to affect respiration response to precipitation.

In arid and semi-arid ecosystems, soil characteristics, such as texture, are important for many different ecological processes, including biogeographical distributions and species interactions, soil water balance, and plant physiological performance (McAuliffe 1994). Soil texture modifies water infiltration, depth of moisture storage, duration of biologically available soil water, and the covariation of moisture and temperature (Noy-Meir 1973; Azzalini and Diggle 1994; McAuliffe 2003; Huxman et al., 2004; Dilustro et al., 2005). Although soil texture translates precipitation events into soil and plant biological activity, the effects on each can differ in response to a pulse (McAuliffe 1994; Parker 1995; Smith et al., 1995; McAuliffe 1999; Hamerlynck et al., 2002). For example, at low mean annual precipitation, coarse-textured soils provide greater plant production ('inverse texture hypothesis' – Noy-Meir 1973; Sala et al., 1988), but fine textured soils have greater soil microbial activity due to greater soil moisture holding capacity and nutrient availability ('inverse-inverse texture hypothesis' – Austin et al., 2004). Thus, how soil texture interacts with plant species to affect the response of respiration to a pulse is not well understood.

The effects of soil texture and plant species on respiration response to rainfall depend on season, due to variation in antecedent soil moisture, plant phenology, and evaporative demand. If antecedent soil moisture is high, such as during the primary growing season, a pulse event may have a different effect than if the soil is dry (Huxman et al., 2004; Potts et al., *in press*). Plant phenology can affect rhizosphere activity,

microclimate through changes in canopy structure, and soil water loss via transpiration (Hibbard et al., 2005; Tang et al., 2005; Flanagan and Johnson 2005; Irvine et al., 2005). Evaporative demand may change the duration of soil moisture in different seasons. How temperature confounds the respiratory response to precipitation is unclear (Conant et al., 1998; Borke et al., 1999; Conant et al., 2004). With higher soil moisture, temperature may become more important in driving respiration (Conant et al., 2004). Therefore, greater understanding of the role of season in the respiration response to a precipitation pulse is needed for arid and semi-arid ecosystems (Raich and Schlesinger 1992).

The objective of this study was to evaluate how soil respiration responds to individual precipitation pulses, with effects of antecedent soil moisture and pulse history, in semi-arid grassland. As part of a rainfall manipulation experiment in southern Arizona, we conducted four experiments over two years where we address the role of plant species and soil texture in how respiration responds to a pulse. In the four experiments we ask: (1) what is the effect of a large pulse after a prolonged drought period on soil respiration? We hypothesize that respiration will increase rapidly with soil moisture, and soil surface will have a greater effect than plant species. (2) What is the effect of pulse size with different antecedent soil moisture conditions on soil respiration? We hypothesize that a larger pulse will result in higher soil respiration but with high antecedent soil moisture, the response to the pulse will be lower compared to the smaller pulse with lower antecedent soil moisture. Plant species and soil surface will have larger effects on respiration following the large pulse. (3) What is the effect of pulse history on how a large pulse after a prolonged drought affects soil respiration? Plant species will

play a larger role due to the pulse history effects on root growth and substrate deposition for respiration. (4) What is the effect of pulse history on how pulse size with different antecedent moisture conditions affects soil respiration? We hypothesize that the large pulse will result in greater respiration rates and less responsiveness than the small pulse, but plant species will play a large role in both water treatments due to substrate deposition and root activity.

To answer these questions, we applied equivalent sized pulses of water prior to and different sized pulses during the height of the North American Monsoon to plots of monospecific stands of a native and the non-native grass species on two contrasting soil surfaces. Additionally, during the monsoon, we compared effects of low and high antecedent soil moisture.

## **Methods**

Soil CO<sub>2</sub> fluxes were measured before and after large experimental irrigation events in plots of native and non-native grass under rain-out shelters at the Santa Rita Experimental Range, south of Tucson, Arizona. Rain-out shelter plots were established on two different soil surfaces (English et al. 2005). Three shelters (161 m<sup>2</sup> covered area) were built on a Pleistocene-aged surface characterized by clay-loam fine textured soil (hereafter, clay loam surface), and three shelters were built on a Holocene-aged surface characterized by sandy-loam coarse-textured soil (hereafter, sandy loam surface).

Each of the three shelters (replicate blocks) within a site covered twelve plots equally divided among non-native grass, native grass, and bare vegetation treatments.

The perimeter of each (1.5 m x 1.8 m) plot was trenched to a depth of 1 m and lined with plastic to isolate soil columns from the surrounding soil environment. Time-domain reflectometry sensors were placed in each plot at 15, 35 and 55 cm depths for measurement of soil water content. During construction, the A horizon was left intact on all plots, but all above-ground plant material was removed before establishment of experimental grassland communities.

In the Spring of 2001, plots were planted with greenhouse-grown transplants of either a native grass (*Heteropogon contortus*) or an invasive grass (*Eragrostis lehmanniana*) at densities similar to that observed in adjacent natural stands (18.6 plants m<sup>-2</sup>). Plots received ~149 mm of irrigation from August 10, 2001 to April 1, 2002. Plots received no irrigation from April 1, 2002 until June 2002. See English et al. (2005), Huxman et al. (2004), Potts et al. (2006) and Potts et al. (in press) for further site details and descriptions of treatments.

Four pulse experiments were carried out: 1. a large pulse was applied after 90 days of drought, 2. pulses of two sizes were applied to plots with dry and wet watering regimes prior to the pulse, 3. a large pulse after 90 days of drought with the previous year's rainfall regime (wet and dry), 4. pulses of two sizes were applied to plots with dry and wet watering regimes prior to the pulse with the previous year's rainfall regime (wet and dry).

For experiments 1 and 3, in June 2002 and 2003, a 39-mm pulse of water was applied to 24 plots (3 replicates of 2 grass species with 2 water treatments on 2 soil types). However, differential water treatments did not begin until July 2002, when half

plots that were well watered in June had a wet monsoon and the remainder had a dry monsoon. For experiments 2 and 4, measurements were focused on a single pulse in a series of pulses that occurred in August. For the plots that had a wet monsoon, measurements were made after they received a large pulse (39mm). For the plots that had a dry monsoon, measurements were made after they received a small pulse (12mm). Thus, the cumulative rainfall for the dry plots was half that of the wet plots. Pulse sizes were generated from a weather generation program, as described in English et al. 2005.

### *CO<sub>2</sub> Efflux Measurements*

Instantaneous measurements of soil CO<sub>2</sub> exchange were made prior to, and 1, 3, 7 and 15 days following each pulse event (for  $n = 3$  plots in each treatment combination, but bare plots that received the dry treatment were not measured). Within each plot, a single soil collar (styrene coupling, 10.2cm in diameter) was installed in the soil to a depth of 5 cm within 30 cm of the edge 4 weeks prior to the first measurement. For measurements in 2002, we used the LI-6400 – 09 standard soil CO<sub>2</sub> efflux chamber. In 2003, a syringe sampling method was employed to measure rates of soil CO<sub>2</sub> efflux. The gas exchange chambers were constructed of white opaque PVC cylinders, 3L in volume, fitted with a female Luer-lok fitting (LUER LOK, BD Syringe). The gas exchange chamber was fitted with 2.5-mm diameter 25mm long capillary tubing vented to atmosphere to relieve pressure differentials (Hutchinson and Mosier 1981; Davidson et al., 2002). A 4.5-V microfan provided mixing of air within the cylinder. Six air samples

(20 mL) were collected from the chamber over a 10-minute measurement interval. Samples were collected with a syringe (LUER LOK) and injected into a LI 820 in a closed loop configuration, and time (seconds) and dry-air CO<sub>2</sub> concentrations (ppm) were recorded. Air temperature (°C) within the cylinder and the top 2cm of the soil within the collar were recorded. The CO<sub>2</sub> concentration data were converted to flux density with volume/area corrections (Pearcy et al., 1990).

### ***Data Analysis***

Volumetric soil moisture, soil temperature and soil CO<sub>2</sub> efflux data were log transformed to meet assumptions of normality for statistical analysis. Data were analyzed with JMP5.1 (SAS Institute) using a multi-way ANOVA model for each experiment and then for each pulse day. For experiment 1, plant species, soil type, and time were crossed, and soil moisture and temperature were included as covariates. For each day, plant species and soil type were crossed, and soil temperature and moisture were covariates. For experiment 2, 3 and 4, plant species, soil type, water treatment, and time were crossed, and soil temperature and moisture were included as covariates. For each day, plant species, soil type, and water treatment were crossed, and soil temperature and moisture were covariates. Significant results for the model across days are presented in tables 1a – 4a, and results for within day model effects are presented in tables 1b - 4b. For illustration of the time-series, CO<sub>2</sub> efflux was standardized to 30°C to account for

variation in temperature across sampling periods within a day using a  $Q_{10}$  function assuming a value of 2. Means are presented with one standard error.

## Results

Experiment 1: The effect of a pulse after a dry period (90 days).

### *Soil Respiration*

Respiration was most influenced by pulse day (partial  $R^2 = 0.28$ , Table 1), where rates on day 1 were 89% greater than on days -1 and 15, which had the lowest respiration rates. Soil surface also significantly influenced respiration where on day 1, respiration from the clay loam surface was 37 % higher than on the sandy loam surface (partial  $R^2 = 0.18$ ,  $F_{1,11} = 8.4765$ ,  $p = 0.0269$ , Figure 1a).

### *Soil Moisture and temperature*

Throughout the pulse period, soil moisture on the clay loam surface was 61% higher than on the sandy loam surface (partial  $R^2 = 0.51$ , Table 1). During the pulse period, soil moisture was 44% and 39% higher on days 1 and 3 compared to the driest day (day -1) (Table 1). Soil moisture was 72% higher on the non-native species plots on the clay loam surface compared to both species plots on the sandy loam surface that had the lowest soil moisture. Intermediate in soil moisture were the native species plots on the clay loam, with 54% wetter soil than the sandy loam plots (Table 1, Figure 1d). Soil temperature was on average 8.6 °C (+/- 0.95) higher on days -1, 7 and 15, compared to

days 1 and 3 (partial  $R^2 = 0.64$ , Table 1). Non-native species plots were  $2.2\text{ }^\circ\text{C}$  ( $\pm 1.4$ ) warmer than the native plots (Table 1, Figure 1e).

Experiment 2: The effect of a pulse combined with the effect of antecedent soil moisture.

### *Soil Respiration*

The main model effects for soil respiration were pulse day and water treatment (partial  $R^2 = 0.10$ , partial  $R^2 = 0.091$ , respectively; Table 2). On days -1 and 7, wet treatment respiration was 55% and 52% greater than dry treatment respiration, respectively (Table 2). The highest respiration rates occurred on days 1 and 3 ( $3.5\text{ ? mol m}^{-2}\text{ s}^{-1} \pm 0.29$ ,  $3.0\text{ ? mol m}^{-2}\text{ s}^{-1} \pm 0.24$ ; Table 2). Important daily variation in respiration across treatments occurred. On day 1, respiration was 42% higher on the clay loam surface compared to the sandy loam surface. On day 3, soil surface amplified the water treatment effects, where the difference between water treatments was 82% greater on the clay loam surface ( $F_{1,22} = 9.0212$ ,  $p = 0.0102$ ). The wet treatment on the clay loam soil had 51% higher respiration rates than the plots with the lowest rates: both water treatments on the sandy loam and the dry treatment on the clay loam surface (Figure 2a). On day 3, soil respiration was highest from both plant species with the wet treatment on the clay loam soil (native  $4.9\text{ ? mol m}^{-2}\text{ s}^{-1} \pm 0.75$ , non-native  $4.3\text{ ? mol m}^{-2}\text{ s}^{-1} \pm 0.01$ ), and lowest from the non-native grass with the dry treatment on the clay loam surface ( $1.7\text{ ? mol m}^{-2}\text{ s}^{-1} \pm 0.39$ , Table 2). On day 7, soil moisture at 15cm was significant, with wetter soil associated with higher respiration rates ( $F_{1,23} = 4.48$ ,  $p =$

0.0416; Figure 2b). Lower soil temperature was associated with greater respiration on days -1 and 7 ( $F_{1,23} = 5.6065$ ,  $p = 0.0271$ ; Figure 2c).

### *Soil moisture and temperature*

Overall, the clay loam surface was 42% wetter than the sandy loam surface (partial  $R^2 = 0.36$ , Table 2). Pulse day, soil surface-by-water treatment, and water treatment-by-pulse day were also significant (Table 2). On days 1 and 3, soil moisture was 39% and 28% higher compared to day 7, the driest day. On days -1, 1, and 3, soil moisture was 27% higher on wet treatment plots compared to dry treatment plots (Table 2). Dry and wet treatments were more different on the sandy loam surface (mean difference sandy loam 3.5% +/- 0.66 vs. mean difference clay loam surface 2.1% +/- 1.1, Table 2, Figure 2d).

On days -1, 1 and 7, the soil from the dry treatment was 3.3°C warmer than the wet treatment (Table 2). Compared to the rest of the pulse period, day 7 had the warmest soil (32.4 °C +/- 0.73) (Table 2). Soil surface x water treatment and plant species were also significant. The difference between dry and wet treatment soil temperatures was amplified on the clay loam surface, the difference in mean temperatures on the sandy loam was 3.1 °C (+/- 1.3) versus the clay loam difference of 5.1 °C (+/- 0.82) (Table 2). Prior to the pulse, soil on non-native species plots was 1.7 °C warmer than the native species. On day 1, the native plants with the dry treatment on the clay loam surface had the highest soil temperature (31.7 °C +/- 0.71), and both species with the wet treatment

on the sandy loam surface had the lowest soil temperature (27.9 °C +/- 0.71) (partial  $R^2 = 0.12$ ,  $F_{1,22} = 4.2796$ ,  $p = 0.0563$ , Figure 2e).

Experiment 3: The effect of a pulse after a 90 day dry period combined with the effects of pulse history from the previous year.

#### *Soil respiration*

Respiration rates on day 1 were 88% higher than on the day prior to the pulse, which had the lowest rates. Compared to the day prior to the pulse (-1), respiration rates were 88% higher on day 1 and then declined to day 15, when rates were still 46% higher than day -1 (partial  $R^2 = 0.32$ , Table 1). In a plant species-by-soil surface interaction on day 3, respiration was 40% higher on the non-native plots on the clay loam surface compared to the lowest rates on the native plots on the clay loam ( $F_{1,31} = 9.3943$ ,  $p = 0.005$ , Figure 3a). There were no water treatment effects from the previous year.

#### *Soil temperature and moisture*

In general, soil moisture was highest on days 1 and 3 (12.3% +/- 1.1, 10.6% +/- 0.84) compared to the remaining pulse days (Table 1). Throughout the pulse period, the clay loam surface had higher soil moisture than the sandy loam surface (partial  $R^2 = 0.44$ , Table 1), and on the day with the highest soil moisture, the clay loam was 61% (day 1) and 59% (day 3) wetter than the sandy loam surface (Table 1). In a plant species-by-soil surface interaction, both species plots on the clay loam soil had 60% higher soil moisture than the driest plots, the non-native species on the sandy loam. Intermediate was the

native species plots on the sandy loam with 29% higher soil moisture than the driest plots (Table 1, Figure 3b). The highest soil temperatures were on days -1, 7 and 15 compared to days 1 and 3 (Table 1, Figure 3c).

Experiment 4: The effect of pulse size, antecedent soil moisture conditions, and pulse history on respiration.

#### *Soil respiration*

Soil respiration was influenced by water treatment and pulse day (partial  $R^2 = 0.13$ , partial  $R^2 = 0.07$ , respectively) (Table 2). There was greater variation in respiration rates throughout the pulse period on the dry plots, but respiration rates were 19% lower than the wet treatment plots (Table 2). Respiration was 41% higher on days -1, 1, and 3 for both soil surfaces, compared to days 7 and 15, where rates were lowest from the clay loam soil (Table 2). There was also a significant effect of soil surface-by-water treatment, and soil moisture at 15cm. Respiration was 58% higher from the wet treatment plots on both soil surfaces compared to the lowest rates from the dry treatment on the clay loam (Table 2, Figure 4a). Wetter soil resulted in higher respiration on days -1, 1, and 3 ( $F_{1,77} = 47.8359$ ,  $p < 0.0001$ , Figure 4b). On days -1, 7, and 15, soil temperature was significant, where higher respiration was associated with cooler soil ( $F_{1,83} = 37.4695$ ,  $p < 0.0001$ , Figure 4c).

### *Soil temperature and moisture*

Overall, soil moisture was 40% higher on the clay loam surface compared to the sandy loam surface (partial  $R^2 = 0.39$ , Table 2). Water treatment-by-pulse day and soil surface-by- water treatment were also significant. On days -1, 1, 3, and 7, volumetric water content on wet treatment plots was 5% (+/- 0.68) higher than on dry treatment plots (Table 2). The wet treatment on the clay loam had 67% higher soil moisture than the dry treatment on the sandy loam, which had the lowest moisture values (Table 2, Figure 4d).

Soil temperature was 8.4°C (+/- 1.1) higher on days 7 and 15 compared to the remaining pulse days (partial  $R^2 = 0.34$ , Table 2). In a soil surface-by-water treatment interaction, the dry treatment on the clay loam soil had 15% warmer soil than the wet treatment on both soil surfaces, which had the coolest soil. Intermediate was the dry treatment on the sandy loam soil, which had 10% higher temperatures (Table 2, Figure 4e).

## **Discussion**

Rainfall in deserts occurs in discrete events or pulses (Noy-Meir 1973). Soil respiration is primarily controlled by temperature in non-water limited ecosystems (Lloyd and Taylor 1994), but in arid and semi-arid ecosystems, water availability likely has overriding control of biological activity (Orchard and Cook 1983; Liu et al., 2002; Fierer and Schimel 2003; Conant et al., 2004). Variation in soil moisture is a function of seasonal timing, frequency, and magnitude of precipitation pulses, and ecosystem factors

such as soil texture and plant community composition (Austin et al., 2004; Huxman et al., 2004). How ecosystem and climate factors control the magnitude and duration of soil respiratory activity following a pulse is unclear.

The objective of this study was to evaluate how soil respiration responds to individual precipitation pulses, with effects of antecedent soil moisture and pulse history, in semi-arid grassland. As part of a rainfall manipulation experiment in southern Arizona, we conducted four projects over two years where we address the role of plant species and soil texture in how respiration responds to a pulse. In the four projects we ask: (1) what is the effect of a large pulse after a prolonged drought period on soil respiration? (2) What is the effect of pulse size with different antecedent soil moisture conditions on soil respiration? (3) What is the effect of pulse history on how a large pulse after a prolonged drought affects soil respiration? (4) What is the effect of pulse history on how pulse size with different antecedent moisture conditions affects soil respiration? In every case, rates of CO<sub>2</sub> efflux from soils were higher with cooler, wetter conditions, and were most influenced by water addition when initial soil moisture and respiratory activity was low (Figure 5). Cumulative carbon loss was greatest with higher mean soil moisture (Figure 6).

We found that a large pulse of water after a prolonged drought resulted in a large and rapid increase in respiration, an increase in soil moisture, and a decrease in soil temperature (Figure 1). A large pulse with higher antecedent soil moisture resulted in higher initial respiration rates but a smaller pulse with lower antecedent soil conditions resulted in higher responsiveness of respiration to the pulse. The fine textured soil had

higher respiration rates, 19.7% greater responsiveness to the pulse, and amplified the effects of pulse size, soil moisture, and temperature (Figure 2). The effect of pulse history on how a large pulse of water after a prolonged period of drought affects soil respiration was to reduce the role of plant species compared to the previous year, when the non-native plants had higher respiration rates on the fine-textured soil (Figure 3). The effect of pulse history on how a large pulse of water with high antecedent soil moisture occurred in a soil surface effect, where the sandy loam surface responded slightly more to the pulse than the previous year. However, the clay loam still had the highest rates. The effect of pulse history on how a small pulse with low antecedent soil moisture affected respiration was through reducing the difference in respiration rates between the soil surfaces (Figure 4).

Soil texture had a strong effect on carbon cycling, similar to its effect on plant community composition, plant production, and seasonal distribution of soil moisture in deserts (McAuliffe 2003). Compared to the sandy loam soil, the clay loam soil had higher respiration rates, greater pulse responsiveness, and stronger effects of plant species and water treatment in how respiration responded to pulses of water. Soil texture differentially affects microbial and plant activity. Plant production is higher on coarse textured soil (Schenk and Jackson 2002; Liao et al. 2004), particularly in arid and semi-arid ecosystems (the inverse texture hypothesis -- Noy-Meir 1973; Sala et al., 1988). However, plant activity may be limited on coarse textured soil depending on soil microorganism activity, such as root parasitic nematodes, where Griffin (1996) found the greatest effects of the parasites on plant growth was primarily in sandy soil. Most soil

microorganisms respond favorably to clay content due to high amounts of organic carbon (Jobaggy and Jackson 2000, Santruckova et al. 2003) resulting in greater respiration responses to wet-dry events (Bouma and Bryla 2000, 'inverse-inverse texture hypothesis' -- Austin et al. 2004). However, microbial activity may become limited by the clay fraction due to the binding of soil organic matter to clay particles, as with Muller and Hoper's (2004) finding that microbial activity was low in clay soils despite high microbial biomass. Variation in the effects of soil type occurred within each part of this study, possibly due to the differential effects of fine textured soil on plant and soil activity.

In this study, larger pulses resulted in higher respiration rates. In all cases, higher respiration from wetter soil occurred in conjunction with lower soil temperature; thus, these two abiotic drivers alternated in their relative importance surrounding a rainfall event. Similar interactions of soil temperature and moisture have been found in other studies, where in dry periods, moisture is more constraining and respiration is less responsive to increases in temperature (Amundson et al., 1989; Conant et al. 1998; Rustad et al. 2001; Conant et al., 2004; Tang and Baldocchi 2005). In this study, after accounting for soil moisture, there was a negative relationship with temperature. Previous research has shown that respiration responds positively to temperature (Lloyd and Taylor 1994; Conant et al., 2004; Xu et al., 2004). Soil moisture and temperature covary in their effects on microbial activity, where high soil temperature is associated with low soil moisture. At high soil temperatures, microbes rapidly use substrates (Eliasson et al., 2005, Leifeld and Fuhrer 2005), but due to low soil moisture, diffusion of

solutes may become the rate limiting step (Skopp et al. 1990). Thus, substrate availability may be inversely related to temperature (Davidson et al. 2006), resulting in the inverse soil respiration-temperature relationship observed in some arid and semi-arid ecosystems. Interestingly, in our study, the clay loam soil had higher temperature and moisture compared to the sandy loam soil, possibly resulting in the amplified soil respiration rates after the pulses. Perhaps declining soil moisture with high temperature does not affect substrate availability as much on the fine textured soil due to more continuous water films.

Soil moisture conditions prior to a rain event were responsible for the differences we measured in respiration response to a pulse across different antecedent moisture conditions. Responsiveness was greatest with lower antecedent soil moisture and lower initial respiration rates (Figure 6). Xu et al. (2004) found similar results in an annual grassland, where the magnitude of the respiratory response to rainfall was inversely related to the pre-rain soil respiration rates. In our study, a pulse applied following a prolonged drought period resulted in the greatest responsiveness of respiration (87.6% increase in rates from day -1 to 1), regardless of pulse history. Where antecedent soil moisture and pulse size were manipulated, pulse history was important. The difference in responsiveness between wet and dry treatments was smaller with pulse history effects, where in the 2003 monsoon season the water treatments had similar responsiveness (17.5%). In the 2002 monsoon season, the dry treatment had 52% greater responsiveness of respiration to the pulse than the wet treatment.

Others have found that increases in soil moisture result in a large soil respiration response (Rochette et al., 1991) most likely due to changes in microbial biomass and rapid upregulation of physiological processes associated with carbon and nitrogen cycling in these organisms (Franzluebbers et al., 2000; Fierer and Schimel 2003). In addition to the activity of microbes, autotrophic respiration can also be significant; it is estimated that nearly 12% of recent photosynthate may be respired by the rhizosphere (Nguyen 2003) and plants in our study up-regulated photosynthetic processes to high levels rapidly (Huxman et al., 2004; Ignace et al. *in prep*). In the monsoon season, the flush of CO<sub>2</sub> is not as dramatic after the pulse, likely due to the impact of multiple soil wet-dry cycles that occurred throughout the primary growing season from multiple rain events. Wet-dry cycles can result in lower overall respiration rates and lower responsiveness to soil wetting due to their effect on the availability of carbon substrates for microbial activity (Fierer and Schimel 2002). Physical displacement of CO<sub>2</sub> from soil pores by infiltrating water has been suggested to be a significant contributor to the loss of CO<sub>2</sub> from soils after a rainfall event (Li et al. *in press*). However, this likely occurs within the first few hours of a rain event, and then biological activity dominates resulting in steady state conditions. Thus, the effect of pulse history was likely through reduction of substrates for microbial activity, limiting the soil respiration response to a pulse of any size or antecedent soil conditions.

Overall, the decrease in respiration rates after the pulse (slope of the line from day 1 to day 15) was fastest on the clay loam soil ( $F_{1,79} = 20.2286$ ,  $p < 0.0001$ ), despite higher soil moisture and higher day 1 respiration rates than the sandy loam soil. There were

some within-experiment variations to this finding. Following a large pulse with dry antecedent soil moisture (premonsoon 2002 and 2003), respiration declined the fastest on the non-native grass plots on the clay loam soil, regardless of pulse history ( $F_{1,35} = 5.3572$ ,  $p = 0.0272$ ). Species did not differ on the sandy loam soil. The combination of pulse history, pulse size, and antecedent soil moisture resulted in rapid decline in respiration on the wet treatment plots on the clay loam soil ( $F_{1,20} = 5.9414$ ,  $p = 0.0299$ ), a result absent the previous year. Rapid declines in respiration after a large peak may be due to limitation in substrate supply (Fierer and Schimel 2002), or binding of organic matter to clay particles, since soil moisture availability remained high. The soil type effects are partially consistent with Austin et al. (2004)'s "inverse-inverse texture" hypothesis that soil microbial activity should be higher on fine textured soil, because the peak respiration rates were higher on fine- than on coarse-textured soil. The duration of biological activity on different soil types is an additional component important for considering carbon cycling in water limited regions.

Comparing the rate of decline in respiration across experiments, the most rapid decline occurred with the pulse after the drought period with no pulse history effects (June 2002). Despite an initial burst of microbial activity following an increase in soil moisture (high responsiveness), the duration of biological activity can be limited by prepulse organic matter inputs restricting the degree of microbial biomass development throughout a pulse (Austin et al., 2004). Because the primary source for organic matter input into soil communities in grasslands is from belowground structures (Hibbard et al.,

2005; Rees et al. 2005), limited plant activity (such as during the premonsoon) can constrain microbial activity.

Higher soil moisture throughout the pulse period was associated with greater cumulative carbon loss following a pulse, where across experiments the clay loam soil had the greatest carbon loss ( $F_{1,82} = 17.9757$ ,  $p < 0.0001$ , Figure 5), and there were within-experiment variations. The combination of pulse size and antecedent soil moisture resulted in greater carbon loss from the wet treatment plots on the clay loam soil ( $F_{1,47} = 12.9665$ ,  $p = 0.0008$ ). The effect of pulse history was a less loss of carbon from this treatment (2003:  $1.43 \text{ mol C day}^{-1} \pm 0.08$ ; 2002:  $1.84 \text{ mol C day}^{-1} \pm 0.1$ ). This may be driven by the interaction of water treatment and the fine textured soil across years, where the wet treatment in 2002 had a large carbon loss and the dry treatment in 2003 had low carbon loss. Thus, higher rainfall will result in greater soil carbon loss, particularly from fine textured soils, and pulse history has a significant impact on this relationship (Figure 6).

We found that a pulse translates into less biological activity when antecedent soil moisture is high, but following a long period of very dry soil, a pulse induces large soil  $\text{CO}_2$  efflux. Xu et al. (2004) found similar results in an annual grassland, where the magnitude of the respiratory response to rainfall was inversely related to the pre-rain soil respiration rates. Due to the upregulation and substrate use of the soil organisms, respiration is stronger after drought and low cellular activity, whereas in the monsoon, organism activity drops to a lower level due to substrate limitation (Fierer and Schimel 2002). An interesting finding from this study is that higher soil temperatures result in

lower respiration rates, differing from previous research (Lloyd and Taylor 1994; Conant et al., 2004; Xu et al., 2004). Due to the covariation of soil moisture and temperature, microbes rapidly use substrates at high soil temperatures (Eliasson et al., 2005, Leifeld and Fuhrer 2005), but due to low soil moisture, diffusion of solutes may become the rate limiting step (Skopp et al. 1990). Thus, substrate availability may be inversely related to temperature (Davidson et al. 2006), resulting in the inverse soil respiration-temperature relationship. Soil texture had the most significant effect on how a pulse, pulse history, and antecedent moisture interacted to affect soil respiration. If more rain falls during the monsoon, as induced with the water treatment differences, more carbon will be lost from fine textured soils.

Arid and semiarid regions are increasing in area globally (Schlesinger et al., 1990) and current predictions of climate change and current land-use practices suggest that trend will continue (Abahussain et al., 2002; Lin and Tang 2002; Geist and Lambin 2004). For many of these regions, global circulation models predict changes in the frequency, magnitude and seasonality of precipitation (IPCC 2001). For example, the frequency of relatively large precipitation events is expected to increase in the Southwestern United States (Easterling et al. 2000; IPCC 2001); currently small events (<5mm) are most common (Sala et al. 1982), and changes in the event size distribution of rainfall events appears important at controlling features such as site water balance (Loik et al., 2004). Shift in features such as the seasonal distribution of precipitation, or interannual variability in total sums, may have consequences for a number of ecosystem processes (Sala et al., 1982; Sala et al., 1992; Schlesinger 1997; Golluscio et al., 1998;

Conant et al., 1998; Borken et al., 1999; Reynolds et al., 2000; Weltzin and Tissue 2003; Weltzin and McPherson 2003; Huxman et al., 2004). Because rainfall indirectly and directly influences soil CO<sub>2</sub> efflux (through characteristics such as substrate supply rate, soil temperature, microbial and plant physiological status, the diffusivity of CO<sub>2</sub>– Davidson et al., 2006), a greater mechanistic understanding is the key to predicting the carbon cycling consequences of changes in precipitation for arid and semiarid regions.

### **Acknowledgements**

The authors thank Nathan English, Bill Cable, Danielle Ignace, Dan Potts, Alex Eilts, Janet Chen, and Mike Mason for technical support. We also acknowledge support from USDA-CSREES (Grant # 00-35101-9308), SAHRA (Sustainability of Semi-Arid Hydrology and Riparian Areas) under the STC program of NSF, and NSF awards DEB 041-5977, DEB 041-8363, and DEB 041-8134 to TEH, JFW, and DGW.

**Literature Cited**

- Abahussain A A, Abdu A S, Al-Zubari W K, El-Deen N A, and Abdul-Raheem M 2002 Desertification in the Arab Region: analysis of current status and trends. *Journal of Arid Environments* 51, 521-545.
- Amundson R G, Chadwick O A, Sowers J M, and Doner H E 1989 Soil evolution along an altitudinal transect in the eastern Mojave desert of Nevada, USA. *Geoderma* 43, 349-371.
- Atwell BJ 1993 Response of roots to mechanical impedance. *Environmental and Experimental Botany*, 27-40.
- Austin A T, Yahdjian L, Stark J M, Belnap J, Porporato A, Norton U, Ravetta D A, Schaeffer S M 2004 Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141, 221-235.
- Azzalini A and Diggle P J 1994 Prediction of soil respiration rates from temperature, moisture-content and soil type. *Applied Statistics-Journal of the Royal Statistical Society Series C* 43, 505-526.
- Borken W, Xu Y-J, Brumme R, and Lamersdorf N 1999 A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: Drought and rewetting effects. *Soil Science Society of America Journal* 63, 1848-1855.

- Cable J M, Ogle K, Eilts J A, McClaran M, Martens D, and Huxman T E *In preparation*  
Heterotrophic and autotrophic respiration response to precipitation pulses in a  
semi-arid grassland.
- Conant R T, Klopatek J M, Malin R C, and Klopatek C C 1998 Carbon pools and fluxes  
along an environmental gradient in northern Arizona. *Biogeochemistry* 43, 43-61.
- Conant R T, Dalla-Betta P, Klopatek C C, and Klopatek J A 2004 Controls on soil  
respiration in semiarid soils. *Soil Biology and Biochemistry* 36, 945-951.
- Craine J M, Wedin D A, and Chapin F S III 1998 Predominance of ecophysiological  
controls on soil CO<sub>2</sub> flux in a Minnesota grassland. *Plant and Soil* 207, 77-86.
- D'Antonio C M and Vitousek P M 1992 Biological invasions by exotic grasses, the  
grass/fire cycle, and global change. *Annual Review in Ecology and Systematics*  
23, 63-87.
- Davidson E A, Verchot L V, Cattanio J H, Ackerman I L, and Carvalho J E M 2000  
Effects of soil water content on soil respiration in forests and cattle pastures of  
eastern Amazonia. *Biogeochemistry* 48, 53-69.
- Davidson E A, Savage K, Verchot L V, and Navarro R 2002 Minimizing artifacts and  
biases in chamber-based measurements of soil respiration. *Agricultural and Forest  
Meteorology* 113, 21-37.
- Davidson E A, Janssens I A, and Luo Y 2006 On the variability of respiration in  
terrestrial ecosystems: moving beyond Q<sub>10</sub>. *Global Change Biology* 12, 154-164.

- Dilustro J J, Collins B, Duncan L, and Crawford C 2005 Moisture and soil texture effects on Soil CO<sub>2</sub> efflux components in southeastern mixed pine forests. *Forest Ecology and Management* 204, 85-95.
- Easterling D R, Meehl G A, Parmesan C, Changnon S A, Karl T R, and Mearns L O 2000 Climate extremes: Observations, modeling, and impacts. *Science* 289, 2068-2074.
- Eliasson P E, McMurtrie R E, Pepper D A, Stromgren M, Linder S, and Agren G I 2005 The response of heterotrophic CO<sub>2</sub> flux to soil warming. *Global Change Biology* 11, 167-181.
- English N B, Weltzin J F, Fravolini A, Thomas L, and Williams D G (2005) The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. *Journal of Arid Environments* 63, 324-343.
- Fierer N and Schimel J P 2002 Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology and Biochemistry* 34, 777-787.
- Fierer N and Schimel J P 2003 Mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Science Society of America Journal* 67, 798-805.
- Fierer N, Schimel J P, and Holden P A 2003 Influence of drying-rewetting frequency on soil bacterial community structure. *Microbial Ecology* 45, 63-71.
- Flanagan L B and Johnson B G 2005 Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology* 130, 237-253.

- Franzluebbers A J, Haney R L, Honeycutt C W, Schomberg H H, and Hons F M 2000  
Flush of carbon dioxide following rewetting of dried soil relates to active organic  
pools. *Soil Science Society of America Journal* 64, 613-623.
- Geist H J and Lambin E F 2004 Dynamic causal patterns of desertification. *Bioscience*  
54, 817-829.
- Giardina C P and Ryan M G 2000 Evidence that decomposition rates of organic carbon in  
mineral soil do not vary with temperature. *Nature* 404, 858-861.
- Golluscio R A, Sala O E, and Laurenroth W K 1998 Differential use of large summer  
rainfall events by shrubs and grasses: a manipulative experiment in the  
Patagonian steppe. *Oecologia* 115, 17-25.
- Griffin GD 1996 Importance of soil texture to the pathogenicity of plant-parasitic  
nematodes on rangeland grasses. *Nematropica* 26, 27-37.
- Hamerlynck E P, McAuliffe J R, McDonald E V, and Smith S D 2002 Ecological  
responses of two Mojave Desert shrubs to soil horizon development and soil  
water dynamics. *Ecology* 83, 768-779.
- Hibbard K A, Law B E, Reichstein M, and Sulzman J 2005 An analysis of soil respiration  
across northern hemisphere temperate ecosystems. *Biogeochemistry* 73, 29-70.
- Hutchinson G L and Mosier A R 1981 Improved soil cover method for field measurement  
of nitrous-oxide fluxes. *Soil Science Society of America Journal* 45, 311-316.
- Huxman T E, Cable J M, Ignace D D, Eilts J A, English N B, Weltzin J, and Williams D  
G 2004 Response of net ecosystem gas exchange to a simulated precipitation

pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141, 295-305.

Ignace D D, Huxman T E, Weltzin J F, and Williams D G *In preparation* Functional response of native and non-native grasses to precipitation manipulation in the Sonoran Desert.

IPCC, Climate Change 2001 The Scientific Basis. Cambridge University Press, Cambridge.

Irvine J, Law B E, and Kurpius M R 2005 Coupling of canopy gas exchange with root and rhizosphere respiration in a semi-arid forest. *Biogeochemistry* 73, 271-282.

Janssens I A, Lankreijer H, Matteucci G, Kowalski A S, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grunwald L, Montagnani L, Dore S, Rebmann C, Moors J, Grelle A, Rannik U, Morgenstern K, Oltchev S, Clement R, Gudmundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen O, Vesala T, Granier A, Schulze E D, Lindroth A, Dolman A J, Jarvis P G, Ceulemans R, and Valentini R 2001 Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7, 269-278.

Jobaggy EG and Jackson RB 2000 The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* 10, 423-436.

Leifeld J and Fuhrer J 2005 The temperature response of CO<sub>2</sub> production from bulk soils and soil fractions is related to soil organic matter quality. *Biogeochemistry* 75, 433-453.

- Li X., Miller, A E, Meixner T, Schimel J, Melack J M, and Sickman J O. Incorporating the mechanism of the rewetting pulse into a biogeochemical model, *Global Change Biology in review*.
- Liao XY, Chen TB, Lei M, Huang ZC, Xiao XY, and An ZZ 2004 Root distributions and elemental accumulations of Chinese brake (*Pteris vittata* L.) from As-contaminated soils. *Plant and Soil* 261, 109-116.
- Lin N F and Tang J 2002 Geological environment and causes for desertification in arid-semiarid regions in China. *Environmental Geology* 41, 806-815.
- Liu X Z, Wan S Q, Su B, Hui D F, and Luo Y Q 2002 Response of soil CO<sub>2</sub> efflux to water manipulation in a tallgrass prairie ecosystem. *Plant and Soil* 240, 213-223.
- Liu H S and Li F M 2005 Root respiration, photosynthesis and grain yield of two spring wheat in response to soil drying. *Plant Growth and Regulation* 46, 233-240.
- Lloyd J and Taylor J A 1994 On the temperature dependence of soil respiration. *Functional Ecology* 8, 315-323.
- Loik M E, Breshears D D, Lauenroth W K, and Belnap J 2004 A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141, 269-281.
- McAuliffe J R 1994 Landscape evolution, soil formation and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs* 64, 111-148.
- McAuliffe J R 1999 The Sonoran Desert: landscape complexity and ecological diversity. *In Ecology of Sonoran Desert Plants and Communities* Eds R Robichaux. pp 87-104. University of Arizona Press, Tucson, AZ.

- McAuliffe J R 2003 The interface between precipitation and vegetation *In* Changing Precipitation Regimes and Terrestrial Ecosystems: a North American Perspective Eds J F Weltzin and G R McPherson. University of Arizona Press, Tucson, AZ.
- Mack M C, D'Antonio C M, and Ley R E 2001 Alteration of ecosystem nitrogen dynamics by exotic plants: A case study of C<sub>4</sub> grasses in Hawaii. *Ecological Applications* 11,1323-1335.
- Melillo J M, Steudler P A, Aber J D, Newkirk K, Lux H, Bowles F P, Catricala C, Magill A, Ahrens T, and Morrisseau S 2002 Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298, 2173-2176.
- Muller T and Hoper H 2004 Soil organic matter turnover as a function of the soil clay content: consequences for model applications. *Soil Biology and Biochemistry* 36, 877-888.
- Nguyen C 2003 Rhizodeposition of organic C by plants: mechanisms and controls. *Agronomie* 23, 375-396.
- Noy-Meir I 1973 Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25-51.
- Orchard V A and Cook F J 1983 Relationship between soil respiration and soil-moisture. *Soil Biology and Biochemistry* 15, 447-453.
- Parker K C 1995 Effects of complex geomorphic history on soil and vegetation patterns on arid alluvial fans. *Journal of Arid Environments* 30, 19-39.
- Pearcy R W, Ehleringer J, Mooney H A, and Rundel P W 1990 *Plant Physiological Ecology: Field Methods and Instrumentation*. Chapman and Hall, London. 457pp.

- Potts D L, Huxman T E, Enquist B J, Weltzin J F, and Williams D G 2006 Resilience and resistance of ecosystem functional response to a precipitation pulse in a semi-arid grassland. *Journal of Ecology* 94, 23-30.
- Potts D L, Huxman T E, Cable J M, English N B, Ignace D D, Eilts J A, Mason M J, Weltzin J F, and Williams D G 2006 Antecedant moisture and seasonal precipitation influence response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. *New Phytologist*, *in press*.
- Raich J W and Schlesinger W H 1992 The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81-99.
- Raich J W and Tufekcioglu A 2000 Vegetation and soil respiration: Correlations and controls. *Biogeochemistry* 48, 71-90.
- Raich J W, Potter C S, and Bhagawati D 2002 Interannual variability in global soil respiration, 1980-94. *Global Change Biology* 8, 800-812.
- Rees R M, Bingham I J, Baddeley J A, and Watson C A 2005 The role of plants and land management in sequestering soil carbon in temperate arable and grassland ecosystems. *Geoderma* 128, 130-154.
- Reynolds J F, Kemp P R, and Tenhunen J D 2000 Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: A modeling analysis. *Plant Ecology* 150, 145-159.
- Rochette P, Desjardins R L, and Pattey E 1991 Spatial and temporal variability of soil respiration in agricultural fields. *Canadian Journal of Soil Science* 71, 189-196.

- Rustad L E, Campbell J L, Marion G M, Norby R J, Mitchell M J, Hartley A E, Cornelissen J H C, and Gurevitch J 2001 A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126, 543-562.
- Rustad L 2001 Matter of time on the prairie. *Nature* 413, 578-579.
- Sala O E, Lauenroth W K, and Parton W J 1982 Plant recovery following prolonged drought in a shortgrass steppe. *Agricultural Meteorology* 27, 49-58.
- Sala O E, Parton W J, Joyce L A, and Lauenroth W K 1988 Primary Production of the central grassland region of the United-States. *Ecology* 69, 40-45.
- Sala O E, Lauenroth W K, and Parton W J 1992 Long-term soil water dynamics in the shortgrass steppe. *Ecology* 73, 1175-1181.
- Santruckova H, Bird M I, Kalaschnikov Y N, Grund M, Elhottova D, Simek M, Grigoryev S, Gleixner G, Arneeth A, Schulze E D, and Lloyd J 2003 Microbial characteristics of soils on a latitudinal transect in Siberia. *Global Change Biology* 9, 1106-1117.
- Schenk HJ and Jackson RB 2002 The global biogeography of roots. *Ecological Monographs* 72, 311-328.
- Schimel J P, Gulledege J M, Clein-Curley J S, Lindstrom J E, and Braddock J F 1999 Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. *Soil Biology and Biochemistry* 31, 831-838.

- Schlesinger W H, Reynolds J F, Cunningham G L, Huenneke L F, Jarrell W M, Virginia R A, and Whitford W G 1990 Biological feedbacks in global desertification. *Science* 247, 1043-1048.
- Schlesinger W H 1997 *Biogeochemistry: An analysis of global change*. Academic Press, New York. 588pp.
- Shaw MR and Harte J 2001 Control of litter decomposition in a subalpine meadow-sagebrush steppe ecotone under climate change. *Ecological Applications* 11, 1206-1223.
- Silvola J, Alm J, Ahlholm U, Nykanen H, and Martikainen P J 1996 The contribution of plant roots to CO<sub>2</sub> fluxes from organic soils. *Biology and Fertility of Soils* 23, 126-131.
- Skopp J, Jawson M D, and Doran J W 1990 Steady-state aerobic microbial activity as a function of soil-water content. *Soil Science Society of America Journal* 54, 1619-1625.
- Smith S D, Herr C A, Leary K L, and Piorkowski J M 1995 Soil-plant water relations in a Mojave desert mixed shrub community- A comparison of 3 geomorphic surfaces. *Journal of Arid Environments* 29, 339-351.
- Tang J W and Baldocchi D D 2005 Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. *Biogeochemistry* 73, 183-207.
- Tang J, Baldocchi D D, and Xu L 2005 Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology* 11, 1298-1304.

- Townsend A R, Vitousek P M, Desmarais D J, and Tharpe A 1997 Soil carbon pool structure and temperature sensitivity inferred using CO<sub>2</sub> and <sup>13</sup>CO<sub>2</sub> incubation fluxes from five Hawaiian soils. *Biogeochemistry* 38, 1-17.
- Trumbore S 2000 Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications* 10, 399-411.
- Weltzin J F and McPherson G R 2003 Predicting the response of terrestrial ecosystems to potential changes in precipitation regimes. *In: Changing Precipitation Regimes and Terrestrial Ecosystems*. Eds J F Weltzin and G R McPherson. pp 3-8. University of Arizona Press, Tucson.
- Weltzin J F and Tissue D T 2003 Resource pulses in arid environments – patterns of rain, patterns of life. *New Phytologist* 157, 171-173.
- Xu L K, Baldocchi D D, and Tang J W 2004 How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochemical Cycles* 18, Art. No. GB4002.
- Zak D R, Holmes W E, White D C, Peakcock A D, and Tilman D 2003 Plant diversity, soil microbial communities, and ecosystem function: are there any links? *Ecology* 84, 2042-2050.

## Tables

Table 1. Experiments 1 and 3 (June 2002, June 2003). Pulse effects on respiration, moisture and temperature. 'Day' is pulse day, 'Plant' is plant species, and 'Soil' is soil surface. Only significant model effects are presented with degrees of freedom, sum of squares, F-statistic, p-value, and  $R^2$ . The partial  $R^2$  values are present for within the full model effects.

<b>Respiration</b>		<b>Df</b>	<b>SS</b>	<b>F</b>	<b>p</b>	<b>R<sup>2</sup></b>
<i>June 2002</i>	Full Model	21,58	48.8	20.051	<0.0001	0.92
	Day	4,58	13.42055	31.521	<.0001	0.2752
	<i>June 2003</i>					
	Full Model	21,151	97.324234	32.8663	<0.0001	0.84
	Day	4,151	30.7457	64.7769	<.0001	0.316
	Plant	1,151	0.59376	5.0039	0.027	0.006
	Plant x Soil	1,151	0.72225	6.0867	0.0149	0.007
<b>Moisture</b>						
<i>June 2002</i>	Full model	19,59	30.682	7.9292	<.0001	0.79
	Day	4,59	4.86648	7.5599	0.0001	0.1586
	Soil	1,59	15.7193	97.6781	<.0001	0.5123
	Plant x Soil	1,59	2.44684	15.2044	0.0004	0.0798
<i>June 2003</i>	Full Model	19,151	55.6218	20.8218	<0.0001	0.75
	Day	4,151	13.7328	32.5665	<.0001	0.2469
	Soil	1,151	24.5529	232.903	<.0001	0.4414
	Plant	1,151	0.60205	5.7109	0.0183	0.0108
	Plant x Soil	1,151	0.90255	8.5614	0.004	0.0162
<b>Temperature</b>						
<i>June 2002</i>	Full Model	19,58	1.5974	4.9035	<0.0001	0.7
	Day	4,58	1.02991	21.303	<.0001	0.6447
	Plant	1,58	0.066	5.4609	0.0247	0.0413
<i>June 2003</i>	Full Model	19,151	6.682	6.6008	<0.0001	0.49
	Day	4,151	2.9638	28.5442	<.0001	0.4436

Table 2. Experiments 2 and 4 (August 2002, August 2003). Pulse effects on respiration, moisture and temperature ‘Water’ is water treatment. Only significant model effects are presented.

<b>Soil R</b>		<b>Df</b>	<b>SS</b>	<b>F</b>	<b>p</b>	<b>R<sup>2</sup></b>
<i>August 2002</i>	Full Model	33,94	31.244	4.8765	<0.0001	0.73
	Water x Day	3,94	2.1277	5.0376	0.0035	0.068
	Soil x water	1,94	0.6223	4.4203	0.0396	0.02
<i>August 2003</i>	Full Model	41,129	47.227	13.1742	<0.0001	0.86
	Water x day	4,129	1.6053	5.3379	0.0007	0.034
	Plant x water	1,129	0.3947	5.2498	0.0243	0.008
	Soil x water	1,129	1.8093	24.0639	<.0001	0.038
	Soil x day	4,129	1.3010	4.326	0.0031	0.028
	Plant x soil x water	1,129	0.2828	3.7608	0.0557	0.006
	Ln Soil Moisture	1,129	0.6168	8.2043	0.0052	0.013
<b>Moisture</b>						
<i>August 2002</i>	Full Model	31,91	21.203	6.6342	<0.0001	0.77
	Water x day	3,91	0.6517	2.7524	0.0499	0.0307
	Soil x water	1,91	0.7526	9.5355	0.003	0.0355
<i>August 2003</i>	Full Model	39,129	32.366	13.9755	<0.0001	0.86
	Day	4,129	3.6816	18.0586	<.0001	0.1138
	Soil x water	1,129	0.3702	7.2637	0.0084	0.0114
	Water x day	4,129	1.7242	8.4574	<.0001	0.0533
	Plant	1,129	0.5752	11.2861	0.0011	0.0178
	Plant x soil	1,129	0.3093	6.0689	0.0157	0.0096
<b>Temperature</b>						
<i>August 2002</i>	Full Model	31,94	0.9199	5.5179	<0.0001	0.73
	Water x day	3,94	0.0371	3.143	0.0313	0.0403
	Soil x water	1,94	0.0230	5.8631	0.0184	0.0251
	Plant	1,94	0.0211	5.3557	0.0239	0.0229
<i>August 2003</i>	Full Model	39,129	5.142	2.6399	<0.0001	0.53
	Day	4,129	1.7523	16.4386	<.0001	0.3408
	Soil x water	1,129	0.1002	3.7617	0.0556	0.0195

### Figure legends

Figure 1. Experiment 1 in June 2002. The interaction of plant species and soil surface over the pulse measurement period following a single large pulse after a prolonged drought period. In the legend, 'native' and 'non-native' refer to the grass species, and sandy and clay refer to the soil types. Circles are on the sandy loam surface, triangles are the clay loam surface, filled symbols are the native grass, and open symbols are the non-native grass. The mean and standard error are presented for all data. The following are plotted over the pulse period: (a) soil respiration, (b) soil moisture, and (c) soil temperature.

Figure 2. Experiment 2 in August 2002. The effects of pulse size and antecedent soil moisture on respiration. Circles are the sandy loam soil, triangles are the clay loam soil, filled symbols are the wet treatment, and open symbols are the dry treatment. In a water treatment-by-soil type interaction, mean and standard error throughout the pulse period are presented for: (a) soil respiration; (d) soil moisture and (e) soil temperature; (b) soil moisture vs. respiration on day 7 (includes all treatments) [ $\ln \text{soil respiration} = 0.42 * \ln \text{soil moisture} - 0.34$ ,  $R^2 = 0.14$ ,  $p = 0.08$ ]; (c) soil temperature vs. respiration on days -1 and 7 (includes all treatments) and data were combined for both days on a single graph because they are not statistically different [ $\ln \text{soil respiration} = -2.75 * \ln \text{soil moisture} + 10.1$ ,  $R^2 = 0.42$ ,  $p < 0.0001$ ].

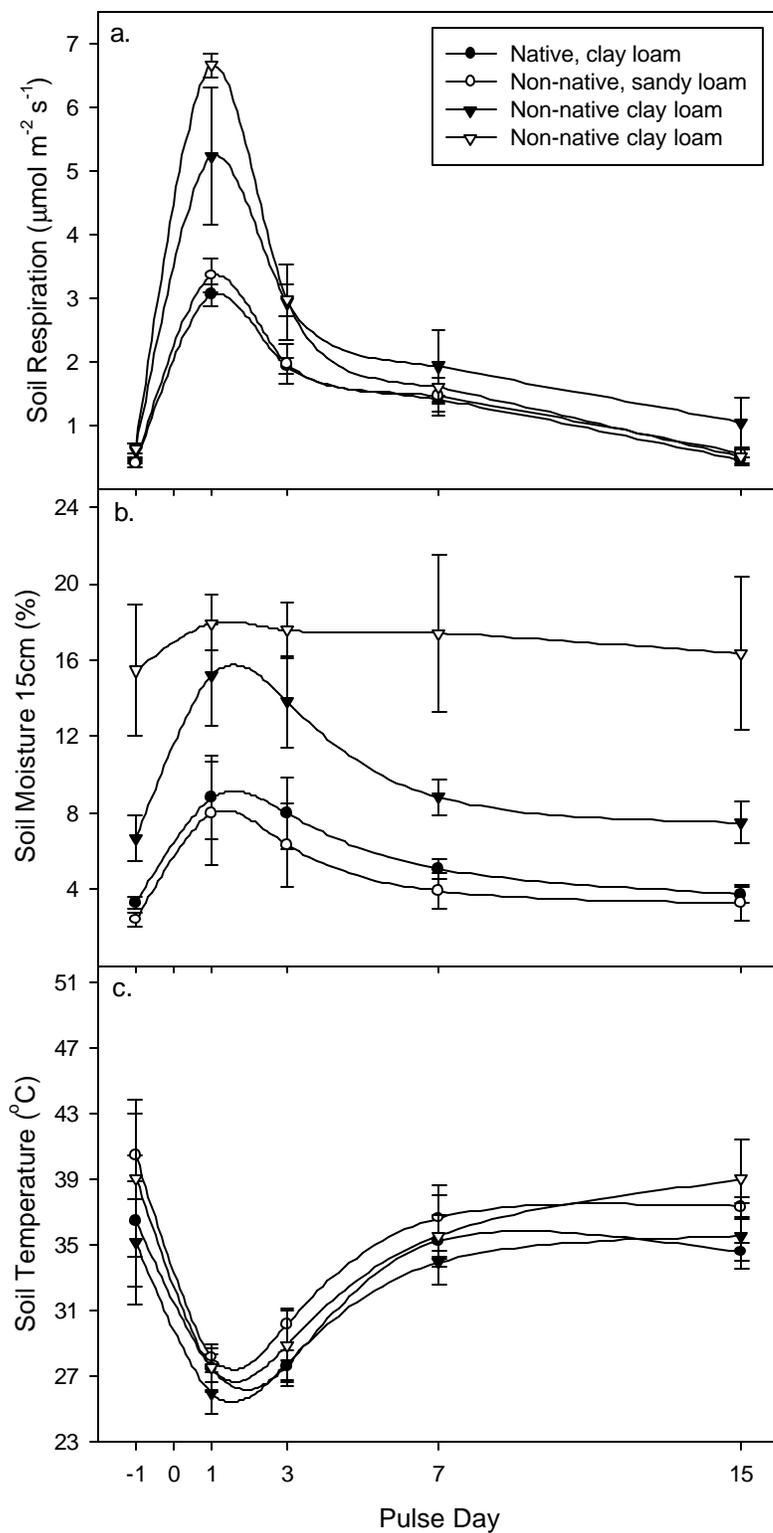
Figure 3. Experiment 3 in June 2003. The effects of pulse history and a large pulse after a prolonged drought on respiration. Plant species-by-soil surface interaction over the pulse period. Circles are on the sandy loam surface, triangles are the clay loam surface, filled symbols are the native grass, and open symbols are the non-native grass. The mean and standard error are presented. The following are presented over the pulse period: (a) soil respiration, (b) soil moisture, and (c) soil temperature.

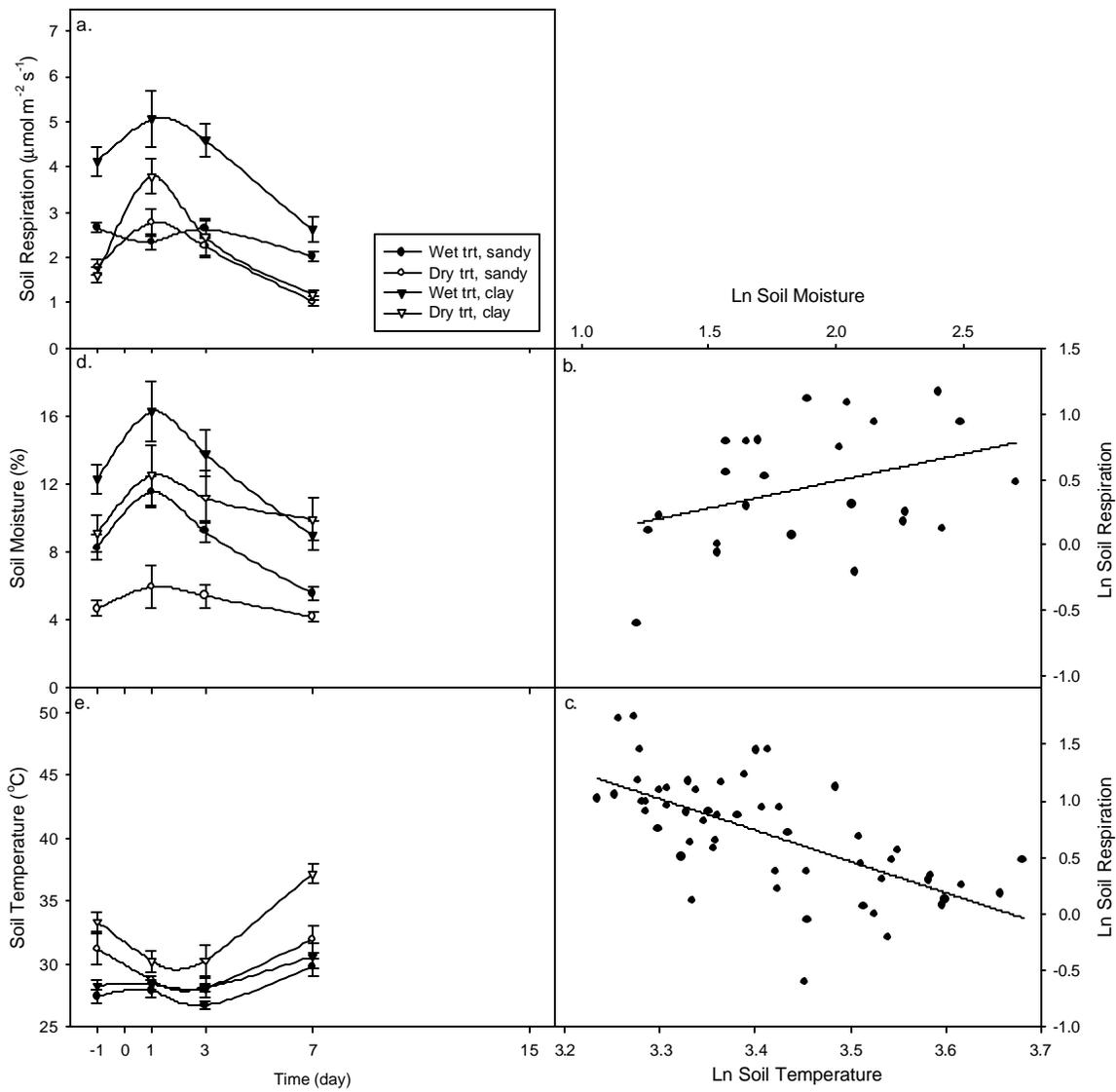
Figure 4. Experiment 4 in August 2003. Effects of pulse history on how pulse size and antecedent soil moisture affect respiration, soil moisture, and soil temperature. Circles are sandy loam, triangles are clay loam, filled symbols are the wet treatment, and open symbols are the dry treatment. In a soil surface-by-water treatment interaction, the mean and standard error throughout the pulse period are presented for: (a) soil respiration, (d) soil moisture, and (e) soil temperature; (b) soil moisture vs. soil respiration on days -1, 1, and 3 for all treatments [ $\ln \text{soil respiration} = 0.16 * \ln \text{soil moisture} + 0.49$ ,  $R^2 = 0.52$ ,  $p < 0.0001$ ]; (c) soil temperature vs. soil respiration on days -1, 7, and 15 for all treatments [ $\ln \text{soil respiration} = -1.73 * \ln \text{soil temperature} + 6.54$ ,  $R^2 = 0.31$ ,  $p < 0.0001$ ].

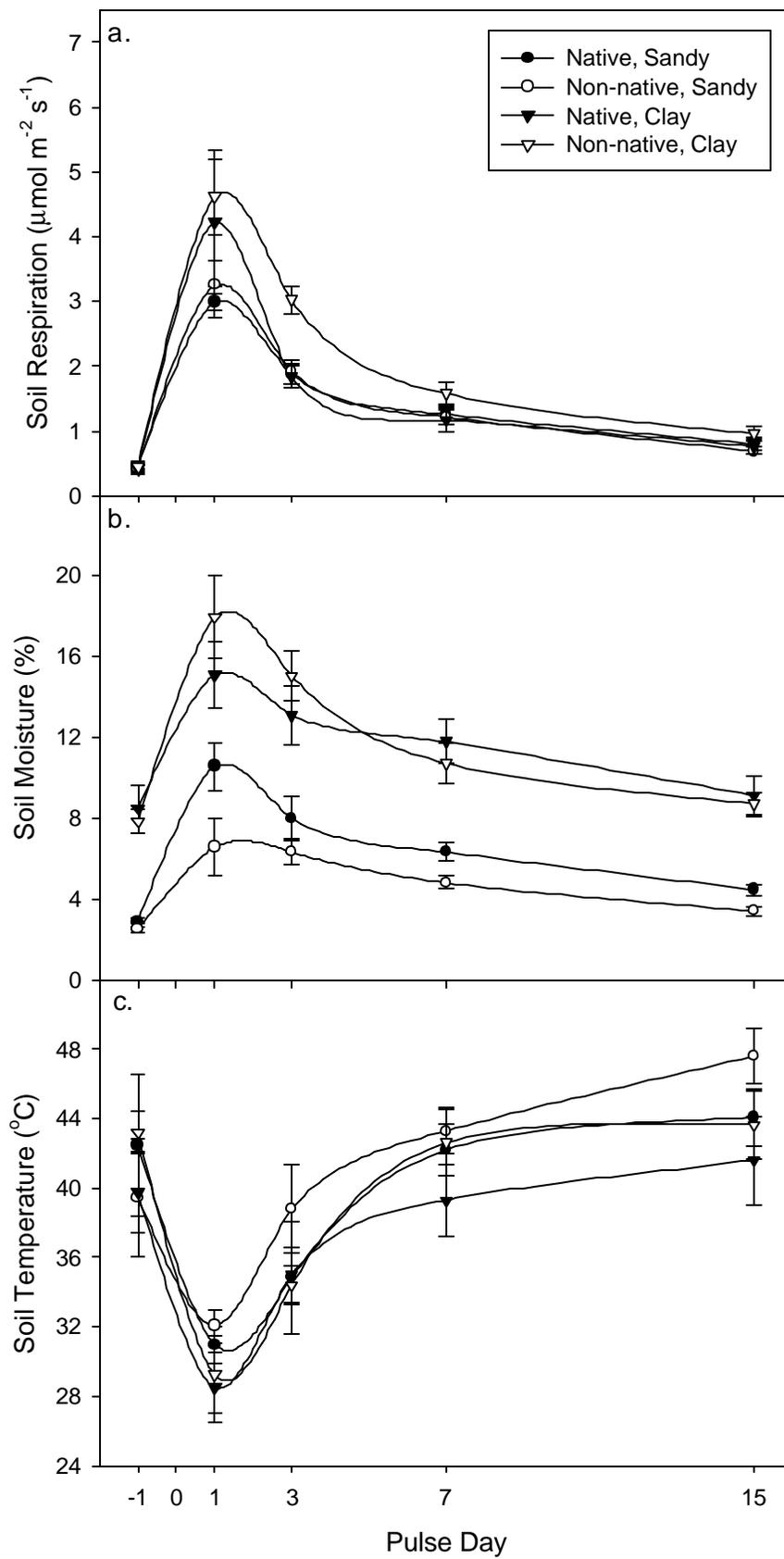
Figure 5. The responsiveness of respiration to a pulse (% increase in respiration from days -1 to 1 relative to day -1; [%increase =  $(R_{-1} - R_1)/R_{-1}$ ]) vs.  $\ln$  initial respiration rates for both seasons and both soil surfaces. Years have been combined for each month.

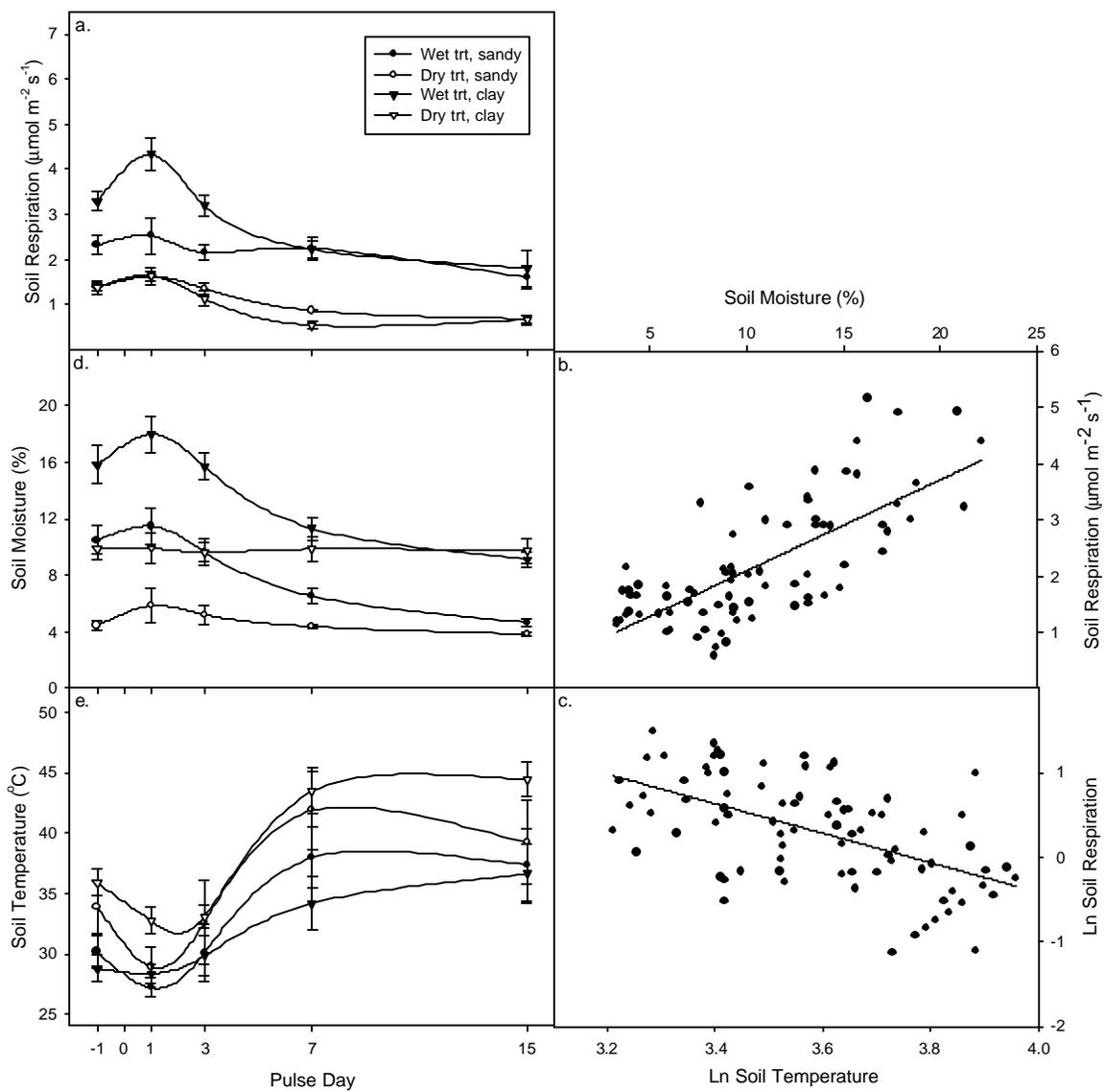
Figure 6. Cumulative carbon loss from days -1 to 7 ( $\text{mol C m}^{-2} \text{d}^{-1}$ ) vs. mean soil moisture at the 15 cm depth from days -1 to 7. Standard errors are presented for the cumulative carbon and soil moisture values. The months are lettered J (June) and A (August); the years are numbered 02 (2002) and 03 (2003); the water treatments are shown as 'dry' or 'wet'; and the soil surfaces are shown as 'sand' for sandy-loam and 'clay' for the clay loam.

Figures

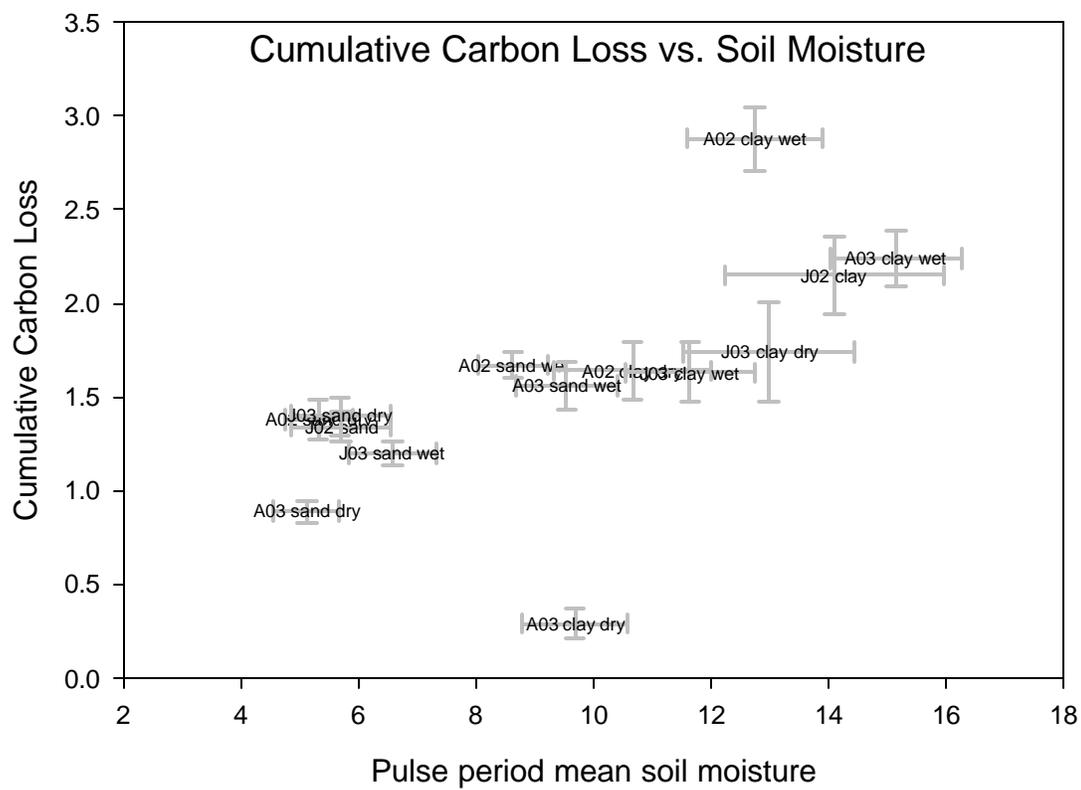












APPENDIX C

EFFECTS OF PRECIPITATION PULSE SEQUENCING ON PLANT AND SOIL

RESPONSE TO PULSE SIZE IN THE SONORAN DESERT

Jessica M. Cable, Mitchell Pavao-Zuckerman, David G. Williams, and Travis E. Huxman

**Abstract**

In pulse driven ecosystems, the combined effect of rainfall event size distribution and sequencing on different ecosystem components is not well understood. Plants and soil microorganisms may be differentially affected by characteristics of rainfall due to differences in upregulation and growth time, their vertical positioning in the soil profile, and resource-use strategies. In this study, we examined how a short sequence of rainfall events precondition the relative activity of microbes and plants and alter their responsiveness to different sized rainfall events. During the dry fore-summer in the Sonoran Desert, we applied an initial “preconditioning” rainfall event followed up with a series of different sized “target” rainfall events delivered following a week of dry-down. We intensively sampled soil, leaf, and root CO<sub>2</sub> exchange, predawn leaf water potentials, soil moisture, and soil temperature on grass plots. We found that preconditioning did not differentially affect the response of soil respiration to target pulse size. However, preconditioning differentially affected the responsiveness and maintenance of activity in plant photosynthesis following different sized target pulses. Rainfall variability is expected to increase in the desert Southwestern US, possibly resulting in non-linear responses of ecosystem carbon processes due to the differential response of plants and soils. Our findings provide novel experimental results that highlight the complex mechanistic components that govern ecosystem responses to rainfall.

**Key Words:** antecedent soil moisture, *Eragrostis lehmanniana*, photosynthesis, respiration, southwest Arizona

## Introduction

Discrete “pulses” of precipitation drive biological activity in arid and semi-arid ecosystems (Noy-Meir 1973), but all pulse events may not have similar effects (Fierer and Schimel 2002, Huxman et al. 2004a, Loik et al. 2004, Schwinning et al. 2004). Pulses differ in their sequence influencing antecedent soil moisture conditions prior to a subsequent rain event that can affect biological responses (Fierer and Schimel 2002, Fierer et al. 2003, Tang and Baldocchi 2005). The size of a precipitation event can affect different ecosystem components. For example, small events tend to activate surface organisms or shallow rooted plants, while large events influence the activity of organisms deeper in the soil (Sala et al. 1982, Cable and Huxman 2004, Austin et al. 2004). How rainfall sequencing interacts with event size to affect biological activity in arid and semi-arid ecosystems has not been extensively examined *in situ* (but see Fay et al. 2003, Harper et al. 2005), but may be important to understand in order to evaluate ecosystem response to precipitation change (Schwinning and Sala 2004, Weltzin et al. 2003). For example, the frequency of large relative to small precipitation events is expected to increase in the future for the Southwestern United States (Easterling et al. 2000, IPCC 2001); currently small events (<5mm) are much more common (Sala et al. 1982).

Major ecosystem components of arid and semi-arid ecosystems, such as plants and soil microbes, respond differently to inputs of precipitation because of variation in metabolic upregulation time, nutrient requirements and availability, and location in the soil profile (Huxman et al. 2004b, Schwinning et al. 2004, Schwinning and Sala 2004).

A single pulse event results in a rapid, large efflux of CO<sub>2</sub> from the soil due to the combination of physical displacement from soil pores as water moves deeper in the soil profile (Li et al. *in review*) and a rapid increase in microbial activity associated with carbon and nitrogen mineralization (Franzuebbers et al., 2000; Fierer and Schimel 2003, Austin et al. 2004). The response from plants may be delayed compared to microbes because of limited leaf area and upregulation of photosynthetic activity after recovery from a low water status (Sala et al. 1982, Flanagan et al. 2002, Schwinning et al. 2002, Huxman et al. 2004a). Huxman et al. (2004b) proposed a hierarchical response of ecosystem components to pulses. Specifically, small pulses are predicted to only activate surface organisms, such as microbes, while larger events or sequences of events are predicted to activate plants through greater amounts of water infiltrating to the active rooting zone.

The preconditioning of plants and soils by sequences of rainfall events may constrain or prime their responsiveness to subsequent events (Fierer and Schimel 2003, Schwinning and Sala 2004). A single wetting event can result in high carbon mineralization due to microbial turnover and consumption of labile substrates (Franzuebbers et al. 2000, Fierer and Schimel 2003, Austin et al. 2004). However, frequent soil wet-dry cycles in grassland soils decreases microbial respiration rates with subsequent rain events, due to a reduced availability of carbon and nitrogen substrate for consumption, and shifts in microbial community structure. Both of these constrain the response of soil microbes to repeated rapid increases in soil moisture (Fierer and Schimel 2002, Mikha et al. 2005). For plants, a series of soil wet-dry cycles can result in

increased water status, photosynthetic performance, growth, and leaf area, possibly 'preconditioning' the responsiveness to utilize subsequent rain events (Kozlowski and Pallardy 1997, Yan et al. 2000, Schwinning et al. 2002). Thus, the sequencing of rainfall may differentially affect plant vs. soil microbe processes, where plants may respond favorably to multiple rain events, but microbes may be constrained by wet-dry cycles.

Determining the effects of multiple rather than single rainfall events may be more biologically meaningful, because sequences of rain events are better predictors of rainfall variability (Reynolds et al. 2004). The combination of biological preconditioning and subsequent pulse size will likely have complex effects on whole ecosystem functioning due to the differential contributions of each component in response to precipitation. Although soils may dry between even short sequences of rainfall events, the history of soil moisture change may affect the responsiveness of plant and soil microbial activity to subsequent rain events.

In this study we ask: what is the response of plant and soil CO<sub>2</sub> exchange to target pulses of different sizes when the system has experienced a recent rainfall event? We hypothesize that an initial watering event will precondition the responsiveness of leaf-level activity in plants to different sized target pulses, specifically plants will be more likely to respond to a small event if they have experienced a recent rainfall event. We further hypothesize that an initial watering event will precondition the responsiveness of bulk soil microbial activity to different sized target pulses, specifically bulk soil microbes will be less likely to respond to *both* small and large events if they have experienced a recent rainfall event.

As compared to those living in the bulk soil, microbes closely associated with roots (rhizosphere) may differentially respond to wet-dry cycles. These organisms are primarily driven by root exudation and thus are expected to respond to immediate plant activity (Chen et al. 2006). A rapid response from stored resources allocated to root growth following rainfall may influence this community (Huang and Fu 2000). A delayed response to rain events could occur if resources are allocated to leaf level function (Gindaba et al. 2005). Preconditioning of root activity by a sequence of rainfall could lead to even greater infiltration of water, so that despite surface drying, deeper roots may remain active (Huang and Fu 2000, DaCosta et al. 2004, Peek et al. 2005). Together these observations drive our last hypothesis, where differences in sequences of rainfall events will result in greater rhizosphere respiration due to the effect of preconditioning on root growth. Specifically, rhizosphere respiration will be more responsive to event size if they have experienced a recent rainfall event.

## **Methods**

Research was conducted at the Santa Rita Experimental Range (SRER) southeast of Tucson, AZ. The mean daytime temperature for May (the month prior to measurements) was 78°F and the most recent rainfall was 0.19 in 9 days prior to the first measurements. We established 30 plots, on a sandy loam soil, in stands dominated by the C<sub>4</sub> grass *Eragrostis lehmanniana*. Plots were 2 m x 1 m, separated by 0.5 m and trenched to 10 cm to minimize water exchange between plots. Plots were randomly separated into two treatment groups: those receiving no preconditioning rainfall event and a 15 mm

preconditioning rainfall event. Within each treatment group, plots were randomly assigned the following target pulse treatments (5 replicates per treatment): 0 mm, 5 mm, and 15 mm. The preconditioning and target pulses were separated by seven days. All measurements were made on the day prior to the target pulse, and days 1, 3, and 7 following the target pulse. Leaf gas exchange was measured at 4 am, 8 am, and 2 pm; soil respiration was measured at 4am and 2pm; rhizosphere respiration was measured at 8 am; and leaf water potential was measured at 4am.

One polyvinyl chloride (PVC) ring (soil collar) 10.2 cm in diameter was placed into each plot one week prior to water application. Soil respiration was measured with a closed loop chamber design, where air was pumped from a PVC lid 3 L in volume, through a Li-820 at a 0.8 L/min flow rate, and returned to the lid. The lid contained a small 5V microfan to mix the air. The lid was placed on the collars for 2 minutes. Soil collar depth, soil moisture to 12 cm (%), Hydrosense, Campbell Scientific), lid air temperature (°C, Type E thermocouple), soil temperature (°C) were measured at the same time. The soil temperature probe was inserted at a shallow angle for the 2 cm reading and vertical for the 12 cm reading. The data were corrected for collar area, lid volume, additional volume from the collar depth, and lid temperature. The flux data were converted to flux density and were volume/area corrected (Pearcy et al. 1990).

Leaf and rhizosphere gas exchange measurements were made with a Li-6400 portable gas exchange system (Li-Cor, Lincoln, NE). For leaf level measurements, the standard cuvette with a Red-Blue light source was used and the conifer chamber was used for rhizosphere respiration. Conditions in the cuvette were set to ambient environmental

conditions for each measurement period (temperature, VPD, PAR, CO<sub>2</sub> concentration). For rhizosphere respiration, the roots with the associated soil were carefully excavated, temperature of the root mass was taken by touching a type K thermocouple, and the roots with the associated rhizosphere soil was placed in a shaded chamber. The Li-6400 block temperature was set to the root temperature. Roots from the chamber were collected, dried, and weighed. These data were used to standardize rhizosphere fluxes. Rhizosphere respiration and photosynthesis at 8am were measured on the same plant but different plants were measured during each measurement period. Predawn leaf water potential measurements were made with a Scholander-type pressure bomb (PMS Instrument Co. Albany, OR) on the grass blades collected at the base of the plant.

Soil respiration, rhizosphere respiration, and leaf level gas exchange data were  $\log_{10}$  transformed to meet statistical assumptions of normality. Data were analyzed with JMP5.1 (SAS Institute) using a multi-way ANOVA model. The explanatory variables for soil respiration were temperature, moisture, time (pulse day), pulse size, preconditioning pulse size, rhizosphere respiration, and photosynthetic rates (8am and 2pm). The explanatory variables for photosynthesis and leaf respiration were time, pulse size, and preconditioning pulse size. The explanatory variables for rhizosphere respiration were time, pulse size, preconditioning pulse size, and photosynthesis (8am and 2pm). Means are presented with the standard error.

## Results

### *Soil moisture*

Greater pulse size resulted in higher soil moisture on days 1 and 3 following the target rainfall event (*15mm vs 5mm*:  $F_{1,78} = 24.96$ ,  $p < 0.0001$ ; *5mm vs. 0mm*:  $F_{1,78} = 7.20$ ,  $p = 0.009$ ; Figure 1). Preconditioning treatment (a rainfall event 7 days prior to the target pulse) had no effect on the time-course. By day 7, soil moisture had returned to pre-target pulse levels.

### *Soil respiration*

The temporal trend in soil respiration ( $R_S$ ) for 4am and 2pm did not differ, and  $R_S$  at 4am and 2pm were also similar across target pulse sizes. For  $R_S$  in both time periods, there was an pulse day x pulse size interaction, where  $R_S$  peaked on day 1 post-pulse and rates increased with increasing pulse size (*4am*:  $F_{6,94} = 13.863$ ,  $p < 0.0001$ ; *2pm*:  $F_{6,79} = 5.7068$ ,  $p < 0.0001$ ; Figure 2). The 15mm target pulse resulted in higher  $R_S$  through day 7. Only on day 1, the 5 mm target pulse resulted in significantly greater  $R_S$  than the control. Higher soil moisture resulted in higher  $R_S$  (*4am*:  $t(57) = 3.73$ ,  $p = 0.0004$ ,  $R^2 = 0.49$ ; *2pm*:  $t(94) = 2.97$ ,  $p = 0.0038$ ,  $R^2 = 0.46$ , Figure 3). For  $R_S$  at 2pm, higher soil temperature (2cm) was associated with lower  $R_S$  ( $t(94) = -1.96$ ,  $p = 0.0525$ ). However, soil moisture explained most of the variation in  $R_S$  (soil temperature  $R^2 = 0.40$ , soil

moisture  $R^2 = 0.46$ ; Figure 3). Interestingly, the preconditioning pulse resulted in slightly higher  $R_S$  in the control plots at 4am ( $F_{1,36} = 5.8227$ ,  $p = 0.021$ , Figure 2). This effect was not seen at 2pm on days 1, 3 and 7, where both controls had similar flux values. On the day prior to the target pulse application,  $R_S$  was greater from plots that received a preconditioning treatment ( $F_{1,79} = 4.19$ ,  $p = 0.0436$ ).

Pulse size explained most of the variation in  $R_S$  on day 1 (peak day) (4am:  $F_{2,12} = 102.16$ ,  $p < 0.0001$ ,  $R^2 = 93\%$ ; 2pm:  $F_{2,24} = 15.117$ ,  $p < 0.0001$ ,  $R^2 = 62\%$ ). Mean  $R_S$  was consistently lowest for the control plots (0mm target pulse) and highest for the 15mm target pulse. At 4am, mean  $R_S$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for the 0mm, 5mm and 15mm target pulses were -1.2 (0.09), -4.8 (0.61), and -6.8 (0.61), respectively, and at 2pm, the mean rates were -0.56 (0.79), -5.33 (0.66), and -7.20 (0.66).

### *Plant water potential*

Plant water potential was influenced by the preconditioning treatment, target pulse size, and time (repeated measures ANOVA:  $F_{1,17} = 8.0636$ ,  $p = 0.006$ ;  $F_{2,17} = 10.8502$ ,  $p < 0.0001$ ;  $F_{3,15} = 14.9834$ ,  $p < 0.0001$ ; respectively; Figure 4). In the absence of a preconditioning pulse, water potential was more negative than with a preconditioning pulse (0 mm = -1.53 MPa +/- 0.060 vs. 15 mm = -1.27 MPa +/- 0.056). With increasing target pulse size, water potential became less negative across both preconditioning treatments ( $F_{2,17} = 4.7093$ ,  $p = 0.0236$ ). As compared to plants that did not receive a preconditioning pulse, the plants that did receive a preconditioning pulse showed greater

responsiveness to the 15mm target pulse (on day 1) ( $F_{1,19} = 4.9252$ ,  $p = 0.0388$ ), and a greater duration of favorable water status (for 5mm target pulse) ( $F_{1,85} = 4.0271$ ,  $p = 0.048$ ).

### *Plant photosynthesis and respiration*

Leaf respiration ( $R_L$ ) was greatest on days -1 and 1, and was marginally higher with a 15mm preconditioning treatment ( $F_{3,94} = 13.56$ ,  $p < 0.0001$ ;  $F_{1,94} = 3.67$ ,  $p = 0.058$ , respectively; Figure 5). There was a trend in  $R_L$  with plants that received the combination of 0mm preconditioning pulse and a 15mm target pulse, where higher  $R_L$  lasted through day 3 and declined to lower levels by day 7 ( $F_{1,10} = 3.95$ ,  $p = 0.07$ ; Figure 5). However, plants that received a 15mm preconditioning pulse responded similarly to the different target pulse sizes. On the days -1 and 1, preconditioning treatment had the greatest effect on  $R_L$ , where the 15mm preconditioning pulse resulted in higher overall rates ( $F_{1,56} = 5.43$ ,  $p = 0.0235$ ).

Photosynthetic rates at 8am and 2pm were influenced by the preconditioning treatment and time x target pulse size interaction. Preconditioning treatment affected photosynthesis more at 2pm than 8am but the pattern across days was the same: higher photosynthesis resulted from a preconditioning pulse (8am:  $F_{1,35} = 3.31$ ,  $p = 0.077$ ; 2pm:  $F_{1,94} = 7.308$ ,  $p = 0.0081$ ). Plants that received a 5mm or 15mm target pulse with no preconditioning had peak photosynthesis at 2pm one day post target pulse ( $F_{6,94} = 13.863$ ,  $p < 0.0001$ ; Figure 6a, Figure 7). However, the duration of high photosynthesis was

greater following the 15mm target pulse continuing through day 3 ( $F_{1,11} = 9.26$ ,  $p = 0.011$ ; Figure 6a).

The response to the target pulses differed for plants that received a 15 mm preconditioning pulse. On day 1, photosynthesis at 8am responded similarly for both the 5 mm and 15mm pulses. Photosynthesis at 2pm showed similar responses to the 5 mm and 15 mm pulses, with a slightly greater response for the 5 mm pulse ( $F_{1,11} = 4.50$ ,  $p = 0.057$ , Figure 6b). By day 3 post target pulse, photosynthetic activity at 2pm was similar for plants that received 5 mm and 15 mm target pulses, but there was a slight trend for higher photosynthetic rates from the plants that received a 15 mm target pulse (Figure 6b). Interestingly, plants that received a preconditioning pulse followed by a 15mm target pulse reached maximum photosynthetic rates on day 3 as compared to plants that did not have a preconditioning pulse ( $F_{1,8} = 5.61$ ,  $p = 0.045$ ).

### *Rhizosphere Respiration*

The highest rates of rhizosphere respiration ( $R_R$ ) occurred on days 3 and 7 post target pulse ( $F_{2,65} = 4.0317$ ,  $p = 0.0108$ , Figure 8).  $R_R$  was greatest for plants that did not receive a preconditioning treatment ( $F_{1,61} = 9.04$ ,  $p = 0.0038$ , Figure 8). Midmorning (8am) photosynthesis one day after the target pulse explained 22% of the variation in day three  $R_R$  values ( $t(16) = -2.11$ ,  $p = 0.05$ ), where lower  $R_R$  was associated with higher photosynthetic rates. Higher soil moisture at 4am was associated with higher  $R_R$ , but

little variation (3%) was explained ( $t(40) = -2.57$ ,  $p = 0.0142$ ). Soil temperature and target pulse size were not a significant covariates.

Combining soil and plant physiological variables, higher  $R_S$  each day at 4am was associated with higher  $P_L$  at 2pm the previous day ( $t(57) = 2.07$ ,  $p = 0.0426$ ,  $R^2 = 0.21$ ). Further,  $R_R$  explained 42% of the variation in  $R_S$  at 2pm on day 1 post-pulse when plots that did not receive a target pulse were excluded from the analysis, and greater  $R_R$  was associated with lower  $R_S$  ( $t(9) = -2.54$ ,  $p = 0.0318$ ).

## **Discussion**

Biological activity in desert ecosystems is driven by episodic inputs of precipitation (Noy-Meir 1973). Characteristics of precipitation, such as sequence and event size distribution, differ in their impacts on individual ecosystem components (Austin et al. 2004, Huxman et al. 2004b). Through differences in the potential for physiological upregulation, nutrient requirements and availability, and location in the soil profile, plants and soil microorganisms likely respond differently to individual rainfall events. Single events often result in a large efflux of  $CO_2$  from the soil due primarily to a rapid increase in microbial activity from nutrient mineralization (Fierer and Schimel 2003, Austin et al. 2004). A slower response from plants generally occurs due to limited leaf area display and upregulation of photosynthetic activity (Sala et al. 1982, Flanagan et al. 2002, Schwinning et al. 2002, Huxman et al. 2004a). Multiple rain events can alter response to a single pulse by affecting antecedent soil moisture conditions and the

physiological state of ecosystem components (Reynolds et al. 2004). In this study, we examined how a short sequence of rainfall events precondition the relative activity of microbes and plants and alter their responsiveness to different sized rainfall events.

We hypothesized that a preconditioning pulse event would prime leaf-level plant activity and alter responsiveness to different sized target pulses. While plants would be expected to respond to the greatest extent for large target rainfall events, preconditioning may prime physiological processes and allow for a greater response to relatively small rainfall events (Sala and Lauenroth 1982). Indeed, when plants were activated by a preconditioning rainfall event, it elevated plant water status (Figure 4) and increased the photosynthetic responsiveness to our smallest target rainfall treatment (Figure 5). We hypothesized that a preconditioning pulse would result in a reduction in soil respiration responsiveness to target pulses due to the effects of wet-dry cycle dynamics on microbes (Fierer and Schimel 2003). We found that precondition did not affect how soil CO<sub>2</sub> efflux responded to target pulses of different sizes (Figure 2).

In our study, soil and plant activity differed in response to the combination of target pulse size and preconditioning treatment. In the Mojave and Sonoran Deserts, Reynolds et al. (2004) found that antecedent soil moisture and pulse size interact to affect plant growth, where high antecedent soil moisture, from a rain event greater than 10 mm, resulted in low plant response to a precipitation event. In our study, high antecedent plant water status resulted in a similar photosynthetic response to both the small and large target pulses. Target pulse size (5 mm versus 15 mm) had little disproportionate effects on plant water status when plants received a precondition pulse. In the absence of a

precondition, the difference in response between the 5 mm and 15 mm target pulses was large. This suggests that priming effects of antecedent rainfall events significantly influences the relationship between physiological activity and rainfall event size distribution, and may be important for seasonally integrated processes (Ogle and Reynolds 2004).

Turnbull et al. (2001) found that dark leaf respiration was lower with wetter soil conditions. In our study, there was greater carbon loss from leaf respiration when antecedent plant water status was high, but rhizosphere respiration showed the opposite trend. Thus, whole plant carbon loss following the target pulses may be similar from both preconditioning treatments due to the differential response of shoots versus roots. Respiration is from tissue growth and cell maintenance processes. Greater rhizosphere respiration in the absence of the preconditioning pulse may indicate rapid allocation of resources and growth in roots following the target pulses. Martinez et al. (2002) found that high soil moisture and nutrient levels resulted in lower root respiration rates (growth and maintenance) due to low carbon content in root tissues. Perhaps the lower rhizosphere respiration rates in plants that received a precondition pulse are due to a shift in allocation of carbon to support growth of the canopy (Albaugh et al. 1998). Greater leaf respiration with a preconditioning pulse is consistent with this hypothesis.

Preconditioning did not affect soil respiration, with consistent responses of soil CO<sub>2</sub> efflux to the different sized target pulses; rates increased with increasing target pulse size. These results stand in contrast to those of Fierer and Schimel (2003), who found that respiration declined with repeated soil wet-dry cycles. Since our study had only one

cycle, we may not have induced substrate limitation of microbial activity. Many studies have found a positive relationship between temperature and respiration (e.g. Lloyd and Taylor 1994). However, in our study, there was an inverse relationship. Pavao-Zuckerman et al. (*in preparation*) found that during a pulse response in a semi-arid savannah, microbial biomass and nematode abundance are positively correlated with soil moisture content, but negatively correlated with soil temperature. Thus, these observed decreases in soil respiration in semi-arid systems may be associated with shifts in soil organism community structure owing to the co-variation between temperature and water. Additionally, because evaporative effects result in a negative relationship between soil temperature and moisture (Pavao-Zuckerman et al. *in preparation*), it is likely that soil organisms and soil respiration are tracking the effects of soil moisture as mediated by shifts in the soil thermal environment. Additionally, at low soil moisture levels, substrate supply may be limiting due to the combined effect of high metabolic activity of microbes and diffusive constraints of substrates with decreasing water films (Skopp et al. 1990, Davidson et al. 2006).

The time of peak activity differed for each ecosystem component. Photosynthesis, leaf and soil respiration peaked the day after the target pulses. While the observed photosynthetic response is rapid compared to other studies (Sala et al. 1982, Huxman et al. 2004a), the timing of the soil respiration response appears to be consistent with other studies (Fierer and Schimel 2003, Huxman et al. 2004a, Steenwerth et al. 2005, Cable et al. *in prep*). Rhizosphere respiration peaked the 3<sup>rd</sup> day after the target pulses, when the other processes began declining, and by day 7 activity from all

components had declined to low levels. The link between each of the plant physiological variables is temporally complex. For example, higher photosynthetic rates on day 1 were correlated with lower rhizosphere respiration rates on day 3. The plants may have already responded to the pulse and as the soil dried, minimal to no root activity may be required (Hayes and Seastedt 1987, Huang and Fu 2000, Craine et al. 2002, Peek et al. 2005, Huang et al. 2005). Earlier development of roots in response to soil moisture availability can result in higher root persistence and activity throughout the growing season (Fay et al. 2003, Peek et al. 2005).

The temporal links between physiological processes above- and below-ground are also not straightforward. It has been estimated that rhizosphere respiration can be 30 to 50% of total soil respiration (Bowden et al. 1993, Andrews et al. 1999, Tang and Baldocchi 2005) and that nearly 12% of recent photosynthate can be respired through the rhizosphere (Nguyen 2003). In this study, the positive association between midday soil respiration and photosynthesis the previous afternoon suggests that the lag time between photosynthate production and transport to the rhizosphere may be within approximately 24 hours. In some trees, the transport time of recent photosynthate to roots is 7-12 hours (Tang et al., 2005). In an African C<sub>4</sub> grass, leaf to root transport rate was 1.4 cm / min (Freckman et al., 1991), suggesting rapid carbohydrate transport is possible in our study. However, rhizosphere respiration may not be a significant contributor to soil CO<sub>2</sub> efflux. On day 1 after the target pulses, rhizosphere respiration explains significant variation in soil respiration from plots that received a target pulse, regardless of size, but greater

rhizosphere respiration was associated with lower soil respiration rates. This suggests that bulk soil microbial respiration may be contributing more to soil CO<sub>2</sub> efflux.

The best support for the large contribution from microbial activity in response to these sequences of rainfall events comes from temporal and spatial separation in rhizosphere and bulk soil activity. Rhizosphere respiration peaked on days 3 and 7. Soil respiration peaked by day 1 and then declined. Thus, rhizosphere respiration may not be a large contributor to soil CO<sub>2</sub> efflux due to the single peak in soil CO<sub>2</sub> efflux. If the rhizosphere were a significant contributor, there would have been a second peak or the duration of high soil CO<sub>2</sub> efflux would have been longer. Thus, the temporal patterning of root and soil respiration is consistent with the expectation that the bulk of the soil respiration response to the target pulse was likely microbial in origin.

We found that the preconditioning treatment 'activated' the plants, causing them to respond more to the small target rainfall events. However, the preconditioning pulse did not affect the response of soil respiration to different sized pulses. The frequency of large precipitation events for the Southwestern United States is expected to increase in the future (IPCC 2001, Easterling et al. 2000). Findings from this study show that plants and soil will likely contribute differently to ecosystem carbon exchange in arid and semi-arid ecosystems with shifts in precipitation. Even a small shift in seasonal precipitation could have significant consequences by differentially influencing components of net ecosystem production, or feedbacks on ecosystem structure by nutrient cycling (Sala et al., 1982; Sala et al., 1992; Schlesinger 1997; Golluscio et al., 1998; Conant et al., 1998, Borken et al. 1999; Reynolds et al., 2000; Weltzin and Tissue 2003; Weltzin and

McPherson 2003; Huxman et al., 2004a). Arid and semiarid regions are predicted to increase in area and soil carbon dynamics are predicted to change from vegetation shifts, so deserts may play large roles in global biogeochemical cycles with shifts in precipitation (Schlesinger et al. 1990).

### **Acknowledgements**

The authors thank D. Potts, A. Eilts, D. Ignace, B. Collins, A. Hazard, and K. Gilliam for project development and field support. We also acknowledge the support of SAHRA (Sustainability of semi-Arid Hydrology and Riparian Areas), under the STC program of the NSF agreement number EAR-9876800 and NSF awards DEB041-5977 and DEB041-8134.

## Literature Cited

- Albaugh TJ, Allen HL, Dougherty PM, Kress LW, and King JS 1998 Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *Forest Science* 44, 317-328.
- Andrews JA, Harrison KG, Matamala R, and Schlesinger WH 1999 Separation of root respiration from total soil respiration using carbon-13 labeling during Free-Air Carbon Dioxide Enrichment (FACE). *Soil Science Society of America Journal* 63, 1429-1435.
- Austin A T, Yahdjian L, Stark J M, Belnap J, Porporato A, Norton U, Ravetta D A, Schaeffer S M 2004 Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141, 221-235.
- Borken W, Xu Y-J, Brumme R, and Lamersdorf N 1999 A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: Drought and rewetting effects. *Soil Science Society of America Journal* 63, 1848-1855.
- Bowden RD, Nadelhoffer KJ, Boone RD, Melillo JM, and Garrison JB 1993 Contributions of aboveground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Canadian Journal of Forest Research – Revue Canadienne de Recherche Forestiere* 23, 1402-1407.
- Cable JM and Huxman TE 2004 Precipitation pulse size effects on Sonoran Desert soil microbial crusts. *Oecologia* 141, 317-324.

- Cable J M, Ogle K, Eilts J A, McClaran M, Martens D, and Huxman TE *In preparation*  
Heterotrophic and autotrophic respiration response to precipitation pulses in a  
semi-arid grassland.
- Chen CR, Condon LM, Xu ZH, Davis MR, and Sherlock RR 2006 Root, rhizosphere  
and root-free respiration in soils under grassland and forest plants. *European  
Journal of Soil Science* 57, 58-66.
- Collier DE and Cummins WR 1993 Effect of osmotic-stress on the respiratory properties  
of shoots and roots of *Arnica-Alpina*. *Canadian Journal of Botany – Revue  
Canadienne de Botanique* 71, 1102-1108.
- Conant R T, Klopatek J M, Malin R C, and Klopatek C C 1998 Carbon pools and fluxes  
along an environmental gradient in northern Arizona. *Biogeochemistry* 43, 43-61.
- Craine JM, Tilman D, Wedin D, Reich P, Tjoelker M, and Knops J 2002 Functional  
traits, productivity and effects on nitrogen cycling of 33 grassland species.  
*Functional Ecology* 16, 563-574.
- DaCosta M, Wang ZL, and Huang BR 2004 Physiological adaptation of Kentucky  
bluegrass to localized soil drying. *Crop Science* 44, 1307-1314.
- Davidson E A, Janssens I A, and Luo Y 2006 On the variability of respiration in  
terrestrial ecosystems: moving beyond  $Q_{10}$ . *Global Change Biology* 12, 154-164.
- Easterling D R, Meehl G A, Parmesan C, Changnon S A, Karl T R, and Mearns L O 2000  
Climate extremes: Observations, modeling, and impacts. *Science* 289, 2068-2074.
- Emmerich W 2003 Carbon dioxide fluxes in a semiarid environment with high carbonate  
soils. *Agricultural and Forest Meteorology* 116, 91-102.

- Fay PA, Carlisle JD, Knapp AK, Blair JM, and Collins SL (2003) Productivity responses to altered rainfall patterns in a C<sub>4</sub>-dominated grassland. *Oecologia* 137:245-251.
- Fierer N and Schimel J P 2002 Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology and Biochemistry* 34, 777-787.
- Fierer N and Schimel J P 2003 Mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Science Society of America Journal* 67, 798-805.
- Fierer N, Schimel J P, and Holden P A 2003 Influence of drying-rewetting frequency on soil bacterial community structure. *Microbial Ecology* 45, 63-71.
- Flanagan LB, Wever LA, and Carlson PJ 2002 Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology* 8, 599-615.
- Flanagan L B and Johnson B G 2005 Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology* 130, 237-253.
- Franzluebbers A J, Haney R L, Honeycutt C W, Schomberg H H, and Hons F M 2000 Flush of carbon dioxide following rewetting of dried soil relates to active organic pools. *Soil Science Society of America Journal* 64, 613-623.
- Freckman DW, Barker KR, Coleman DC, Acra M, Dyer MI, Strain BR, and McNaughton SJ (1991) The use of the <sup>11</sup>C technique to measure plant response to herbivorous soil nematodes. *Functional Ecology* 5:810-818.

- Gindaba J, Rozanov A, and Negash L (2005) Photosynthetic gas exchange, growth and biomass allocation of two Eucalyptus and three indigenous tree species of Ethiopia under moisture deficit. *Forest Ecology and Management* (1-3): 127-138.
- Golluscio R A, Sala O E, and Laurenroth W K 1998 Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia* 115, 17-25.
- Hanson PJ, Edwards NT, Garten CT, and Andrews JA 2000 Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry* 48, 115-146.
- Harper CW, Blair JM, Fay PA, Knapp AK, and Carlisle JD 2005 Increased rainfall variability and reduced rainfall amount decreases soil CO<sub>2</sub> flux in a grassland ecosystem. *Global Change Biology* 11, 322-334.
- Hayes DC and Seastedt TR (1987) Root dynamics of tallgrass prairie in wet and dry years. *Canadian Journal of Botany* 65 (4): 787-791.
- Huang BR and Fu JM (2000) Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying. *Plant and Soil* 227 (1-2): 17-26.
- Huang XM, Lakso AN, and Eissenstat DM 2005 Interactive effects of soil temperature and moisture on Concord grape root respiration. *Journal of Experimental Botany* 56, 2651-2660.
- Huxman T E, Cable J M, Ignace D D, Eilts J A, English N B, Weltzin J, and Williams D G 2004a Response of net ecosystem gas exchange to a simulated precipitation

pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141, 295-305.

Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, and Schwinning S 2004b Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141, 254-268.

IPCC, Climate Change 2001 The Scientific Basis. Cambridge University Press, Cambridge.

Li X., Miller, A E, Meixner T, Schimel J, Melack J M, and Sickman J O. Incorporating the mechanism of the rewetting pulse into a biogeochemical model, *Global Change Biology in review*.

Lloyd J and Taylor J A 1994 On the temperature dependence of soil respiration. *Functional Ecology* 8, 315-323.

Loik M E, Breshears D D, Lauenroth W K, and Belnap J 2004 A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141, 269-281.

Martinez F, Lazo YO, Fernandez-Galiano JM, and Merino J 2002 Root respiration and associated costs in deciduous and evergreen species of *Quercus*. *Plant Cell and Environment* 25, 1271-1278.

McLean MA and Huhta V 2000 Temporal and spatial fluctuations in moisture affect humus microfungus community structure in microcosms. *Biology and Fertility of Soils* 32, 114-119.

- Mikha MM, Rice CW, and Miliken GA 2005 Carbon and nitrogen mineralization as affected by drying and wetting cycles. *Soil Biology and Biochemistry* 37, 339-347.
- Nguyen C 2003 Rhizodeposition of organic C by plants: mechanisms and controls. *Agronomie* 23, 375-396.
- Noy-Meir I 1973 Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25-51.
- Olsson P, Linder S, Giesler R, and Hogberg P 2005 Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. *Global Change Biology* 11, 1745-1753.
- Pavao-Zuckerman MA, Cable J, Yopez E, Potts DL, Huxman TE, Williams D. Plant species cover mediates soil community and ecosystem carbon cycling responses to altered precipitation regimes (*in preparation* for *Global Change Biology*).
- Pearcy R W, Ehleringer J, Mooney H A, and Rundel P W 1990 *Plant Physiological Ecology: Field Methods and Instrumentation*. Chapman and Hall, London. 457pp.
- Kozlowski TT and Pallardy SG 1997 *Growth Control in Woody Plants*. Academic Press. 641pp.
- Peek MS, Leffler AJ, Ivans CY, Ryel RJ, and Caldwell MM (2005) Fine root distribution and persistence under field conditions of three co-occurring Great Basin species of different life form. *New Phytologist* 165 (1): 171-180.

- Reynolds J F, Kemp P R, and Tenhunen J D 2000 Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: A modeling analysis. *Plant Ecology* 150, 145-159.
- Reynolds JF, Kemp PR, Ogle K, and Fernandez RJ 2004 Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141, 194-210.
- Rochette P, Desjardins R L, and Pattey E 1991 Spatial and temporal variability of soil respiration in agricultural fields. *Canadian Journal of Soil Science* 71, 189-196.
- Sala OE and Lauenroth WK 1982 Small rainfall events: An ecological role in semiarid regions. *Oecologia* 53, 301-304.
- Sala O E, Lauenroth W K, and Parton W J 1982 Plant recovery following prolonged drought in a shortgrass steppe. *Agricultural Meteorology* 27, 49-58.
- Sala O E, Lauenroth W K, and Parton W J 1992 Long-term soil water dynamics in the shortgrass steppe. *Ecology* 73, 1175-1181.
- Schwinning S and Ehleringer JR 2001 Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology* 89, 464-480.
- Schwinning S, Davis K, Richardson L, and Ehleringer JR 2002 Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia* 130, 345-355.
- Schwinning S and Sala OE 2004 Hierarchy of responses to resource pulses in and semi-arid ecosystems. *Oecologia* 141 (2): 211-220.

- Schwinning S, Sala OE, Loik ME, and Ehleringer JR 2004 Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141, 191-193.
- Schlesinger W H, Reynolds J F, Cunningham G L, Huenneke L F, Jarrell W M, Virginia R A, and Whitford W G 1990 Biological feedbacks in global desertification. *Science* 247, 1043-1048.
- Schlesinger W H 1997 *Biogeochemistry: An analysis of global change*. Academic Press, New York. 588pp.
- Skopp J, Jawson M D, and Doran J W 1990 Steady-state aerobic microbial activity as a function of soil-water content. *Soil Science Society of America Journal* 54, 1619-1625.
- Steenwerth KL, Jackson LE, Calderon FJ, Scow KM, and Rolston DE 2005 Response of microbial community composition and activity in agricultural and grassland soils after a simulated rainfall. *Soil Biology and Biochemistry* 37, 2249-2262.
- Tang J W and Baldocchi D D 2005 Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. *Biogeochemistry* 73, 183-207.
- Tang JW, Baldocchi DD, Xu L (2005) Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology* 11 (8): 1298-1304.
- Turnbull MH, Whitehead D, Tissue DT, Schuster WSF, Brown KJ, and Griffin KL 2001 Responses of leaf respiration to temperature and leaf characteristics in three

deciduous tree species vary with site water availability. *Tree Physiology* 21, 571-578.

Weltzin J F and McPherson G R 2003 Predicting the response of terrestrial ecosystems to potential changes in precipitation regimes. *In: Changing Precipitation Regimes and Terrestrial Ecosystems*. Eds J F Weltzin and G R McPherson. pp 3-8. University of Arizona Press, Tucson.

Weltzin J F and Tissue D T 2003 Resource pulses in arid environments – patterns of rain, patterns of life. *New Phytologist* 157, 171-173.

Yan SG, Wan CG, Sosebee RE, Wester DB, Fish EB, and Zartman RE 2000 Responses of photosynthesis and water relations to rainfall in the desert shrub creosote bush (*Larrea tridentata*) as influenced by municipal biosolids. *Journal of Arid Environments* 46, 397-412.

Zhang QH and Zak JC 1998 Effects of water and nitrogen amendment on soil microbial biomass and fine root production in a semi-arid environment in West Texas. *Soil Biology and Biochemistry* 30, 39-45.

### Figure legends

Figure 1. The change in soil moisture (volumetric water content) throughout the pulse period; the pulse was applied on day 0 (not shown). The errors bars are one standard error,  $n = 5$  per treatment. The following convention for symbols will be the same for all figures unless otherwise noted. Triangles are the 0mm prepulse treatment, and circles are the 15mm prepulse treatment. Different colored symbols represent the target pulse treatments: white (0mm target pulse), grey (5mm target pulse), and black (15mm target pulse). The main effect on soil moisture is from pulse size but prepulse treatment was not significant.

Figure 2. The effects of pulse size and preconditioning pulse on soil respiration. The 4am data are presented here because the trends are the same for 2pm soil respiration. The main effect was an interaction between pulse day and pulse size, where respiration peaked on day 1 post-pulse and rates increased with increasing pulse size. The errors bars are one standard error,  $n = 5$  per treatment.

Figure 3. (3a) The effect of soil moisture on soil respiration (4am and 2pm). Data for the entire pulse period are included. The main result is that wetter soil is correlated with higher respiration rates and the difference between the 4am and 2pm results are likely due to the covariation of moisture and temperature. For 4am data,  $R^2 = 0.50$ ,  $y = 0.61x - 2.16$ ,  $p < 0.0001$ ; and for 2pm date,  $R^2 = 0.45$ ,  $y = 0.93x - 1.9$ . (3b) Higher soil temperature

(2cm deep) is correlated with lower respiration rates at 2pm ( $R^2 = 0.44$ ,  $y = 47.0 + 2.0x - 0.02x^2 - 47.02$ ,  $p < 0.0001$ ). The errors bars are one standard error,  $n = 5$  per treatment.

Figure 4. The response of predawn water potentials to precipitation pulse size and preconditioning pulse. Less negative values indicate less water stress. (4a) The response of predawn leaf water potential with no preconditioning ('prepulse' in the figure) pulse to different target pulse sizes. The plants that received the 15mm target pulse sustained higher leaf water status until day 7. The trend matches the photosynthesis values. (4b). The response of predawn water potential with a 15mm preconditioning pulse to different target pulse sizes. The water potentials are higher (less negative) on average are higher than plants that did not receive a preconditioning pulse. The temporal trends for the 5mm and 15mm target pulses are similar.

Figure 5. The effect of preconditioning water treatment on leaf respiration. Pulse size data were grouped because of statistical similarity. Following the 15mm preconditioning treatment, leaf respiration was highest on day 1 post pulse, ( $F_{1,17} = 3.81$ ,  $p = 0.06$ ).

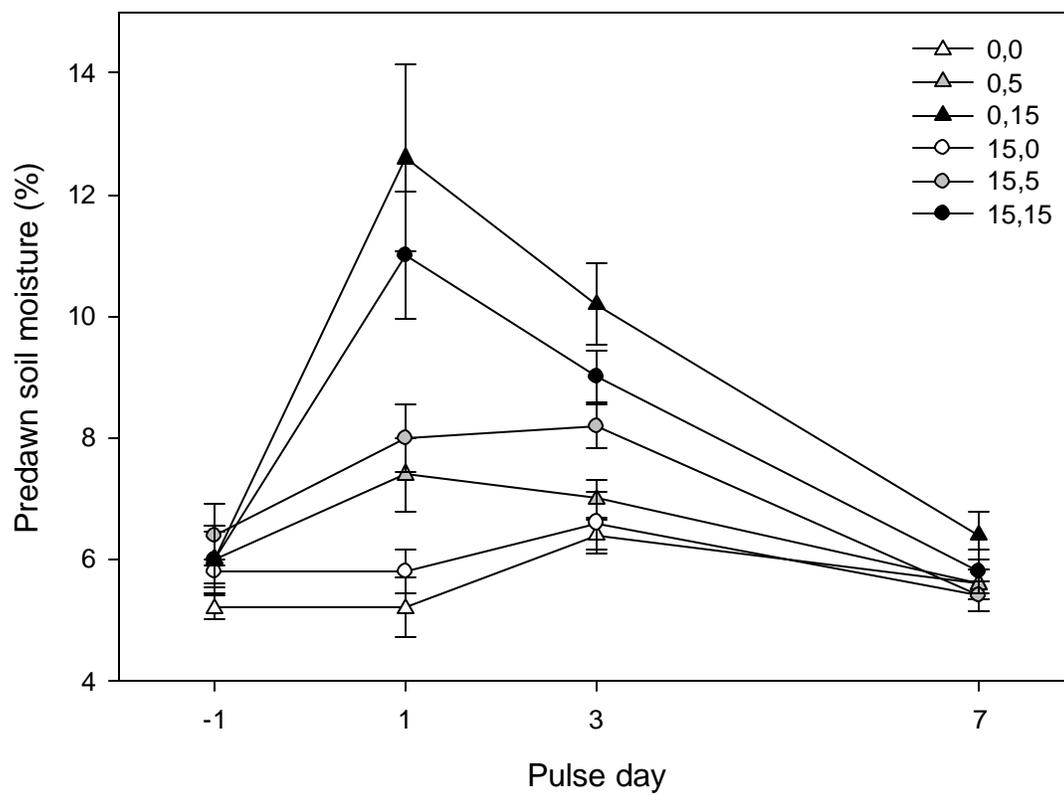
Figure 6. The effect of pulse size and preconditioning pulse on photosynthesis at 2pm. The data were combined for graphical representation on day -1 (5a and 5b) because the plants had low leaf area and made it difficult to measure. (6a). The absence of a preconditioning treatment resulted in longer duration of high photosynthetic activity

following the 15mm target pulse. (6b) A 15mm preconditioning treatment resulted in a shift in the photosynthetic response to the 15mm target pulse, with lower day 1 rates.

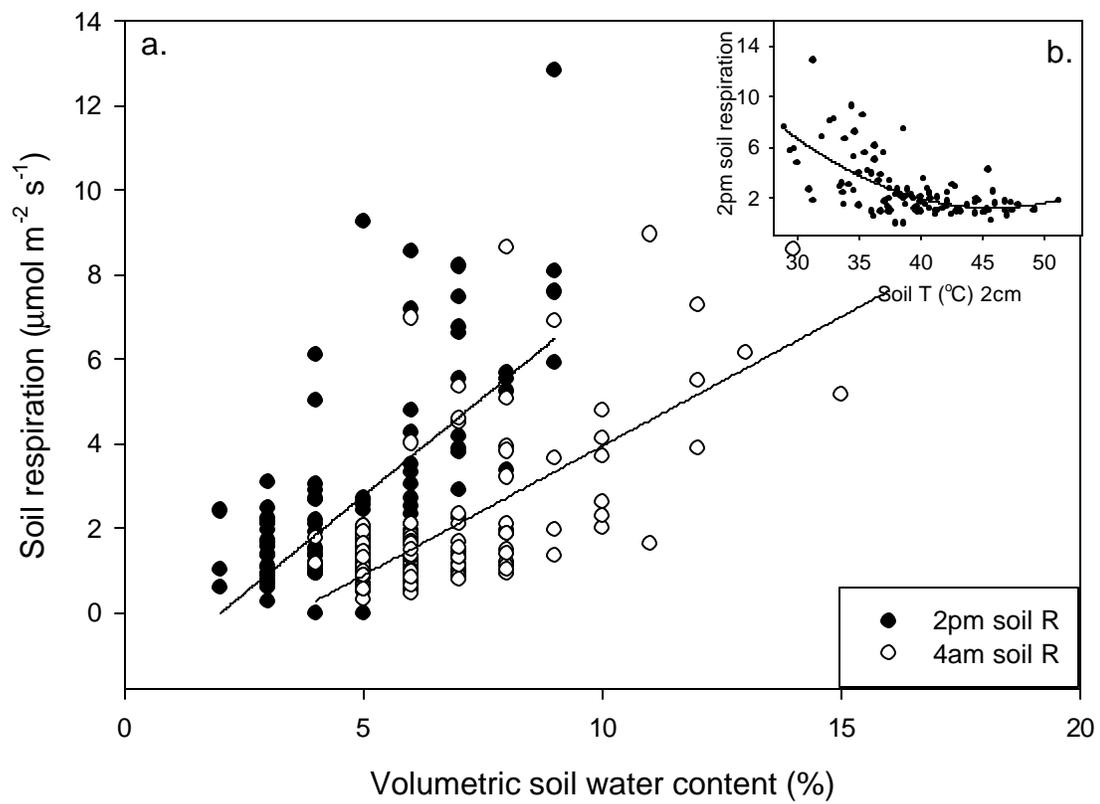
Figure 7. The effect of the preconditioning pulse on day 1 (peak day) photosynthetic responses to 5mm and 15mm target pulses. The 15mm preconditioning water treatment reduced the photosynthetic response to the 15mm target pulse. Asterisks denote statistical differences at  $p < 0.05$ . Grey bars are plants that received a 15mm preconditioning pulse, and hashed bars represent plants that received a 15mm target pulse.

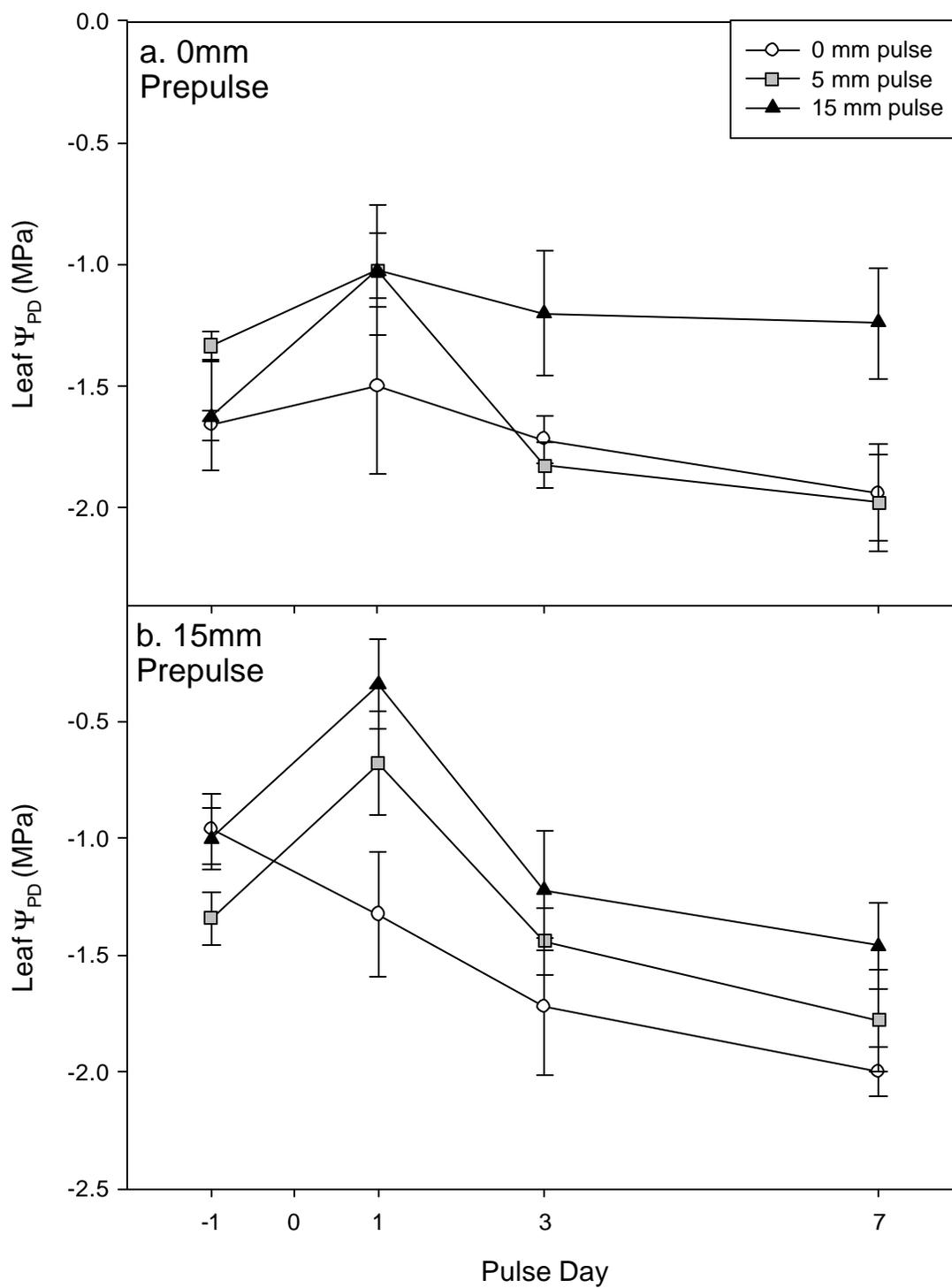
Figure 8. Preconditioning pulse effect on rhizosphere respiration throughout the pulse period. In the absence of a preconditioning treatment, rhizosphere respiration was higher on day 3 after the target pulses were applied. The effect of pulse size was not statistically significant so these data were grouped for graphical representation.

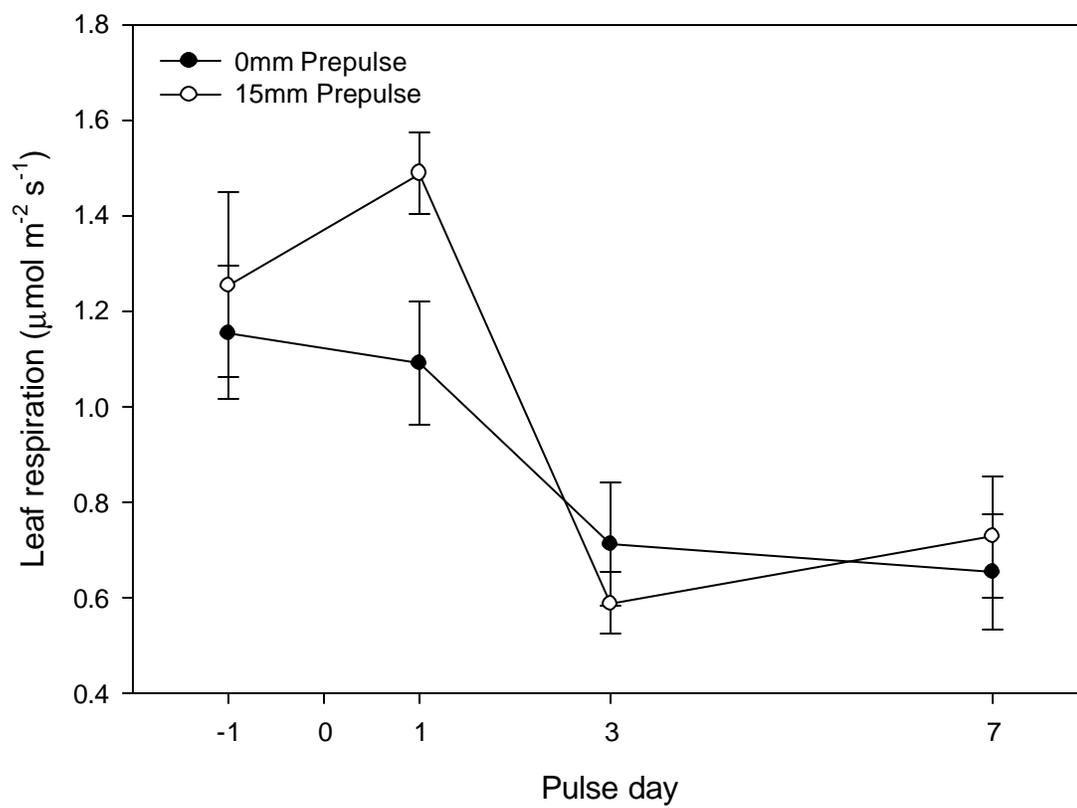
Figures

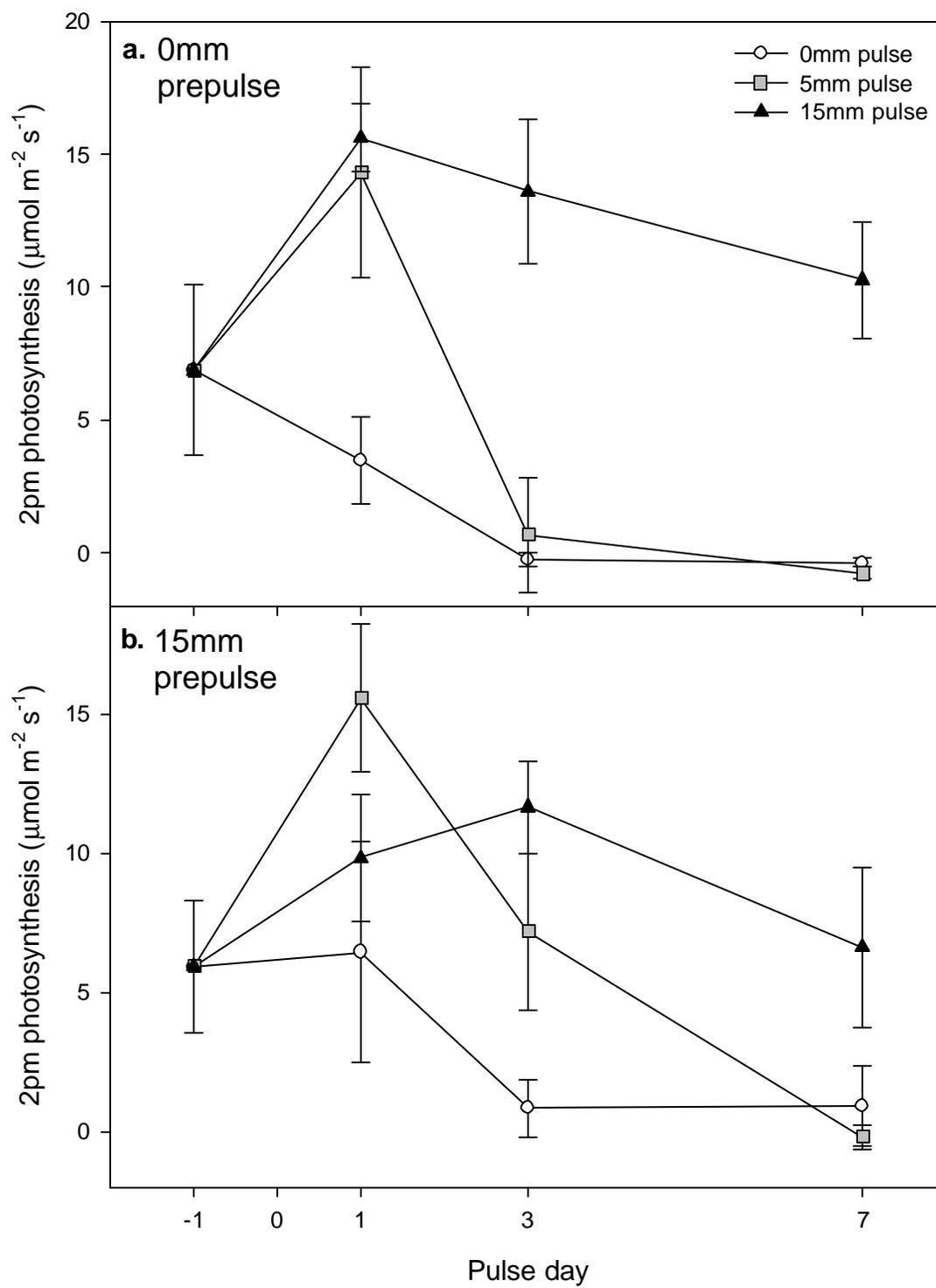


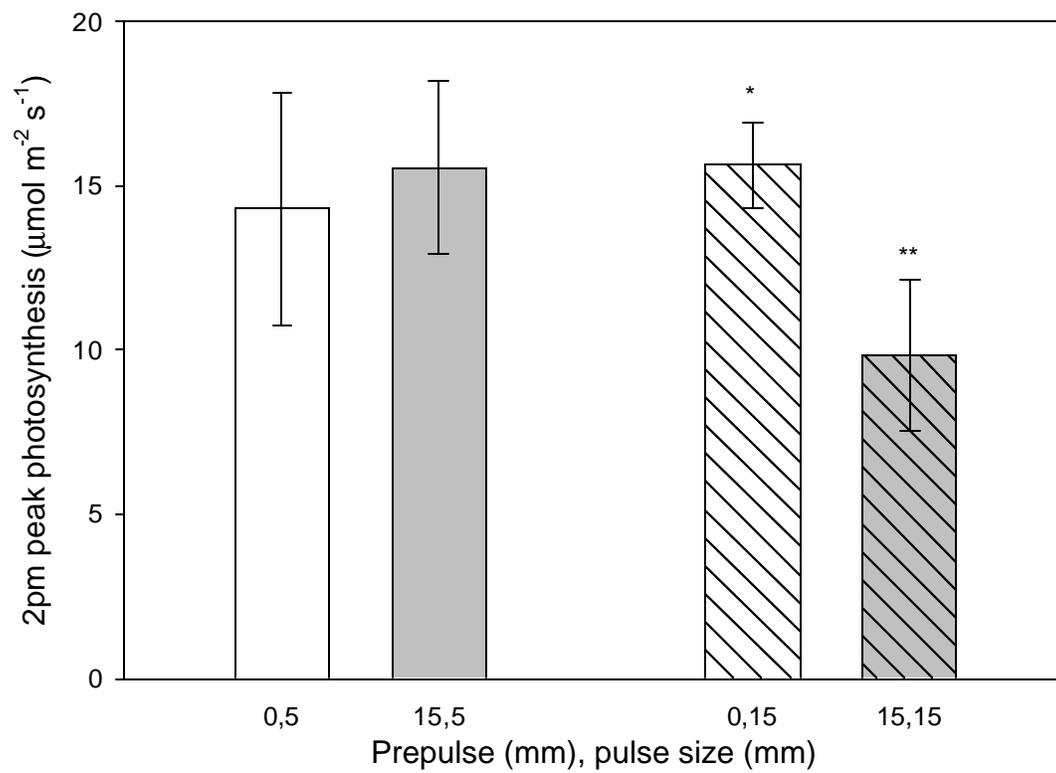


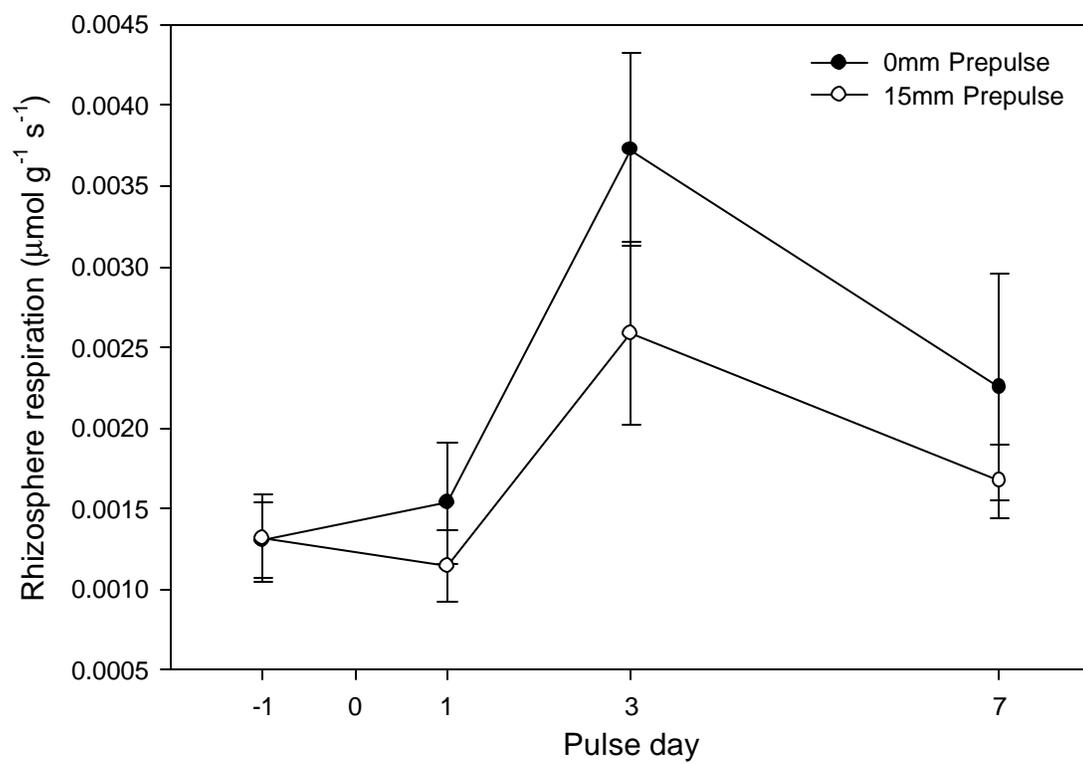












## APPENDIX D

PRECIPITATION PULSE EFFECTS ON SOIL RESPIRATION IN SEMI-ARID  
ECOSYSTEMS: THE ROLE OF WOODY PLANT ENCROACHMENT

Jessica M. Cable, Daniel L. Potts, William L. Cable, Mitchell Pavao-Zuckerman, Evan  
Lu, Russell L. Scott, David G. Williams, and Travis E. Huxman

**Abstract**

In semi-arid savannas, the relative proportion of herbaceous to woody plants affects nutrient distribution and soil microclimate, two key drivers of soil respiration. This makes vegetation change a potentially important factor in soil carbon cycling. In this study, we ask how shrub and grass microsites affect the response of soil respiration to precipitation in the context of woody plant encroachment. In southeastern Arizona, USA, we measured soil CO<sub>2</sub> efflux in five microsites created by the vegetation cover at a site co-dominated by the C<sub>3</sub> shrub *Prosopis velutina* shrubs (mesquite) and the C<sub>4</sub> bunchgrass *Sorobolus wrightii* (sacaton). The microsites were located to represent a gradient in nutrients and microclimates - ranging from open inter-canopy space (hot, dry, low soil carbon and nitrogen pools) to beneath large mesquite shrubs (cool, wet, high soil C and N pools), with intermediate microsites created by grass and medium-sized mesquite. We found that soil CO<sub>2</sub> efflux similarly responds to rainfall inputs for both open, intercanopy spaces and beneath medium-sized shrubs. The largest response of soil CO<sub>2</sub> efflux following rainfall was from soil near the trunks of large shrubs. The loss of CO<sub>2</sub> to the atmosphere from beneath grasses was intermediate in magnitude between the open areas/medium shrubs and large shrubs. These results suggest that during the transition from grasslands to mesquite shrublands, the sensitivity of respiratory processes in soils to precipitation initially decreases due to the loss of grass microsites, and is followed by a recovery of sensitivity to rainfall as woody plants mature. This non-linearity suggests we need to focus on how vegetation change and precipitation change may interactively affect soil carbon cycling.

**Key words:** mesquite, shrub islands, microclimate, litter, grassland

## **Introduction**

In desert ecosystems, soil physiological processes, such as respiration from microbial activity, rapidly respond to precipitation because increases in soil moisture bring microbes out of dormant states (Borken et al. 1999, Davidson et al. 2000, Austin et al. 2004). Spatial and temporal variation in soil processes arises from the interaction of climate (precipitation and temperature) with ecosystem vegetation structure (functional type). Patchy distributions of plants affect spatial patterns of soil microbial activity through microclimate and litter (Schlesinger et al. 1996). The timing and magnitude of rainfall events determine variation in soil moisture and the hierarchical response of ecosystem components (Huxman et al. 2004). Thus, the effect of precipitation on soil processes likely depends on the spatial and temporal interaction between soil moisture, temperature, and nutrient availability, all of which can vary with ecosystem vegetation structure (Lloyd and Taylor 1994, Martens et al. 2000, Rustad 2001, Austin et al. 2004) and seasonal patterns of precipitation.

Soil moisture promotes plant production, which provides substrates for microbial activity, resulting from decomposition of labile carbon of plant litter, fine roots, and root exudates (Raich and Schlesinger 1992, Raich et al. 2002, Townsend et al. 1997, Trumbore 2000, Janssens et al. 2001). Soil moisture also increases nutrient availability for microorganisms by promoting microbial biomass turnover (Austin et al. 2004, Saetre

and Stark 2005). Rapid changes in soil moisture determine microbial community size and activity due to differences in the sensitivity of microbial species to water status (Schimel et al. 1999). However, it is unclear how temperature confounds the respiratory response to precipitation (Borken et al. 1999, Conant et al. 1998, Conant et al. 2004).

Variation in soil moisture is a function of the timing, sequence and magnitude of rainfall events likely influencing soil carbon cycling (Huxman et al. 2004). Small events are not accessible for plants, and drive microbial respiration (Freckman et al. 1987, Schwinning and Sala 2004, Scott et al. 2004), whereas large events have the added contribution of plant activity (Golluscio et al. 1998). In general, desert ecosystem activity increases with larger rainfall events (Loik et al. 2004). Clusters of rainfall events from storm systems may be more important in driving biological activity than individual events (Reynolds et al. 2004). Seasonality of rainfall events is also important, where higher evaporative demand in the summer results in less infiltration and a smaller proportional response of vegetation growth to compared to winter precipitation, depending on plant rooting depth (Loik et al. 2004). However, summer rains can still affect whole ecosystem function because soil microbial activity increases following soil wetting, contributing significantly to ecosystem carbon loss (Saetre and Stark 2005, Huxman et al. 2004). Precipitation pulse effects on ecosystem carbon cycling also depend on antecedent soil moisture conditions, which relates to both the timing and magnitude of rain events (Loik et al. 2004). If a soil is already moist from clusters of rainfall events, further wetting may alter the response from plant and soil components

(Freckman et al. 1987, Schwinning and Sala 2004); emphasizing the importance of understanding the role of seasonal precipitation.

Through changes in soil microclimate and litter, plants of different functional types alter soil moisture, temperature, and substrate availability for microbial activity (Raich and Tufekcioglu 2000, Mungai et al. 2005, Concilio et al. 2005). Such variation in ecosystem vegetation structure is often a function of the relative abundance of herbaceous and woody plants. Throughout water-limited regions of the world, a shift from native grasslands to shrublands has been occurring (Buffington and Herbel 1965, Archer et al. 1988). In the southwestern U.S., grazing by cattle and alterations in fire regimes have fueled the expansion of mesquite (*Prosopis spp*) into many historic grasslands (Buffington and Herbel 1965, Archer et al. 1988, Brown and Archer 1989, Archer 1989, Van Auken 2000). Shrub encroachment concentrates soil nutrients into fertility islands by the accumulation of high quality litter under shrub canopies (Garcia-Moya and McKell 1969, Schlesinger et al. 1996, Paruelo and Lauenroth 1996, Schlesinger and Pilmanis 1998, Cross and Schlesinger 1999). Mesquites are legumes with high litter nitrogen, which increases the decomposability (Austin et al. 2004), compared to grass litter. The litter effect of mesquite may strongly influence microbial activity in these microsites. The fertile island effect also occurs through soil microclimate, where heterogeneity of temperature and soil moisture is increased (Breshears et al. 1998, Stoyan et al. 2000, McLain and Martens 2006). These effects likely vary with plant size, where factors such as precipitation interception by canopies may affect the distribution of soil moisture (Huxman et al., 2004).

In this study, we asked how soil microclimate and litter interact to affect the response of soil respiration to precipitation during the growing season. To address this, we made replicated measurements of soil respiration, moisture, and temperature along gradients in microclimate and litter created by the differences in woody plant and grass plant canopies. We partitioned the gradient into five microsites created by open spaces, and canopies of grass and different sized / aged shrubs. In this study, microclimate effects are canopy effects on soil temperatures and soil moisture from shading and rain interception. Litter effects are the change in quality or quantity with plant size / type. Thus, we hypothesize that respiration in open spaces will have the lowest rates after rainfall and respiration beneath mesquites, near the canopy edge, will have the highest rates.

## **Methods**

*Site description* – Measurements were made near Upper San Pedro River Basin in southeastern Arizona, near Sierra Vista, at an elevation of 1200 m (Scott et al. 2004; Scott et al., 2006). Mean summer temperature is 26°C and the climate is semi-arid with a mean annual rainfall of 350 mm. Rainfall occurs bimodally, with 60% falling during the monsoon (June to September) (Scott et al. 2004). Measurements were made in a medium dense shrub-grass ecosystem with a mix of velvet mesquite (*Prosopis velutina*) (1 to 4.5 m tall) and sacaton bunchgrass (*Sporobolus wrightii*), with canopy cover ranging from 30-60% (Scott et al. 2006). Medium sized mesquites are 1.5 – 3 m tall and large

mesquites are greater than 3 m tall. Intercanopy spaces are greater than approximately 0.5 m from the drip line of any plant canopy. This research site is equipped with an eddy covariance system measuring ecosystem level CO<sub>2</sub> and H<sub>2</sub>O exchange, basic meteorological sensors, and water content probes over a profile of 5 to 100 cm (see Scott et al., 2006 for further details).

Soil respiration – *in situ* measurements

Replicate soil collars (PVC, 10cm diameter) were installed into the soil (5 cm deep) beneath five medium-sized mesquite, five sacaton bunchgrass, in three open spaces, and beneath five large mesquite (paired collars, five within 50 cm of the trunk and 5 within 25 cm of the canopy edge), within a 20 m radius of the eddy covariance tower. Measurements of soil CO<sub>2</sub> flux were made with a closed loop static chamber system from 8 am to 9:30 am (MST) at about bi-weekly intervals from June 2, 2005 to October 2, 2005. A white 3L PVC (polyvinyl chloride) lid was fitted tightly upon soil collars 10.16 cm in diameter. The lid formed a closed loop system with a LI-820 IRGA (LiCOR Inc., Lincoln, NE, USA), where air was drawn from the lid through a LI-820 and then returned to the chamber with a pump (0.8L/min flow rate). The lid was fitted with 2.5-mm wide, 25 mm long capillary tubing vented to atmosphere to relieve pressure differentials (Hutchinson and Mosier 1981; Davidson et al., 2002). A 4.5-V microfan provided mixing of air within the cylinder. Measurements were logged every second for 2 minutes on a laptop computer interfaced with the IRGA. Within 10 cm of the soil collars, concurrent measurements of chamber air temperature, soil temperature integrating from

the surface to 2 cm and 12 cm (DiGi-Sense, Eutech Instruments, Vernon Hills, IL, USA) and soil moisture (volumetric water content, %, CS620 HydroSense, Campbell Scientific, Inc, Logan, UT) integrating from the surface to 12 cm were made. Three measurements of soil moisture were averaged for per collar to account for spatial heterogeneity of soil water. The CO<sub>2</sub> concentration data were converted to flux density with volume/area corrections (Pearcy et al., 1990). Precipitation data were collected with a tipping bucket rain gauge (TE525, Texas Electronics) on the eddy covariance tower.

Soil respiration – root-free incubations

Two soil cores to a depth of 10 cm were taken from 25 randomly selected areas at the study area – focusing on the five micro-sites (i.e. grass, inter-canopy, small mesquite, near the trunk and canopy edge of big mesquite). Roots were removed by hand following transport to the laboratory. Each soil core was placed in a 5.1 cm diameter, 25 cm deep PVC pipe with one open end. Then 10 mL of water was added to half of the tubes and the remaining were left dry. These tubes of soil were placed in a growth chamber and CO<sub>2</sub> flux was measured following a short period of acclimation using the same techniques as in the field. Fluxes were measured at 15 °C, 25 °C, 35 °C, and 45 °C in order to replicate the temperature range seen in the field over the course of the season. Samples were held at a constant temperature for greater than 2 hours, beginning at 15°C, measurements were made, and then the chamber temperature was increased to the next value. The CO<sub>2</sub> concentration data were converted to flux density with volume/area corrections (Pearcy et al., 1990), and an ANOVA was used to determine the difference

between the means of flux rates between the wet and the dry cores. To determine how respiration responded to temperature,  $Q_{10}$  values were calculated for each 10°C increment (Eq. 1).

$$Q_{10} = (R_2 / R_1)^{10 / (T_2 - T_1)} \quad \text{Eq. 1}$$

where  $R_1$  and  $R_2$  are the respiration rates at temperatures  $T_1$  and  $T_2$ , respectively.

## Results

### Soil moisture and temperature

The 2004 monsoon season began on July 18<sup>th</sup> (National Weather Service) in southern Arizona. We recorded rainfall at our research site on July 16<sup>th</sup> and consistently wet periods lasted through September 19<sup>th</sup> (Figure 1a). Total precipitation in this period was 235 mm. Soil temperatures at both depths did not differ within each microsite, but microsites had different temperature regimes throughout the study period. Surface temperatures were lowest beneath the large mesquite (mean 22.9°C +/- 0.26 near trunk and 23.4°C +/- 0.30 canopy edge) and the bunchgrass (mean 23.4°C +/- 0.34), highest in the open space (mean 27.5°C +/- 0.83), and intermediate under the medium mesquite (mean 24.9°C +/- 0.47) ( $F_{4,315} = 17.9790$ ,  $p < 0.0001$ ;  $F_{4,315} = 8.3577$ ,  $p < 0.0001$ , respectively). Despite day-to-day variation in soil moisture across all sites within the season, microsites did not differ in their season-average soil moisture values (Figure 1b).

### Soil respiration

Overall, rates of CO<sub>2</sub> efflux near the trunk of the large mesquite shrubs (season mean 5.0 μmol m<sup>-2</sup> s<sup>-1</sup> +/- 0.39) were 60% greater than the other microsites combined. Respiration from beneath the large mesquite near the canopy edge and beneath the sacaton grass were similar (season combined mean 3.64 μmol m<sup>-2</sup> s<sup>-1</sup> +/- 0.23), and rates from beneath the medium mesquite and in open spaces were the lowest (season combined mean 2.43 μmol m<sup>-2</sup> s<sup>-1</sup> +/- 0.15) ( $F_{4,247} = 48.0392$ ,  $p < 0.0001$ ). From July 19<sup>th</sup> to September 6<sup>th</sup>, mean respiration rates (5.2 μmol m<sup>-2</sup> s<sup>-1</sup> +/- 0.17) were 75% greater compared to pre- and post-monsoon rates ( $F_{13,247} = 174.1893$ ,  $p < 0.0001$ , Figure 1c). Mean soil moisture from July 26<sup>th</sup> through September 6<sup>th</sup> (16.4% +/- 0.4) was 75% higher than in the pre- and post-monsoon periods ( $F_{13,306} = 181.4597$ ,  $p < 0.0001$ ).

The effect of soil temperature on rates of CO<sub>2</sub> efflux was not as strong as volumetric soil moisture content ( $R^2 = 0.005$ ,  $R^2 = 0.38$ , respectively). The interactive effects of microsite and soil moisture explained 49% of the variation in respiration ( $F_{1,295} = 6.6673$ ,  $p = 0.0103$ ). Despite similar soil moisture levels across microsites, the sensitivity of respiration to moisture differed, suggesting that resource pool sizes control the response of respiration to precipitation. For a given soil temperature, the sensitivity of respiration to soil moisture varied, where the slopes and confidence intervals from respiration beneath large mesquite and sacaton were the most sensitive to increases in soil moisture (Table 1). For a given soil temperature, soil moisture explained the most variation in respiration beneath large mesquite (Table 1, Figure 2).

### Root-free Soil Incubations

Wet soil respiration was between 63% and 67% times greater than dry soil respiration at 25, 35, and 45°C incubation temperatures (25°C:  $F_{1,48} = 33.2517$ ,  $p < 0.0001$ ; 35°C:  $F_{1,48} = 38.0366$ ,  $p < 0.0001$ ; 45°C:  $F_{1,48} = 70.1706$ ,  $p < 0.0001$ ).

Interestingly, for each microsite, the percent increase in respiration with soil wetting was similar for all incubation temperatures. The exception to this was in the 15°C incubations, where the sacaton soil had a negative response to wetting (decline of 80% +/- 0.16 in rates) and the medium and large mesquite soil had the largest increase (increase in rates: 48% medium mesquite, 62% near the large mesquite trunk, and 73% near the large mesquite canopy edge). The open spaces had a 2% increase in respiration ( $F_{4,20} = 14.5015$ ,  $p < 0.0001$ ) (Figure 3).

For comparison to the incubations, we compared *in situ* measurements of soil respiration on one day prior to the monsoon (dry soil) to one day just following the onset of the monsoon (wet soil). Dry soil respiration was nearly identical for all microsites, and CO<sub>2</sub> efflux was 60% times greater during the monsoon (mean  $3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  +/- 0.09) ( $F_{1,252} = 299.1957$ ,  $p < 0.0001$ ). In particular, respiration increased to the greatest extent for the large mesquite (mean  $4.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  +/- 0.28), to a similar extent for the medium mesquite and sacaton ( $3.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  +/- 0.17), and to the least for the open spaces ( $2.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  +/- 0.15) ( $F_{4,91} = 8.8017$ ,  $p < 0.0001$ ). In the root-free cores, the response of respiration to wetting (e.g. the increase in respiration from dry to wet soil conditions) followed a similar trend for each microsite (in the 35°C incubations) as the *in situ* results, except for soil from medium mesquite microsite. In this case, respiration

responded less to increased soil moisture in the incubations than from *in situ* measurements. These patterns suggest that roots may be a significant contributor to soil CO<sub>2</sub> efflux below medium sized mesquite canopies (Figure 3).

In dry soil conditions at incubation temperatures between 15-25°C, soil from the medium mesquite microsite had the highest Q<sub>10</sub> (7.6) ( $F_{1,20} = 14.6346$ ,  $p = 0.0011$ ). In the 25-35°C range, there were no differences in Q<sub>10</sub> values. In the 35-45°C range, the soil from the open space had the highest Q<sub>10</sub> (4.3) ( $F_{1,20} = 8.6363$ ,  $p = 0.0081$ ). In wet soil conditions, at incubation temperatures 15-25°C, soil from the medium mesquite (4.9), grass (5.0), and from open spaces (4.6) had higher Q<sub>10</sub> values than soil from the large mesquite (2.9 near trunk, 2.4 canopy edge) ( $F_{1,20} = 3.9032$ ,  $p = 0.062$ ). In the 25-35°C range, there were no differences in Q<sub>10</sub> values. In the 35-45°C range, soil from the open spaces had the highest Q<sub>10</sub> (2.0) and soil from the large mesquite had the lowest (1.2 canopy edge, 0.9 near trunk) ( $F_{1,20} = 18.2058$ ,  $p = 0.0004$ , Figure 4).

## Discussion

Vegetation change is a ubiquitous feature of global change (Neilson et al. 2005). In the arid and semi-arid regions of North American, one type of vegetation change is the encroachment or thickening of woody plant life forms into herbaceous or grass-dominated systems (Breshears 2006). How this vegetation change affects carbon cycling is an important question with large-scale ramifications (Jackson et al., 2002; Huxman et al., 2005). In this study, we evaluated patterns of CO<sub>2</sub> efflux from soils as a function of

different canopy cover locations for grass, shrub and bare-ground microsites in a semi-arid mesquite savanna. We used variation in temperature and soil moisture throughout the season, along with root-free incubations of soil respiration in the laboratory to evaluate the drivers of soil carbon cycling in this system. Because of the differential inputs of organic matter, we hypothesized that respiration in bare-ground open spaces would have the lowest response to rainfall, and respiration beneath mesquite shrubs, near the canopy edge, will have the largest response. We found that while CO<sub>2</sub> efflux rates were similar for all microsites during dry periods, the values measured near the trunks of large mesquite shrubs were the greatest throughout the summer monsoon rainfall period. There were large microsite effects with an unexpected pattern of medium-sized mesquites having efflux rates similar to that of bare-ground open spaces. The sensitivity of CO<sub>2</sub> efflux to soil moisture was greatest from beneath large mesquite and sacaton grass, and soil temperature was not as important as soil moisture as a predictive variable. Similar interactions of soil temperature and moisture have been found in other studies, where in dry periods, moisture is more constraining and respiration is less responsive to increases in temperature (Amundson et al., 1989; Conant et al. 1998; Rustad et al. 2001; Conant et al., 2004; Tang and Baldocchi 2005).

Small early monsoon rainfall events did not significantly increase soil moisture but soil respiration appeared to increase anyway. These small, early events may not have been reflected in the soil moisture measurements if wetting was isolated to the litter layer. This supports the idea of hierarchical responses of ecosystem components to rainfall (Huxman et al. 2004), because only microbial activity in the litter layer was activated by

the small rainfall events. Similarly, desert crusts respond to small rainfall events that are unavailable to other ecosystem components (Cable and Huxman 2004, Belnap et al. 2004). Small rainfall events (< 5 mm) occur the most frequently, compared to large events (Huxman et al. 2004, Reynolds et al. 2004), and thus are significant drivers of biological activity of surface organisms.

Others found that soil respiration in woody ecosystems is lower than in paired grasslands (McCarron et al. 2003, Mills and Fey 2004) as a result of lower surface soil temperatures and a decreased sensitivity of respiration to variation in temperature (Smith and Johnson 2004, McLain and Martens 2006). It has also been found that soil moisture, mineralizable soil C and N, biomass C, and root biomass did not differ between grassland and woodland ecosystems (McCarron et al. 2003, Lett et al. 2004, Smith and Johnson 2004). It is unclear if the woody plants evaluated in the above studies have symbiotic associations with nitrogen fixing bacteria. The *Prosopis* spp. in our study fixes nitrogen and the litter deposited as shrubs develop not only influences the quantity of litter inputs into the system, but the quality of that litter (e.g. Wilson and Thompson 2004, McLain and Martens 2006). Carbon rather than nitrogen limitation beneath shrubs has been shown in previous studies, where rates of nitrogen cycling depended on carbon availability (Schaeffer et al. 2003).

The unexpectedly low soil CO<sub>2</sub> efflux patterns from beneath the medium-sized mesquite shrubs have implications for carbon cycling during vegetation transitions. Combined with the greater leaf level photosynthetic rates achieved by these shrubs as compared to grass canopies throughout the summer growing season (Potts et al., in

review), these data suggest developing mesquites are significant patches of accumulating carbon. Alternatively, Hibbard et al. (2001) found that recently developed woodlands may have greater carbon and nitrogen losses than more developed woodlands. However, in our study the combination of sparse canopy development and a thin litter layer likely resulted in little soil shading and limited resources for microbes. Root-free incubations and high photosynthetic rates suggest that root activity may be a more significant contributor to soil respiration than microbial respiration. These two studies suggest that root deposition may be an important feature of change in the soil with woody plant encroachment (Hibbard et al. 2001). However, soil respiration from microbes can be a significant fraction of ecosystem CO<sub>2</sub> loss (Davidson et al. 2006).

Shrub expansion and high photosynthetic activity results in high litter deposition, which stimulates microbial respiration and alters the response of these ecosystems to rainfall (Scott et al. 2006). With further expansion of shrubs into native grasslands, at what stage of canopy development does a shrub start to affect soil processes? It appears that there may be two important thresholds, one at either end of a gradient of shrub development. Data from this study suggests that respiration from grasslands and shrublands with large mesquite have higher respiration rates than a shrubland dominated by young and small mesquite. Thus, given the changes in ecosystem scale photosynthetic processes (Scott et al., 2006), ecosystem carbon gain may be greatest in young, developing shrublands with little co-dominance by grasses.

Arid and semi-arid regions of the southwestern US are undergoing landscape scale changes in ecosystem structure and regional climate (Breshears et al. 2005). In

combination with continued woody plant expansion, precipitation patterns are predicted to shift in the southwestern US to a greater frequency of large events (Easterling et al. 2000; IPCC 2001). The response of ecosystem processes to such shifts will be affected by the change in soil carbon (Hibbard et al. 2001, Scott et al. 2006). For example, variation in ecosystem responses to rainfall may be due to the spatial variation in soil litter and microclimate affecting the response of respiration to rainfall. Gaining a mechanistic understanding of the changes in soil carbon processes with vegetation change will be important in determining how variation in other drivers of ecosystem function, such as precipitation, will affect arid and semi-arid regions.

### **Acknowledgements**

The authors thank D. Goodrich, B. Collins, N. Pierce, and K. Gilliam for project development and field support. We also acknowledge the support of SAHRA (Sustainability of semi-Arid Hydrology and Riparian Areas), under the STC program of the NSF agreement number EAR-9876800 and NSF awards DEB041-5977 and DEB041-8134.

**Literature Cited**

- Amundson R G, Chadwick O A, Sowers J M, and Doner H E 1989 Soil evolution along an altitudinal transect in the eastern Mojave desert of Nevada, USA. *Geoderma* 43, 349-371.
- Austin AT, Yahdjian L, Stark JM, Belnap J, Proporato A, Norton U, Ravetta DA, and Schaeffer SM 2004 Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221-235.
- Archer S, Scifres C, and Bassham CR 1988 Autogenic succession in a subtropical savannah: conversion of grassland to thorn woodland. *Ecological Monographs* 58(2):111-127.
- Archer S 1989 have southern Texas savannahs been converted to woodlands in recent history? *The American Naturalist* 134(4):545-561.
- Borken W, Xu Y-J, Brumme R, and Lamersdorf N 1999 A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: Drought and rewetting effects. *Soil Science Society of America Journal* 63:1848-1855.
- Breshears DD, Nyhan JE, Heil CE, and Wilcox BP 1998 Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Sciences* 159(6):1010-1017.

- Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balics RG, Romme WH, Kastens JH, Floyd ML, Belnap J, Anderson JJ, Myers OB, and Meyer CW 2005 Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America* 102(42), 15144-15148.
- Brown, J.R. and Archer, S. 1989 Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80:19-26.
- Buffington LC and Herbel CH 1965 Vegetational changes on a semidesert grassland range from 1858-1963. *Ecological Monographs* 35(2):139-164.
- Conant R T, Klopatek J M, Malin R C, and Klopatek C C 1998 Carbon pools and fluxes along an environmental gradient in northern Arizona. *Biogeochemistry* 43, 43-61.
- Conant R T, Dalla-Betta P, Klopatek C C, and Klopatek J A 2004 Controls on soil respiration in semiarid soils. *Soil Biology and Biochemistry* 36, 945-951.
- Davidson EA, Verchot LV, Cattanio JH, Ackerman IL, and Carvalho JEM 2000 Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* 48:53-69.
- Davidson EA, Savage K, Verchot LV, and Navarro R 2002 Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agricultural and Forest Meteorology* 113:21-37.

- Davidson EA, Janssens IA, and Luo YQ 2006 On the variability of respiration in terrestrial ecosystems: moving beyond Q(10). *Global Change Biology* 12, 154-164.
- Conant RT, Klopatek JM, Malin RC, and Klopatek CC 1998 Carbon pools and fluxes along an environmental gradient in northern Arizona. *Biogeochemistry* 43:43-61.
- Conant RT, Dalla-Betta P, Klopatek CC, and Klopatek JA 2004 Controls on soil respiration in semiarid soils. *Soil Biology and Biochemistry* 36(6):945-951.
- Concilio A, Ma SY, Li QL, LeMoine J, Chen JQ, North M, Moorhead D, and Jensen R 2005 Soil respiration response to prescribed burning and thinning in mixed-conifer and hardwood forests. *Canadian Journal of Forest Research* 35, 1581-1591.
- Cross AF and Schlesinger WH 1999 Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. *Plant Ecology* 145:11-25.
- Easterling D R, Meehl G A, Parmesan C, Changnon S A, Karl T R, and Mearns L O 2000 Climate extremes: Observations, modeling, and impacts. *Science* 289, 2068-2074.
- Freckman DW, Whitford WG, Steinberger Y 1987 Effect of irrigation on nematode population-dynamics and activity in desert soils. *Biology and Fertility of Soils* 3(1-2):3-10.
- Garcia-Moya E and McKell CM 1969 Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51(1):81-88.

- Golluscio RA, Sala OE, and Lauenroth WK 1998 Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia* 115, 17-25.
- Hibbard KA, Archer S, Schimel DS, and Valentine DW 2001 Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82, 1999-2011.
- Hutchinson GL and Mosier AR 1981 Improved soil cover method for field measurement of nitrous-oxide fluxes. *Soil Science Society of America Journal* 45(2):311-316.
- Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, and Schwinning S 2004 Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254-268.
- Huxman T E, Cable J M, Ignace D D, Eilts J A, English N B, Weltzin J, and Williams D G 2004b Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141, 295-305.
- IPCC, Climate Change 2001 The Scientific Basis. Cambridge University Press, Cambridge.
- Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grunwald L, Montagnani L, Dore S, Rebmann C, Moors J, grelle A, Rannik U, Morgenstern K, Oltchev S, Clement R, Gudmundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen O, Vesala T, Granier A, Schulze ED, Lindroth A, Dolman

- AJ, Jarvis PG, Ceulemans R, and Valentini R 2001 Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7:269-278.
- Lett MS, Knapp AK, Briggs JM, and Blair JM 2004 Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland. *Canadian Journal of Botany* 82, 1363-1370.
- Lloyd J and Taylor JA 1994 On the temperature dependence of soil respiration. *Functional Ecology* 8:315-323.
- Loik ME, Breshears DD, Lauenroth WK, and Belnap J 2004 A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141:269-281.
- Martens SN, Breshears DD, and Meyer CW 2000 Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. *Ecological Modeling* 126, 79-93.
- McCarron JK, Knapp A, and Blair JM 2003 Soil C and N responses to woody plant expansion in a mesic grassland. *Plant and Soil* 257, 183-192.
- McLain JEM and Martens DA 2006 Moisture controls on trace gas fluxes in semiarid riparian soils. *Soil Science Society of America Journal* 70, 367-375.
- Mills A and Fey M 2004 Transformation of thicket to savanna reduces soil quality in the Eastern Cape, South Africa. *Plant and Soil* 265, 153-163.

- Mungai NW, Motavalli PP, Kremer RJ, and Nelson KA 2005 Spatial variation of soil enzyme activities and microbial functional diversity in temperate alley cropping systems. *Biological Fertility of Soils* 42, 129-136.
- Neilson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, and Thompson K 2005 Forecasting regional to global plant migration in response to climate change. *Bioscience* 55, 749-759.
- Noy-Meir I 1973 Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25-51.
- Paruelo JM and Lauenroth WK 1996 Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecological Applications* 6(4):1212-1224.
- Pearcy R W, Ehleringer J, Mooney H A, and Rundel P W 1990 *Plant Physiological Ecology: Field Methods and Instrumentation*. Chapman and Hall, London. 457pp.
- Raich JW and Schlesinger WH 1992 The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B:81-99.
- Raich JW and Tufekcioglu A 2000 Vegetation and soil respiration: Correlations and controls. *Biogeochemistry* 48:71-90.
- Reynolds JF, Kemp PR, Ogle K, and Fernandez RJ 2004 Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141:194-210.
- Rustad L E, Campbell J L, Marion G M, Norby R J, Mitchell M J, Hartley A E, Cornelissen J H C, and Gurevitch J 2001 A meta-analysis of the response of soil

respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126, 543-562.

Rustad L 2001 Matter of time on the prairie. *Nature* 413:578-579.

Saetre P and Stark JM 2005 Microbial dynamics and carbon and nitrogen cycling following re-wetting of soils beneath two semi-arid plant species. *Oecologia* 142, 247-260.

Schaeffer SM, Billings SA, and Evans RD 2003 Responses of soil nitrogen dynamics in a Mojave Desert ecosystem to manipulations in soil carbon and nitrogen availability. *Oecologia* 134 (4), 547-553.

Schimel JP, Gullledge JM, Clein-Curley JS, Lindstrom JE, and Braddock JF 1999 Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. *Soil Biology and Biochemistry* 31:831-838.

Schlesinger WH, Raikes JA, Hartley AE, and Cross AF 1996 On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77(2):364-374.

Schlesinger WH and Pilmanis AM 1998 Plant-soil interactions in deserts. *Biogeochemistry* 42:169-187.

Schwinning S and Sala OE 2004 Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141:211-220.

Scott RL, Edwards EA, Shuttleworth WJ, Huxman TE, Watts C, and Goodrich DC 2004 Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Agricultural and Forest Meteorology* 122:65-84.

- Scott RL, Huxman TE, Williams DG, and Goodrich DC 2006 Ecohydrological impacts of woody-plant encroachment: seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment. *Global Change Biology* 12, 311-324.
- Smith DL and Johnson L 2004 Vegetation-mediated changes in microclimate reduce soil respiration as woodlands expand into grasslands. *Ecology* 85, 3348-3361.
- Stoyan H, De-Polli H, Bohm S, Robertson GP, and Paul EA 2000 Spatial heterogeneity of soil respiration and related properties at the plant scale. *Plant and Soil* 222:203-214.
- Tang J, Baldocchi D D, and Xu L 2005 Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology* 11, 1298-1304.
- Townsend AR, Vitousek PM, Desmarais DJ, and Tharpe A 1997 Soil carbon pool structure and temperature sensitivity inferred using CO<sub>2</sub> and <sup>13</sup>CO<sub>2</sub> incubation fluxes from five Hawaiian soils. *Biogeochemistry* 38:1-17.
- Trumbore S 2000 Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications* 10(2):399-411.
- Van Auken, O.W. 2000 Shrub invasions of North American semiarid grasslands. *Ann. Rev. Ecol. Syst.* 31:197-215.
- Wilson TB and Thompson TL 2005 Soil nutrient distributions of mesquite-dominated desert grasslands: changes in time and space. *Geoderma* 126, 301-315.

## Tables

Table 1. The residual variation from the relationship between soil respiration and temperature (R below) was plotted against log soil moisture (SW below). The equation of the regression (Line eqn.) is presented with the 95% confidence interval of the slopes to show the sensitivity of respiration to soil moisture. The top value is the lower CI and the bottom value is the upper CI. All regressions are significant, and the most variation is explained by soil moisture in the big mesquite microsite.

Microsite	Line eqn.	95%CI slope	R <sup>2</sup>	t(df)	p
Big Mesquite Far	R = -2.02 + 0.99 SW	0.77 1.22	0.54	t(68) = 8.85	<0.0001
Big Mesquite Near	R = -1.65 + 1.02 SW	0.8 1.25	0.55	t(67) = 9.11	<0.0001
Medium Mesquite	R = -1.67 + 0.66 SW	0.43 0.89	0.33	t(67) = 5.77	<0.0001
Sacaton	R = -1.48+ 0.81 SW - 0.38 SW <sup>2</sup>	0.61 1.02	0.50	t(64) = 7.97	<0.0001
Open Space	R = -1.40 + 0.55 SW	0.27 0.84	0.28	t(40) = 3.99	0.0003

### Figure legends

Figure 1. Precipitation, soil moisture, and soil respiration throughout the 2005 dry for-summer, monsoon, and post-monsoon periods. (1a) Precipitation (mm/day) throughout the summer season. For (1b and c), circles represent measurements from beneath large mesquite, and filled are from near the canopy edge ('far' from the trunk) and open circles are near the trunk. Squares with a dot are measurements from beneath medium sized mesquite; triangles with a dot are from beneath sacaton grass; and open diamonds are from open, inter-canopy spaces. The error bars are one standard error of the mean. (1b) Soil moisture (%) across the different microsites throughout the season. (1c) Soil respiration across the microsites throughout the season.

Figure 2. The residual variation from the relationship between respiration and soil temperature (2 cm and 12 cm) plotted against  $\ln$  soil moisture. Large mesquite near the trunk  $R^2 = 0.55$ , big mesquite far (near the canopy edge)  $R^2 = 0.54$ , sacaton  $R^2 = 0.5$  (non-linear polynomial fit), medium-sized mesquite  $R^2 = 0.33$ , and open space  $R^2 = 0.28$ . For further statistics, see Table 1.

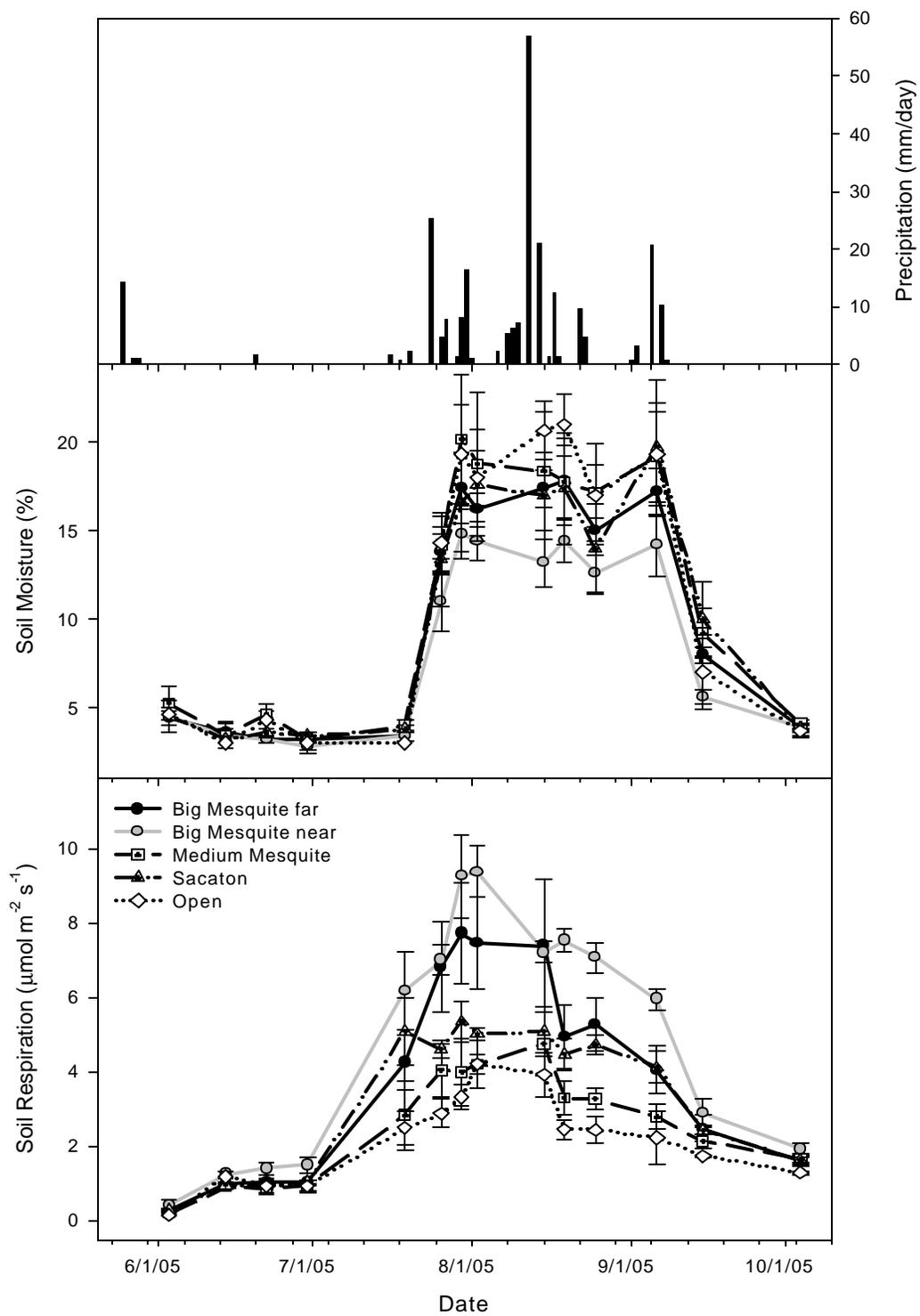
Figure 3. (Top) *In situ* measurements of soil respiration across five microsites. BM near is under large mesquite near the trunk, BM far is under large mesquite near the canopy edge, MM is under medium mesquite, grass is beneath sacaton bunchgrass, and open is in inter-canopy spaces. Wet soils are measurements taken on one day during the monsoon,

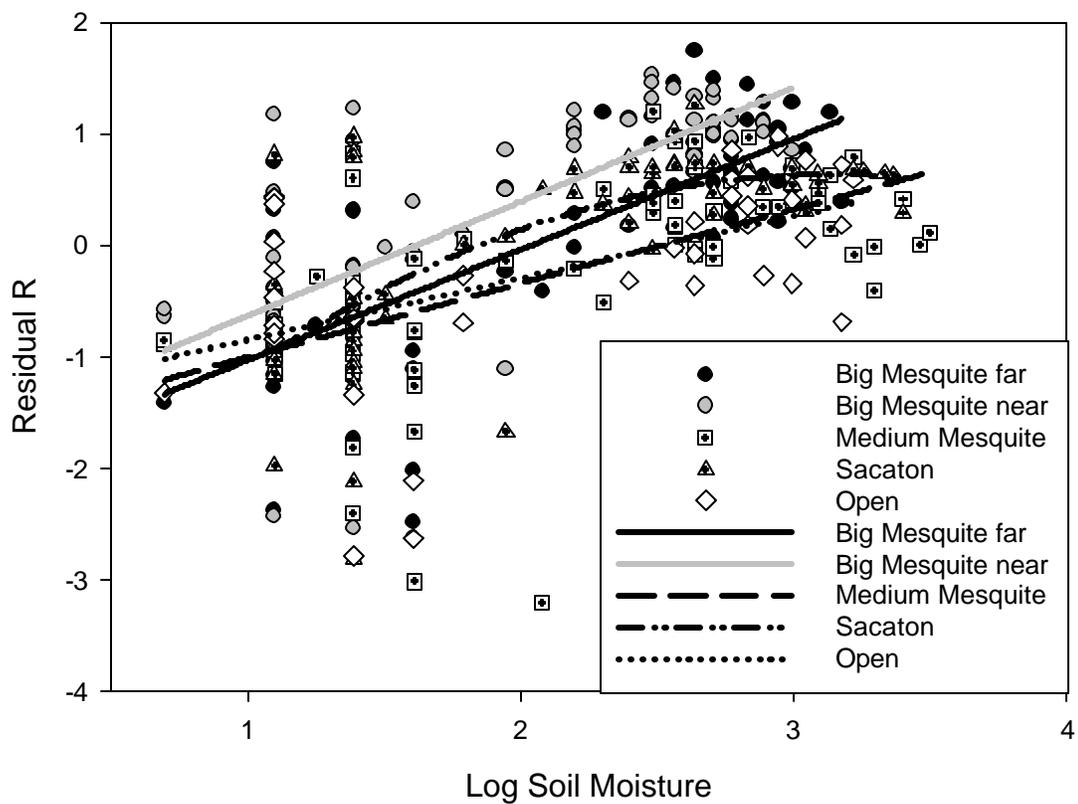
and dry soils are measurements taken on day during the dry fore-summer. (Bottom)

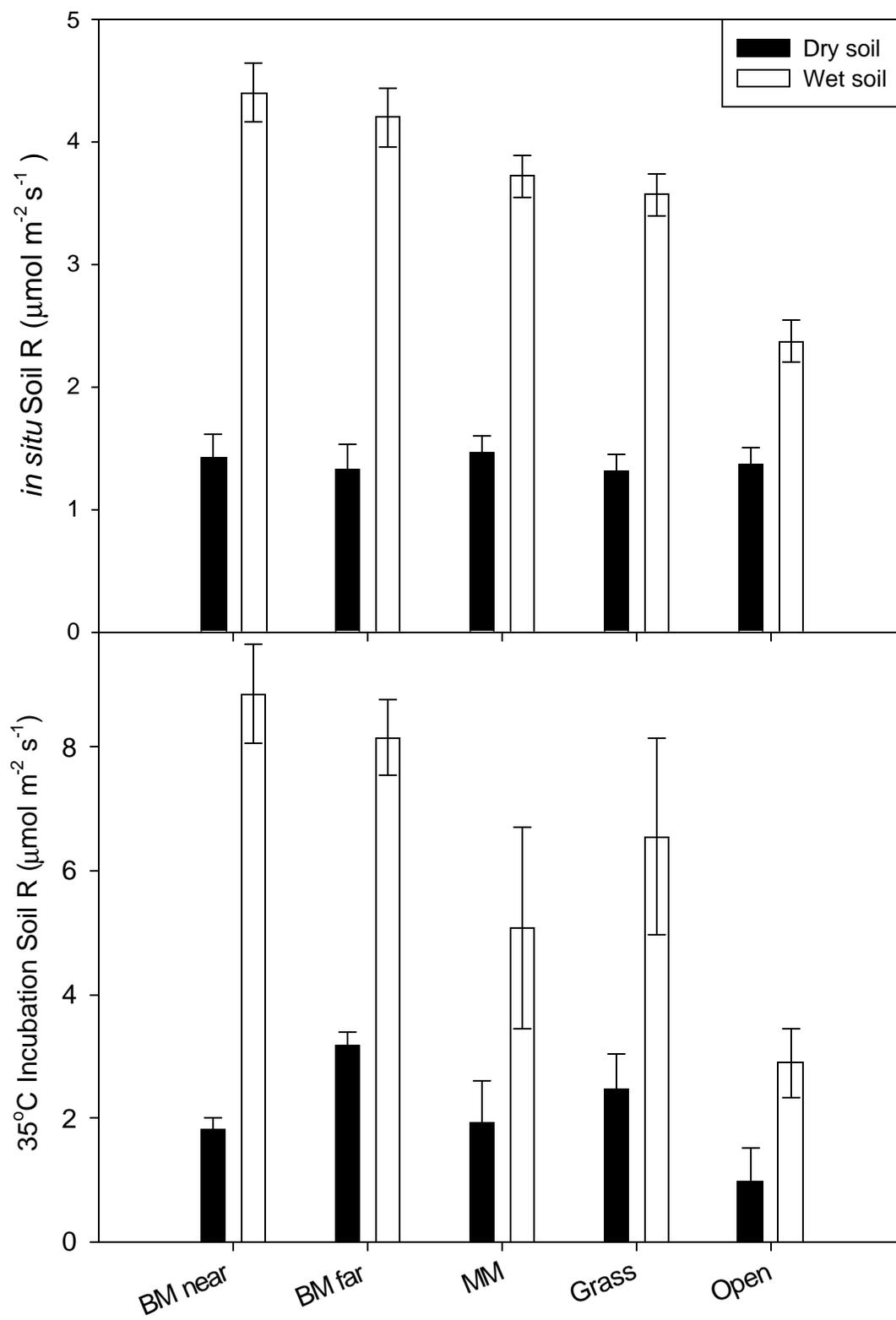
Incubation of root free wet and dry soil at 35°C for samples from each microsite.

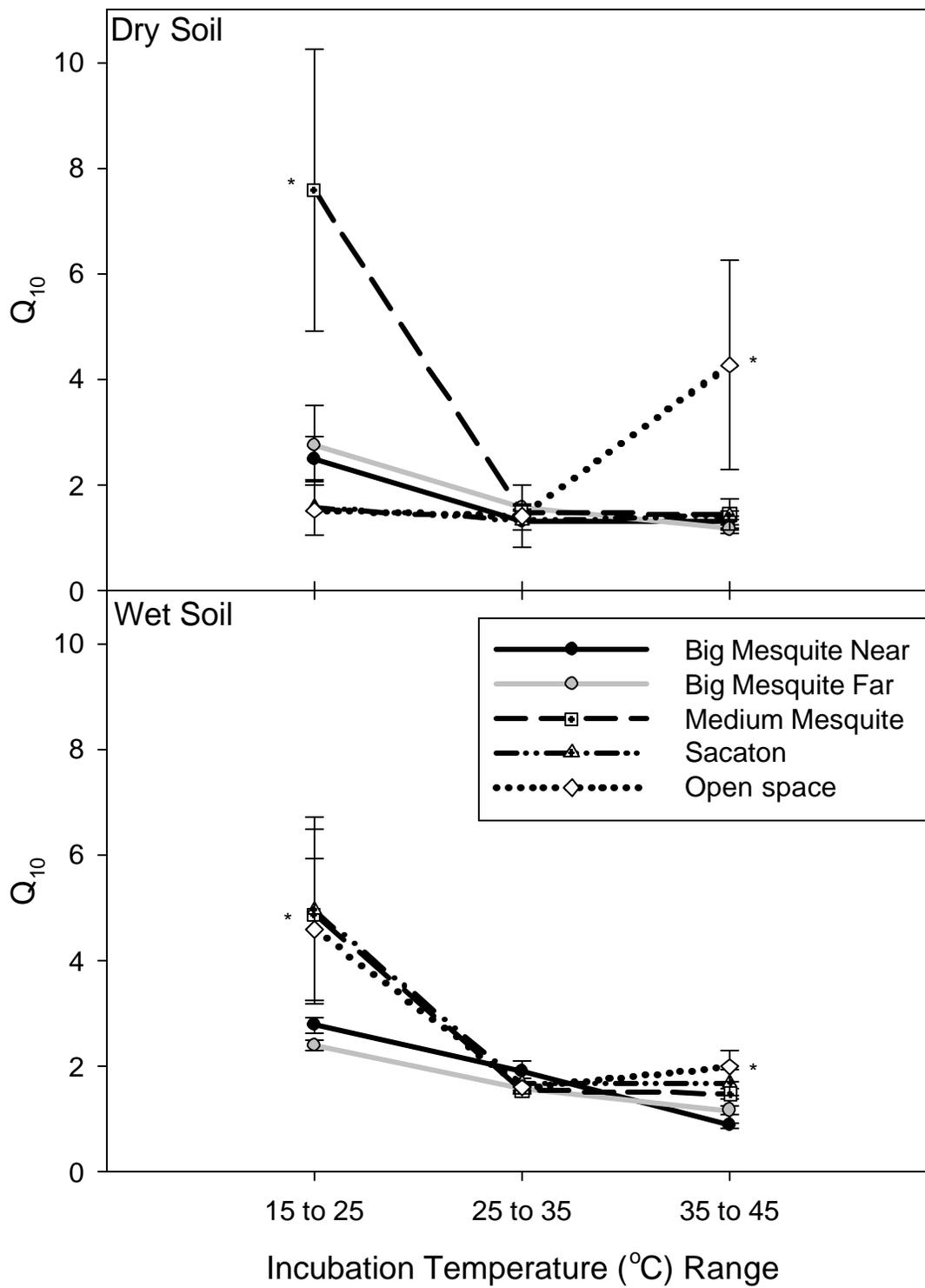
Figure 4. The  $Q_{10}$  of respiration from the incubations of dry soil (top) and wet soil (bottom) for each microsite.

Figures









## APPENDIX E: PERMISSION FROM JOURNAL

The following is an email from Springer-Verlag Publishing Company in response to my request for permission to include Appendix A in this dissertation.

\*\*\*\*\*

Dear Ms. Cable,

With reference to your request (copy herewith) to re-use material on which Springer controls the copyright, our permission is granted free of charge, on the following condition:

\* full credit (journal title, volume, year of publication, page, chapter/article title, name(s) of author(s), figure number(s), original copyright notice) is given to the publication in which the material was originally published by adding: With kind permission of Springer Science and Business Media.

With best regards,

—

Alice Essenpreis  
Springer  
Rights and Permissions

—

Tiergartenstrasse 17 | 69121 Heidelberg GERMANY  
FAX: +49 6221 487 8223  
Alice.Essenpreis@springer.com  
[www.springeronline.com/rights\\_](http://www.springeronline.com/rights_)

-----Ursprüngliche Nachricht-----

Von: Jessica Cable [mailto:[cableje@email.arizona.edu](mailto:cableje@email.arizona.edu)]

Gesendet: Mittwoch, 26. April 2006 15:44

An: Permissions Heidelberg

Betreff: URGENT! Needed for dissertation

To whom it may concern:

I have an urgent request. I need a permission statement from you for a journal article I wrote for inclusion in my dissertation. However, I am on a very tight deadline, as I need it by Monday May 1st. I have been informed that even an email or FAX from you would suffice. Below is the article information.

Please help!

Oecologia Volume 141, Number 2, Oct 2004, pages: 317 - 324, Title: Pulse size effects on Sonoran Desert soil microbial crusts, Authors: Jessica M. Cable and Travis E. Huxman

Thank you for your time.  
Sincerely,  
Jessica Cable

\*\*\*\*\*

Jessica M. Cable  
Graduate Student  
Department of Ecology and Evolutionary Biology University of Arizona Tucson, AZ  
85721 (office)520-621-8220 cableje@u.arizona.edu

Journal cover page

## Issue



### Oecologia

Publisher: Springer Berlin / Heidelberg  
 ISSN: 0029-8549 (Paper) 1432-1939 (Online)  
 Issue: Volume 141, Number 2  
 Date: October 2004

**Export Selected Citations:** RIS | Text

Select All Unselect All

#### Editorial

-   **Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems** (191 - 193)  
 Susan Schwinning, Osvaldo E. Sala, Michael E. Loik, James R. Ehleringer  
 DOI: 10.1007/s00442-004-1683-3

#### Pulse Events and Arid Ecosystems

-   **Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses** (194 - 210)  
 James F. Reynolds, Paul R. Kemp, Kiona Ogle, Roberto J. Fernández  
 DOI: 10.1007/s00442-004-1524-4

#### Pulse Events and Arid Ecosystems

-   **Hierarchy of responses to resource pulses in arid and semi-arid ecosystems** (211 - 220)  
 Susanne Schwinning and Osvaldo E. Sala  
 DOI: 10.1007/s00442-004-1520-8

#### Pulse Events and Arid Ecosystems

-   **Water pulses and biogeochemical cycles in arid and semiarid ecosystems** (221 - 235)

Amy T. Austin, Laura Yahdjian, John M. Stark, Jayne Belnap, Amilcare Porporato, Urszula Norton, Damián A. Ravetta, Sean M. Schaeffer  
 DOI: 10.1007/s00442-004-1519-1

#### Pulse Events and Arid Ecosystems

-   Resource pulses, species interactions, and diversity maintenance (236 - 253) in arid and semi-arid environments  
 Peter Chesson, Renate L. E. Gebauer, Susan Schwinning, Nancy Huntly, Kerstin Wiegand, Morgan S. K. Ernest, Anna Sher, Ariel Novoplansky, Jake F. Weltzin  
 DOI: 10.1007/s00442-004-1551-1

#### Pulse Events and Arid Ecosystems

-   Precipitation pulses and carbon fluxes in semiarid and arid ecosystems (254 - 268)  
 Travis E. Huxman, Keirith A. Snyder, David Tissue, A. Joshua Leffler, Kiona Ogle, William T. Pockman, Darren R. Sandquist, Daniel L. Potts, Susan Schwinning  
 DOI: 10.1007/s00442-004-1682-4

#### Pulse Events and Arid Ecosystems

-   A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA (269 - 281)  
 Michael E. Loik, David D. Breshears, William K. Lauenroth, Jayne Belnap  
 DOI: 10.1007/s00442-004-1570-y

#### Pulse Events and Arid Ecosystems

-   Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays (282 - 294)  
 Kiona Ogle and James F. Reynolds  
 DOI: 10.1007/s00442-004-1507-5

#### Pulse Events and Arid Ecosystems

-  □ Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture (295 - 305)  
 Travis E. Huxman, Jessica M. Cable, Danielle D. Ignace, J. Alex Eilts,  
 Nathan B. English, Jake Weltzin, David G. Williams  
 DOI: 10.1007/s00442-003-1389-y

#### Pulse Events and Arid Ecosystems

-  □ Response of desert biological soil crusts to alterations in precipitation frequency (306 - 316)  
 Jayne Belnap, Susan L. Phillips, Mark E. Miller  
 DOI: 10.1007/s00442-003-1438-6

#### Pulse Events and Arid Ecosystems

-  □ **Precipitation pulse size effects on Sonoran Desert soil microbial crusts** (317 - 324)  
**Jessica M. Cable and Travis E. Huxman**  
**DOI: 10.1007/s00442-003-1461-7**

#### Pulse Events and Arid Ecosystems

-  □ Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs (325 - 334)  
 K. A. Snyder, L. A. Donovan, J. J. James, R. L. Tiller, J. H. Richards  
 DOI: 10.1007/s00442-003-1403-4

#### Pulse Events and Arid Ecosystems

-  □ Water conservation in *Artemisia tridentata* through redistribution of precipitation (335 - 345)  
 R. J. Ryel, A. J. Leffler, M. S. Peek, C. Y. Ivans, M. M. Caldwell  
 DOI: 10.1007/s00442-003-1421-2

#### Pulse Events and Arid Ecosystems

-   Experimental separation of resource quantity from temporal variability: seedling responses to water pulses (346 - 352)  
Jeremy T. Lundholm and Douglas W. Larson  
DOI: 10.1007/s00442-003-1454-6

#### Pulse Events and Arid Ecosystems

-   The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments (353 - 362)  
Anna A. Sher, Deborah E. Goldberg, Ariel Novoplansky  
DOI: 10.1007/s00442-003-1435-9

#### Pulse Events and Arid Ecosystems

-   Minimum recruitment frequency in plants with episodic recruitment (363 - 372)  
Kerstin Wiegand, Florian Jeltsch, David Ward  
DOI: 10.1007/s00442-003-1439-5