

Direct and Indirect Effects
of Precipitation on Soil Respiration
in an Arid Ecosystem

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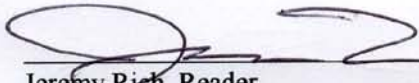
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Abstract

Climate change is expected to impact precipitation regimes; models specifically reveal reduced precipitation in North America. This study looks at the impacts of changes in precipitation quantity and nutrient levels on soil respiration in the Chihuahuan Desert in New Mexico. Specifically, soil respiration is measured to examine the effects on belowground activity of changing precipitation levels in past and current years, and the effects of nitrogen fertilization. Rainout shelters and irrigation systems were used to change rainfall quantity by -80%, -50%, 0, +50% and +80% in the 2007-2008 growing season, and then treatments either remained the same or reversed for the 2009 growing season at -80%, 0, or +80%. Soil respiration was measured in each of the 22 precipitation treatments with four replicated 2.5 x 2.5 m plots. Plots were also measured in treatments with consistently +80%, 0, or -80% precipitation, and with or without nitrogen addition, with six replicates each. In 14 select plots, soil respiration rates were measured for 16 days after irrigation to examine the time response of soil respiration. The results of the rainfall experiment revealed that soil respiration increased with precipitation in the current year ($p < 0.05$), and in the previous years, revealing a legacy effect, ($p < 0.05$). This is expected to be partially due to increased root growth in wet treatments, which also creates additional substrate for increased microbial activity. Nitrogen had no significant effect on soil respiration rates ($p > 0.05$). This may be due to continued water limitations or may be due to CO_2 limitations on photosynthesis when low water availability results in reduced stomatal conductance. The results of the time response experiment revealed that soil respiration decreased over time after an experimental precipitation event. This increased difference in soil respiration rates between irrigated and control plots after rainfall may be initially due to displacement of CO_2 with soil water saturation. These results give us insight on how belowground activity and a specific carbon flux between the soil and the atmosphere may change with changes in water availability.

Introduction

Climate change has varying effects on environmental variables across ecosystems. Global precipitation patterns are expected to be impacted by these changes. Many scientists not only hypothesize that there will be fewer rainfall events, but that the size of rainfalls will increase, with larger and longer pulses (Schwinning and Sala 2004, Karl and Knight 1998). Additionally, precipitation is expected to decrease in the North American southwest with an increased number of droughts (Bates et al. 2008), and the majority of models predict a drier North American southwest (Seager et al. 2007). Changes in precipitation due to climate change are particularly important because rainfall is considered a primary control on production throughout a large portion of world, where water availability is the most important control in the majority of vegetation biomes (Churkina and Running 1998).

An important consideration in the limitations of ecosystems is if water availability is the most pertinent limiting factor, or if there are indirect effects of water that create lags in the response to increased or decreased water availability. If there do exist time lags in response, it is important to understand how these will impact production. It is also possible that in some systems, belowground activity is limited by nitrogen availability (Burton et al. 2002), or the interaction between water and nitrogen levels (Schwinning and Sala 2004). The importance of nitrogen availability compared to water in productivity is another important relationship to observe, as other studies have found the importance of nitrogen to soil respiration (Burton et al. 2002, Conant et al. 1998, Illeris et al. 2002, Irvine et al. 2005).

Drylands make up 40% of land area worldwide (UNDP 1997), and desertification will lead to more semi-arid and arid regions over time (Mielnick et al. 2005), making these regions particularly important to study. Forty percent of land area

is susceptible to desertification (Reynolds and Stafford Smith 2007), with future drought expected in the North American southwest and the southern Europe-Mediterranean-Middle East (Seager et al 2007). Additionally, climate models predict that southwestern North America will become more arid (Seager et al. 2007). The IPCC predicts reductions in precipitation in the southwest of the United States with reduced summer and increased winter rainfall (Bates et al. 2008). With increased variability and uncertainty in rainfall patterns, it is likely that the frequency at which wet years could follow dry years and dry years could follow wet years could increase, making precipitation legacy an important factor in climate change. An environmental legacy refers to the conditions in an ecosystem in a preceding time period. For instance, a precipitation legacy may refer to rainfall patterns in the previous two years, as was studied in this experiment. In this study we saw how past precipitation variability affects belowground activity through the legacy effect.

Soil respiration is an important ecosystem process expected to change with changes in climate, and potentially providing a feedback to climate change. Soil respiration, also known as carbon dioxide efflux, is the production of carbon dioxide from intact soil due to belowground activities in roots and soil organisms and the oxidation of carbon-containing materials (Raich and Schlesinger 1992). It is the main source of carbon dioxide to the atmosphere from ecosystems and is an important part of the carbon cycle because of its impact on net carbon uptake from the atmosphere and net ecosystem production (Ryan and Law 2005). Soil respiration includes root respiration, litterfall decomposition and microbial respiration (Raich and Nadelhoffer 1989), and therefore provides an estimate for an upper limit on BNPP (belowground net primary production). Root production cannot be any greater than soil respiration since it

is a combination of these three elements. Therefore, soil respiration constrains root production estimates.

The two major components of soil respiration are heterotrophic and autotrophic respiration. Both are controlled by substrate availability, and make up belowground activity. Nearly half of soil respiration is composed of autotrophic respiration, which is the metabolic activity of roots in the rhizosphere (Ryan and Law 2005). Some mycorrhizae are included in measurements of autotrophic respiration because they feed off root carbohydrates, and measurements are generally unable to separate the respiration of these mycorrhizae from the root respiration (Hanson et al. 2000). Slightly less than half of overall soil respiration is composed of heterotrophic respiration, which is carbon produced from microbes using new organic materials as substrate (Ryan and Law 2005). The remaining approximately 10% of soil respiration is made of the decomposition of older carbon compounds in certain ecosystems (Giardina et al. 2004).

The objective of this study was to examine how altering water and nutrient availability in this ecosystem changes belowground activity. Specifically I studied how precipitation legacies and fertilization affect belowground activity, measured through soil respiration. There were three goals: (1) To understand how water availability during the current growing season and previous growing seasons affects belowground activity; (2) To determine whether fertilization affects belowground activity in this ecosystem; and (3) To observe how soil respiration rates change over time with one event of increased precipitation.

First, I hypothesized that soil respiration is a function of current-year rainfall input, where soil respiration would be greater with consistently higher soil moisture compared to consistently drier conditions and controls. Past studies have found precipitation to positively affect soil respiration (Conant et al. 1998, Illeris et al. 2002,

Mielnick et al. 2005, Huxman et al. 2004, Irvine et al. 2005, Tang and Boldocchi 2005).

Increased respiration is due to increased plant and root growth, which leads to additional substrate for respiration and microbes, increasing microbial activity.

Precipitation has the potential to increase both heterotrophic and autotrophic respiration.

Also, in this arid ecosystem I expected soil respiration to be a function of precipitation legacy, which is known as the legacy effect. Soil respiration was expected to increase with increasing precipitation in previous years. A legacy of wet conditions should increase soil respiration again due to increased root growth and microbial activity.

During wet years, I expected accumulation of roots and organic matter in the soil that will serve as a substrate for current-year soil respiration. During dry years, the opposite mechanism could occur with a negative legacy on soil respiration, where belowground biomass was expected to decrease. I predicted that soil respiration would decrease with past dry conditions mainly due to a decrease in roots, and soil respiration would decrease with current dry conditions due to the decrease in microbial activity and overall plant biomass.

Next, I hypothesized that soil respiration is a function of the amount of nutrients, specifically nitrogen, in the soil. I expected there to be a significant interaction between fertilization and water availability. In treatments with greater precipitation, I expected nitrogen to have a positive effect on soil respiration rates due to overall increased plant growth with more nutrients. However, in water-limited plots, I expected nitrogen not to have an effect on soil respiration because growth would be constrained by the lack of soil moisture. Soil respiration has been found to increase with nitrogen addition in other North American ecosystems (Burton et al. 2002). Additionally, primary production in arid grasslands has been found to increase with nitrogen, water, and the interaction of the two resources in past studies (Lauenroth et al. 1978). Increased plant growth leads to

more roots, increasing autotrophic respiration, which again increases the amount of substrate for microbes, increasing heterotrophic respiration. I looked at the interaction between precipitation and fertilization treatment, and expected to see higher soil respiration rates with greater precipitation levels and in fertilized plots, and similarities in soil respiration in fertilized and unfertilized plots with lower than average precipitation.

Lastly, I hypothesized that soil respiration is negatively related to time after rainfall. I expected soil respiration to decrease in plots over time after a rainfall or irrigation event as the soils got drier. Additionally, after a certain period of time after rainfall, I expected the difference between soil respiration of plots that experienced the single rainfall event and plots that did not to approach zero.

Past research has looked at soil respiration across environmental gradients by precipitation and changes in nitrogen levels (Burton et al. 2002, Conant et al. 1998, Illeris et al. 2002, Irvine et al. 2005). This study looks more extensively at the interaction between precipitation and nitrogen levels in a semiarid grassland. Additionally, studying the legacy effect will allow an increased understanding of the effect of variations in climate on future belowground activity.

This study determined changes in soil respiration rates for the three areas of interest using overall soil respiration rates, which include autotrophic and heterotrophic respiration. A manipulative experiment was used by creating a precipitation gradient across plots and adding nitrogen to soils to measure soil respiration rates across conditions.

Materials and Methods

Study Site and Experimental Design

The location of study was the Jornada Basin LTER research site (+32.5°N, -106.8°W, 1188 meters elevation), located in the Northern Chihuahuan Desert in New Mexico. Vegetation at the study site mainly consists of perennial grasses and shrubs, dominated by *B. eriopoda* (black grama) and *P. glandulosa* (mesquite). Seasonal variation includes hot, rainy summers and cool, dry winters. The mean annual precipitation over the past 80 years is 245 mm, where about half of rainfall is derived from late summer monsoonal storms (Havstad et al. 2006). Additionally, the study site is protected from livestock grazing.

There are three blocks at the study site to account for spatial heterogeneity across the Jornada Experimental Range. Plots are 2.5 x 2.5 m, positioned with a large mesquite at the center of each. The precipitation treatments can be seen in Table 1, below. Each of these precipitation treatments were treated with $2.5 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ twice per season, or remained as controls for nutrients. Within each block, there are two replicates of each treatment type, leading to a total of 44 plots per block. We applied nitrogen using an aqueous solution of NO_3NH_4 . We treated plots with increased precipitation using a PVC pipe irrigation system with sprinklers. Either 50% or 80% additional precipitation was added the morning after a rainfall for precipitation events exceeding 2 mm. We treated plots with decreased precipitation using rainout shelters. Shelters constructed over each plot had plastic, v-shaped, tilted shingles to intercept either 50% or 80% of rainfall. I used these plots, created in 2007 to answer the first two questions of the study: how precipitation legacies change belowground activity, and whether fertilization affects belowground activity.

Table 1: Precipitation Treatments

| | | | | | | | | | | | |
|----------------|------|------|------|------|------|------|----|------|------|------|------|
| Legacy '07-'08 | -80% | -80% | -50% | -50% | 0% | 0% | 0% | +50% | +50% | +80% | +80% |
| Current '09 | -80% | +80% | -80% | +80% | -80% | +80% | 0% | -80% | +80% | -80% | +80% |

To answer the question of how soil respiration rates change over time with one event of increased precipitation, I created ten additional 1 x 1 m plots within one of the experimental blocks previously mentioned. These plots contained grass and bare soil, but no mesquite. I installed soil collars in each of these plots. Half of these plots were treated with the equivalent of 10 mm of rain as a single precipitation event. I measured soil respiration before and for 15 days after the precipitation treatment in all 14 plots.

Measurements

I used a LICOR-6400XT (LI-COR Inc, Nebraska, USA) with a soil CO₂ chamber attachment to measure soil respiration rates and soil temperature. The LICOR measures soil respiration and soil temperature simultaneously. The LICOR averages soil temperature from 15 cm below to the surface. I installed soil collars, 10.2 cm diameter and 7.6 cm height in all sample plots on July 3rd, 2009. The soil collars remained stationary and were used for soil respiration measurements throughout the period of study. I placed soil collars in bare soil approximately 46 cm from the base of the mesquite, which was located at the center of each plot.

I also measured soil moisture when possible. In the 2.5 x 2.5 m plots I measured volumetric soil water content at two depths for the plots in which measurement systems were installed. We used ECH₂OTM moisture probes and an ECH₂OTM check handheld at 5-10 cm and 30-50 cm to measure soil moisture. For the 1 x 1 m plots, I measured soil moisture to a depth of about 8 cm using a Hydrosense® Soil Water Measurement System (CD-620 HydroSense Display Unit System and CS-620 Water Content Probe, Campbell Scientific Inc.).

Precipitation Effect

To measure the effect of current and past precipitation levels, I used four replicates of each precipitation treatment listed in Table 1. This included all unfertilized plots in blocks 1 and 3, two out of the three total blocks. In these 44 plots I measured soil respiration and temperature, and volumetric water content for the plots where ECH₂OTM moisture probes had been installed. I took measurements on July 6th, 15th, 22nd and 24th of 2009.

Fertilization Effect

To identify whether fertilization had an effect on belowground activity, I measured soil respiration, temperature, and soil moisture (where ECH₂OTM moisture probes had been installed) in 18 fertilized and 18 unfertilized plots. This included all fertilized and unfertilized plots with precipitation treatments of consistently +80% precipitation, consistently -80% precipitation and controls. I took measurements for these 36 plots in all three blocks on July 20th and 23rd of 2009.

Time Effect

I measured soil respiration, temperature, and soil moisture (0-8 cm) in the 14 1 x 1 m plots, where 7 were irrigated and 7 were left as controls, to determine the effects of time after a large precipitation event on belowground activity. I irrigated 7 plots with the equivalent of 10 mm of precipitation on the afternoon of July 20th, 2009. I took measurements directly before irrigation on July 20th, twice 1 day after irrigation (July 21st), and once in the afternoon (around 5:00 pm) 2, 3, 4, 5, 6, 7, 10, 14 and 17 days after irrigation. Any natural rainfall events within this measurement period were experienced by both the control and once irrigated plots.

Statistical Techniques

I used JMP 5.0.1 software to analyze the effects of environmental variables on soil respiration. To determine if soil respiration was correlated to current precipitation levels and past precipitation levels, I ran a linear regression for each variable on each day studied, and for all the days combined. To test the effect of the combination of current and past precipitation levels on soil respiration, I carried out multivariate regressions for each day studied, and a multivariate regression with all data nested by date. I added temperature, block and an interaction term between current and past precipitation quantities to determine if these variables had a statistically significant impact on soil respiration.

To test the effect of fertilization on soil respiration, I also carried out multivariate regressions for each day studied, and a multivariate regression with all data nested by date using fertilization level and precipitation quantity 2007-2009 as independent variables. Again, I added temperature, block and an interaction term between fertilization and precipitation quantities to determine if these variables had a statistically significant impact on soil respiration.

For the time series study, I tested the correlation between soil moisture and soil respiration rate across all measurement periods. Additionally, I looked at the averages of controlled and irrigated plots to observe the time it takes for the difference between these two values to become statistically insignificant.

To determine if the precipitation treatments led to the expected effect on soil moisture in each plot, I compared the soil moisture means of each precipitation treatment using an LSMeans Differences Tukey's HD test. I determined regression significance for all tests at the 0.05 level.

Results

During the growing season (July 1st to September 30th), there was 133 mm of rain in 2007, 264 mm of rain in 2008, and 63 mm of rain in 2009. The measuring period for soil respiration took place from July 6th, 2009 through August 6th, 2009. Growing season rainfall in 2009 accumulated to 18 mm by the end of the measurement period. During the growing season, precipitation generally occurs in large rainfall events. Soil temperatures to a depth of 15 cm had a mean of 30.7°C with a 95% confidence interval of [30.3°C, 31.0°C]. Maximum temperatures were reached around the middle of the measurement period, with highest measurements on July 20th, occurring in unsheltered plots. The average soil respiration measurements taken across days was 0.672 $\mu\text{mol}/(\text{m}^2)/\text{s}$ with a 95% confidence interval of [0.612, 0.732]. The average shallow volumetric water content (5-10 cm) was 5.57%, with a 95% confidence interval of [5.14, 6.01] and the average deep volumetric water content (30-50 cm) was 9.93 with a 95% confidence interval of [9.33, 10.53].

The treatments of rainout shelters and the irrigation system are effective at changing soil moisture. In comparing the shallow volumetric water content of the soil (5-10 cm), the VWC of irrigated (+80%) plots were significantly higher than the control and sheltered (-80%) plots across the four days that 44 measurements were taken to test the legacy effect ($p < 0.05$). The mean shallow soil moisture is higher for the irrigated plots than for the controls, which is higher than the mean for the sheltered plots.

Soil Respiration and the Legacy Effect

In response to the first question of the study of how current precipitation affects soil respiration rates, I found a positive correlation between soil respiration and current year (2009) growing season precipitation level (figure 1). Coefficients are significant on all measurement days except July 22nd. Shallow (5-10 cm) volumetric water content

(VWC) can also be used to observe the effects of the current season's precipitation. We see a similar positive trend between shallow VWC and soil respiration (figure 2), significant ($p < 0.05$) on all days except July 6th, July 22nd and in combining all days including July 22nd. It may be important to note that plots experienced 5.3 mm of rain the evening of July 21st, which was no more than 6 hours before soil respiration and soil moisture measurements were taken on July 22nd.

In testing the legacy effect, I found a positive correlation between soil respiration and past (2007-2008) growing season precipitation levels (figure 3). Coefficients are found to be significant ($p < 0.05$) on all days except July 6th, July 22nd, and the model including July 22nd.

From these relationships, I created a multivariate model to combine the effects for each measurement date (figure 4), from all sets of measurements together (figure 5), and for all measurement sets excluding the morning after the large rainfall (July 22nd) when the soils were most likely saturated with water for a day (figure 5). The coefficients of both variables in this model are significant ($p < 0.05$) on all days except July 22nd, and the model of all dates including July 22nd. Another model for efflux accounts for legacy and current precipitation treatments with the current treatment nested under day ($R^2 = 0.62$). The coefficients of legacy treatment ($p = 0.054$), current treatment ($p = 0.0027$), and date ($p < 0.0001$) were all nearly significant at the 5% level, and were all significant at the 10% level. These models combine the two precipitation treatments for past (2007-2008) versus current (2009) year precipitation to see how each affect overall soil respiration rates.

Soil Respiration and Fertilization Treatments

To understand the effect of fertilization and its interaction with precipitation in its effects on soil respiration, I regressed soil respiration based on 2007-2009

precipitation separated by fertilization treatment (figure 6). In the multivariate regressions taking both fertilization treatment and precipitation levels as variables to determine soil respiration, I found no significant correlation between soil respiration and fertilization treatment on either of the days measurements were taken ($p > 0.05$), but a strong correlation between rainfall over the past three years and soil respiration rates ($p < 0.05$) on July 23rd, the second day measurements were taken. A model with precipitation and fertilization treatment as variables, with precipitation level nested under date had an $R^2 = 0.56$. The coefficient of date ($p < 0.0001$) and 2007-2009 growing season precipitation ($p < 0.0001$) were significant at the 5% level; however, the coefficient on fertilization was not ($p = 0.118$).

Soil Respiration over Time

Results from the time series study are displayed in figure 7. Figure 8 displays the means of the control and irrigated plots, independently, with error bars for 1 standard error. I irrigated on day 0 directly after soil respiration measurements were taken. Soil respiration was equivalent between irrigated and control plots on day 0, directly before irrigation, and then again on day 2 ($p < 0.05$), following a natural rainfall the night before. As stated previously, large rainfalls initially increase soil respiration rate due to the displacement of carbon dioxide from the soil matrix to the atmosphere and enhanced microbial activity (Huxman et al. 2004). This may account for the similarity in soil respiration rates across treatments on day 2. There is again a significant difference in soil respiration rates 3 days after irrigation ($p > 0.05$). The rates in irrigated and control plots converge again with a statistically insignificant difference between the two treatments by day 14 ($p < 0.05$). I found an overall linear positive correlation between soil moisture measurements (0-8 cm) and soil respiration rates over 11 separate measurement periods, as can be seen in figure 8 ($p < 0.05$).

I found no significant effect in other variables measured. The effect of temperature was not statistically significant in testing for the effect of past and current precipitation treatments on July 6th, July 15th or July 24th ($p>0.05$), but were found to be significant on July 22nd (when the other variables were not significant) and in the models including multiple dates ($p<0.05$). Including the difference in location between the three blocks for the multivariate regressions of past and current precipitation and for the regressions of fertilization and precipitation were not significant on the majority of measurement days ($p>0.05$). Additionally, the effect of the interaction term between past and current precipitation and of the interaction term between fertilization level and precipitation were insignificant ($p>0.05$). Therefore, it was unnecessary to include these variables in the regressions.

Discussion

Soil respiration measurements were found to be comparable to other studies of the same area, and other areas studied around the world, where the average value measured from June 6, 2009 through August 3, 2009 was $0.672 \mu\text{mol}/(\text{m}^2)/\text{s}$. This is greater than the overall average found for the Chihuahuan Desert grassland of $0.394 \mu\text{mol}/(\text{m}^2)/\text{s}$ measured over five years (Mielnick et al. 2005); however, our measurements took place during the rainy growing season, so we would expect soil respiration to be higher than the average. Mielnick et al. highlight the difference in soil respiration over the course of the year, where rates are nearly zero for most of the year, and larger positive values are measured during the growing season (Mielnick et al. 2005). Soil respiration rates measured in other regions are included in table 2. While different measurement methods may under or over estimate soil respiration rates, our results appear to be in a reasonable range compared to other studies.

Table 2: Average Soil Respiration Rates across Ecosystems

| Avg soil respiration $\mu\text{mol}/(\text{m}^2)/\text{s}$ | Ecosystem type, location, references |
|--|---|
| 0.672 | Chihuahuan Desert, New Mexico USA, <i>this study</i> |
| 0.394 | Chihuahuan Desert, New Mexico USA, <i>Mielnick et al. 2005</i> |
| 0.51 to 2.29 | Oak-grass savanna, California USA, <i>Tang and Baldocchi 2005</i> |
| 0.317 | White spruce forest, Alaska USA, <i>Raich and Schlesinger 1992</i> |
| 0.241 | Aspen forest, Ottawa, Canada, <i>Raich and Schlesinger 1992</i> |
| 0.904 | Red pine forest, Japan, <i>Raich and Schlesinger 1992</i> |
| 0.937 | Pine forest, Florida USA, <i>Raich and Schlesinger 1992</i> |
| 0.598 | Eucalyptus forest, Victoria, Australia, <i>Raich and Schlesinger 1992</i> |
| ~0 to 2 | Temperate hardwood forest, Massachusetts USA, <i>Boone et al. 1998</i> |

Results from our study suggest that soil respiration is positively correlated with soil moisture and past and current precipitation levels. The general result of our study is similar to a study across ecosystems, where mean annual precipitation level and soil respiration are positively correlated ($p < 0.0001$) (Raich and Schlesinger 1992). It differs, however, from a study in the Harvard Forest in Massachusetts that finds a negative correlation between volumetric water content and soil respiration ($p < 0.05$). Unlike our experiment, soil respiration in this forest is sensitive to soil temperature, which is negatively correlated with volumetric water content, making this result difficult to interpret (Davidson et al. 1998). Increased rainfall in both past and current years has a positive effect on belowground activity in the Jornada Experimental Range. Especially unique to this study is the finding that increased precipitation levels in previous years was important to current soil respiration values, which we here call the legacy effect. As stated earlier, this effect was expected due to increased plant growth and microbial activity with increased water availability, as water is an important resource in arid ecosystems.

Additionally, nitrogen levels were found to have little to no impact on soil respiration rates. Nitrogen has no net effect on soil respiration rates, so microbial life and root production are assumed to remain constant with changing levels of nitrogen across precipitation treatments. This deviates from the hypothesis that nitrogen would have a positive effect on soil respiration in wet treatments. The lack of correlation greatly differs from results found in North American forests, where root respiration rates are correlated with nitrogen concentrations with a significance of 99.9% (Burton et al. 2002), but is comparable to results from a 27-year old nitrogen fertilized *Pinus rigidus* forest in Massachusetts which was irrigated and found no effect of fertilization on soil respiration in the first two years of study (Raich and Schlesinger 1992). While it was hypothesized that nitrogen would affect underground activity in wet treatments, arid and semi-arid ecosystems are known to be water-limited, and this part of the study reveals a larger magnitude of importance of water than of nitrogen to belowground activity. This result agrees with other studies that find increasing leaf nitrogen at low levels of water availability leads to diminishing returns in photosynthesis due to CO₂ limitations (Mooney and Gulmon 1979). Additionally, in other semiarid grasslands there have been studies that show an increase in nutrient use efficiency with decreased nutrient levels, which could be a factor in the lack of an effect of nitrogen on soil respiration (Yuan et al. 2006).

Lastly, a single precipitation event compared to controls that do not experience this specific precipitation event has a decreasing effect over time on belowground activity. There is a lasting effect of a single precipitation event for at least 10 days in this study. There could potentially be a longer effect as future precipitation events may cause the soil respiration rates of these two treatments to separate as was observed after the precipitation event 2 days after irrigation (figure 7). This prolonged impact may

reinforce the legacy effect in that past precipitation regimes affect current soil respiration rates, as can be seen from the effects of the 2007-2008 precipitation treatments. This difference in soil respiration rates between the controls and once-irrigated plots does; however, appear to decrease over time, making current precipitation levels very important to immediate soil respiration rates.

Overall, evidence on precipitation and fertilization effects suggests that water is important for belowground activity in arid ecosystems, especially when compared to nitrogen levels. However, there are a few deviations from this general trend. Similar trends are found every day for soil respiration measurements looking at the precipitation legacy and current precipitation effects except on July 22nd, 2009, as can be seen in figure 4. July 22nd was the only day measurements were taken after a significant rainfall event. On the evening of July 21st, there were 5.3 mm of precipitation. Large rainfalls lead to an initially elevated soil respiration rate due to the displacement of carbon dioxide from the soil matrix to the atmosphere and enhanced microbial activity (Huxman et al. 2004). These rates, therefore, may not directly relate to belowground activity, and may instead be dominated by the carbon dioxide displacement. There was also a very weak correlation between precipitation and soil respiration on July 20th, which may relate to the 0.8 mm of rain on July 15th.

Temperature, block location, and interaction terms (2007-2008ppt*2009ppt and ppt*fertilization) were found to have no significant effect on soil respiration rates. The lack of an effect of temperature allows us to discount a potential treatment effect of the rainout shelters. One potential worry is that the rainout shelters, constructed with a clear plastic barrier, would create a greenhouse effect and raise temperatures in treated plots. Since soil temperature does not appear to affect soil respiration rates, this portion of a treatment effect is not considered an issue.

Further research on the overall direction of the change in carbon fluxes between the soils of semiarid and arid ecosystems and the atmosphere with predicted climate change would be helpful to better understand feedback mechanisms. From this study, we can predict the direction of changes in soil respiration with precipitation changes based on climate models. A next step is to find the scale of CO₂ efflux with precipitation changes predicted by climate models to determine the direction and magnitude of change of the release of CO₂ from ecosystems.

From this study we better understand the importance of precipitation patterns on belowground activity in arid and semi-arid ecosystems. This reminds us of the importance of the changes in precipitation that will result as a consequence of climate change. Precipitation changes today will affect belowground activity both now and years from now, as is confirmed with the study of the legacy effect on soil respiration. If this ecosystem experiences fewer rainfall events and reduced annual mean precipitation, as is predicted by many climate models (Seager et al. 2007, Bates et al. 2008), there could be long-lasting implications of decreased carbon fluxes and reduced belowground activity.

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References

- Bates, B.C., Z.W. Kundzewicz, S. Wu and J.P Palutikof, Eds., 2008: Climate Change and Water. Technical Paper of the Intergovernmental Panel on Climate Change, IPCC Secretariat, Geneva, 210 pp.
- Boone, R.D., Nadelhoffer, K.J., Canary, J.D., & Kaye, J.P. (1998). Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature*, 396, 570-572.
- Burton, A.J., Pregitzer, K.S., Ruess, R.W., Hendrick, R.L., & Allen, M.F. (2002). Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes. *Oecologia*, (131), 559-568.
- Churkina G. & Running S.W. 1998. Contrasting climatic controls on the estimated productivity of global terrestrial biomes. *Ecosystems* 1:206-15.
- Conant, R.T., Klopatek, J.M., Malin, R.C., & Klopatek, C.C. (1998). Carbon pools and fluxes along an environmental gradient in northern Arizona. *Biogeochemistry*, (43), 43-61.
- Davidson, E.A., Belk, E., & Boone, R.D. (1998). Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, 4(217-227),
- Giardina, C.P., Binkley, D., Ryan, M.G., Fownes, J.H., & Senock, R.S. (2004). Belowground carbon cycling in a humid tropical forest decreases with fertilization. *Oecologia*, 139(4), 545-550.
- Hanson, P.J., Edwards, N.T., Garten, C.T., & Andrews, J.A. (2000). Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry*, (48), 115-146.
- Havstad, K.M., Huenneke, L.F., & Schlesinger, W.H. (2006). *Structure and function of a chihuahuan desert ecosystem*. New York, NY: Oxford University Press, Inc..
- Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., & Schwinning, S. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141, 254-268.
- Karl, T. & Knight, R. (1998). Secular trends of precipitation amount, frequency. and intensity in the United States. *Bulletin of the American Meteorological Society*, 79(2), Retrieved from <http://www.umces.edu/president/hypoxiapubs/Karl%20Knight%201998.pdf> s
- Illeris, L., Michelsen, A., & Jonasson, S. (2002). Soil plus root respiration and microbial biomass following water, nitrogen, and phosphorous application at a high arctic semi desert. *Biogeochemistry*, 65, 15-29.

- Irvine, J., Law, B.E., & Kurpius, M.R. (2005). Coupling of canopy gas exchange with root and rhizosphere respiration in a semi-arid forest. *Biogeochemistry*, (73), 271-282.
- Lauenroth, W.K., Dodd, J.L., & Sims, P.L. (1978). The Effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia*, 36(2), 211-222.
- Mielnick, P., Dugas, W.A., Mitchell, K., & Havstad, K. (2005). Long-term measurements of CO₂ flux and evapotranspiration in a Chihuahuan desert grassland. *Journal of Arid Environments*, (60), 423-436.
- Mooney, H.A., & Gulmon, S.L. (1979). Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. *Topics in Plant Population Biology*. Columbia University, New York. 316-337.
- Raich, J.W., & Nadelhoffer K.J. (1989). Belowground carbon allocation in forest ecosystems: global trends. *Ecology*, 70(5), 1346-1354.
- Raich, J.W., & 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., et al. (2007). Global desertification: building a science for dryland development. *Science*, 316, 847-851.
- Ryan, M.G., & Law B.E. (2005). Interpreting, measuring, and modeling soil respiration. *Biogeochemistry*, 2005(73), 3-27.
- Schwinning, S., & Sala, O.E. (2004). Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia*, (141), 211-220.
- Seager, R.; Ting, M.; Held, I.; Kushnir, Y.; Lu, J.; Vecchi, G.; Huang, H-P.; Harnik, N.; Leetmaa, A.; Lau, N-C.; Li, C.; Velez, J. & Naik, N. (2007, May 25). Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, 316, 1181-1184.
- Tang, J., & Baldocchi, 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.
- UNSO/UNDP. 1997. Office to Combat Desertification and Drought/ United Nations Development Programme. An assessment of population levels in the world's drylands: Aridity zones and dryland populations. Office to Combat Desertification and Drought. New York, NY. 23.
- Yuan, Z-Y, Li, L-H, Han, X-G, Chen, S-P, Wange, Z-W, Chen, Q-S, & Bai, W-M.. (2006). Nitrogen response efficiency increased monotonically with decreasing soil resource availability: a case study from a semiarid grassland in northern China. *Oecologia*, (148), 564-572.

Figures

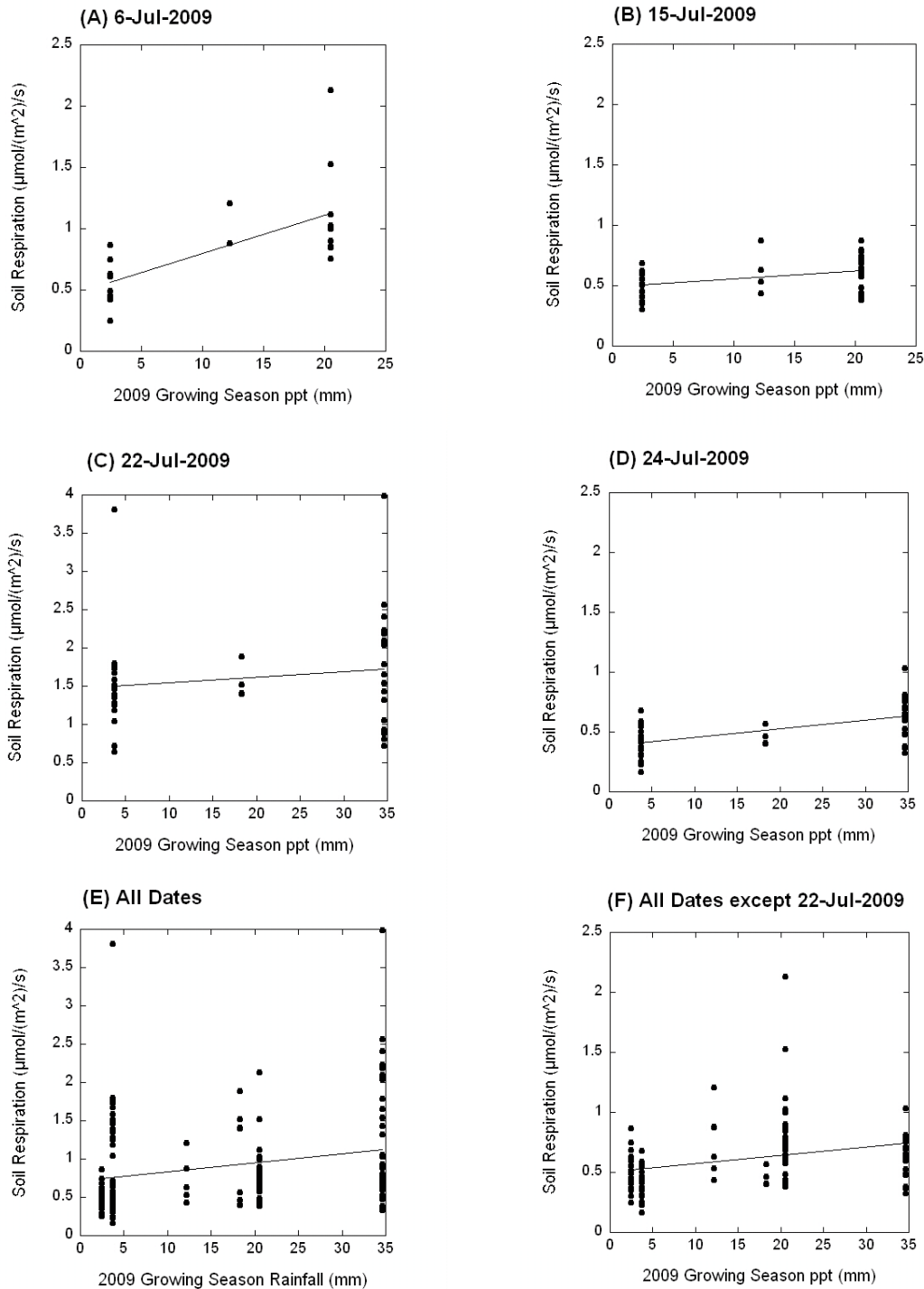


Figure 1 Soil respiration rate by current year growing season rainfall (starting July 1, 2009). Results from July 6, 2009 are shown in (A) with the relationship $y = 0.490 + 0.0308x$, $R^2=0.42$ ($p<0.05$); July 15, 2009 is shown in (B) with the relationship $y = 0.492 + 0.00638x$, $R^2=0.14$ ($p<0.05$); July 22, 2009 is shown in (C) with the relationship $y = 1.48 + 0.00714x$, $R^2=0.025$ ($p>0.05$) following a 5.3 mm rainfall on July 21, note: scale of y-axis is different in this plot; July 24, 2009 is shown in (D) with the relationship $y = 0.387 + 0.00711x$, $R^2=0.35$ ($p<0.05$); measurements for all dates are combined in (E) with the relationship $y = 0.714 + 0.0118x$, $R^2=0.060$ ($p<0.05$), note: scale of y-axis is different in this plot; and all dates excluding July 22 are shown in (F) with the relationship $y = 0.502 + 0.00703x$, $R^2=0.10$ ($p<0.05$).

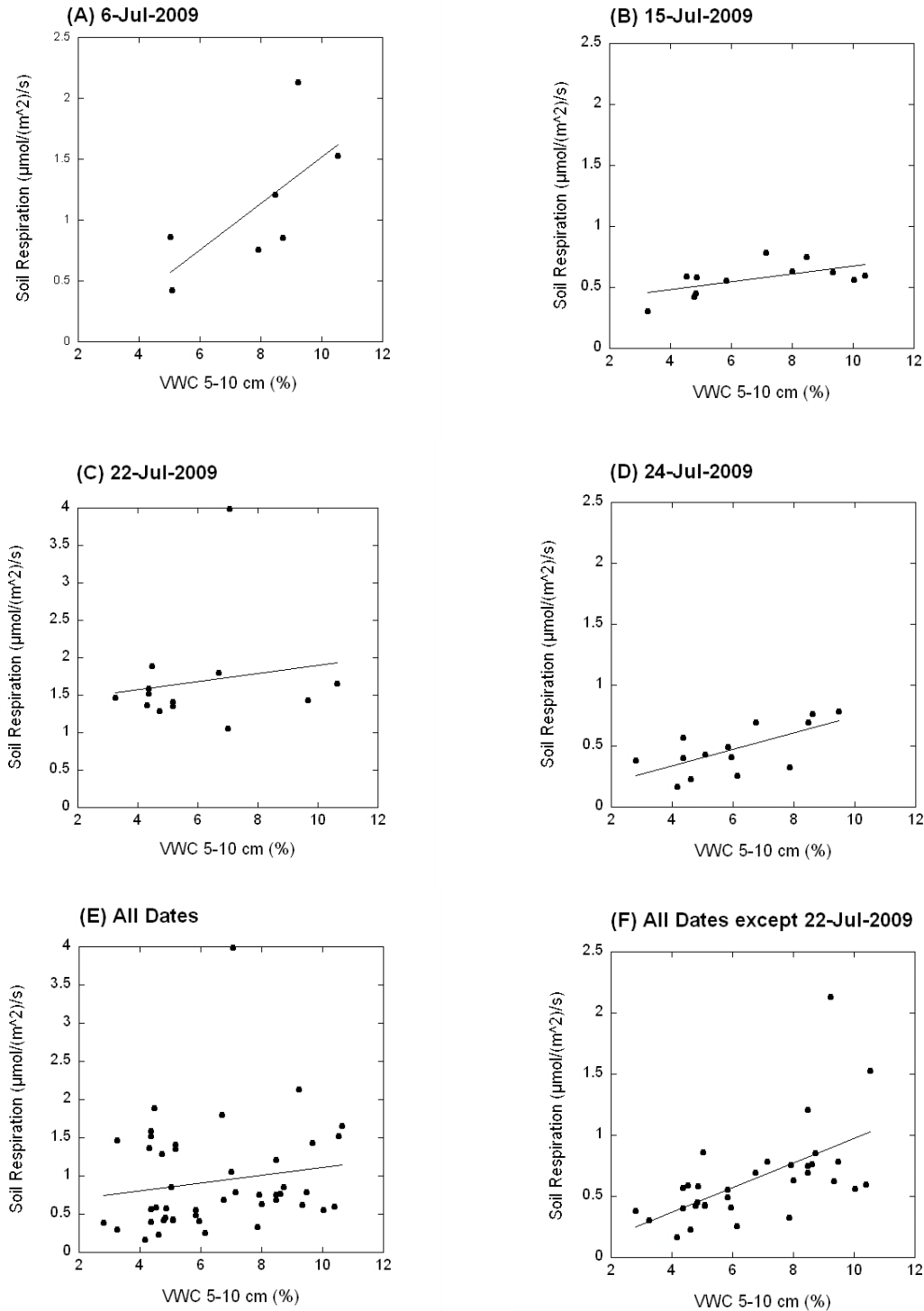


Figure 2 Soil respiration by percent shallow volumetric water content (5-10 cm) by date. Results from July 6, 2009 are shown in (A) with the relationship $y = -0.397 + 0.192x$, $R^2=0.48$ ($p>0.05$); July 15, 2009 is shown in (B) with the relationship $y = 0.353 + 0.0322x$, $R^2=0.35$ ($p<0.05$); July 22, 2009 is shown in (C) with the relationship $y = 1.36 + 0.0535x$, $R^2=0.026$ following a 5.3 mm rainfall on July 21 ($p>0.05$), note: scale of y-axis is different in this plot; July 24, 2009 is shown in (D) with the relationship $y = 0.0628 + 0.0678x$, $R^2=0.44$ ($p<0.05$); measurements for all dates are combined in (E) with the relationship $y = .606 + 0.0510x$, $R^2=0.027$ ($p>0.05$), note: scale of y-axis is different in this plot; and all dates excluding July 22 are shown in (F) with the relationship $y = -0.0294 + 0.100x$, $R^2=0.34$ ($p<0.05$).

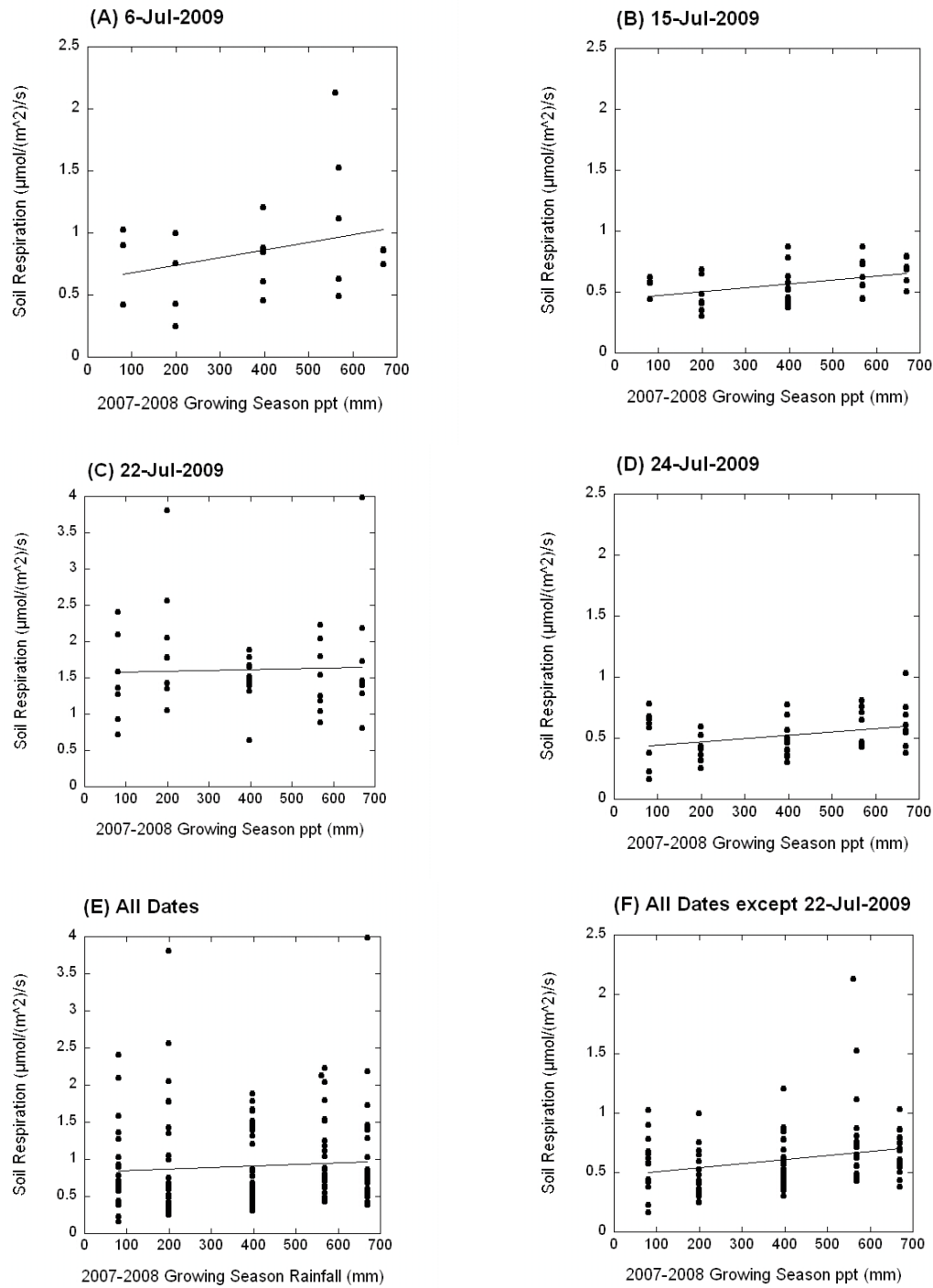


Figure 3 Soil respiration by past (2007-2008) growing season rainfall (July 1 through September 30). Results from July 6, 2009 are shown in (A) with the relationship $y = 0.618 + 0.000613x$; $R^2=0.089$ ($p>0.05$); July 15, 2009 is shown in (B) with the relationship $y = 0.444 + 0.000308x$; $R^2=0.17$ ($p<0.05$); July 22, 2009 is shown in (C) with the relationship $y = 1.57 + 0.000110x$; $R^2=0.0012$ ($p>0.05$), following a 5.3 mm rainfall on July 21, note: scale of y-axis is different in this plot; July 24, 2009 is shown in (D) with the relationship $y = 0.418 + 0.000272x$; $R^2=0.10$ ($p<0.05$); measurements for all dates are combined in (E) with the relationship $y = 0.824 + 0.000208x$; $R^2=0.0046$ ($p>0.05$), note: scale of y-axis is different in this plot; and all dates excluding July 22 are shown in (F) with the relationship $y = 0.470 + 0.000350x$; $R^2=0.071$ ($p<0.05$).

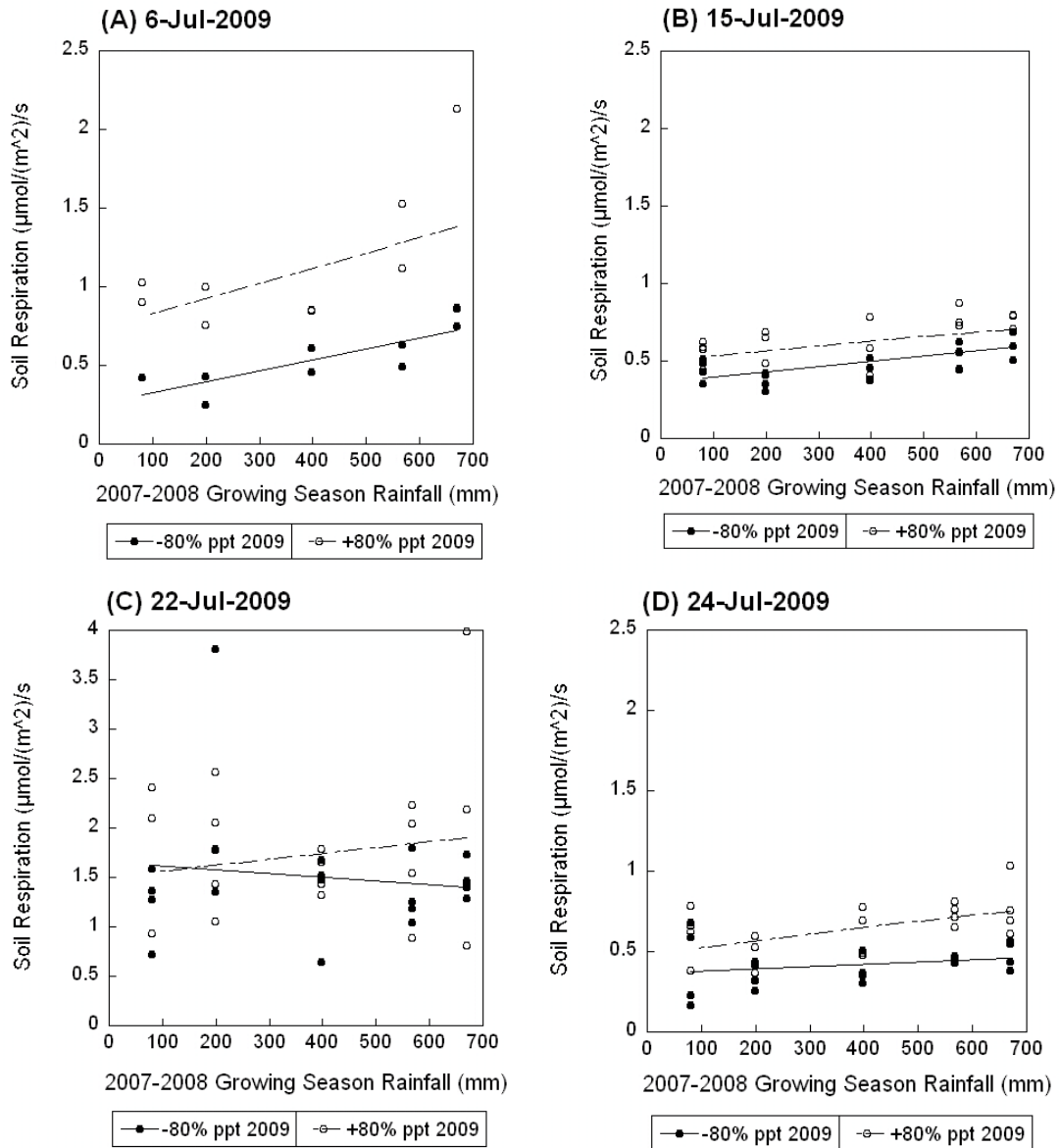


Figure 4 Soil respiration by past (2007-2008) growing season rainfall, separated by current year precipitation treatment. Results from July 6, 2009 are shown in (A) with a relationship of $\text{Efflux} = 0.167 + 0.000765 * (\text{Rainfall}_{2007-2008}) + 0.0327 * (\text{Rainfall}_{2009})$, $R^2=0.56$, ($p<0.05$); July 15, 2009 is shown in (B) with a relationship of $\text{Efflux} = 0.319 + 0.000371 * (\text{Rainfall}_{2007-2008}) + 0.00793 * (\text{Rainfall}_{2009})$, $R^2=0.38$ ($p<0.05$); July 22, 2009 is shown in (C) with a relationship of $\text{Efflux} = 1.44 + 0.000110 * (\text{Rainfall}_{2007-2008}) + 0.00714 * (\text{Rainfall}_{2009})$, $R^2=0.026$ ($p>0.05$), following a 5.3 mm rainfall on July 21, note: scale of y-axis is different in this plot; and July 24, 2009 is shown in (D) with a relationship of $\text{Efflux} = 0.283 + 0.00711 * (\text{Rainfall}_{2007-2008}) + 0.000273 * (\text{Rainfall}_{2009})$, $R^2=0.45$ ($p<0.05$).

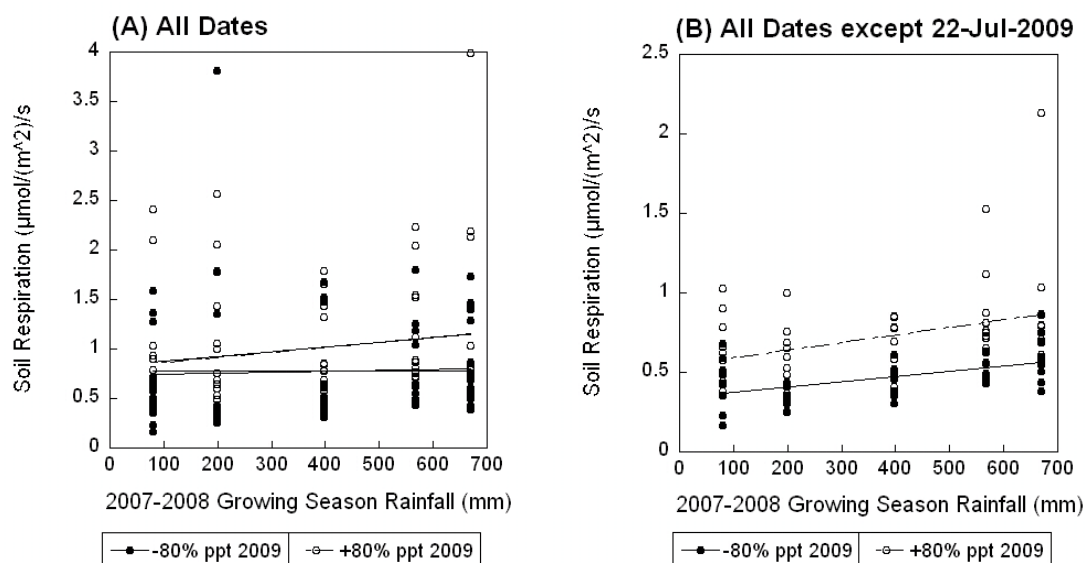


Figure 5 Soil respiration by past (2007-2008) growing season rainfall, separated by current year precipitation treatment. Results for all dates combined are shown in (A) with a relationship of $\text{Efflux} = 0.612 + 0.000250 * (\text{Rainfall}_{2007-2008}) + 0.0120 * (\text{Rainfall}_{2009})$, $R^2=0.067$ ($p>0.05$); and for all dates excluding July 22 are shown in (B) with a relationship of $\text{Efflux} = 0.342 + 0.000384 * (\text{Rainfall}_{2007-2008}) + 0.00753 * (\text{Rainfall}_{2009})$, $R^2=0.19$ ($p<0.05$). By nesting current precipitation by date, we get a model combining all dates with $R^2=0.62$, $p_{2009\text{rainfall}}=0.0027$, $p_{07-08\text{rainfall}}=0.054$, and $p_{\text{date}}<0.0001$.

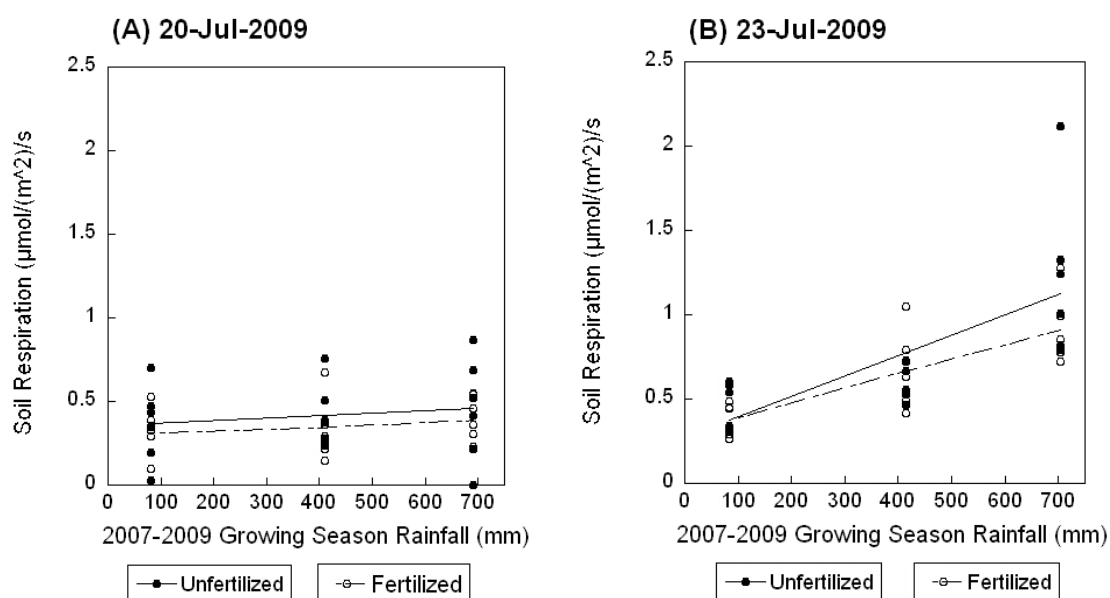


Figure 6 Soil respiration by 2007-2009 growing season rainfall, separated by fertilization treatment. Results from July 20, 2009 are shown in (A) which has a relationship of $\text{Efflux} = 0.0361 + -0.0597 * (\text{Fertilization}) + 0.000134 * (\text{Rainfall}_{2007-2009})$, $R^2=0.052$ ($p>0.05$); and results from July 23, 2009 are shown in (B) which has a relationship of $\text{Efflux} = 0.344 + -0.112 * (\text{Fertilization}) + 0.00104 * (\text{Rainfall}_{2007-2009})$, $R^2=0.54$ ($p_{\text{rainfall}}<0.05$, $p_{\text{fertilization}}>0.05$). By nesting precipitation by date, we get $R^2=0.56$, $p_{\text{date}}<0.0001$, $p_{2007-2009\text{rainfall}}<0.0001$, and $p_{\text{fertilization}}=0.12$.

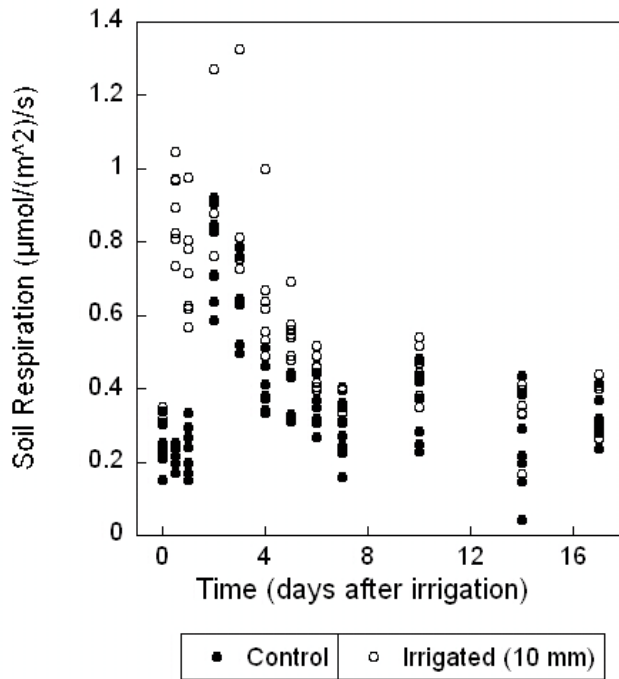


Figure 7 Soil respiration by date, starting on day 0, immediately before irrigating the equivalent of 10 mm of precipitation to half of the plots. Measurements lasted until 17 days after irrigation. Note that there was 5.3 mm of rainfall the evening before measurements were taken on day 2.

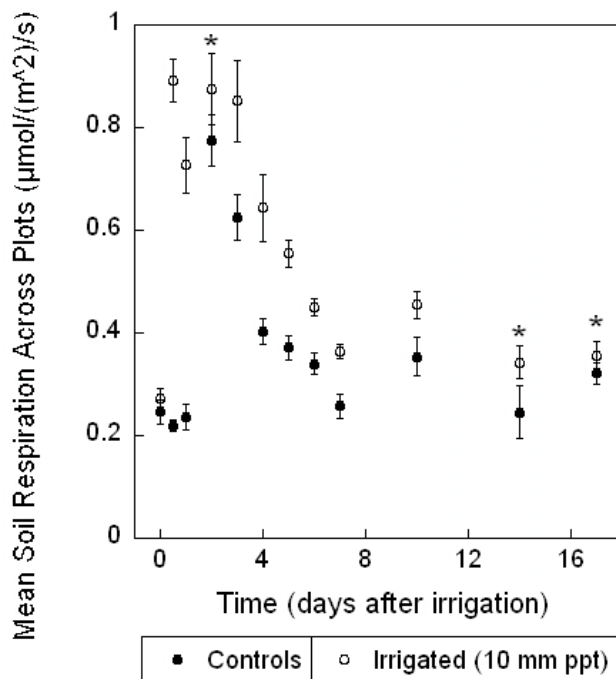


Figure 8 Means and standard errors of soil respiration for irrigated and control plots, separately. The difference between the means is statistically insignificant ($p < 0.05$) on the days marked with (*), including 2, 14 and 17 days after irrigation. Note that soil respiration rates in the irrigated and control plots come together ($p > 0.05$) after the natural 5.3 mm rainfall event before day 2.

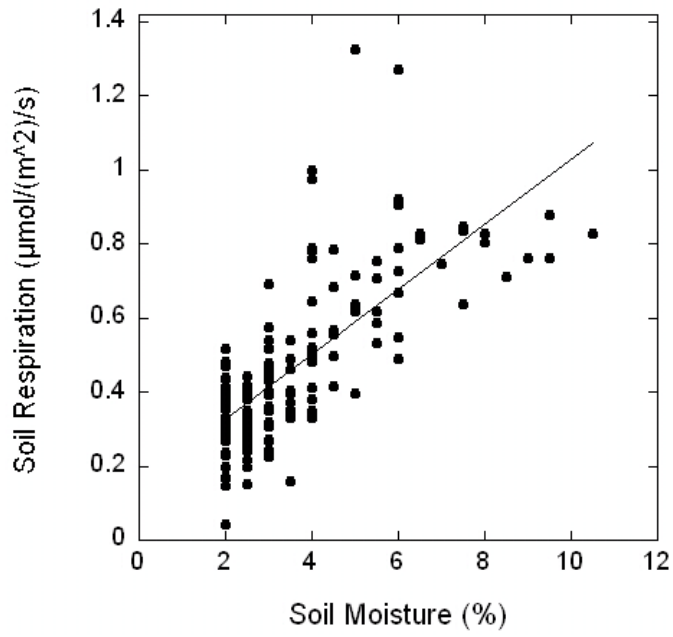


Figure 9 Soil respiration by soil moisture from 0 cm to 8 cm below the surface with values from 12 individual measurement periods, with a relationship of $y = 0.150 + 0.0878x$, $R^2 = 0.52$, ($p < 0.05$).