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Effects of three global climate change factors on soil water and sap flow of *Larrea tridentata* in the Mojave Desert

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By

Christopher Dale Holmes

Dr. Robert S. Nowak/Thesis Advisor

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Robert S. Nowak, Ph.D., Advisor

Wally Miller, Ph.D., Committee Member

George Fernandez, Ph.D., Graduate School Representative

Marsha H. Read, Ph. D., Associate Dean, Graduate School

May, 2009

ABSTRACT

Water availability is the primary control of plant productivity and composition in arid plant communities. Effects of simulated global changes on soil water and sap flow of *L. tridentata* in a natural Mojave Desert ecosystem were measured over five years and two years respectively. Global change treatments were summer irrigations that imitated a northward shift of summer monsoons associated with global warming, nitrogen additions that imitated increased nitrogen deposition from anthropogenic sources, and biological crust disturbance that imitated disturbance from increased land use. Averaged over all data, irrigated plots had 40% and 24% more soil water than non-irrigated plots at 0.2 m and 0.4 m depths, respectively. Soil water from irrigation treatments consistently reached 0.6 m depth but only persisted in irrigated plots until October or November and hence is unlikely to benefit deeper rooted C_3 vegetation that is active during late winter and spring. At no time during the study did soil water infiltrate beyond the rooting zone, suggesting that deep percolation of soil water is very rare for this ecosystem. A significant year-long effect of intact biological soil crusts was not found. However within 2-4 days following summer irrigation, plots with intact biological soil crusts were wetter than plots with disturbed biological soil crusts to 0.6 m depths. No consistent effects of nitrogen deposition on soil water content were found.

Larrea tridentata is one of the most abundant and widespread perennial plants in deserts of southwestern North America. Averaged over all treatments, *L. tridentata* exposed to summer irrigation treatments have significantly greater sap flow than plants in non-irrigated plots. This irrigation effect lasts approximately seven weeks after the last irrigation when a transition is made and plants in non-irrigated plots begin to have significantly greater sap flow until the irrigations of the following year. Not only is *L. tridentata* able to respond to an increase in soil water during the hot summer months, but evidence is also presented that suggests *L. tridentata* has an additional physiological response to the increase in soil water within a two week period. *L. tridentata* plants exposed to the highest nitrogen addition consistently had the greatest rates of sap flow. The effect of the biological soil crust treatment on sap flow of *L. tridentata* was variable and dependant on interactions with the irrigation and nitrogen treatments. These results demonstrate that predicted impacts of global changes have the potential to have important effects on the Mojave Desert by affecting the primary production of *L. tridentata* and the ecohydrology of the ecosystem.

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Chapter 1

Soil water content of a Mojave Desert ecosystem in response to global change factors

ABSTRACT

Water availability is the primary control of plant productivity and composition in arid plant communities. Effects of simulated global changes on soil water for a natural Mojave Desert ecosystem were measured over five years. Global change treatments were summer irrigations that imitated a northward shift of summer monsoons associated with global warming, nitrogen additions that imitated increased nitrogen deposition from anthropogenic sources, and biological crust disturbance that imitated disturbance from increased land use. Averaged over all data, irrigated plots had 40% and 24% more soil water than non-irrigated plots at 0.2 m and 0.4 m depths, respectively. Soil water from irrigation treatments consistently reached 0.6 m depth but only persisted in irrigated plots until October or November and hence is unlikely to benefit deeper rooted C_3 vegetation that are active during late winter and spring. At no time during the study did soil water infiltrate beyond the rooting zone, suggesting that deep percolation of soil water is very rare for this ecosystem. A significant year-long effect of intact biological soil crust disturbance treatment was not found. However within 2-4 days following summer irrigation, plots with intact biological soil crusts were wetter than plots with disturbed biological soil crusts to 0.6 m depths. No consistent effects of nitrogen deposition on soil water content were found. These results demonstrate that predicted impacts of global changes have potential to influence plant production or species composition in the Mojave Desert by altering the ecohydrology of the ecosystem.

INTRODUCTION

Water availability is often recognized as the primary control of plant productivity and composition in semi-arid and arid land plant communities (Noy-Meier, 1973). In arid ecosystems where evapotranspiration (ET) accounts for more than 90% of water loss, timing, seasonal distribution, and intensity of precipitation play a major role in the availability of water within soil profiles, thus strongly influencing arid land plant productivity and composition (Comstock and Ehleringer 1992, Ehleringer *et al.* 1999, Weltzin *et al.* 2003, Wilcox *et al.* 2006). Precipitation that falls in winter is more likely to percolate deeper into the soil profile, whereas summer precipitation has a high probability of evaporating before infiltrating below the soil surface layer (Schwinning *et al*. 2003).

Paleobotanical evidence indicates that the Mojave Desert region changed from desert grassland to desert scrub by ~5,000 years ago. This shift in community types coincided with the southern displacement of the "monsoon front" and therefore a significant decrease in summer rainfall in the region (Spaulding and Graumlich 1986, Tyler *et al.* 1996). As a result of this displacement of the monsoon front, the Mojave Desert climate became dominated by winter rains with only sporadic summer thunderstorms. This shift in climatic patterns is thought to be responsible for the current physiognomy of the Mojave Desert, which is dominated by deep-rooted, drought-tolerant perennials such as *Larrea tridentata, Ambrosia dumosa*, *Lycium andersonii*, and *Lycium pallidum.*

Future global changes could have profound consequences for plant production and species composition by altering available water and nutrients. Climate change as a result of anthropogenic activities is predicted to alter precipitation regimes throughout the world (Easterling *et al.* 2000, NAST 2000, IPCC 2001). Early general circulation models (GCM's) suggested that amount of winter and early-spring precipitation in desert regions of North America would remain relatively constant, but amounts of summer rainfall would increase (Taylor and Penner 1994). However, recent predictions indicate that amount of summer precipitation may actually remain relatively constant or slightly decline (Bell *et al.* 2004, Christensen *et al*. 2007, Meehl *et al.* 2007). Another global change phenomenon is increased nitrogen deposition. Nitrogen deposition has increased 10-fold since the late nineteenth century, nearly doubling total nitrogen input into terrestrial desert ecosystems downwind of major south-western cities in the USA (Smil 1990, Fenn and Bytnerowicz 1993, Vitousek *et al*. 1997, Galloway 1998, Galloway *et al*. 2004). Land use change is another global change phenomenon that has potential to alter ecosystem functions (Schlesinger *et al.* 1990). Off-road vehicles, grazing, and other uses destroy biological soil crusts (BSC) that are present at the surface of most desert soils (Belnap and Lange 2001, Belnap 2003). Land use changes that destroy BSCs tend to alter the hydrologic cycle and exacerbate the desertification process (Evans and Belnap 1999).

The Mojave Global Change Facility (MGCF) was created in 2001 as a long-term manipulative global change experiment designed to study responses of a natural Mojave Desert ecosystem to global change factors other than increasing CO_2. Manipulations at the MGCF involve: (1) increased summer monsoon rainfall; (2) increased nitrogen deposition; and (3) disturbance of BSCs. These global changes may interact in complex ways to affect the ecohydrology of the Mojave Desert. For example, how increased nitrogen deposition affects desert ecosystems may depend on patterns of water availability and plant response to increased nitrogen. The ability of BSC to fix nitrogen depends on precipitation patterns and could be negatively affected by nitrogen deposition. Thus, it is difficult to predict how a change in timing of precipitation events combined with nitrogen additions and BSC disturbance will affect the ecohydrology of the Mojave Desert.

The aim of the current study was to determine how the treatments imposed at the MGCF affect soil water content. We were particularly interested in how long the irrigation effect would persist into the following growing season. If water from summer irrigation treatments were to persist in the soil until the beginning of the next growing season, then summer monsoons would benefit nearly all plants in the ecosystem rather than benefit only evergreen and summer active species. We were also interested in soil water content for plots with and without BSC as this may be important for summer-active annual species and the BSC itself.

METHODS

Study site

The MGCF is located in the northern Mojave Desert within the boundaries of the Nevada Test Site (NTS), which is a U.S. Department of Energy facility. The NTS lies within Nye County, Nevada, U.S.A. (36°49′ N, 115°55′ W), approximately 90 km north-west of Las Vegas. Study plots are arrayed on a broad bajada (alluvial fan) along the southern end of Frenchman Flat at an elevation of 960-975 m. The bajada slopes 2-2.5% to the N-NNW. This area of the northern Mojave Desert has been closed to the public and to livestock grazing for over 50 years and consequently provides a secure and relatively undisturbed ecosystem.

The MGCF study area is characteristic of the northern Mojave Desert and is dominated by the evergreen shrub *Larrea tridentata* and several species of drought-deciduous shrubs (*Ambrosia dumosa*, *Lycium andersonii*, *Lycium pallidum,* and *Krameria erecta*). Other important species found at the MGCF include a C_3 bunchgrass (*Achnatherum hymenoides*), a C_4 bunchgrass (*Pleuraphis rigida*), a C_3 exotic annual grass (*Bromus madritensis* ssp. *rubens*), and a number of native C_3 winter annuals (most notably *Camissonia* spp., *Eriogonum* spp., and the grass *Vulpia octoflora*) (Turner and Randall 1989, Rundel and Gibson 1996). For all perennial species, plant density averages approximately 1 individual m^{-2}, plant cover 16%, and standing aboveground biomass 84 g m^{-2} (Turner and Randall 1987, Jordan *et al.* 1999). Up to 75 species of annual and perennial forbs may occur, depending on amount and seasonality of rainfall (Beatley 1974a, Beatley 1975, Beatley 1976, Jordan *et al.* 1999).

The northern Mojave Desert experiences low precipitation with average annual rainfall of ~150 mm. Winter rains account for the majority of annual precipitation (60-70%) and usually occur as widespread events that last up to several days. Summer storms generally occur in July and August and are often local, intense and unpredictable. All year long, relative humidity is low (< 20% is common), resulting in very high average annual potential evapotranspiration (PET). Temperatures are extreme regardless of season, with minimum winter temperature of -10° C and maximum summer temperature > 47°C. Large diurnal temperature fluctuations occur throughout the year (Smith and Nowak 1990, Smith *et al.* 1997). To characterize meteorological conditions, a weather station (Campbell Scientific Inc., Logan, UT, USA) was located at the center of the study area, and four data-logging tipping rain gauges (Onset Corp., Bourne, MA, USA) were located equidistant from each other throughout the study area.

Soil at the MGCF is an Aridisol derived from calcareous alluvium with sandy loam surface texture (sand 53%, silt 19%, clay 10%), 18% gravel content in the shallow A1 horizon (0–10 cm), and average bulk density in the A1 horizon of 1.23 g cm^{-3} (Meadows *et al.* 2006). Soils show very little development of discernable horizons, and caliche layers or any other layers that limit downward flux of water are absent (Jordan *et al.* 1999, Marion *et al.* 2008). Soil pH is alkaline, ranging from 8 to 9 at all depths (Jordan *et al.* 1999). Pinnacled BSCs are present at the soil surface throughout the MGCF with cover estimates ranging from 13–65% depending on available soil water (Jordan *et al.* 1999, Belnap *et al.* 2007).

Plot design

Individual study plots are 14 x 14 m (196 m^2). For each plot, a 16 x 16 m area was treated, which provided a 1-m wide treated buffer around the entire 14 x 14 m plot. The overall experiment involves a 2x2x3 factorial, completely-randomized block design with 8 replicates per treatment. Experimental treatments include two summer rainfall treatments (irrigated and non-irrigated; +/- I), two BSC disturbance treatments (disturbed crust and intact crust; +/- C), and three nitrogen deposition treatments (N applied at 0, 10, 40 kg-N ha^{-1} yr^{-1}; 0/10/40 N) and all two and three way combinations of these treatments for a total of 12 treatment combinations. Eight blocks with 12 plots per block are arrayed across the bajada, and each block contains all treatment combinations. Within each block, treatments were randomly assigned to individual plots. Within each plot, two walkways that are perpendicular to each other transect the plot, providing access within the plot.

Summer rainfall treatments were applied using a sprinkler system located in the center of each plot. Summer rainfall treatments consist of three applications of 25 mm each that are supplied at three week intervals during July and August, for total annual supplemental water treatment of 75 mm. Given that the site averages about 150 mm of rainfall per year with most occurring in winter months, this treatment represents a 50% increase in precipitation on an annual basis and a 3- to 5-fold increase in summer rain. Table 1.1 summarizes the total amount of natural precipitation received at the MGCF during the study period on a hydrologic year basis as well as the increase in precipitation due to the irrigation treatment. The irrigation treatment was applied at a rate that did not exceed the infiltration rate, and application occurred under still air conditions. Amount and uniformity of applied water was monitored and verified with randomly-placed rain gauges throughout MGCF plots and with a plot instrumented with collection cups on a 1 m grid. Water source for irrigation and fertilization treatments was analyzed in 2004-2005 and found to contain 3.95 mg L^{-1} of nitrate. Thus, MGCF plots received an additional 0.23 - 3.74 kg N ha^{-1} yr^{-1} depending on treatment due to the amount of nitrate in water used for irrigations and nitrogen fertilization.

BSC disturbance and nitrogen treatments were both applied in fall of each year. BSC disturbance involved repeated disruption of BSC by individuals scuffing their feet throughout a plot in a systematic fashion until no visible BSC was present. BSC disturbance was applied each fall prior to application of nitrogen deposition treatments and before germination of winter annuals. Nitrogen deposition treatments consisted of supplemental nitrogen at rates of 10 and 40 kg-N ha^{-1} yr^{-1}. These rates are slightly higher than rates of N deposition recorded for a site in southern Nevada and for a site east of Los Angeles (Fenn and Bytnerowicz 1993). Nitrogen was added as $CaNO_3$ in solution via sprinklers with a single application in late fall that used less than 10 mm of water (the same amount of water was also applied to all non-fertilized plots to ensure uniformity). Application of nitrogen in fall allows natural winter precipitation to move applied nitrogen down into the soil profile, where it then becomes available for plants. Under natural conditions, we recognize that nitrogen deposition occurs throughout the year, but in the Mojave Desert, this nitrogen would most likely stay near the soil surface until winter rains, which comprise 60-70% of the annual precipitation (Smith and Nowak 1990), move it into the soil profile. All three treatments (irrigation, BSC disturbance, and nitrogen addition) were initiated in 2001 and have continued to the present time.

Soil water measurements

Volumetric soil water content for each plot was monitored with a neutron probe (Model 503 Hydroprobe, Campbell Pacific Nuclear Corporation, Martinez, CA, USA). A 2-meter long neutron probe access tube was installed in a bare-ground area between plants near the center of each of the 96 MGCF plots. Neutron probe measurements began in March 2001 and have continued until present time; data from March 2001 to June 2006 are included in this paper. Neutron probe measurements typically were taken at 4-week intervals, except during summer irrigation treatments and following specific rainfall events when measurements occurred at shorter intervals to better characterize rates of water gain and loss. Measurements were made at 0.2 m soil depth and then at 0.2 m depth increments to a soil depth of 1.80 m. In addition to measurements at individual soil depths, we also determined the total amount of water (TSWC) in the soil profile from the surface to a depth of 1.90 m (i.e., half the 0.2 m depth increment past the 1.80 m depth reading) following procedures in Anderson *et al.* (1987) and Nowak *et al.* (2004).

Statistical analyses

We used two approaches to compare and analyze experimental data. The first approach analyzed the entire data set using longitudinal (time series) data analysis coupled with a radial smoothing technique (SAS Proc Glimmix, type = rsmooth) to model covariance for each plot through time (SAS 9.1, © SAS Institute 2002). The basic ANOVA model included all experimental treatments (+/- irrigation, +/- BSC, and 0/10/40 nitrogen additions) and their interactions. However to maximize predictive power of the radial smoothing model, we also included three continuous variables (cumulative precipitation between soil water measurement dates, time (days) since irrigation, and measurement date) and all interactions of these factors with themselves as well as with experimental treatment factors. We used two factors to describe time (days since irrigation, measurement date) because these factors actually describe two different aspects of soil water measurements. Days Since Irrigation (DSI) reflects a specific time of year regardless of the year of measurement because DSI is always referenced to the first irrigation, which occurred at the same time each year. Measurement date, on the other hand, reflects weather conditions that are unique to each year because “Date” is referenced to the calendar. Thus, a significant DSI factor implies significant effects during specific times of year, whereas a significant “Date” factor implies significant effects for a specific year.

The second data analysis approach divided data into time periods that focused either on sampling dates during summer irrigation treatments (July – August) or on sampling dates between irrigations (September – June). By splitting data in this manner, we were better able to focus on short-term effects of irrigation treatments on soil water dynamics and on effects of all experimental treatments on soil water dynamics. To maximize predictive power of these analyses, we also included two additional factors in the analyses: one continuous factor to account for cumulative precipitation between soil water measurements and one categorical factor to account for time during the data series (irrigation number for the first data set and month for the second). For detailed analyses of soil water responses during irrigation months (July – August), we omitted data from non-irrigated plots; in the absence of precipitation, soil water was extremely low and constant in non-irrigated plots, and variance was proportionally low, resulting in very unequal variances between irrigated and non-irrigated plots (thus preventing convergence of the statistical model). Nitrogen addition treatment, irrigation number (first, second or third), BSC disturbance, and precipitation were fixed effects. Random effects were block and plot. Detailed analysis of time periods between irrigations (September – June) included data from non-irrigated plots, and thus had the full complement of experimental treatments (+/- irrigation, +/- BSC, and 0/10/40 nitrogen addition). As with earlier analyses, cumulative precipitation between soil water measurements was included as a continuous factor. To account for time using an equally-spaced repeated measures analysis, we selected measurement dates that occurred at 4-week intervals since the last irrigation date.

For both approaches, total soil water over the 1.9 m soil profile and water content for each of the nine individual depths were analyzed. In all cases, we modeled data using a lognormal error distribution in Proc Glimmix (this method is equivalent to performing a log transformation on raw data to normalize distribution and running a Gaussian or normal model). For all analyses, random effects were blocks and plots, and we used the Random _residual_ option of Proc Glimmix (SAS 9.1, © SAS Institute 2002) to model covariance structure (either a spline fit for the radial smoother or an autoregressive model for repeated measures analyses). We considered $P \leq 0.05$ as significant, and mean comparisons for significant factors in ANOVAs were made with the "lsmeans/diff" command in SAS.

RESULTS

Time series analysis of entire dataset

When analyzing the entire dataset, we found no significant treatment main effects on soil water except for an irrigation effect on total soil water content (TSWC) and at 0.2 and 0.4 m depths (Table 1.2). Averaged over all 5 years of measurement, TSWC for irrigated plots (80mm) was 9 % greater than that for non-irrigated plots (73 mm). For 0.2 and 0.4 m depths, irrigated plots averaged 40% (+I = 3.64%, -I = 2.59%) and 24% (+I = 4.83%, -I = 3.88%) more soil water than non-irrigated plots, respectively. However, irrigation significantly interacted with Days Since Irrigation (DSI), Precipitation, DSI x Precipitation, Date, and Precipitation x Date for TSWC and individual depths (Table 1.2).

Significant I x DSI effects were due to greater soil water content on +I plots following irrigation treatments, but this irrigation effect decreased through time (Figure 1.1). The extent of the irrigation effect varied depending on amount of precipitation (I x Precipitation, I x DSI x Precipitation) (Table 1.2, Figure 1.1) such that precipitation reduced the difference in soil water content between +I and –I plots. Finally, significant I x Date and I x Date x Precipitation interaction terms suggest that the irrigation effect varies from year to year. These irrigation effects and interactions are discussed in more detail in the following sections. BSC and nitrogen treatments were not significant and did not have any significant interactions with any other factors (Table 1.2).

The continuous variables DSI, Precipitation, and Date were significant for TSWC or individual depths and sometimes significantly interacted with each other (Table 1.2). Because these are continuous factors, significant main effects indicate a general linear relationship between soil water content and the factor. For example, soil water content declines with days since irrigation for all experimental treatments, as expected. When two or more of these continuous factors significantly interact, soil water content has a multiple regression relationship with those factors. For example, the DSI x Precipitation interaction indicates that decline in soil water content with days since irrigation is influenced by how much precipitation occurred during the intervening time period.

One interesting aspect of the significant Date factor and its interaction with precipitation is the extent that soil water content varied from year to year (Figure 1.1). The greatest TSWC and longest period of wet soils occurred in October 2004 through July 2005 following an unusually large 38 mm precipitation event in October 2004. This large precipitation event was the only time that water permeated to 0.8 m depth and below. As seen in Figure 1.1, it took approximately seven months (October 2004 to May 2005) for soil water from this unusually large precipitation event to reach our deepest measurement depth. It is also interesting to note that an increasingly smaller amount of soil water reached each successive depth.

During summer irrigation treatments (July – August)

To focus on short-term effects of irrigation treatments, we narrowed our data to measurements immediately before, during, and immediately after irrigation treatments. Furthermore, because soil water content of non-irrigated plots was less than irrigated plots and did not change in the absence of precipitation, we excluded non-irrigated plots from this analysis. For TSWC and 0.2, 0.4, and 0.6 m depths, Irrigation Number (1, 2, or 3) was significant (Table 1.3, Figure 1.2). This significant irrigation number effect means that, as expected, soil water content increased with subsequent irrigations. For TSWC and 0.4 m depth, soil water content significantly increased with each successive irrigation. At 0.2 m depth, soil water content significantly increased from irrigation one to two but not from number two to number three (Figure 1.2). At 0.6 m depth, soil water content did not significantly increase between the first and second irrigations, but only between the second and third. This additive effect with subsequent irrigations results from water being driven deeper into the soil profile with each 25 mm irrigation event (wetting front increased from about 0.4 to 0.6 to 0.8 m from the first to third irrigation) (Figure 1.3). By the end of the third irrigation (mid-August), irrigated plots had approximately 40% more soil water in the entire 1.9 m soil profile than non-irrigated plots. Also by the end of the third irrigation, irrigated plots had approximately 3.3 and 1.3 times greater soil water content at 0.2 and 0.4 m depths respectively and 20% greater soil water content at 0.6 m depth (Figure 1.3).

One interesting finding from our analysis of irrigated plots during irrigations was a significant BSC effect for TSWC and 0.2, 0.4, and 0.6 m depths (Table 1.3, Figure 1.4) immediately following the third irrigation (measurement taken within 2-4 days after irrigation). Plots with intact BSC were wetter than plots with disturbed BSC (4%, 12%, 16%, and 6% for TSWC, 0.2, 0.4, and 0.6 m respectively). This BSC effect was short lived, and no significant differences were detected between plots with and without BSC at the next sampling date approximately 4 weeks after the third irrigation.

We are unable to adequately explain some significant factors and interactions that occur at deeper depths. Significant factors such as Nitrogen at 1.4 m depth and Nitrogen x Crust at 1.0 and 1.2 m depths are difficult to interpret because no depth above or below show a similar pattern (Table 1.3). These significant factors do not seem to be biologically relevant and may simply be due to transient fluctuations in soil water.

After summer irrigation treatments (September – June)

The irrigation factor was significant only for the 0.4 m depth (Table 1.4). However, the Irrigation x Month interaction term also was significant, which indicates that irrigated plots were significantly wetter than non-irrigated plots for only part of the time period (Figure 1.5). For 0.4 m depth, irrigated plots were significantly wetter than non-irrigated plots from immediately following irrigation only through October. For TSWC and at 0.6 m depth, irrigated plots were significantly wetter than non-irrigated plots only through October or November (Figure 1.5). No difference between irrigated and non-irrigated plots could be detected at 0.2 m depth, presumably due to rapid dry down of the top 0.2 m of soil after the conclusion of irrigations. Thus, irrigation effects on soil water content did not persist very late into the fall, and hence additional water was not available at the beginning of the next spring growing season, even at the deeper soil depths.

The ANOVA factor of Month was also significant (Table 1.4). For all measurement dates and across all treatment types for the top 0.6 m of soil, February, March, and April were months with more soil water, with March being the wettest. May and June were consistently drier months. For 0.8 m depth and below, many months did not differ from one another because soil water content at these depths is usually fairly constant throughout the year (Figures 1 and 3).

As with summer irrigation analyses, we are unable to adequately explain some significant factors and interactions that occur at deeper depths in our post-irrigation statistical analyses. Significant factors such as Nitrogen, Nitrogen x Crust, and Irrigation x Nitrogen x Crust at individual deeper depths are difficult to interpret because no depth above or below show a similar pattern (Table 1.4). Again, these significant factors do not seem to be biologically relevant and may simply be due to transient fluctuations in soil water.

DISCUSSION

Our results clearly show that summer irrigation treatments significantly increase soil water content during the irrigation period. In order for summer irrigation to influence arid land plant productivity and composition, species must be present that utilize additional available water. One study at the MGCF showed that *Larrea tridentata* increased rates of CO_2 assimilation on a leaf area basis and uses water from summer irrigation treatments (Barker *et al.* 2006). Several studies in the Chihuahuan Desert, where a significant natural monsoon weather pattern exists, have shown that *L. tridentata* shifts its' vegetative growth to take advantage of winter/spring or late summer monsoon precipitation, depending on when sufficient soil water is present (Cunningham *et al.* 1979, Fisher *et al.* 1988, Reynolds *et al.* 1999). Muldavin *et al.* (2008) showed that a C_4 grassland (which consisted mainly of black grama (*Bouteloua eriopoda*) along with other C_4 grasses, forbs, shallow rooted sub-shrubs, and CAM succulents) was very responsive to summer monsoon precipitation because annual net primary productivity peaked in the summer/fall period and only responded weakly to winter/spring precipitation. C_4 and CAM species are present at the MGCF (e.g., *Pleuraphis rigida* and *Opuntia ramosissima*) and can respond to increased summer monsoon precipitation. However, these species are only a small proportion of current vegetation (e.g., *Pleuraphis rigida* constitutes about 5% of total plant cover, unpublished data). In contrast, C_3 grasses, forbs, and sub-shrubs are particularly adept at taking advantage of soil water that is stored from winter precipitation during spring (March – May) before rising temperatures and drying soils limit C_3 photosynthesis (Kurc and Small 2004). Thus, potential for species composition shifts exists in the Mojave Desert if a significant amount of annual precipitation were to occur in summer months (i.e. return of the summer monsoon).

Another possible effect of the return of reliable summer monsoons would be to negatively affect reproductive success of the dominant shrub *L. tridentata*. Although fruit production in *L. tridentata* occurs mainly during the spring growing season and seems to be tied to photoperiod or temperature rather than soil water and nutrient content (Fisher *et* *al.* 1988), the relationship between seed germination and soil water is very important (Barbour 1968, Beatley 1974b, McGee and Marshall 1993). Soil water requirements for *L. tridentata* germination have been described as mesic, with too little or too much soil water being detrimental (Beatley 1974b, McGee and Marshall 1993). High germination rates occur when total precipitation from late September to June of the following year is between 80 and 150 mm (Beatley 1974b). If less than 80 mm or more than 150 mm of precipitation occur, germination rates will be less than 20%. However, Boyd and Brum (1983) show that a monthly total of at least 35 mm of precipitation triggers high germination events in August and September, but with low seedling survival. Consequently, reproductive success of *L. tridentata* is reduced by reduced rates of recruitment and depletion of its seed bank. Fortunately, these large precipitation events in August or September are rare in the Mojave Desert under current climate patterns, occurring only 5 out 41 years in Boyd and Brums' (1983) study area. A monthly precipitation total of at least 35 mm during August or September never occurred naturally at the MGCF over the 5-year period of our study, although it did occur in irrigated plots for three of five years during our experiment. Thus, if global warming results in increased summer precipitation similar to that in our irrigation treatments, then *L. tridentata* may experience reduced reproductive success.

In addition to intra-seasonal effects of summer irrigation, we were also interested if irrigation effects would persist in soil into the next growing season. If increased soil water from irrigation lasted into the next growing season (March – May), then C_3 plants in irrigated plots would most likely show increased production or reproduction. Our analyses of soil water following the last irrigation treatment indicated that irrigated plots were wetter than non-irrigated plots, but the duration of the effect only lasted until late fall (October or November), depending on depth in the soil profile (Figure 1.5). These results indicate that even deep-rooted C_3 perennial species, which use water early in the spring growing season (Cunningham *et al.* 1979, Fisher *et al.* 1988, Reynolds *et al.* 1999), are not likely to benefit greatly from the summer irrigation treatments.

A significant year-long effect of intact BSCs was not present in this data set. BSC treatment effects were only apparent among irrigated plots, with intact BSCs plots being slightly wetter for a brief period immediately following irrigations (within 2-4 days) for TSWC and 0.2, 0.4, and 0.6 m depths (Figure 1.4). No significant differences were detected between plots with and without BSC at approximately 4 weeks after the last irrigation treatment. Furthermore, differences detected between plots with and without BSCs were small. For example, TSWC of plots with intact BSC averaged 3.4 mm more water than plots without BSC, which only amounts to about 2% of average annual total precipitation. Crust disturbance by trampling, as used in our study, changes the structure of surface soils, thereby altering hydrologic characteristics of the soil (Eldridge 2003, Warren 2003). A conceptual model put forth by Belnap (2006) illustrates that pinnacled BSC, such as those present at the MGCF, increase surface area available for infiltration and increase soil water retention. Our data corroborates this conceptual model in that plots with intact soil BSCs absorbed more water or retained soil water longer than plots with disturbed BSCs at relatively short time scales (less than one month). Although plots with intact BSCs remain wetter for only a brief time, this finding may be important for summer-active annual plants during high water stress summer months.

The main effect of Nitrogen as well as interactions with other factors was significant at only a few depths during or after summer irrigation treatments (Tables 1.2, 1.3). As indicated in the results section, significant factors such as Nitrogen, Nitrogen x Crust, and Irrigation x Nitrogen x Crust at individual deeper depths are difficult to interpret because none of the depths above or below show a similar pattern (Tables 2, 3). In a similar study to the MGCF, Fisher *et al.* (1988) showed that *L. tridentata* had significantly more above-ground production in response to water and nitrogen additions. Presumably, this increase in above-ground production increases water use by *L. tridentata*, which translates to less water in the soil. At this time, we do not have production data for *L.tridentata* in our study plots that corroborate the findings of Fisher *et al.* (1988). Because our results do not indicate consistent Nitrogen or Nitrogen interaction effects, the observed significant factors may simply be due to transient fluctuations in soil water and do not seem to be biologically relevant.

The largest precipitation event (38 mm) that occurred during the sampling period happened in late October 2004. This large pulse event occurred in fall when evaporative demand is relatively low, which allowed water to percolate down to our deepest measurement depth (1.8 m). It is interesting to note that it took approximately seven months for soil water to reach our deepest measurement depth and that progressively less soil water reached subsequent depths until it was barely detectable at 1.8 m (Figure 1.1). In order for deep percolation of soil water to occur, annual precipitation must exceed annual evapotranspiration (ET) and water must move past the rooting zone of vegetation (Small 2005). Rooting zone for *L. tridentata* at MGCF reaches at least 6 m depth (Hartle *et al.* 2006). Thus, our data corroborates other studies (Phillips 1994, Yoder and Nowak

1999, Izbicki *et al.* 2000, Scanlon *et al.* 2005a, Scanlon *et al.* 2005b, Seyfried *et al.* 2005), which show that deep percolation of soil water in naturally vegetated arid or semi-arid landscapes occurs only under rare conditions.

Similar to other studies of soil water in the Mojave Desert and other arid environments, our evidence suggests that whatever water is present in the soil profile will be effectively used by vegetation (Anderson *et al.* 1987, Yoder and Nowak 1999, Huxman *et al*. 2004, Nowak *et al.* 2004). The top 0.6 m of soil showed dynamic changes in soil water over the five year sampling period. Precipitation events, irrigation treatments, evaporation, and transpiration all play important roles in determining the ecohydrology of this environment (Figure 1.1). With the exception of the pulse of soil water from the large October 2004 precipitation event, soil depths at or below 0.8 m remained relatively constant at approximately 4% soil water (Figure 1.1). These findings illustrate that Mojave Desert vegetation effectively removes soil water from the top 0.6 m of soil and are also capable of utilizing soil water at deeper depths (>0.6 m) as well.

In conclusion, this study has shown that in the Mojave Desert, predicted changes in climate (return of the summer monsoon) or land use (particularly BSC destruction) have potential to change plant production or species composition by altering the ecohydrology of the ecosystem. Water from simulated summer monsoons was largely used by plants or lost through evaporation by late fall, and increased soil water from summer irrigation did not persist into winter and spring and hence was not available to the spring-active, deeper-rooted plant species. In addition, intact BSCs have a very transitory influence on the ecohydrology of the MGCF, potentially benefiting plant species that are only active during late summer. Further, this study clearly shows that deep percolation of soil water is not occurring at the MGCF and that it is highly unlikely to occur unless climate or land use drastically changes.

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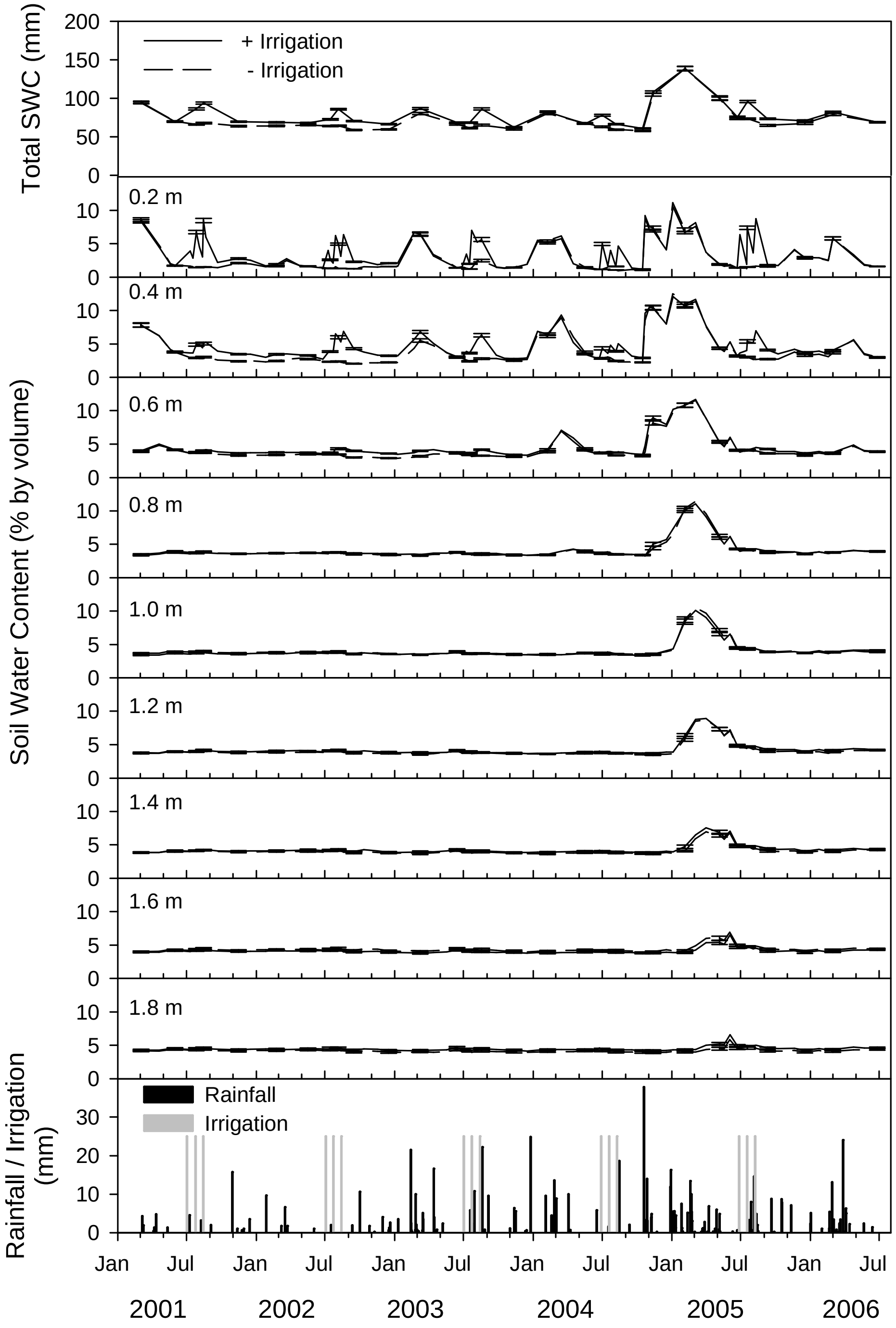

Figure 1.1. Total amount of water in soil profile (mm of water, top panel) and soil water content for each depth (% by volume, middle 9 panels) from March 2001 to June 2006 for summer irrigated (solid lines) and non-irrigated (dashed lines) treatments, averaged over all other treatments. Error bars are 1 SE. Bottom panel shows precipitation and irrigation events.

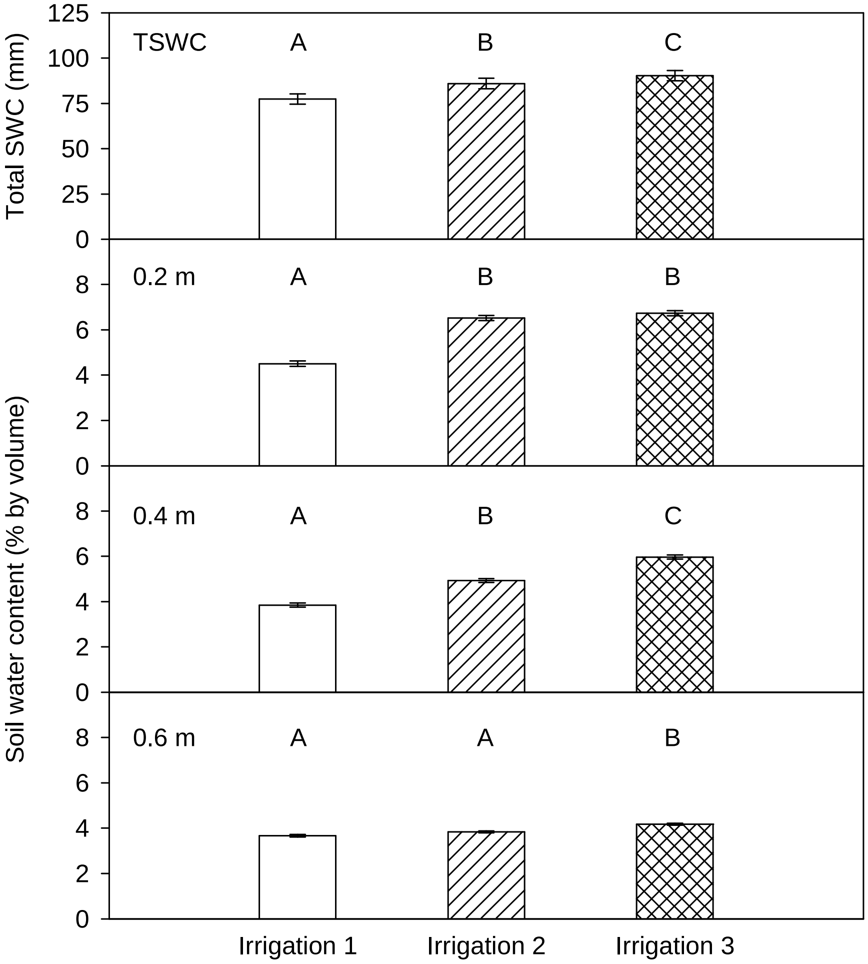

Figure 1.2. Total amount of water in soil profile (mm of water, top panel) and soil water content at 0.2, 0.4, and 0.6 m depths (% by volume, lower three panels) after first, second, and third summer irrigations. Data are from all irrigated plots (regardless of other treatments) immediately after each irrigation and averaged over 5 years of measurements. Bars with same letter are not significantly different ($P \leq 0.01$). Error bars are 1 SE.

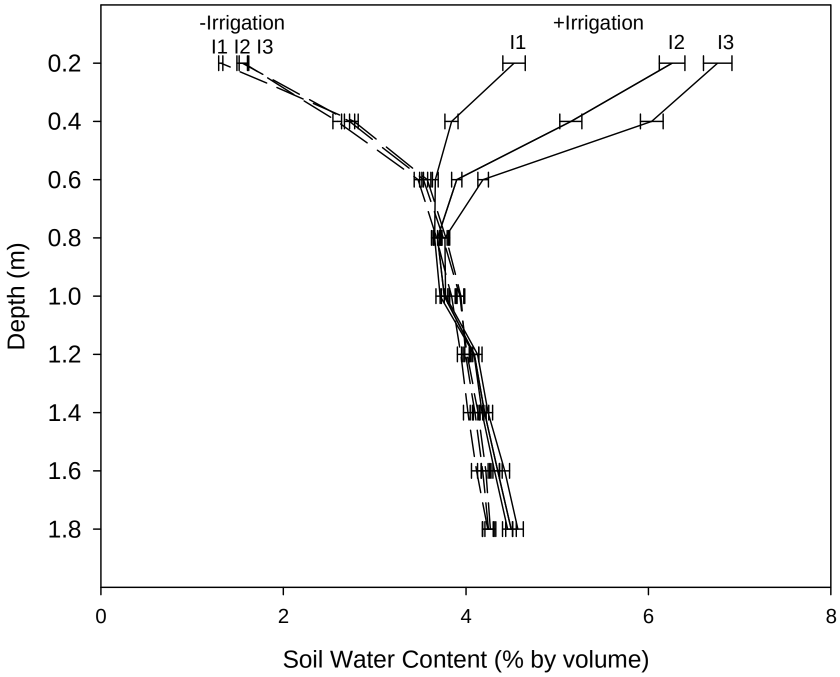

Figure 1.3. Depth profile of soil water content (% by volume) for irrigated (solid lines) and non-irrigated (dashed lines) plots following the first (I1), second (I2), and third (I3) irrigation treatments. Data are averaged over all other treatments and over 5 years of measurements. Error bars are 1 SE.

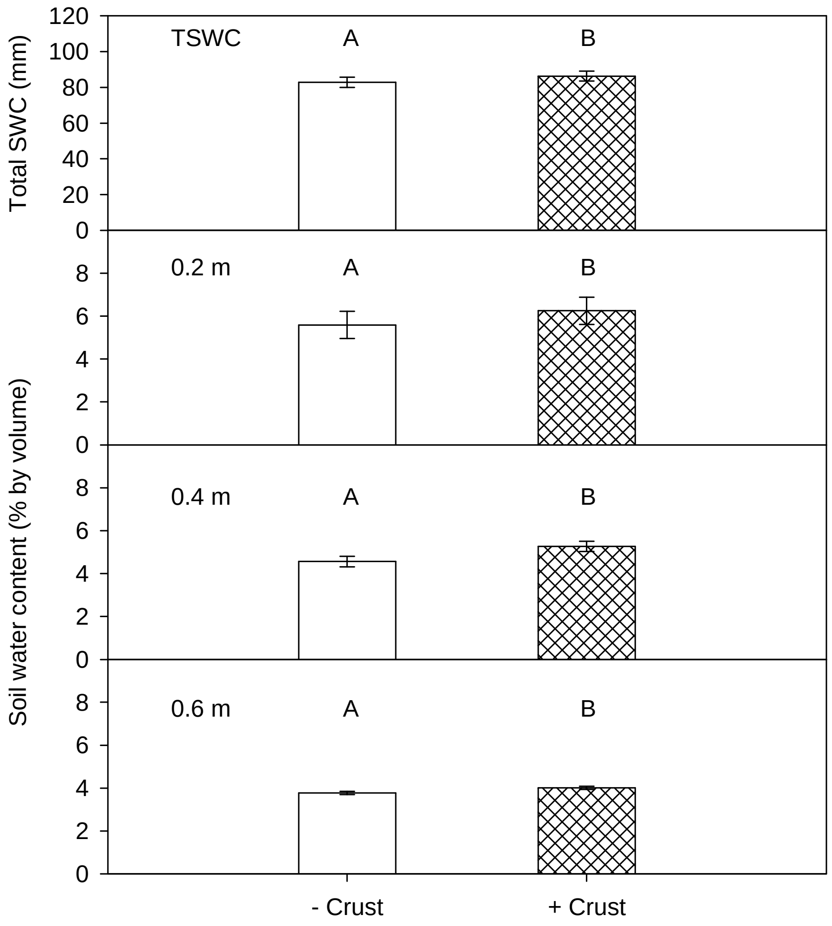

Figure 1.4. Total amount of water in soil profile (mm of water, top panel) and soil water content at 0.2, 0.4, and 0.6 m depths (% by volume, lower three panels) for plots with disturbed soil crust (-Crust, open bars) and with (+Crust) biological soil crust. Data are from all crust disturbance plots (regardless of other treatments) immediately after the third irrigation and averaged over 5 years of measurements. Bars with same letter are not significantly different ($P \leq 0.01$). Error bars are 1 SE.

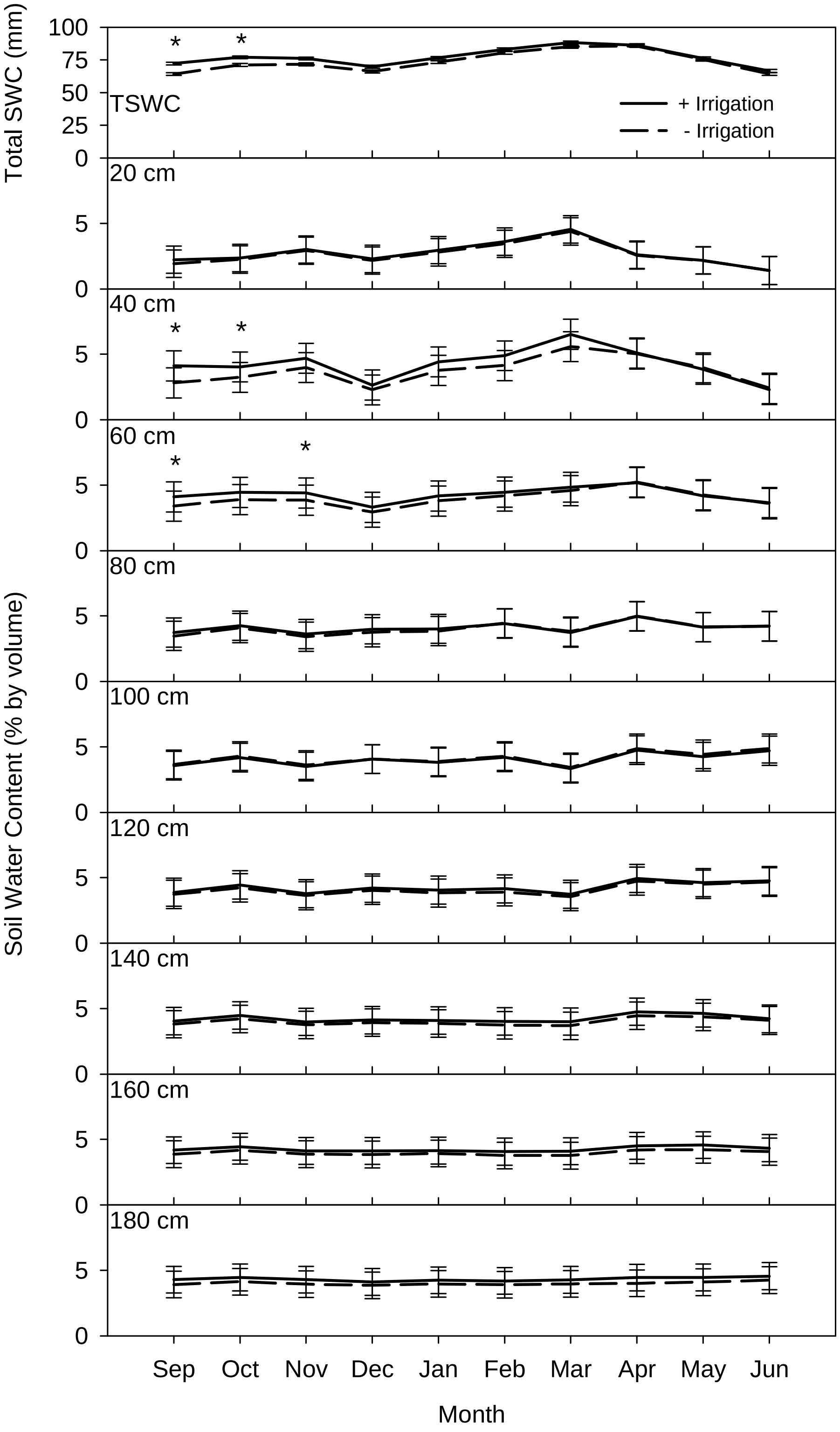

Figure 1.5. Total amount of water in soil profile (mm of water, top panel) and soil water content for each depth (% by volume, lower 9 panels) following the final summer irrigation for irrigated (solid lines) and non-irrigated (dashed lines) treatments, averaged over all other treatments and over 5 years of measurements. Asterisk denotes significant difference ($P \leq 0.01$) between irrigated and non-irrigated plots. Error bars are 1 SE.

Table 1.1. Natural precipitation (mm) and the percentage increase in precipitation from irrigations for each hydrologic year during the experiment. Hydrologic year is defined as October 1st through September 30th.

Hydrologic Year (Oct. 1 –Sep. 30)	Natural Precipitation (mm)	Increase in Precipitation From Irrigations (%)
2000-01	102	74
2001-02	47	160
2002-03	149	50
2003-04	123	61
2004-05	242	31
2005-06	113	66

Table 1.2. ANOVA tables for total soil water content (TSWC) and each individual depth (0.2-1.8 m) from March 2001 – June 2006. Data were analyzed with a longitudinal (time series) data analyses on the entire data set using a radial smoothing technique, where “days since irrigation” was the repeated measure and irrigation, nitrogen addition, and crust disturbance treatments were fixed effects. Random effects were block and plot. P values with $P \leq 0.05$ and their corresponding effects are bolded.

		TSWC		0.2 m		0.4 m		0.6 m		0.8 m		1.0 m		1.2 m		1.4 m		1.6 m		1.8 m	
Effect	ndf	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value
Irrigation (Irrig)	1	84	**0.044**	**84**	**<.001**	**84**	**0.003**	84	0.148	84	0.819	84	0.757	84	0.813	84	0.813	84	0.4865	84	0.440
Crust	1	84	0.859	84	0.618	84	0.875	84	0.632	84	0.646	84	0.948	84	0.529	84	0.499	84	0.563	84	0.212
Irrig*Crust	1	84	0.759	84	0.681	84	0.928	84	0.842	84	0.729	84	0.473	84	0.426	84	0.579	84	0.980	84	0.680
Nitrogen (N)	2	84	0.931	84	0.506	84	0.979	84	0.913	84	0.994	84	0.883	84	0.946	84	0.877	84	0.558	84	0.072
Irrig*N	2	84	0.984	84	0.538	84	0.989	84	0.992	84	0.975	84	0.987	84	0.934	84	0.886	84	0.854	84	0.722
Crust*N	2	84	0.967	84	0.911	84	0.921	84	0.923	84	0.875	84	0.729	84	0.930	84	0.974	84	0.576	84	0.529
Irrig*Crust*N	2	84	0.956	84	0.815	84	0.975	84	0.967	84	0.949	84	0.932	84	0.804	84	0.902	84	0.797	84	0.326
Days Since Irrigation (DSI)	1	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	7788	0.107
DSI*Irrig	1	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	7788	0.028	7788	0.793	7788	0.452	7788	0.810	7788	0.608	7788	0.256	7788	0.560
DSI*Crust	1	7788	0.314	7788	0.450	7788	0.325	7788	0.541	7788	0.686	7788	0.751	7788	0.970	7788	0.527	7788	0.455	7788	0.321
DSI*Irrig*Crust	1	7788	0.254	7788	0.385	7788	0.144	7788	0.449	7788	0.339	7788	0.599	7788	0.823	7788	0.789	7788	0.240	7788	0.154
DSI*N	2	7788	0.653	7788	0.739	7788	0.576	7788	0.684	7788	0.708	7788	0.509	7788	0.747	7788	0.793	7788	0.184	7788	0.137
DSI*Irrig*N	2	7788	0.592	7788	0.495	7788	0.887	7788	0.889	7788	0.942	7788	0.582	7788	0.662	7788	0.636	7788	0.906	7788	0.228
DSI*Crust*N	2	7788	0.888	7788	0.980	7788	0.564	7788	0.873	7788	0.849	7788	0.639	7788	0.718	7788	0.592	7788	0.061	7788	0.245
DSI*Irrig*Crust*N	2	7788	0.986	7788	0.977	7788	0.422	7788	0.917	7788	0.931	7788	0.855	7788	0.921	7788	0.826	7788	0.847	7788	0.608
Precipitation (Precip)	1	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**0.002**	7788	0.637	7788	0.106	7788	0.035	7788	0.208	**7788**	**0.01**
Precip*Irrig	1	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	7788	0.427	7788	0.277	7788	0.634	7788	0.730	7788	0.784	7788	0.799	7788	0.872
Precip*Crust	1	7788	0.510	7788	0.862	7788	0.494	7788	0.718	7788	0.575	7788	0.511	7788	0.861	7788	0.511	7788	0.924	7788	0.617
Precip*Irrig*Crust	1	7788	0.792	7788	0.936	7788	0.321	7788	0.312	7788	0.562	7788	0.374	7788	0.425	7788	0.664	7788	0.531	7788	0.504
Precip*N	2	7788	0.687	7788	0.777	7788	0.659	7788	0.289	7788	0.414	7788	0.925	7788	0.988	7788	0.871	7788	0.993	7788	0.663
Precip*Irrig*N	2	7788	0.845	7788	0.867	7788	0.951	7788	0.812	7788	0.529	7788	0.987	7788	0.375	7788	0.858	7788	0.862	7788	0.679
Precip*Crust*N	2	7788	0.924	7788	0.897	7788	0.991	7788	0.895	7788	0.688	7788	0.902	7788	0.967	7788	0.997	7788	0.709	7788	0.593
Precip*Irrig*Crust*N	2	7788	0.895	7788	0.828	7788	0.991	7788	0.897	7788	0.805	7788	0.999	7788	0.995	7788	0.962	7788	0.7990	7788	0.923
DSI*Precip	1	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	7788	0.676	7788	0.482	**7788**	**0.010**	7788	0.325	7788	0.513
DSI*Precip*Irrig	1	**7788**	**0.004**	**7788**	**<.001**	**7788**	**<.001**	7788	0.143	7788	0.146	7788	0.570	7788	0.609	7788	0.723	7788	0.911	7788	0.957
DSI*Precip*Crust	1	7788	0.223	7788	0.412	7788	0.293	7788	0.418	7788	0.685	7788	0.596	7788	0.970	7788	0.662	7788	0.995	7788	0.599
DSI*Precip*Irrig*Crust	1	7788	0.616	7788	0.964	7788	0.178	7788	0.174	7788	0.577	7788	0.549	7788	0.635	7788	0.641	7788	0.386	7788	0.485
DSI*Precip*N	2	7788	0.506	7788	0.709	7788	0.327	7788	0.243	7788	0.632	7788	0.833	7788	0.999	7788	0.821	7788	0.814	7788	0.533
DSI*Precip*Irrig*N	2	7788	0.612	7788	0.698	7788	0.910	7788	0.721	7788	0.571	7788	0.877	7788	0.319	7788	0.830	7788	0.770	7788	0.803
DSI*Precip*Crust*N	2	7788	0.879	7788	0.750	7788	0.983	7788	0.831	7788	0.813	7788	0.839	7788	0.994	7788	0.903	7788	0.492	7788	0.438
DSI*Precip*Irrig*Crust*N	2	7788	0.734	7788	0.891	7788	0.702	7788	0.698	7788	0.760	7788	0.991	7788	0.916	7788	0.887	7788	0.742	7788	0.976
Measurement date (Date)	1	**7926**	**<.001**	**8275**	**<.001**	7921	0.060	**7922**	**0.035**	**7917**	**<.001**	**7916**	**<.001**	**7916**	**<.001**	**7928**	**<.0001**	**7952**	**0.013**	8014	0.126
Date*Irrig	1	7926	0.749	**8275**	**<.001**	7921	0.381	7922	0.547	7917	0.938	7916	0.903	7916	0.925	7928	0.861	7952	0.817	8014	0.348
Date*Crust	1	7926	0.964	8275	0.470	7921	0.926	7922	0.953	7917	0.902	7916	0.875	7916	0.788	7928	0.839	7952	0.822	8014	0.145
Date*Irrig*Crust	1	7926	0.762	8275	0.871	7921	0.899	7922	0.846	7917	0.893	7916	0.668	7916	0.655	7928	0.689	7952	0.774	8014	0.543
Date*N	2	7926	0.982	8275	0.788	7921	0.979	7922	0.983	7917	0.978	7916	0.957	7916	0.954	7928	0.981	7952	0.940	8014	0.418

		TSWC		0.2 m		0.4 m		0.6 m		0.8 m		1.0 m		1.2 m		1.4 m		1.6 m		1.8 m	
Effect	ndf	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value
Date*Irrig*N	2	7926	0.998	8275	0.213	7921	0.987	7922	0.987	7917	0.993	7916	0.999	7916	0.931	7928	0.842	7952	0.948	8014	0.723
Date*Crust*N	2	7926	0.999	8275	0.926	7921	0.985	7922	0.993	7917	0.994	7916	0.979	7916	0.995	7928	0.989	7952	0.959	8014	0.906
Date*Irrig*Crust*N	2	7926	0.978	8275	0.729	7921	0.988	7922	0.999	7917	0.986	7916	0.978	7916	0.892	7928	0.968	7952	0.890	8014	0.765
DSI*Date	1	**7788**	**<.001**	**7788**	**0.040**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**0.008**	7788	0.156
DSI*Date*Irrig	1	7788	0.519	7788	0.463	7788	0.226	7788	0.364	7788	0.228	7788	0.147	7788	0.481	7788	0.893	7788	0.297	7788	0.449
DSI*Date*Crust	1	7788	0.887	7788	0.809	7788	0.731	7788	0.841	7788	0.780	7788	0.786	7788	0.766	7788	0.780	7788	0.996	7788	0.586
DSI*Date*Irrig*Crust	1	7788	0.758	7788	0.954	7788	0.520	7788	0.553	7788	0.364	7788	0.706	7788	0.898	7788	0.407	7788	0.675	7788	0.136
DSI*Date*N	2	7788	0.895	7788	0.986	7788	0.847	7788	0.894	7788	0.640	7788	0.488	7788	0.661	7788	0.674	7788	0.148	**7788**	**0.007**
DSI*Date*Irrig*N	2	7788	0.649	7788	0.686	7788	0.596	7788	0.912	7788	0.916	7788	0.871	7788	0.982	7788	0.996	7788	0.950	7788	0.062
DSI*Date*Crust*N	2	7788	0.798	7788	0.925	7788	0.967	7788	0.867	7788	0.712	7788	0.546	7788	0.477	7788	0.370	7788	0.340	7788	0.125
DSI*Date*Irrig*Crust*N	2	7788	0.892	7788	0.863	7788	0.926	7788	0.897	7788	0.983	7788	0.869	7788	0.694	7788	0.387	7788	0.991	7788	0.204
Precip*Date	1	7788	**<.001**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**<.001**	7788	0.746	7788	**<.001**	**7788**	**<.001**	**7788**	**<.001**	7788	0.066	7788	0.638
Precip*Date*Irrig	1	7788	**0.004**	**7788**	**<.001**	**7788**	**<.001**	**7788**	**0.029**	7788	0.059	7788	0.497	7788	0.370	7788	0.406	7788	0.928	7788	0.620
Precip*Date*Crust	1	7788	0.472	7788	0.934	7788	0.441	7788	0.676	7788	0.506	7788	0.479	7788	0.557	7788	0.450	7788	0.890	7788	0.508
Precip*Date*Irrig*Crust	1	7788	0.922	7788	0.747	7788	0.601	7788	0.302	7788	0.613	7788	0.274	7788	0.300	7788	0.323	7788	0.461	7788	0.459
Precip*Date*N	2	7788	0.484	7788	0.623	7788	0.523	7788	0.272	7788	0.301	7788	0.957	7788	0.898	7788	0.658	7788	0.795	7788	0.586
Precip*Date*Irrig*N	2	7788	0.750	7788	0.753	7788	0.903	7788	0.736	7788	0.480	7788	0.996	7788	0.326	7788	0.692	7788	0.946	7788	0.503
Precip*Date*Crust*N	2	7788	0.887	7788	0.884	7788	0.995	7788	0.882	7788	0.609	7788	0.954	7788	0.804	7788	0.994	7788	0.853	7788	0.600
Precip*Date*Irrig*Crust*N	2	7788	0.857	7788	0.795	7788	0.961	7788	0.962	7788	0.899	7788	0.969	7788	0.955	7788	0.892	7788	0.810	7788	0.933
DSI*Precip*Date	1	7788	**<.001**	**7788**	**<.001**	**7788**	**<.001**	7788	0.071	7788	0.361	7788	0.013	**7788**	**0.024**	**7788**	**0.010**	7788	0.148	7788	0.238
DSI*Precip*Date*Irrig	1	7788	0.278	7788	0.570	7788	0.120	7788	0.719	7788	0.767	7788	0.577	7788	0.558	7788	0.329	7788	0.493	7788	0.922
DSI*Precip*Date*Crust	1	7788	0.532	7788	0.670	7788	0.724	7788	0.695	7788	0.957	7788	0.613	7788	0.814	7788	0.801	7788	0.418	7788	0.479
DSI*Precip*Date*Irrig*Crust	1	7788	0.755	7788	0.993	7788	0.938	7788	0.635	7788	0.920	7788	0.694	7788	0.766	7788	0.599	7788	0.483	7788	0.755
DSI*Precip*Date*N	2	7788	0.553	7788	0.667	7788	0.801	7788	0.724	7788	0.801	7788	0.980	7788	0.768	7788	0.748	7788	0.749	7788	0.289
DSI*Precip*Date*Irrig*N	2	7788	0.744	7788	0.688	7788	0.991	7788	0.965	7788	0.866	7788	0.980	7788	0.729	7788	0.948	7788	0.785	7788	0.837
DSI*Precip*Date*Crust*N	2	7788	0.957	7788	0.976	7788	0.923	7788	0.979	7788	0.941	7788	0.905	7788	0.994	7788	0.995	7788	0.918	7788	0.652
DSI*Precip*Date*Irrig*Crust*N	2	7788	0.834	7788	0.834	7788	0.809	7788	0.903	7788	0.932	7788	0.981	7788	0.918	7788	0.884	7788	0.757	7788	0.990

Table 1.3. ANOVA tables for total soil water content (TSWC) and each individual depth (0.2-1.8 m) for subset of data only from irrigated plots during July and August (i.e. during summer irrigation treatment period) in 2001 - 2005. Data were analyzed with a mixed model repeated measures analyses, where nitrogen addition, irrigation number (first, second or third), and crust disturbance were fixed effects. Random effects were block and plot.

		TSWC		0.2 m		0.4 m		0.6 m		0.8 m		1.0 m		1.2 m		1.4 m		1.6 m		1.8 m	
Effect	ndf	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value
Irrigation # (Irrig)	2	**126**	**<.001**	**126**	**<.001**	**126**	**<.001**	**126**	**<.001**	126	0.601	126	0.869	126	0.963	126	0.892	126	0.789	126	0.848
Nitrogen (N)	2	126	0.708	126	0.985	126	0.421	126	0.5728	126	0.148	126	0.162	126	0.392	**126**	**0.030**	126	0.154	126	0.312
Irrig*N	4	126	0.988	126	0.997	126	0.917	126	0.873	126	0.997	126	0.990	126	0.995	126	0.999	126	0.998	126	0.999
Crust	1	**126**	**0.007**	**126**	**0.009**	**126**	**<.001**	**126**	**0.009**	126	0.632	126	0.508	**126**	**0.004**	126	0.385	126	0.608	126	0.414
Irrig*Crust	2	126	0.981	126	0.939	126	0.776	126	0.536	126	0.986	126	0.957	126	0.989	126	0.866	126	0.977	126	0.985
N*Crust	2	126	0.376	126	0.672	126	0.936	126	0.169	126	0.242	**126**	**<.001**	**126**	**0.005**	126	0.181	126	0.143	126	0.896
Irrig*N*Crust	4	126	0.993	126	0.918	126	1.000	126	0.955	126	0.999	126	0.999	126	0.972	126	0.994	126	0.997	126	0.999
Precipitation (Precip)	1	**575**	**<.001**	**575**	**<.001**	575	0.175	575	0.396	**575**	**0.001**	**575**	**<.001**	**575**	**<.001**	**575**	**<.001**	**575**	**0.003**	**575**	**<.001**

Table 1.4. ANOVA tables for total soil water content (TSWC) and each individual depth (0.2-1.8 m) for subset of data only from September - June (i.e. after third summer irrigation treatment) in 2001 - 2006. Data were analyzed with a mixed model repeated measures analyses, where “months since irrigation” (month) was the repeated measure, and nitrogen addition, irrigation, and crust disturbance treatments were fixed effects. Random effects were block and plot.

		TSWC		0.2 m		0.4 m		0.6 m		0.8 m		1.0 m		1.2 m		1.4 m		1.6 m		1.8 m	
Effect	ndf	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value
Irrigation (Irrig)	1	84	0.071	84	0.925	**84**	**0.021**	84	0.115	84	0.758	84	0.463	84	0.148	84	0.082	84	0.068	84	0.083
Months since irrigation (Month)	9	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**
Irrig*Month	9	3635	0.069	3635	0.275	**3635**	**<.001**	3635	0.064	3635	0.101	3635	0.971	3635	0.993	3635	0.719	3635	0.475	**3635**	**0.020**
Nitrogen (N)	2	84	0.362	84	0.468	84	0.547	84	0.861	84	0.688	84	0.465	84	0.370	84	0.477	84	0.207	84	0.146
Irrig*N	2	84	0.752	84	0.681	84	0.168	84	0.853	84	0.964	84	0.741	84	0.675	84	0.489	84	0.874	84	0.705
Month*N	18	3635	0.485	3635	0.741	3635	0.912	3635	0.858	3635	0.902	3635	0.987	3635	0.759	3635	0.929	3635	0.681	3635	0.740
Irrig*Month*N	18	3635	0.994	3635	0.997	3635	0.905	3635	0.999	3635	0.985	3635	0.999	3635	0.996	3635	0.989	3635	0.998	3635	0.709
Crust	1	84	0.477	84	0.138	84	0.185	84	0.169	84	0.422	84	0.765	84	0.153	84	0.505	84	0.847	84	0.623
Irrig*Crust	1	84	0.947	84	0.586	84	0.640	84	0.985	84	0.805	84	0.831	84	0.639	84	0.674	84	0.534	84	0.903
Month*Crust	9	3635	0.541	3635	0.256	3635	0.525	3635	0.486	3635	0.799	3635	0.992	3635	0.937	3635	0.648	3635	0.942	3635	0.110
Irrig*Month*Crust	9	3635	0.986	3635	0.998	3635	0.953	3635	0.777	3635	0.893	3635	0.929	3635	0.607	3635	0.921	3635	0.967	3635	0.999
N*Crust	2	84	0.512	84	0.639	84	0.392	84	0.121	84	0.151	84	0.023	84	0.195	84	0.778	84	0.315	84	0.441
Irrig*N*Crust	2	84	0.645	84	0.895	84	0.886	84	0.793	84	0.444	84	0.811	84	0.103	84	0.185	84	0.579	84	0.370
Month*N*Crust	18	3635	0.962	3635	0.999	3635	0.999	3635	0.735	3635	0.969	3635	0.981	3635	0.937	3635	0.989	3635	0.555	3635	0.610
Irrig*Month*N*Crust	18	3635	0.999	3635	1.000	3635	0.996	3635	0.998	3635	0.991	3635	0.999	3635	0.936	3635	0.939	3635	0.936	3635	0.785
Precipitation	1	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**<.001**	**3635**	**0.007**	3635	0.540	3635	0.305	3635	0.083	3635	0.177	**3635**	**<.001**

CHAPTER 2

Sap flow of *Larrea tridentata* in response to three global climate change factors.

ABSTRACT

Larrea tridentata is one of the most abundant and widespread perennial plants in deserts of southwestern North America. Effects of simulated global climate change on sap flow of *L. tridentata* in a natural Mojave Desert ecosystem were measured over two years. Global change treatments were summer irrigations that imitated a northward shift of summer monsoons associated with global warming, nitrogen additions that imitated increased nitrogen deposition from anthropogenic sources, and biological crust destruction that imitated disturbance from increased land use. Averaged over all treatments, *L. tridentata* exposed to summer irrigation treatments have significantly greater sap flow than plants in non-irrigated plots. This irrigation effect lasts approximately seven weeks after the last irrigation when a transition is made and plants in non-irrigated plots begin to have significantly greater sap flow until the irrigations of the following year. Not only is *L. tridentata* able to respond to an increase in soil water during the hot summer months, but evidence is also presented that suggests *L. tridentata* has an additional physiological response to the increase in soil water within a two week period. *L. tridentata* plants exposed to the highest nitrogen addition consistently had the greatest rates of sap flow. The effect of the biological soil crust treatment on sap flow of *L. tridentata* was variable and dependant on interactions with the irrigation and nitrogen treatments. These results demonstrate that predicted impacts of global changes have the

potential to have important feedbacks on primary production of *L. tridentata* and consequently the Mojave Desert as a whole.

INTRODUCTION

Larrea tridentata, an evergreen xerophytic shrub, is one of the most abundant and widespread perennial plants in deserts of southwestern North America. The abundance, distribution, and growth habit of *L. tridentata* in these deserts is influenced by its' adaptations to the xeric environment. The most important adaptations are those that help *L. tridentata* cope with low amounts of available soil water (Oechel *et al.* 1972).

Numerous studies have investigated physiological adaptations that allow *L. tridentata* to thrive in xeric habitats (Runyon 1934, Odening *et al.* 1974, Meinzer *et al.* 1986, Meinzer *et al.* 1988, Sharifi *et al.* 1988, Hyder *et al.* 2002). These adaptations include a high protoplasmic tolerance to water stress, high net photosynthesis rates at low water potentials (Odening *et al.* 1974), and the ability to maintain a constant turgor pressure over a broad range of leaf water potentials (Meinzer *et al.* 1986). *L. tridentata* also has various morphological adaptations to xeric environments. These morphological adaptations include a resinous coating on outside layers of palisade cells and lining the stomatal cavity, lip formation on guard cells that reduces the external aperture and matting of the epidermal hairs in the cuticular resin to form a leaf coating both of which limit stomatal conductance, and the presence of a thick, compact layer of palisade tissue with few spongy mesophyll cells and intercellular spaces that limits internal gas exchange

(Dalton 1962, Sharifi *et al.* 1988, Hyder *et al.* 2002). All of these factors, and possibly others, combine to allow *L. tridentata* to thrive under drought conditions.

Although many studies have examined morphological and physiological adaptations of *L. tridentata* to low soil water availability, relatively few have studied responses of *L. tridentata* to global climate or land use changes. Global climate and land use changes have the potential to affect precipitation patterns, nitrogen deposition, biogeochemical cycling (Schlesinger *et al.*, 1990), and the length of the growing season (Cleeland *et al.* 2006). It is unknown how these global climate and land use changes will affect the ecology of *L. tridentata*.

The Mojave Desert climate is currently dominated by winter rains and sporadic summer monsoon thunderstorms. The Mojave Desert in southern Nevada and southeastern California in the driest desert of North America (Smth *et al.* 1997). Early general circulations models (GCM's) indicated that climate change would alter precipitation patterns (Easterling *et al.* 2000, NAST 2000, IPCC 2001). Predictions for the desert southwest United States indicated that winter and early spring precipitation would remain relatively constant, but summer monsoon thunderstorms would increase precipitation during the hottest months of the year (Taylor and Penner 1994). However, more recent GCM predictions indicate that summer precipitation may remain closer to historic averages or slightly decline (Bell *et al.* 2004, Christensen *et al.* 2007, Meehl *et al.* 2007). Increased nitrogen deposition is another global change phenomenon. Nitrogen deposition has steadily increased since the late nineteenth century, particularly in terrestrial desert ecosystems downwind of major southwestern cities of the USA (Smil, 1990; Fenn *et al*., 1993; Vitousek *et al*., 1997; Galloway, 1998; Galloway *et al*., 2004).

Another global change that has the potential to alter ecosystem function is land use changes (Schlesinger *et al.* 1990). Off-highway vehicles (OHV's), grazing, and other uses can potentially destroy biological soil crusts (BSC) that are present at the surface of most desert soils. BSC has been shown to be a critical component of most desert ecosystems by fixing atmospheric nitrogen and increasing water infiltration, which can alter the nutrient and hydrologic cycles (Evans and Belnap 1999, Belnap and Lange 2001, Belnap 2003, Belnap *et al.* 2007).

The Mojave Global Change Facility (MGCF) is a long-term manipulative global change experiment designed to study responses of an undisturbed Mojave Desert ecosystem to select global change factors. Manipulations at the MGCF involve the potential effects of (1) increased summer monsoon rainfall associated with global climate change, (2) increased nitrogen deposition that would occur near major cities, and (3) disturbance of N-fixing BSC intended to mimic land-use changes such as grazing and off-road recreational use.

The aim of the current study was to determine how transpiration of *L. tridentata* responds to treatments imposed at MGCF. Specifically, we hypothesized that *L. tridentata* would have the highest rates of daily mean transpiration when exposed to the combination of irrigation, N addition, and disturbed soil crust. We know from previous studies (Fisher *et al.* 1988, Lajtha and Whitford 1989) that desert vegetation is very adept at using any available soil water, and thus we would expect an increase in sap flow in response to the summer irrigation treatment. We also expected increased sap flow from the nitrogen addition treatments because increased N usually increases leaf area or the number of leaves, which in turn increases available conductive surface area for sap flow

(Fisher *et al.* 1988, Lajtha and Whitford 1989). We also know that BSC can act as a barrier to soil water evaporation (Barger *et al.* 2005, Belnap *et al.* 2007) for brief periods of time, and thus *L. tridentata* in disturbed plots would have greater rates of sap flow because these plants are expected to use soil water as quickly as possible.

METHODS

Study site

The MGCF (36°49′ N, 115°55′ W; altitude 960-975m) is located 90 km north-west of Las Vegas, Nevada within the boundaries of the Nevada Test Site (NTS), a Department of Energy facility. This area of the northern Mojave Desert has been closed to the public and to livestock grazing for over 50 years and consequently provides a secure and relatively undisturbed ecosystem. Vegetation at the MGCF is characteristic of the northern Mojave Desert and consists of perennial and annual forbs and grasses and perennial shrubs. The landscape is dominated by the evergreen shrub *Larrea tridentata* and several species of drought-deciduous shrubs (e.g., *Ambrosia dumosa*, *Lycium andersonii* and *Lycium pallidum*). Across all perennial species, plant density averages approximately 1 individual m^{-2}, plant cover 16%, and standing aboveground biomass 84 g m^{-2} (Turner and Randall 1989). Up to75 species of annual and perennial forbs may occur, depending on amount and seasonality of rainfall (Beatley 1974, Beatley 1975, Beatley 1976).

Mean annual precipitation at the MGCF is ~ 150 mm. Winter rains account for the majority of annual precipitation (60-70%) and typically occur as widespread precipitation events. Summer monsoon storms generally occur in July and August and are usually local, intense and sporadic. Water is the primary limitation to plant growth in the Mojave Desert (Turner & Randall, 1989; Smith *et al.*, 1997). Relative humidity is low (< 20% is common), resulting in very high potential evaporation. Temperatures are extreme regardless of the season (winter -10° C; summer > 47°C), and large diurnal temperature fluctuations occur throughout the year (Smith and Nowak 1990). To help characterize environmental conditions, a weather station (Campbell Scientific Inc., Logan, UT, USA) is located at the center of the study area and four rain tipping gauges (Onset Corp., Bourne, MA, USA) are placed equidistant from each other throughout the study area.

Soils at the MGCF plots are Aridisols comprised of loamy to coarse sands derived from calcareous alluvium. Soils show very little development of discernable horizons, and no caliche layers or any other layers that limit the downward flux of water are present (Jordan *et al.* 1999, Marion *et al.* 2008). Soils are characterized by spatial heterogeneity in nutrients, and soil pH ranges from 8 to 9 across all depths to 1 m (Romney *et al.* 1980, Titus *et al.* 2002 Jordan *et al.* 1999). Pinnacled BSCs are present at the soil surface throughout the MGCF with cover estimates ranging from 13–65% (Jordan *et al.* 1999, Belnap *et al.* 2007).

Plot design

Permanent, individual study plots at the MGCF are 14 x 14 m (196 m^2). Treatments for each plot are applied to a 16 x 16 m area, which provides a 1-m wide treated buffer around the entire 14 x 14 m plot. The overall experiment involves a 2x2x3 factorial, completely-randomized block design with 8 replicates per treatment. However, for the purposes of this study, only two blocks were utilized. Experimental treatments include two summer rainfall treatments (irrigated and non-irrigated; +/- I), two BSC disturbance treatments (intact crust and disturbed crust; +/- C), and three nitrogen deposition treatments (N applied at 0, 10, and 40 kg-N ha^{-1} yr^{-1}; 0N/10N/40N) and all two and three way combinations of these treatments for a total of 12 treatment combinations. To minimize disturbance to the soil surface, two walkways that are perpendicular to each other transect the plot and strategically-placed stepping stones provide access within the plot.

Summer rainfall treatments are applied using an oscillating sprinkler system located in the center of each plot. Summer rainfall treatments are supplied at three week intervals during July and August and consist of three applications of 25 mm each for a total annual supplemental water treatment of 75 mm. Given that the site averages about 150 mm of rainfall per year with most occurring in winter months, this treatment represents a 50% increase in precipitation on an annual basis and a 3- to 5-fold increase in summer rain. Water is applied under still air conditions and at a rate that does not exceed the infiltration rate. Water source for irrigation and fertilization treatments was analyzed in 2004-2005 and found to contain 3.95 mg L^{-1} of nitrate. Thus, MGCF plots received an additional 0.23 - 3.74 kg N ha^{-1} yr^{-1} depending on treatment due to the amount of nitrate in water used for irrigations and nitrogen fertilization.

BSC disturbance and nitrogen treatments are both applied in fall of each year. BSC disturbance involves disruption of BSC by individuals scuffing their feet throughout a plot in a systematic fashion until the entire soil surface has been disturbed. BSC disturbance is performed each fall (usually in October) prior to application of nitrogen deposition treatments and before germination of winter annuals. Nitrogen deposition treatments consist of supplemental nitrogen at rates of 0 (0N), 10 (10N) and 40 (40N) kg-

N ha^{-1} yr^{-1}. The 10N and 40N rates are meant to simulate typical and maximum, respectively, observed rates and are similar to rates of N deposition recorded for a site in southern Nevada and for a site east of Los Angeles (Fenn and Bytnerowicz 1993). Nitrogen was added as $CaNO_3$ in solution via the oscillating sprinkler system with a single application in late fall that used less than 10 mm of water (the same amount of water was also applied to all non-fertilized plots to ensure uniformity of water application). Application of nitrogen in fall allows natural winter precipitation to move applied nitrogen down into the soil profile, where it then becomes available for plants. All three treatments (irrigation, BSC disturbance, and nitrogen addition) were initiated in 2001 and have continued to the present time.

Sap flow measurements

In May 2004, an 8-12 mm sap flow sensors (EMS Inc., Turisticka, Brno, Czech Republic) were installed on each of three *Larrea tridentata* individuals in each plot of two complete blocks (72 total sensors). Sap flow sensors operated on the stem heat balance principle at a constant temperature differential (4° C) (Cienciala and Lindroth 1995, Lindroth *et al.* 1995). Sensors were placed on the smoothest section of a stem that was at least 20 cm long and as far as possible from the ground to reduce the effect of any temperature gradient at the ground surface (Grime and Sinclair 1999). Once sensors were installed, they were covered with a reflective Mylar shield (supplied by sensor manufacturer) to protect the sensor from weather as well as act as an insulator from the aforementioned temperature gradient. Sap flow data were collected every 10 minutes using data loggers (EMS Inc., Turisticka, Brno, Czech Republic), and the daily mean for each sensor were calculated. Sensors were allowed to run continuously until November 2005. However, due to the precarious nature of sap flow sensors, sensor and data logger malfunctions as well as installation errors led to missing or incomplete data throughout the measurement period. Unfortunately, these missing time periods precluded statistical analyses that followed an individual plant or an individual plot. Thus, sap flow data was averaged for each plot, then over both plots to calculate sap flow for each treatment.

Leaf area measurements

Because the long-term nature of the MGCF study precluded destructive harvest of branches or leaves from our study plants, we estimated leaf area using the integrating sphere method (Serrano *et al.* 1997). We measured leaf area of each branch with a sap flow sensor three times during the study to monitor changes in leaf transpirational area. We also measured the cross-sectional area of each branch with a sap flow sensor using calipers. Based on previous studies (Pataki *et al.* 2000), we assumed the entire cross-sectional area of each branch was conductive sapwood. Sap flow measurements were expressed on a transpirational surface-area basis (J_s, $g*m^{-2}*sec^{-1}$) using our calculations of daily mean sap flow in combination with our leaf area measurements.

Statistical analyses

In order to test effects of irrigation, BSC disturbance, and nitrogen additions on sap flow rates at different times of the year, we split data into a pre-irrigation time period (21 May – 27 June 2004 and 2005), an irrigation period (28 Jun – 28 Aug 2004 and 2005), a post-irrigation period (29 Aug – 16 Oct 2004 and 2005), and a rest of year period (17 Oct 2004 – 20 May 2005). The beginning date of the pre-irrigation period (21 May 2004) was chosen because it corresponded to the date when the majority of sap flow sensors were operational after installation. Irrigation time period dates were chosen to include each irrigation and its' corresponding three week interval, that allowed us to focus on immediate and short-term irrigation effects. Post-irrigation time periods began three weeks after the last irrigation and ended before the majority of the winter rains began. These post-irrigation periods allowed us to monitor how long the irrigation effects lasted before being influenced by winter rains. The rest of year time period dates were simply the remaining dates between the post and pre-irrigation dates, but analysis of data from this time period also allow us to evaluate the effect of the winter rains on sap flow. To help data conform to assumptions of analysis of variance (ANOVA), we used SAS Proc Transreg (SAS 9.1, © SAS Institute 2002) to determine the most appropriate lambda parameter of the Box-Cox transformation for each data set. For each of the time periods, we used a radial smoothing technique (SAS Proc Glimmix, type = rsmooth) to model covariance for each plot through time (SAS 9.1, © SAS Institute 2002). The basic ANOVA model included all experimental treatments (+/- irrigation, +/- BSC, and 0/10/40 nitrogen additions) and their interactions. However to maximize predictive power of the radial smoothing model, we also included two continuous variables (time (days) since irrigation and year) and all interactions of these factors with themselves as well as with experimental treatment factors. We used days since irrigation (DSI) to reflect a specific time of year regardless of the year of measurement because DSI is always referenced to the first irrigation, which occurred on the same date each year. We also ran statistical analyses for each time period with soil water as an additional covariate to discern how much of the irrigation response could be accounted for simply by changes in soil water. Mean comparisons for significant factors in ANOVAs were made with the "lsmeans/diff" command in SAS with a Tukey adjustment for multiple comparisons. Because large sample sizes and many sampling dates led to high denominator degrees of freedom for F tests, $P \leq 0.01$ was considered significant.

RESULTS

Irrigation treatment effects

During the irrigation period in both 2004 and 2005, sap flow was significantly greater for plants in irrigated plots compared to plants in non-irrigated plots when averaged over all other factors (Irrigation main effect in Table 2.1A, Figure 2.1). However, the significant Irrigation x DSI interaction (Table 2.1A) indicates that this increase in sap flux occurred within 2 days after the irrigation treatment began. When the statistical models are re-run with soil water as a covariate (Table 2.1B), significant differences between irrigation treatments take longer to occur (7-14 days after the first irrigation), suggesting that the increase in sap flow within 2 days after the first irrigation is primarily a plant response to increased soil water and that an additional plant response occurs to increase sap flow over a 1-2 week time period. The Irrigation effect also significantly interacted with other main effects, especially Crust (Table 2.1A, B), but in nearly all cases the interaction did not alter the overall effect of irrigated plots having greater sap flow than non-irrigated plots.

During the post-irrigation period, the overall Irrigation effect continued to be significant with plants in irrigated plots having greater sap flow than plants in non-irrigated plots (Table 2.1C, Figure 2.1). However, the Irrigation effect became not significant as time passed for both statistical models with and without soil water.

Approximately 7 weeks after the last irrigation (late September), the Irrigation effect was no longer statistically detectable (Figure 2.1). Irrigation also interacted with other factors such as Year, Crust x Year and Nitrogen x Year (Table 2.1C, D), but in almost every case, the overall effect of irrigated plants having greater sap flow than non-irrigated plants held true, although the difference was not always statistically significant.

During the rest of year, the overall Irrigation effect is the reverse order of that during the irrigation treatments for both statistical models, i.e. that plants in non-irrigated plots have significantly more sap flow than in irrigated plots when averaged over all other factors (Table 2.1E, F, Figure 2.1). The Irrigation effect significantly interacted with Nitrogen during this period (Table 2.1E, F). At 40N, plants in non-irrigated plots had significantly greater sap flow rates, but although plants in non-irrigated plots had greater mean sap flow at 0N and 10N, differences were not significant.

During the pre-irrigation period, the Irrigation effect was again significant for both models (Table 2.1G, H), and the difference between irrigation treatments was a continuation of the rest of year time period (i.e., -I > +I) (Figure 2.1). For the statistical model without soil water content, the Irrigation x DSI interaction was significant (Table 2.1G). Although the Irrigation x DSI interaction was significant, the significantly greater sap flow for plants in non-irrigated plots observed from the Irrigation main effect consistently occurred across all dates during the pre-irrigation time period. Effects of the irrigation treatment were consistent across all whole-plot N treatment interactions but not for plots with intact BSC. Plants in irrigated plots with intact BSC had greater sap flow rates than plants with disturbed BSC.

Nitrogen treatment effects

During the irrigation period, the Nitrogen effect was significant (Table 2.1A, B, Figure 2.2), and plots that received 40N had significantly greater sap flow than 0N, which in turn was significantly greater than 10N. This overall result (40N > 0N > 10N) is most apparent in 2005. Nitrogen also interacts significantly with Crust (Table 2.1A, B). Plants in plots that do not have BSC show the overall nitrogen effect (40N > 0N >10N), however the 40N and 0N exchange order for plants in plots that have intact BSC. Irrigation also has a small additional effect: for plants in plots without BSC, the 0N and 10N treatments exchange order (40N > 10N > 0N). Nitrogen also interacted significantly with other effects such as Irrigation x DSI, Irrigation x Crust x DSI, Year, and others (Table 2.1A, B). In almost every case, over all interactions the ordering of nitrogen treatments remained the same (40N > 0N > 10N), although they were not always significant. Over all DSI interactions, the ordering of nitrogen treatments (40N > 0N > 10N) were maintained for approximately two months after the last irrigation, after which the 0N and 10N treatments are no longer statistically significantly different.

During the post-irrigation period, the overall Nitrogen effect changed slightly from the results during the irrigation period (Table 2.1C, D, Figure 2.2). The 40N treatment still had the greatest sap flow, but the 0N and 10N treatments were no longer significantly different from one another for both statistical models (i.e., 40N > 0N = 10N). The N x DSI interaction was also significant during the post-irrigation period. The N x DSI interaction for the statistical model without soil water indicated no significant difference between the nitrogen treatments across all dates. However, the statistical model with soil water indicates that initially the three nitrogen treatments are significantly different from one another (40N > 0N > 10N), but over time the 0N and 10N treatments become not significantly different from one another. Plants that received the 40N treatment had significantly greater sap flow than the other two treatments across all dates during the time period. Nitrogen also significantly interacts with Crust and with Crust x Year (Table 2.1C, D). For plots with disturbed BSC, a consistent effect appears for both 2004 and 2005 with the statistical ordering of 40N > 10N > 0N. However, plants in plots with intact BSC vary between years, with 2004 showing the overall result (40N > 0N = 10N) but 2005 showing 40N > 0N > 10N. For the interaction of Nitrogen x Crust x Irrigation x Year, the ordering is consistent among all treatments (40N, 0N, 10N) but the statistical grouping is not always significant.

The results for the Nitrogen effect during the rest of year period were similar to the other time periods in that the Nitrogen main effect was significant and that plants in the 40N treatment consistently had the greatest sap flow for both statistical models (Table 2.1E, F). However, the 0N and 10N treatment switched order in the statistical grouping (40N > 10N > 0N) (Figure 2.2) compared to the irrigation and post-irrigation periods. Although the N x DSI interaction term was significant, the difference between nitrogen treatments was not significant across all dates and for both statistical models during the rest of year time period. However, despite no statistical difference between the nitrogen treatments for the N x DSI interaction, the ordering of the treatments remained the same as the overall Nitrogen effect (40N > 10N > 0N). The Irrigation x N and the Irrigation x N x Crust interaction terms were also significant during this time period (Table 2.1E, F), with the most important interaction dependent on the Irrigation and Crust. For both non-irrigated and irrigated plots with BSC present, plants in the 0N and 10N treatments switch order (40N > 0N >10N); but for plants at both levels of irrigation and disturbed BSC, the overall main effect (40N > 10N > 0N) was obtained.

The Nitrogen effect during the pre-irrigation period was again very similar to other time periods in that plants in the 40N treatment had the greatest rates of sap flow followed by the 0N and 10N treatment (i.e., 40N > 0N > 10N; Table 2.1G, H Figure 2.2) for the statistical model without soil water. However, for the statistical model with soil water the 40N and the 0N treatment were no longer statistically different (40N = 0N > 10N). This overall effect was readily apparent in 2005 where a clear separation between the nitrogen treatments can be seen during the pre-irrigation period (Figure 2.2). Similar to the rest of year period the N x DSI interaction term was significant, but the difference between nitrogen treatments was not significant across all dates and for both statistical models during the pre-irrigation time period. However, despite no statistical difference between the nitrogen treatments for the N x DSI interaction, the ordering of the treatments remained the same as the overall Nitrogen effect (40N > 0N > 10N). The Nitrogen effect also significantly interacted with Irrigation and Crust. In nearly all cases, the overall Nitrogen effect (40N > 0N > 10N) occurred across these interactions except for irrigated plots with intact BSC, where treatment the ordering of nitrogen treatments was different (0N > 40N > 10N).

Crust treatment effects

During the irrigation period, the Crust main effect was significant, but the significant Crust x Year interaction confounded the main effect for both statistical models

(Table 2.1A, B). Plants in plots without BSC had greater sap flow than plots with intact BSC during the 2004 irrigation period (Figure 2.3). However, the reverse order occurred during the 2005 irrigation period: plants in plots without BSC had lower sap flow than those with BSC. The Crust x DSI interaction was significant for both statistical models and showed that plants in plots with disturbed BSC had greater rates of sap flow than plants in plots with intact BSC for approximately three weeks after the first irrigation. The Irrigation x Crust effect was significant for both statistical models during the irrigation period (Table 2.1G, H). For both models, plants in non-irrigated plots with disturbed BSC had greater rates of sap flow than plants in non-irrigated plots with intact BSC; the opposite was true for plants in irrigated plots (+C > -C). The Irrigation x N x Crust interaction was also significant for both models during the irrigation period (Table 2.1G, H). The Irrigation x N x Crust interaction is complex in that for both models, for 0N and both levels of irrigation the opposite of the overall effect was obtained (+C > -C). However, at 10N and 40N the overall result (-C > +C) was obtained.

During the post-irrigation period, the Crust main effect was not significant for both models (Table 2.1C, D). The Crust x N interaction term was significant for both models (Table 2.1G, H). At 0N, plants in plots with intact BSC had greater sap flow (+C > -C). However, at 10N and 40N, the opposite result was obtained (-C > +C). Other significant Crust interaction terms included Irrigation x Crust x Year, N x Crust x Year, and Irrigation x N x Crust x Year for both models. Although these interaction terms involving Crust, Year and other main treatment effects were significant, the overall result (-C = +C) was obtained for the model without soil water. However, for the model with soil water, the results were variable from year to year, but in general as more nitrogen is added to the plot the plants in the disturbed BSC treatments had greater sap flow.

During the rest of year time period, plants in plots with intact BSC had significantly greater sap flow than plants in plots with disturbed BSC for both models (Table 2.1E, F Figure 2.3). The Irrigation x N x Crust interaction term was significant during this time period for both models (Table 2.1E, F). At all levels of nitrogen and for irrigated plots the overall crust effect was the result (+C > -C). However, for all levels of nitrogen and non-irrigated plots the opposite was the result (-C > +C). The Irrigation x Crust x DSI, N x Crust x DSI, and the Irrigation x N x Crust x DSI interaction terms were also significant during this time period. Although these interaction terms were significant, no significant difference between the terms could be determined across all dates that were tested.

During the pre-irrigation period, the overall Crust main effect was significant (Table 2.1G, H). Both models, with and without soil water, were similar to other time periods in that plants in plots with intact BSC had greater sap flow than plants in plots with disturbed BSC (Figure 2.3). The Irrigation x Crust interaction was significant for both models (Table 2.1G, H). For both models, plants in plots that were non- irrigated and had disturbed BSC had greater rates of sap flow than plants in plots with intact BSC. However, for plants in plots that received irrigation, the overall main crust effect was obtained (+C > -C). The N x Crust interaction term was also significant for both models (Table 2.1G, H). At 0N and 10N plants in plots with intact BSC had greater rates of sap flow than plants in plots with disturbed BSC (+C > -C), but at 40N the opposite was the result (-C > +C). For all significant interaction terms involving Crust and DSI, no significant difference between the terms could be determined across all dates that were tested. The Irrigation x Crust x Year interaction was also significant. For the model without soil water, plants in non-irrigated plots and disturbed BSC had greater rates of sap flow in both 2004 and 2005. However, the opposite was true of plants in irrigated plots with intact BSC (+C > -C). For the model with soil water, plants in non-irrigated plots and disturbed crust had greater rates of sap flow but were not statistically different in both 2004 and 2005. However, the opposite was true of plants in irrigated plots with intact BSC (+C > -C), 2005 being the only year that was significant.

DISCUSSION

Irrigation treatment effects

Our results clearly show that summer irrigation treatments significantly increase sap flow during the irrigation period (Figure 2.1). Elevated levels sap flow in *L. tridentata* occurred within the first two days after irrigation, which indicates an almost immediate response of sap flow to the increase in soil water. We know from the results of our soil water study (Chapter 1), that water from the first irrigation reaches a depth of about 0.4m. It is interesting to note that *L. tridentata* are able to utilize soil water from such shallow depths (0 – 0.4m).Thus, *L. tridentata* plants are able to quickly take advantage of available soil water during the peak of the summer monsoon season, as has been reported in other studies (Meinzer *et al.* 1988, Franco *et al.* 1994).

When soil water is accounted for in the statistical model, the irrigation effect does not become significant until approximately 7-14 days after the irrigation. Thus, we infer that *L. tridentata* express additional physiological responses to additional soil water. Possible explanations for this additional physiological response include an increase in roots, an increase in vascular tissue, an increase in leaf area, or an increase in leaf gas exchange. An increase in root tissue would presumably lead to increase in the ability to uptake soil water, but rapid (< two weeks) increases in roots in response to soil water has not been observed at our site (Phillips *et al.* 2006, Verburg *et al.* in review). An increase in vascular tissue also is probably not a likely explanation for the increase in sap flow because changes in xylem production can only be detected from year to year, not on the time scale of weeks (Jones *et al.* 2004). An increase in leaf area of *L. tridentata* in response to irrigation treatments or natural precipitation events has been documented (Reynolds *et al.* 1999, Barker *et al.* 2006, Muldavin *et al.* 2008), but in each of these cases, the leaf production was spread over approximately two months. Thus, increased leaf area could partially explain the increase in sap flow that we observed during the later portions of the irrigation period (August – September). The most probable mechanism to account for additional sap flow in *L. tridentata* plants receiving the irrigation treatment is an increase in leaf gas exchange. Many studies have shown a positive relationship between maximum assimilation (A_{max}) and maximum stomatal conductance (g_{max}) (*e.g.* Wong *et al.* 1979, Ogle and Reynolds 2002, Allen *et al.* 2008). Ogle and Reynolds (2002) investigated this relationship specifically for *L. tridentata* and found this same positive relationship between A_{max} and g_{max}. Barker *et al.* (2006), working at the MGCF, also found this positive relationship between A_{max} and g_{max} for *L. tridentata* in response to the summer irrigation treatment and is the most probable explanation for the delayed increase in sap flow that we see in our results.

Increased sap flow in *L. tridentata* plants exposed to the irrigation treatment was significantly greater than those plants in non-irrigated plots until approximately the last week of September of each year (Figure 2.1). No significant difference can be detected between irrigated and non-irrigated plants from approximately the end of September to the first of November. Beginning around the week of November, plants that did not receive the irrigation treatments began to have significantly greater sap flow until the beginning of the irrigation period the following year. This result is counterintuitive, especially considering that irrigated plots have been shown to be wetter at certain depths (0.4 and 0.6m) than plots not receiving irrigation even into March of the year after the irrigations (Chapter 1). Barker *et al.* (2006), working at the MGCF, showed that the irrigation treatment relieves stomatal limitation to photosynthesis in the summer months, but leads to increased stomatal limitation the following spring. This is presumably due to rapid growth in response to the irrigation treatment resulting in a dilution of leaf nitrogen content. Non-irrigated plants exhibited greater leaf nitrogen content and greater rates of assimilation than irrigated plants during the spring months. Barker et al. (2006) hypothesized that greater leaf nitrogen content may have positively affected photosynthetic capacity in non-irrigated plants by increasing the content of proteins associated with carbon fixation and electron transport (Wong *et al.* 1979, Evans and Seemann 1989). This explanation certainly seems plausible and is supported by the elevated levels of sap flow we see in non-irrigated plants during the months between the summer irrigation treatments.

Nitrogen treatment effects

The most consistent and dominant nitrogen treatment effect on sap flow of *L. tridentata* was that plants receiving 40N had the highest rates of sap flow (Figure 2.2). Rates of sap flow in plants receiving the 10N and 0N treatments were variable and dependant on the irrigation and crust disturbance treatments. Other studies have shown that both individually and interactively, water and nitrogen additions have increased leaf production in *L. tridentata* (Fisher *et al.* 1988, Sharifi *et al.* 1988, Meinzer *et al.* 1988, Lajtha and Whitford 1989). Observational data (B. Newingham and S. Smith, unpubl.) as well as leaf area and stem diameter data used to calculate sap flows (data not shown) show that plants exposed to the 40N treatment have larger stems and leaf area that could potentially explain the elevated levels of sap flow relative to the 0N and 10N treatments.

Contrary to the consistent results of the 40N treatment, sap flow in the 10N and 0N treatments were variable and dependant on the time of year and the irrigation treatment. The 0N treatment was significantly greater than the 10N treatment during both 2004 and 2005 irrigations and during the pre-irrigation period of 2005 (Figure 2.2). The 10N treatment consistently had the lowest rates of sap flow throughout the year, albeit not always statistically significant. It is also interesting to note that the statistical grouping, albeit not always significant, between the 0N and 10N treatments is variable depending on the presence or absence of BSC. In general when BSC was present the 0N treatment had greater rates of sap flow although not always significantly as compared to when BSC were not present the 10N treatment had greater rates of sap flow. Cyanobacteria present in BSCs are known to fix nitrogen and have been shown to be the dominant source of nitrogen for some arid land plant and soil communities (Evans and

Ehleringer 1993, Evans and Belnap 1999). Our results suggest that the presence of BSC is approximately equivalent to the 10N treatment in terms of sap flow, as plants in plots with intact BSCs and receiving 0N generally had greater rates of sap flow.

Crust treatment effects

The crust treatment effects on sap flow were the variable and the most difficult to interpret out of the three treatment combinations. BSC effects were dependant on interactions with the irrigation treatment, the nitrogen treatment and the year. For example, plants in plots with disturbed BSC had greater rates of sap flow than plants in plots with intact BSC during the 2004 irrigation period. However, the exact opposite result was the case during the 2005 irrigation period (Figure 2.3). BSCs do have a positive effect on soil water with intact BSC plots remaining wetter during the irrigation period for a brief time (see Chapter 1). Because it is so difficult to identify a consistent pattern in the effects of BSC on sap flow, we think that this effect is less important in determining the rates of sap flow in *L. tridentata.*

Summary

In conclusion we have shown that *L. tridentata* are clearly capable of responding to simulated increased summer monsoon rains through increased sap flow. We have also shown that *L. tridentata* is not only able to respond to the increase in soil water during the hot summer months, but is also able to physiologically respond to the increase in soil water within a two week period. Another important finding from our results is that our data is in agreement with results obtained by Barker *et al.* (2006), in which an apparent leaf nitrogen dilution effect inhibits the maximum photosynthesis of *L. tridentata* during the winter and spring months before the next growing season. We have also presented data that shows that plants exposed to the 40N treatment consistently had greater rates of sap flow throughout the year presumably due to an increase in plant size or leaf area from the nitrogen additions.

Our data has shown that the most significant and overriding effect is the additional simulated summer monsoon treatment. If a significant increase in summer rains were to occur in an environment with a long term history of winter precipitation, it is possible that *L. tridentata's* growth and allocation patterns and habits have the potential to change and adapt. Similarly, log term nitrogen deposition has the potential to affect the physiology of *L. tridentata* and the biogeochemical cycle as a whole. While the BSC effect seems to be less important than the other treatment effects, all of them have the potential to have important feedbacks on primary production of *L. tridentata* and consequently the Mojave Desert as a whole.

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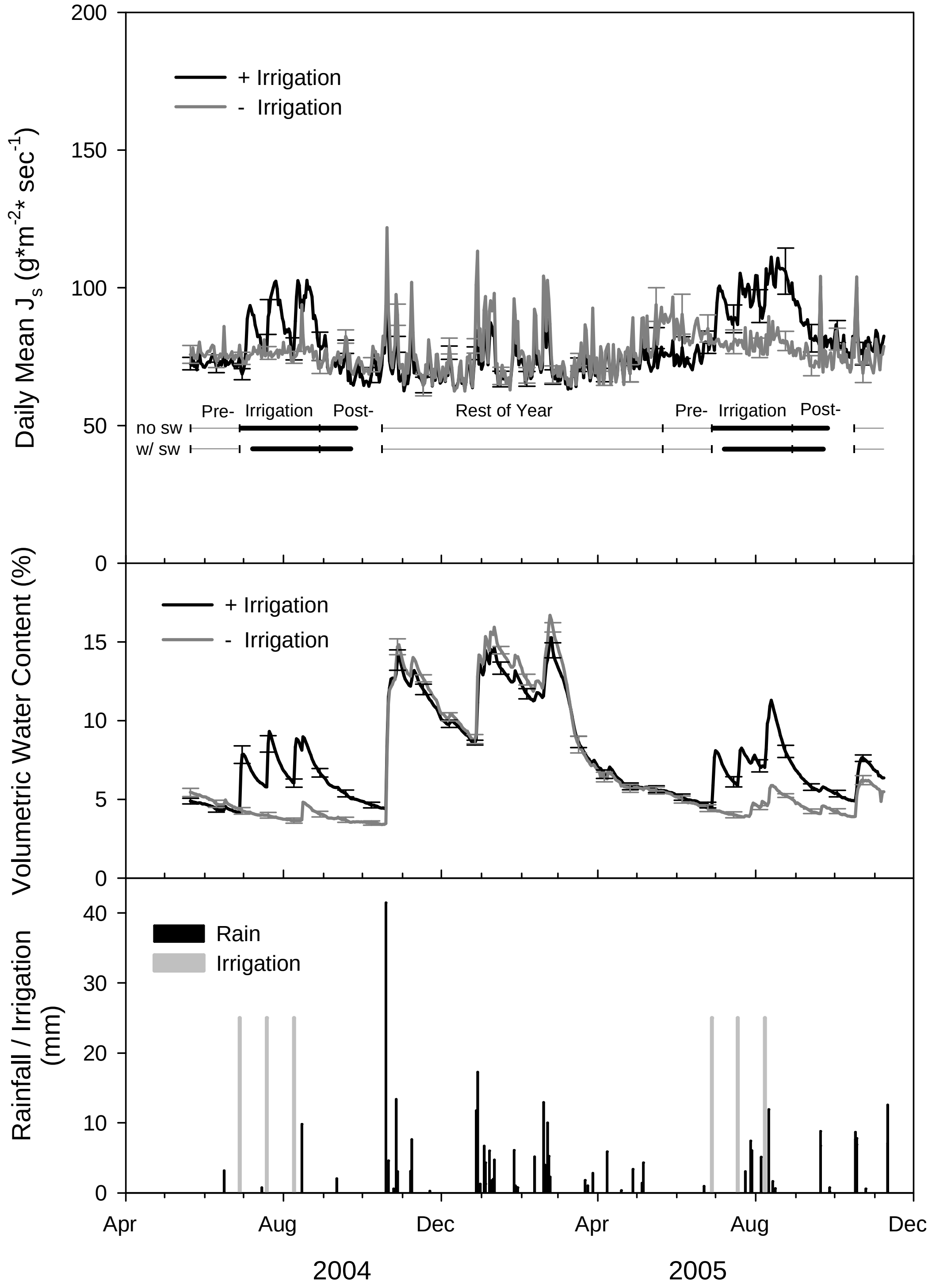

Figure 2.1. Daily average sap flow (g*m^{-2}*sec^{-1}, top panel) and soil water content (% by volume, middle panel) from May 2004 to November 2005 for irrigated (black lines) and non-irrigated (grey lines) treatments, averaged over all other treatments. Error bars are 1 SE. Within the top panel, results from statistical analyses of the irrigation main effect and of the irrigation X time interaction term are shown for each time period over which data were analyzed (beginning and end dates of time periods are marked by vertical lines). Thick horizontal lines indicate that irrigated plots had significantly greater sap flow than non-irrigated; thin lines indicate that non-irrigated had greater sap flow; and no line indicates that irrigation treatments were not significantly different. The top set of lines are for statistical analyses when soil water was NOT included in the ANOVA, and the lower set of lines are for the statistical analyses when soil water was included as a co-variate. Bottom panel shows precipitation and irrigation events.

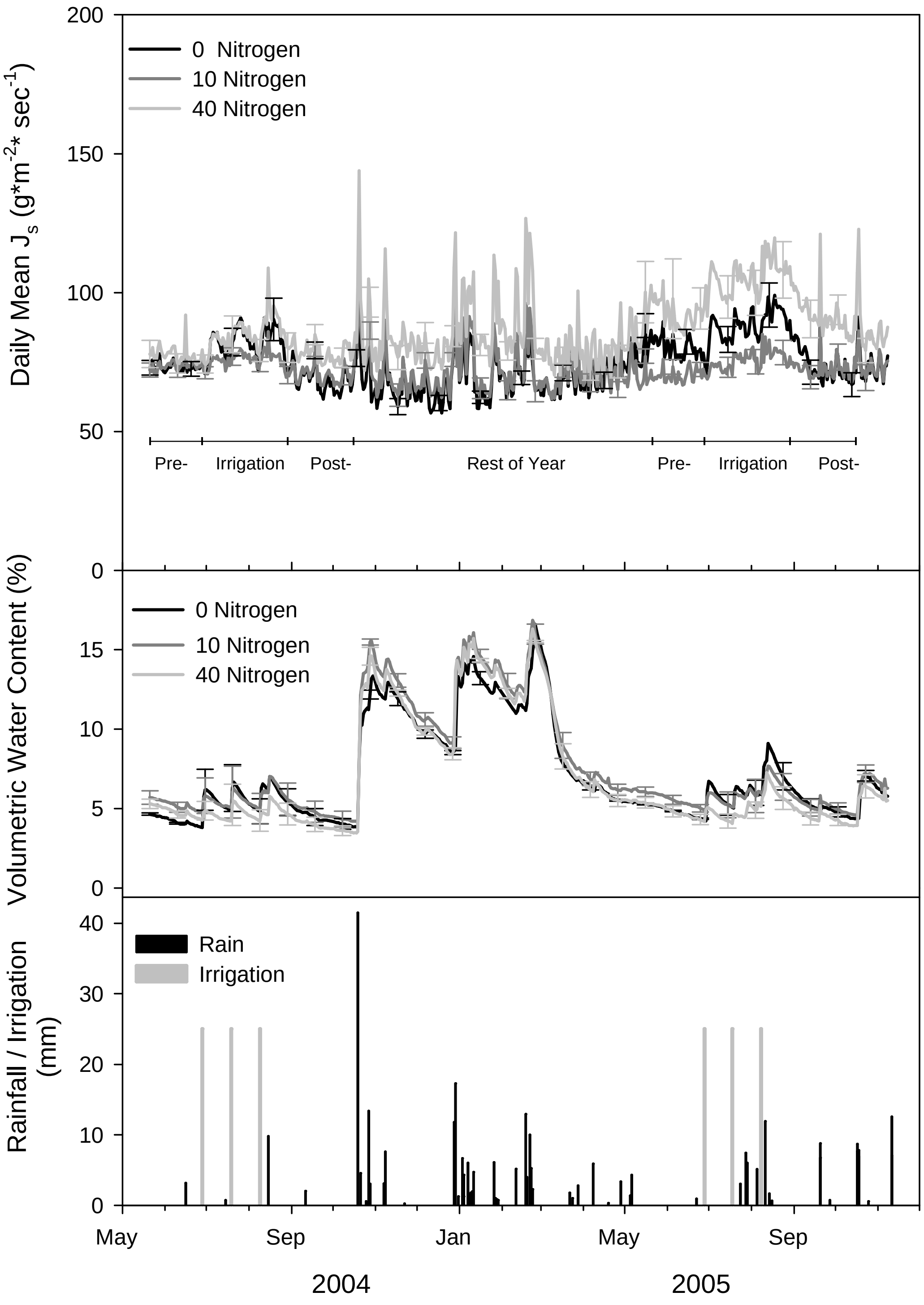

Figure 2.2. Daily average sap flow ($g*m^{-2}*sec^{-1}$, top panel) and soil water content (% by volume, middle panel) from May 2004 to November 2005 for 0 Nitrogen (solid lines), 10Nitrogen (dashed lines), and 40 Nitrogen (dot dash lines) treatments, averaged over all other treatments. Error bars are 1 SE. Bottom panel shows precipitation and irrigation events.

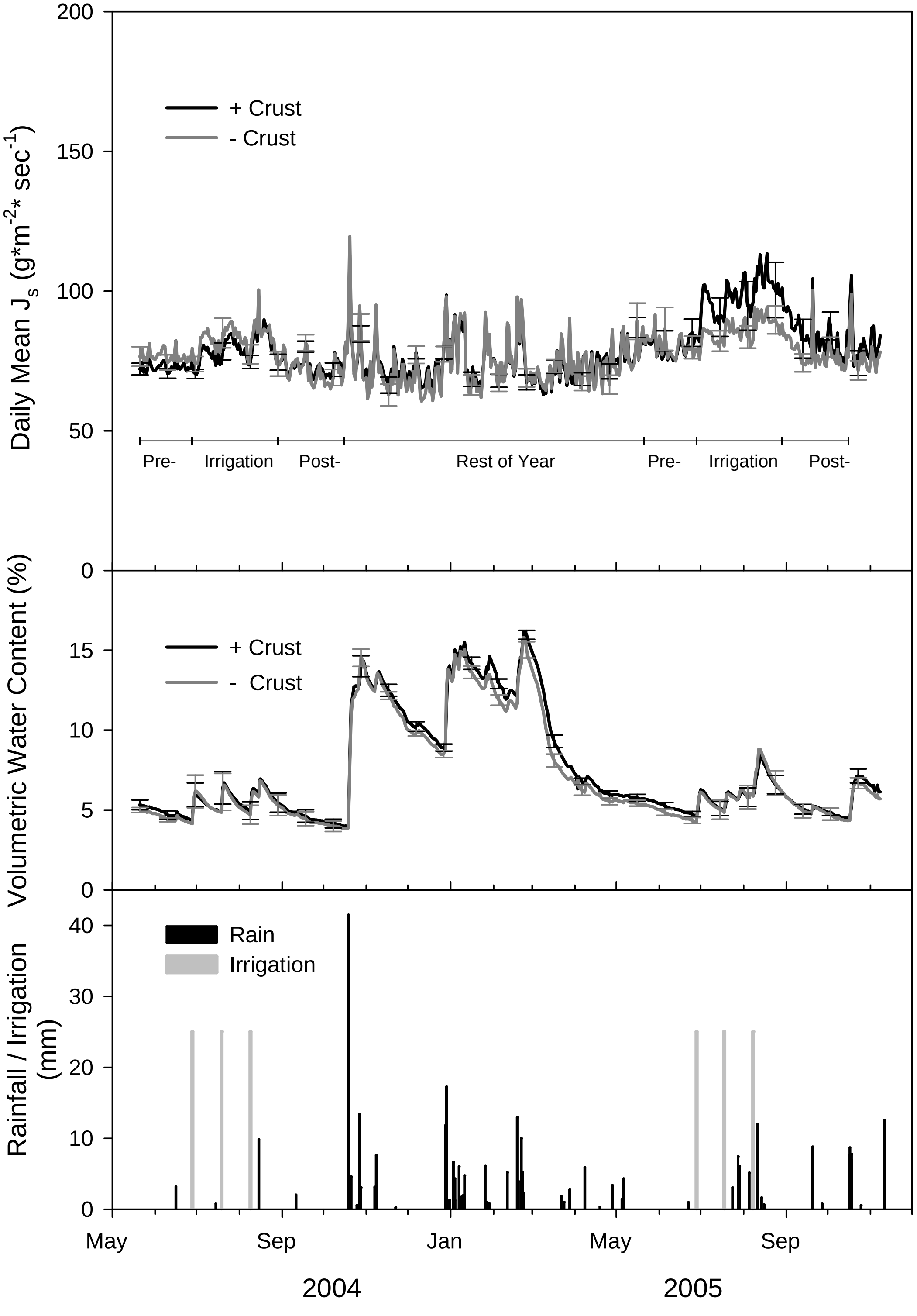

Figure 2.3. Daily average sap flow (g*m^{-2}*sec^{-1}, top panel) and soil water content (% by volume, middle panel) from May 2004 to November 2005 for intact biological soil crust (solid lines) and disturbed biological soil crust (dashed lines) treatments, averaged over all other treatments. Error bars are 1 SE. Bottom panel shows precipitation and irrigation events.

Table 2.1. ANOVA tables for sap flow from May 2004 to November 2005. Data were analyzed with a longitudinal (time series) analyses on the entire data set using a radial smoothing technique, where "days since irrigation" (DSI) was the repeated measure and irrigation, nitrogen addition, and crust disturbance treatments were fixed effects. Bolded P values are <0.05 and are considered significant.

		(A) Irrigation Period (without soil water)		**(B)** Irrigation Period (with soil water)		**(C)** Post-irrigation (without soil water)		**(D)** Post-irrigation (with soil water)		**(E)** Rest of Year (without soil water)		**(F)** Rest of Year (with soil water)		**(G)** Pre-irrigation (without soil water)		**(H)** Pre-irrigation (with soil water)	
Effect	ndf	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value	ddf	P value
Irrigation (Irrig)	1	1450	**<0.0001**	1450	0.0243	1680	**<0.0001**	1667	**<0.0001**	2524	**0.0029**	2300	**0.0017**	864	**<0.0001**	863	**0.0081**
Nitrogen (N)	2	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	2524	**<0.0001**	2298	**<0.0001**	864	**0.0002**	863	**<0.0001**
Irrig*N	2	1450	0.2801	1450	0.0549	1680	0.7331	1667	0.7865	2524	**<0.0001**	2298	**<0.0001**	864	**<0.0001**	863	**<0.0001**
Crust	1	1450	**<0.0001**	1450	**<0.0001**	1680	0.0206	1667	0.0718	2524	**<0.0001**	2298	**<0.0001**	864	**0.0053**	863	**0.0002**
Irrig*Crust	1	1450	**<0.0001**	1450	**<0.0001**	1680	0.7670	1667	0.0115	2524	0.2224	2297	0.4036	864	**<0.0001**	863	**<0.0001**
N*Crust	2	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	2524	0.1986	2298	0.5011	864	**<0.0001**	863	**<0.0001**
Irrig*N*Crust	2	1450	**<0.0001**	1450	**0.0005**	1680	0.0517	1667	0.0118	2524	**<0.0001**	2298	**<0.0001**	864	0.0878	863	0.5838
Days Since Irrigation (DSI)	1	1450	**<0.0001**	1450	**<0.0001**	1680	0.3144	1667	**0.0009**	71	0.9819	62	0.9799	864	**0.0005**	863	**<0.0001**
Irrig*DSI	1	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	2524	0.1660	2301	0.3247	864	**<0.0001**	863	0.0354
N*DSI	2	1450	0.0668	1450	0.0318	1680	**<0.0001**	1667	**<0.0001**	2524	**<0.0001**	2299	**<0.0001**	864	**0.0002**	863	**0.0010**
Irrig*N*DSI	2	1450	**<0.0001**	1450	**<0.0001**	1680	0.7331	1667	0.5945	2524	**<0.0001**	2299	**<0.0001**	864	**<0.0001**	863	**<0.0001**
Crust*DSI	1	1450	**<0.0001**	1450	**<0.0001**	1680	0.0206	1667	0.0205	2524	0.2796	2298	0.8704	864	**0.0050**	863	**0.0006**
Irrig*Crust*DSI	1	1450	**<0.0001**	1450	**<0.0001**	1680	0.7670	1667	0.6350	2524	**<0.0001**	2298	**<0.0001**	864	**<0.0001**	863	**<0.0001**
N*Crust*DSI	2	1450	0.7770	1450	0.8621	1680	**<0.0001**	1667	**<0.0001**	2524	**0.0002**	2298	**<0.0001**	864	**<0.0001**	863	**<0.0001**
Irrig*N*Crust*DSI	2	1450	**0.0003**	1450	**0.0004**	1680	0.0517	1667	0.0598	2524	**<0.0001**	2298	**0.0029**	864	0.0985	863	0.6696
Year	1	1450	**<0.0001**	1450	**<0.0001**	1680	0.3144	1667	**0.0002**	-	-	-	-	864	**<0.0001**	863	0.0868
Irrig*Year	1	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	-	-	-	-	864	**<0.0001**	863	**<0.0001**
N*Year	2	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	-	-	-	-	864	**<0.0001**	863	**<0.0001**
Irrig*N*Year	2	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	-	-	-	-	864	**<0.0001**	863	**<0.0001**
Crust*Year	1	1450	**<0.0001**	1450	**<0.0001**	1680	0.1692	1667	0.1705	-	-	-	-	864	**<0.0001**	863	**0.0002**
Irrig*Crust*Year	1	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	-	-	-	-	864	**<0.0001**	863	**<0.0001**
N*Crust*Year	2	1450	**<0.0001**	1450	**<0.0001**	1680	**0.0001**	1667	**<0.0001**	-	-	-	-	864	0.0116	863	**0.0065**
Irrig*N*Crust*Year	2	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	-	-	-	-	864	0.0916	863	0.0137
DSI*Year	1	1450	0.5010	1450	**0.0083**	1680	**<0.0001**	1667	0.1094	-	-	-	-	864	**<0.0001**	863	**<0.0001**
Irrig*DSI*Year	1	1450	0.6341	1450	0.6435	1680	0.0193	1667	**0.0057**	-	-	-	-	864	**<0.0001**	863	**<0.0001**
N*DSI*Year	2	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	-	-	-	-	864	**<0.0001**	863	**<0.0001**
Irrig*N*DSI*Year	2	1450	**<0.0001**	1450	**<0.0001**	1680	**<0.0001**	1667	**<0.0001**	-	-	-	-	864	**<0.0001**	863	**<0.0001**
Crust*DSI*Year	1	1450	0.0620	1450	**0.0059**	1680	0.0125	1667	0.0125	-	-	-	-	864	**<0.0001**	863	**0.0016**
Irrig*Crust*DSI*Year	1	1450	0.2063	1450	0.0793	1680	**<0.0001**	1667	**<0.0001**	-	-	-	-	864	**<0.0001**	863	**<0.0001**
N*Crust*DSI*Year	2	1450	**0.0019**	1450	**0.0004**	1680	0.1467	1667	0.1691	-	-	-	-	864	**0.0030**	863	**0.0021**
Irrig*N*Crust*DSI*Year	2	1450	**<0.0001**	1450	**<0.0001**	1680	0.1413	1667	0.1085	-	-	-	-	864	0.0361	863	**0.0074**
Soilwater	1	-	-	1450	**<0.0001**	-	-	1667	**0.0011**	-	-	2358	**0.0052**	-	-	863	**<0.0001**

Appendix

Appendix 1. SAS code.

Sample SAS code for the different statistical approaches used in both the neutron probe and sap flow data sets.

```
title 'Neutron Probe. Irrigation period. ';
ods html;
ods graphics on;
proc glimmix data =postirrig_I plots=studentpanel;
        class irrig irrigation__ block plot N crust year;
        model tswc = irrigation__|N|crust precipitation;*/ ddfm = kr;
        random int / subject=block(irrigation__*N*crust);
        random year /subject = block(irrigation__*N*crust)
        type = ar (1) residual;
run;
title;
ods graphics off;
ods html close;
```

```
title 'Neutron Probe. Irrigation period. RSmooth covariate';
ods html;
ods graphics on;
proc glimmix data= swc_plots; plots=studentpanel;
class block irrig crust N plot;
model tswc = irrig|crust|N|DSI|precipitation|days/distribution=lognormal;
random intercept / subject=block(irrig*crust*N);
random days / subject=block(irrig*crust*N) type=rsmooth
     knotmethod=kdtree (bucket= 3000);
run;
title;
ods graphics off;
ods html close;
```

```
title 'Sap Flow. Irrigation period. Box-Cox transformed. With SW. limited interactions. RSmooth covar.';
  ods html;
  ods graphics on;
proc glimmix data = work.Irrig_0405_bothblock plots=studentpanel;
class Irrigation N crust year;
model boxdependent = Irrigation|N|crust|DSI|year soilwater /ddfm=kr;
   nloptions tech=congra;
   random int / subject=year;
   random dsi(year) / type=rsmooth knotmethod=kdtree;
run;
title;
ods graphics off;
ods html close;
```