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**Precipitation and Soil Impacts on Partitioning of Subsurface Moisture in *Avena
barbata*: Observations from a Greenhouse Experiment**

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Abstract

The primary objective of this study was to assess the impact of two grassland soils and precipitation regimes on soil-moisture dynamics. We set up an experiment in a greenhouse, and monitored soil moisture dynamics in mesocosms planted with *Avena barbata*, an annual species found in California grasslands. By repeating the precipitation input at regular intervals, we were able to observe plant manipulation of soil moisture during well-defined periods during the growing season. We found that the amount of water partitioned to evapotranspiration, seepage, and soil storage varied among different growth stages. Further, both soil type and precipitation regimes had a significant impact on redistributing soil moisture. Whereas in the low-precipitation treatments most water was released to the atmosphere as evapotranspiration, major losses from the high-precipitation treatment occurred as gravity drainage. Observations from this study emphasize the importance of understanding intra-seasonal relationships between vegetation, soil, and water.

1. Introduction

Recent interdisciplinary research exploring the influence of hydrological processes on the dynamics of biological communities (e.g., *Newman et al.*, 2006, and references therein) has shown that ecosystems respond in a complex manner to changes in environmental conditions (*Borgogno et al.*, 2007). The numerous processes (including those associated with anthropogenic climate change) that contribute to the nonlinearity of hydrological and ecological phenomena make it difficult to capture a realistic representation of the terrestrial water cycle. Therefore, our ability to assess spatial and temporal dynamics through models that link vegetation and hydrological processes is severely limited. While it is now well established that vegetation plays a pivotal role in the global water balance, an understanding of the interactions between vegetation, water, and soil is far from complete (*Newman et al.*, 2006).

Precipitation and temperature (of soil and air), key factors that influence primary production in terrestrial ecosystems, have been identified by various general circulation models to be extremely sensitive to climate change. These models also suggest that the global atmosphere will continue to warm as annual precipitation amounts change in the foreseeable future (*IPCC*, 2007). In addition, the frequency of extreme rainfall events is projected to increase while the number of individual events decrease, resulting in longer intervening dry periods (*Sun et al.*, 2007). As insights into these potential changes to the global climate unfold, there is also increasing awareness that alterations to the precipitation regime will lead to changes in the structure and functioning of terrestrial ecosystems (*Knapp et al.*, [2002], and references therein). This has led to research that has focused on how climate change impacts ecosystem processes (*Mooney*, 1991; *Sala et*

al., 2000; *Frank*, 2007). While most of this research initially explored the effects of increased temperature and CO₂, recent efforts have focused on how anticipated changes in precipitation could affect terrestrial ecosystems (e.g., *Weltzin et al.*, 2003, *Harper et al.*, 2005; *Harpole et al.*, 2007; *Wan et al.*, 2007; *Chou et al.*, 2008; *Niu et al.*, 2008).

Grasslands are attractive venues for climate-change-related research, as (1) they are extensive biomes, occupying one-third of the world's area under natural vegetation (*Aires et al.*, 2008), and (2) they are among the most responsive of terrestrial ecosystems to interannual variability in precipitation (*Knapp et al.*, 2002). With respect to these ecosystems, research has largely been directed towards understanding how climatic variability, particularly changes in precipitation amounts and shifts in seasonality, influence above-ground net primary productivity (ANPP). The main approach has been to evaluate ecosystem productivity in response to either multiyear trends in natural rainfall events (e.g., *Knapp and Smith*, 2001; *Frank*, 2007; *Swemmer et al.*, 2007), manipulation studies in natural study systems (e.g., *Fay et al.*, 2000; *Knapp et al.*, 2002; *Nippert et al.*, 2006; *Chou et al.*, 2008; *Fay et al.*, 2008), or controlled studies in greenhouse environments (e.g., *Zavaleta et al.*, 2003; *English*, 2005; *Yepez et al.*, 2005). These research efforts have provided valuable insights into the impact that altered precipitation regimes can have on grassland productivity. However, there is much to be learned about the hydrology of these systems, particularly the effect of vegetation in regulating the hydrologic response in grassland ecosystems.

In this study, we evaluated soil-moisture dynamics associated with *Avena barbata*, a species found in annual grasslands in California. The primary objective was to assess the hydrologic response in *A. barbata* monocultures to two precipitation regimes and two

contrasting grassland soil types. Of particular interest were the temporal trends in soil moisture that developed with the prescribed precipitation and soil treatments, and the role of vegetation in controlling soil moisture

2. Methods

2.1. Mesocosms:

The experimental unit for this study was a mesocosm; a 0.60 m tall cylindrical column of soil contained in a 0.57 m ID PVC pipe (Figure 1a). Forty-eight mesocosms were filled with grassland soil from one of two University of California research facilities. The Hopland soil was excavated from the Hopland Research and Extension Center, a University of California research facility located in Mendocino County, ~100 miles north of San Francisco, California. The Sedgwick soil was excavated at the Sedgwick Ranch in Santa Ynez, CA. This reserve is part of the UC Natural Reserve System and is located ~ 45 km north of Santa Barbara (CA). Soil from both locations was excavated with a back-hoe to a depth of 0.75 m, and the A, B₁, and B₂ horizons were collected separately. The soil from each horizon was homogenized and packed (at measured field bulk densities) into the mesocosms sequentially to a depth of 20 cm for each horizon. In each mesocosm, a 0.05 m thick layer of fine sand was first spread along the bottom to facilitate gravity-induced drainage.

A summary of the texture and chemical attributes of the two soils measured immediately after the soil was excavated from the field sites is presented in Table 1. While the Hopland soil had a relatively uniform sandy loam texture along the ~ 60 cm vertical profile, the Sedgwick soil transitioned from loam to clay loam over a similar

vertical profile. The A horizon in the Hopland soil had relatively large amounts of N and C along with concentrations of ammonium (NH_4^+) and nitrate (NO_3^-), which dropped significantly as the soil transitioned to the lower horizons. In the Sedgwick soil, the chemical properties of the soils did not vary with depth. No additional nutrients were added to the soil after the first growing season.

Soil moisture in the mesocosms was monitored with 0.30 m long TDR probes that were installed horizontally at 0.10, 0.25, and 0.50 m depths. Dielectric (K_a) values obtained from TDR measurements were converted to volumetric moisture content (θ) using the following empirical third-order polynomial equation developed by Topp et al. (1980):

$$\theta = -5.3 \times 10^{-2} + 2.92 \times 10^{-2} K_a - 5.5 \times 10^{-4} K_a^2 + 4.3 \times 10^{-6} K_a^3 \quad (1)$$

This relation has been shown to be accurate within a few percent for a wide variety of soils (Dalton, 1992) and has eliminated the need for soil-specific calibrations for most routine applications (Ghezzehei, 2008).

TDR signals were recorded at 1-hour intervals using multiplexers (Campbell Scientific Inc., Model SDMX50), data loggers (Campbell Scientific Inc., Model CR10X) and reflectometers (Campbell Scientific Inc., Model TDR100).

2.2. Experimental Design

This investigation was part of a larger experiment set up as a randomized block design. During the first year of this two-year study, 24 mesocosms were randomly assigned precipitation (high and low) and soil (Hopland and Sedgwick) treatments within six blocks (Figure 1b, c, and d). Blocks 1–5 were the main experimental mesocosms,

while Block 6 was maintained throughout the experiment as spare mesocosms to refill soil cores sampled from Blocks 1–5. The mesocosms were seeded with *A. barbata*, an annual species that is widespread and ecologically important in California’s grasslands. Seeds were applied at a density of 4,000 seeds per square meter and covered with a layer of homogenized leaf litter (100 g per mesocosm). These “vegetated” mesocosms were located in a 3.4 m × 8.5 m room within a greenhouse facility in Richmond, California. During the second year of the study, 24 additional mesocosms were randomly assigned the rainfall and soil treatments, but were left bare. The non-vegetated, “bare” mesocosms were located in a separate room within the same greenhouse.

The greenhouse temperature regime and the precipitation treatments were based on conditions at the Hopland Field Station where it is cool and rainy in the winter (November to late April), and warm and dry in May and June. Daily mean temperatures in the greenhouse ranged between 5 and 20°C during the growing season while the relative humidity was initially high (>95%) in the winter, before gradually dropping to less than 80% late in spring (Figure 2). During this time, the daily potential evaporation rate fluctuated for the most part between 1 and 3 mm per day.

The precipitation treatments used in this study represented wetter and drier conditions observed at the Hopland Field Station over the past 30 years, and were constructed to capture plausible future precipitation scenarios. The two precipitation treatments were defined by the total precipitation received during the growing season, length of dry spells between precipitation events, and the duration of the rainfall season.

For each treatment, the timing and amount of water applied was patterned into a 21-day watering cycle, with an 11-day watering period followed by a 10-day dry period (see

Figure 3A). The low and high irrigation treatments were subject to six and eight watering cycles, respectively (Figure 3B). A fixed amount of water, i.e., 15 mm (3.8 L), was released into the mesocosms during each watering event. In the low precipitation treatment, there were three watering events per watering cycle, while in the high precipitation treatment there were 10 events during Year I, and 8 events during Year II. Before the watering cycles began, fixed amounts of water were released into the mesocosms over several days to facilitate germination (i.e., pre-germination irrigation). The total amount of water released during the first and second year for low precipitation treatment was 315 mm and 297 mm. For the high precipitation treatment the seasonal totals were 1,245 mm versus 987 mm for Year I and II. These totals include 45 mm and 27 mm of pre-germination wetting in Year I and II. The watering cycles in both years began in December and continued through April (low precipitation) and May (high precipitation).

An automated watering system was designed to irrigate the 48 mesocosms. Two key elements in the design of this system were (1) the partitioning of precise amounts of water associated with each irrigation event, and (2) the uniform, slow release of water across the soil surface of each mesocosm. Air-activated pinch valves, programmable pumps, and a control and recording system were the key components of the water-supply system. The pinch valves were pneumatically actuated via air lines controlled by solenoids. Computer-controlled electronic relays operated the solenoids and the pumps. The computer system also incorporated a remote-control capability, so that the system could be started and controlled from any networked computer. Water was released on the

soil surface of each mesocosm via two drip irrigation rings with a total of nine release ports.

Here, we refer to the four treatments as HH (Hopland soil with high precipitation totals), HL (Hopland soil with low precipitation totals), SH (Sedgwick soil with high precipitation totals) and SL (Sedgwick soil with low precipitation totals).

2.3. Schedule of events

Soil for the mesocosms was excavated from the Hopland and Sedgwick field reserves during the summer of 2005 and transported to the greenhouse, where 24 mesocosms were prepared. Each of these mesocosms was seeded in late November 2005. The first watering cycle began in mid-December 2005. Mesocosms subject to low- and high-precipitation treatments were harvested in the first and third week of May 2006, during Year 1.

During the summer of 2006, an additional 24 mesocosms were prepared for the “bare soil” treatment. During the last week of November 2006, the 24 vegetated mesocosms used in the previous year were reseeded at a density similar to the previous year. The vegetated mesocosms with the low-rainfall treatment were harvested during the second week of May 2007, while the high-rainfall treatments were harvested two weeks later, after the 8th watering cycle. During each harvest, all vegetation in the mesocosm was cut at soil level, dried, and weighed to give an estimate of total aboveground biomass.

3. Observations

For this study we focus primarily on observations from both vegetated and bare soil treatments made during Year II of the experiment. Some observations from Year I are included to enhance our analyses.

3.1 Aboveground biomass

The aboveground biomass (AGB) harvested at the end of Years I and II was significantly greater in the Hopland soils than in Sedgwick soils (Figure 4). Within the Hopland soils, biomass production was more in the high-precipitation treatment for both years, while in the Sedgwick soils during the first year the low-precipitation treatment had significantly more biomass. In Year II, there were significant drops in biomass production in three of the four treatments, with the single exception (the Sedgwick soils with high rainfall) producing almost similar amounts of biomass in the two years. The largest drop in productivity was measured in the Sedgwick soils with low rainfall.

Soil-nitrate levels were higher in Year I compared to Year II in all treatments except in the Sedgwick high rain treatment (D. Herman, S. Placella, and M. Firestone, unpublished data). The higher nitrate levels in Year 1 were likely caused by soil disturbance associated with the excavation and repacking of soils in the mesocosms. In Year II, soil nitrate levels were similar across all treatments, with the differences in biomass likely caused by differences in soil water content.

3.2 Temporal patterns of soil moisture (Year II: 2006-2007)

Following the early season irrigation, there was a rapid increase in the amount of water retained along the entire soil profile of all mesocosms. Subsequently, close to the soil surface, θ fluctuated in response to individual irrigation events associated with the

two phases in each watering cycle. With the onset of each phase of the irrigation cycles, θ rapidly increased and then declined sharply during the ensuing period of “drought.” In the deeper soil, the temporal pattern of θ followed the shallow soil profile, with significantly less variability imposed by individual watering events.

In the vegetated Hopland soil mesocosms with low precipitation, θ increased during the early watering cycles before dramatically decreasing (Figure 5a). Superimposed on this seasonal trend were increasingly large fluctuations centered on individual watering events which resulted in progressively drier soils as the growth season progressed. In vegetated mesocosms with Hopland soil and high precipitation, fluctuations associated with wetting events progressively dampened with depth. In this treatment, a consistently wet soil persisted for most of the growing season (Figure 5b). In the low-rainfall-Sedgwick soil treatment, there were relatively small increases in θ in the shallow soil that corresponded to individual precipitation events during the six watering cycles (Figure 5c). Each of these increases was immediately followed by a steady decrease. In the deeper profile, θ increased to a peak value by the middle of the second watering cycle before gradually decreasing during subsequent cycles. When the *A. barbata* was harvested from mesocosms with this treatment, the soil in the shallow profile was much drier than at the start of the experiment—unlike the deeper profile, which was as wet as at the start of the growing season.

The deeper soil profile in the high-precipitation-Sedgwick soil treatment reached saturation levels during the first water cycle and persisted in this state (Figure 5d). Closer to the surface, there were small increases in moisture content during irrigation events, which then gradually decreased until the start of the next watering cycle. At the end of

the watering cycles, the near-surface soil profile was slightly drier than it was at the start, while the deeper profile was much wetter.

3.2. Soil moisture in bare versus vegetated mesocosms

In the bare soil treatments, mesocosms that were subject to high precipitation had similar temporal responses in θ as the vegetated mesocosms, with the soil remaining close to saturation in the deeper profile. In the low-precipitation treatments, while the mesocosms with Sedgwick soils also maintained a temporal θ pattern similar to the corresponding vegetated mesocosms, the bare-soil mesocosms with the Hopland soils subject to the low-precipitation treatment were consistently wetter than the vegetated mesocosm.

During the early stages of the growing season in Year II, the bare and vegetated mesocosms received the same amount of water to facilitate germination. Following this “pre-germination” irrigation, the first watering cycle was initiated. In response to these early-season irrigation events, a wetting front developed that migrated vertically downwards. In the Hopland soils, there were relatively small differences in the time the water took to reach the 0.50 m depth of the bare and vegetated mesocosms (Figure 6). In the Sedgwick soils, the vertical migration of the wetting front was slower in the bare soils, with a difference of ~2 and ~20 days (to travel a distance of 0.50 m) in high and low precipitation treatments, respectively. The difference in the travel time and wetting pattern between the bare and vegetated mesocosms (with the same precipitation and soil

treatment) likely resulted from the alterations to soil hydrologic properties by vegetation during Year I.

Using the 21-day watering cycles as periodic markers, we determined the average soil-moisture content for both vegetated and bare soil treatments. The largest differences in θ between the bare soil mesocosms and vegetated mesocosms, subject to the same soil and precipitation treatment, were in the Hopland soil mesocosms under low precipitation (Figure 7). Here, the amount of soil moisture in vegetated mesocosms began to decrease by the middle of the second watering cycle, and continued to decline relative to the bare soil treatment. Throughout the season, the difference in θ between vegetated and bare soil treatments was consistently largest in the deeper soil profile and smallest closer to the soil surface. These observations suggest that in Hopland soils subject to low precipitation, *A. barbata* altered the subsurface hydrology to a depth of at least 0.50 m, such that the amount of soil moisture was consistently less than in similar soil subject to the same rainfall amounts in the absence of vegetation. Differences between the bare and vegetated soils in the other three treatments were not as large as in the low-rain Hopland soil treatment.

It is important to note here, that even though our intention was to observe moisture dynamics during above and below ‘average’ annual precipitation regimes, the soil moisture data suggests that we did not reach water-limiting condition. As such our water treatments represent water-sufficient and water-excess conditions.

4. Components of a Water-Balance for Year II

Water entering the mesocosms had three paths: it could occupy soil pore spaces, exit the surface as evaporation and/or transpiration, or seep through the bottom as gravity drainage. Lateral flow out of the mesocosms was not possible because of the impermeable PVC walls. Therefore, the water balance for each 21-day watering cycle ($C_{(n)}$) can be expressed as:

$$I_{C(n)} = [\Delta SMC + ET + SEEP]_{C(n)} \quad (2)$$

Where, I is the amount of water introduced into the mesocosm as precipitation, ΔSMC is the change in stored soil water, ET is water released as evapotranspiration, and $SEEP$ is water lost to seepage.

For the two rainfall treatments, the volume of water released into individual mesocosms during each cycle was (respectively) 11.5 L and 30.6 L for the low- and high- precipitation treatments (during Year II). This translates to a daily recharge rate of 2.1 mm and 5.7 mm for the two treatments. To determine the amount of additional water retained as storage and lost to ET , we used estimates of θ from TDR probes installed at 0.10, 0.25 and 0.50 m depths. Δ_{SMC} , the amount of additional water retained as storage in the soil, was determined from the difference in θ over the 21-day period.

From the precipitation pattern defined for this experiment (Figure 3), there was no water released to the mesocosms during the last ten days of each watering cycle. As there was no observable seepage two–three days after the last irrigation event, changes in θ measured during the last seven days of each watering cycle were likely due to transpiration and evaporation. To assess the amount of water removed by ET from each mesocosm, we determined changes in θ in the three soil horizons over the last seven days

of each cycle. Water removed from each mesocosm was determined as the sum of water lost from each of the three soil horizons. Water loss calculated for the seven-day period was increased by a factor of three to estimate ET for the 21-day period. (In doing so, we make the assumption that ET rates remained relatively constant over the duration of each watering cycle.) With known amounts for three of the parameters in Equation 2, we were then able to estimate the amount of water lost to seepage.

4.1 Storage of soil moisture

During the first watering cycle, a large volume of irrigated water (i.e., 2-5 L) was retained by the soil in all four treatments such that increased by $\theta \sim 0.1$ in the low rainfall treatments and by ~ 0.2 in the high rainfall treatments (Figure 8). In subsequent watering cycles, the amount of water stored in the soil remained relative consistent in the vegetated and bare soil mesocosms subject to high-precipitation treatments. In the low-precipitation treatments, soil water storage continued to increase over the next two cycles. In the vegetated Hopland soils with low precipitation, the amount of water retained in the soil dropped significantly during the fourth and fifth watering cycles (~ 5 L), unlike the other low-precipitation treatments, in which moisture amounts remained relatively consistent until the end of the growing season.

4.2 Evaporation and transpiration

The largest volume of water removed as ET in the vegetated mesocosms was from the Hopland soils under low precipitation (Figure 9a). In this treatment, there was on average, a gradual increase in ET losses (from 30 to 60 mm, which translates to $\sim 4 - 6$ L per mesocosm) during each of the first four watering cycles. In the Hopland soil with

high-precipitation treatment, the pattern of ET losses was similar to the low-precipitation treatment, but the volume of water released was less (9b). In both the Sedgwick soil treatments, ET losses were lower than the Hopland soils, with almost no losses observed in the second half of the growing season in the high-precipitation treatment (9c and d). The bare soil treatments show that even without the vegetation, among the four treatments, the Hopland soils consistently lost more water (9e-h). However, while the amount of water lost to evaporation in the bare Hopland soils was less than that lost to ET in the vegetated Hopland soils, evaporation losses in the bare Sedgwick soils were greater than the losses to ET in the vegetated Sedgwick soils.

4.3 Seepage

We estimated seepage across two horizontal planes along the soil profile of the mesocosms, i.e., at depths of 0.25 m and 0.50 m below the soil surface. We first determined seepage at the shallow depth, from estimates of Δ_{SMC} and ET calculated for the top 0.25 m of the soil profile. We then used this estimate of seepage as the amount of water recharging the lower soil profile (i.e., below 0.25 m) to determine seepage out of the base of the mesocosms. As seen in Figure 10 a, in all vegetated and bare soils with high irrigation treatments, a significant portion of the incoming water migrated to the deeper soil profile. In the lower irrigation treatments with Hopland soils, there was noticeably less water that recharged the lower profile in the vegetated mesocosms than in the bare soil mesocosms. In the Sedgwick soils, these differences were minor.

A significant volume of water that recharged the lower profile in the high-precipitation treatments in both types seeped out the bottom of the mesocosms. In the

low- rainfall treatments, there were small amounts of seepage in the Sedgwick soils, but not for more than the first half of the growing season in the Hopland soil.

4.4. Water budget for duration of the growing season

The water budget for the duration of the growing season estimated for each treatment in both vegetated and bare soils is shown in Figure (10). Table 2 depicts the percentage of total precipitation that was partitioned to evaporation and/or transpiration, deep seepage and soil storage during the entire growth season for *A. barbata*.

While most water in the high-precipitation treatment exited the mesocosms as gravity drainage, in the low-precipitation treatment ET losses were generally the largest. Both the bare soils with high precipitation had relatively similar amounts of seepage (i.e., 700-890 mm, which is ~77–79% of total irrigation). However, vegetated Hopland soils with high irrigation had much less seepage than the Sedgwick soils (706 versus 883 mm), suggesting that *A. barbata* had a significant role in redistributing water in Hopland soils. A similar effect of Hopland soils is seen in the low precipitation treatment where almost 95% (i.e., 257 mm) of the water supplied to the mesocosms was released to the atmosphere, as opposed to only 52 % in the Sedgwick soils. In the low-precipitation treatment, evaporation losses in bare mesocosms with both soil types were relatively similar, (i.e., 136 mm Hopland versus 149 mm Sedgwick). Unlike the Sedgwick soils, there were larger losses of water to ET (in vegetated mesocosms) relative to evaporation (in bare mesocosms) in the Hopland soils. This suggests that in the Sedgwick soils, *A. barbata* provided enough shade to reduce evaporation, but in the more nutritious Hopland soils, the more abundant production of biomass resulted in transpiration rates that exceeded bare soil evaporation rates.

4.5 Water use by A. barbata

Biomass yield per unit of water has been used as a measure of the functionality of semi-arid and grassland communities (Emmerich, 2007) and is expressed as the ratio of carbon uptake to plant transpiration (water use efficiency, WUE, [Schlesinger, 1991]), or total annual precipitation (rain use efficiency, RUE, [Huxman et al., 2004]). While WUE reflects the actual amount of water consumed by plants during biomass production, RUE includes all water that is available for plant growth. Both measures originate from the economic sense of productivity—how much of a particular resource should be expended to produce a ‘good’ or ‘service’. In general, the lower the resource input required per unit output, the higher the efficiency

We estimated WUE and RUE for the four treatments by using air-dried biomass (Figure 4) irrigation totals and estimated fluxes associated with evapotranspiration (Figure 9). WUE was largest for the high-precipitation treatment in the Sedgwick soils and lowest for the low-precipitation treatment in the same soil. The estimated WUE was the same in the Hopland soils, for both precipitation treatments. As would be expected, WUE was higher than RUE for each of four treatments. However, there was no discernable relationship between WUE and RUE among the four treatments. While in low precipitation Hopland soils this difference was relatively small (i.e., <1 g/L) it differed significantly among the other three treatments (Figure 11). WUE was three fold greater in the low precipitation treatments than the corresponding high-precipitation treatment in both soils. Further, the high-precipitation Sedgwick soil treatment, which had the highest WUE, had the smallest RUE.

5. Conclusions

In grasslands, the effect of intra-annual climate patterns on productivity and other fundamental ecosystem processes has rarely been quantified. For the most part, the emphasis has been on an integrated response over longer time scales, i.e., comparisons between annual productivity and rainfall, where the overriding conclusion has been that interannual variations in net primary productivity is largely influenced by interannual variations in precipitation (e.g., *Swemmer et al., 2007*). While this relationship has proven useful for regional-scale predictions (e.g., *Burke et al., 1991*), it remains weak at the site scale. In this study we were able to explore soil-moisture dynamics in a grassland environment at a finer temporal (intra-seasonal) and spatial scale than has been reported in most previous studies that have looked at water distribution in grasslands. This was possible because of two main advantages over most early investigations. First, by incorporating multiple replicates, we were able to quantify the variance associated with measurements of soil moisture, and therefore determine, with greater confidence, possible impacts of soil type and rainfall on fundamental ecosystem processes. Second, we were able to continuously record, over a period of two years, the moisture status at multiple soil depths, which allowed us to quantify the amount of water partitioned to various flow paths in a grassland ecosystem. However, through this experimental set-up we had a significant drawback; we were not able to achieve water-limiting soil conditions in the low precipitation treatment. As such our analysis reflects conditions under water-

sufficient (rather than water-limited) versus water-excess conditions that can be found in grasslands in California.

Our results show that both soil and precipitation treatments and a possible interaction between the two, influenced aboveground biomass production, and moisture status along the root zone in *A. barbata* monocultures. A positive relationship between soil-water content and biomass production was observed only in the Hopland soils, where less biomass was produced in the low rainfall treatment during both years, and θ also remained low over extended periods. This trend follows that observed in most ecosystems where ANPP increases across biomes with increasing mean annual precipitation (Huxman *et al.*, 2004). By contrast, in the Sedgwick soils, excess water, as suggested by the prolonged saturated profile, may have inhibited biomass production. Such anoxic conditions have been reported to depress growth and yield in dryland species (e.g., Drew 1997, Kato-Noguchi, 2002, St. Clair *et al.*, 2009).

The impact of *A. barbata* on soil moisture was observed in the wetting pattern of the soils at the start of the growing season. In Sedgwick soil, water from early events in the first watering cycle of Year I took much longer to reach the lower soil profile (i.e., to a depth of 0.50 m) than in the Hopland soils. However at the start of Year II, this travel time was significantly reduced. Vegetation has been shown to enhance soil infiltration by mitigating compaction of soils by raindrops (e.g., Mualem *et al.*, 1990), and by root activity (e.g., Devitt and Smith, 2002). Because water was released along the soil surface through drip rings, there were no mitigating effects of the *A. barbata* canopy on splash compaction during this investigation. Rather, it is plausible that the observed increased infiltration capacity was from preferential flow paths associated with the development of

roots (*Gish et al.*, 1998). One consequence of the increased soil permeability was that more water moved into the deeper soil profile in the low-rainfall Sedgwick soil treatment during the early watering events than in the previous year. As a result, in mesocosms with this treatment, unlike the previous year, a near-saturated soil profile persisted for the remainder of the Year II growth season.

The impact of *A. barbata* on soil moisture, largely influenced by soil type and rainfall treatment, was also apparent when subsurface water dynamics were compared (a) in the bare and vegetated mesocosms and (b) among the vegetated mesocosms with different treatments. Surprisingly, only one treatment, the Hopland soil with low-rainfall, had a significantly drier soil profile than the corresponding bare soil treatment. In both the high-rainfall treatments, the near-surface profile remained significantly wetter in the vegetated mesocosms than in the bare mesocosms.

Evaporation and transpiration are important processes that release water from ecosystems to the atmosphere. Because it is difficult to separate evaporation and transpiration losses from field measurements, the exchange of water between the land surface and atmosphere is usually estimated as evapotranspiration. However, as suggested by Kurc and Small (2007), insights into the manner in which ET is partitioned into evaporation and transpiration is critical for understanding water-cycle dynamics, especially in drier climatic regimes. In this study, we were able not only to determine the amount of water released to the atmosphere at periodic intervals during the course of the *Avena barbata* growing season, but also partition this flux to contributions from evaporation and transpiration. Surprisingly, in the Sedgwick soils which had relatively low fertility, there was consistently more water lost to evaporation (as indicated by the

bare soils) than to evapotranspiration (as indicated by the vegetated soils). This is likely the result of reduced evaporation losses resulting from the shade provided by the aboveground biomass (*Scholes and Archer, 1997*). Some crops can reduce evaporation losses by ~0.5–2.0 mm per day (e.g., *Todd et al., 1991*). Further our analysis shows that in the more fertile Hopland soils, for most of the growing season, the volume of water lost to evapotranspiration was higher in the lower rainfall treatment. These observations suggests that ET cannot be assumed to be the simple sum of measured evaporation and transpiration, but is rather a more complex, non-linear relationship influenced by soil properties and biomass.

In developing water budget, we found that the dominant flow paths to which precipitation was partitioned varied between treatments. While in both high-precipitation treatments, most water in the bare and vegetated soils was lost to seepage, in the low-precipitation Sedgwick soils, relatively similar amounts were portioned to ET and seepage. Unlike these three treatments, in the vegetated Hopland soil with low rainfall, most rainfall was lost to the atmosphere.

In our evaluation of the efficiency of water use, the lower productivity Sedgwick soil with high precipitation was most effective. However, when productive efficiency was evaluated from annual precipitation totals, this treatment was the least effect. While not as dramatic in the Hopland soils, this disparity suggests caution, particularly as these types of measures are deployed to understand how grassland systems take up carbon, interactand function.

Observations from this study suggest that even in a “simplified” grassland ecosystem, there is a complex relationship between vegetation, soil, and water. In particular, our

results emphasize the importance of precipitation patterns and soil type, and the possible interactive effects of these parameters, for soil-moisture dynamics in *A. Barbata* monocultures. This study further emphasizes the need for a better understanding of biosphere–hydrosphere interactions. This is particularly true given the compelling need for accurate forecasts of potential biosphere feedback to natural and anthropogenic changes in climate systems (*Huxman et al.*, 2004).

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Tables

Table 1. Texture and chemical attributes of the and Sedgwick soils.

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Figures

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Figure 7. Volumetric soil moisture content (θ) averaged over 21-day periods for both bare (grey lines) and vegetated mesocosms (black lines). Each row represents the depth from which TDR measurements were made. In this and subsequent figures, consecutive water cycles are numbered C1-C8, for both bare and vegetated mesocosms. The four columns identify the response from each of the four treatments, i.e., Hopland soil with low precipitation (HL), Hopland soil with high precipitation (HH), Sedgwick soil with low precipitation (SL) Sedgwick soil with high precipitation (SH).

Figure 8. Change in volumetric soil moisture content over the course of each 21-day watering cycle in both vegetated (a-d) and bare soil treatments (e-h). This change in volume was determined as the difference in soil water between the first and last day of each cycle.

Figure 9. Amount of water removed as ET from vegetated (a-d) and evaporation from bare soil (e-f) mesocosms. Note the volume of water loss was determined from TDR measurements during periods of prolonged drought at the end of each water cycle.

Figure 10. Amount of water partitioned to evaporation and/or ET, seepage and soil storage in vegetated (a-d) and bare soil (e-h) treatments during the course of the growing season in Year II of the experiment.

Figure 11. Water use efficiency (WUE) and rain use efficiency (RUE) calculated from above ground biomass, ET and irrigation totals.

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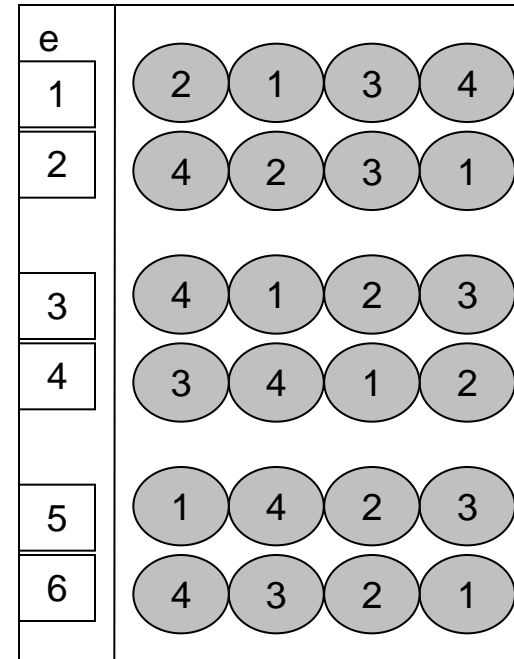
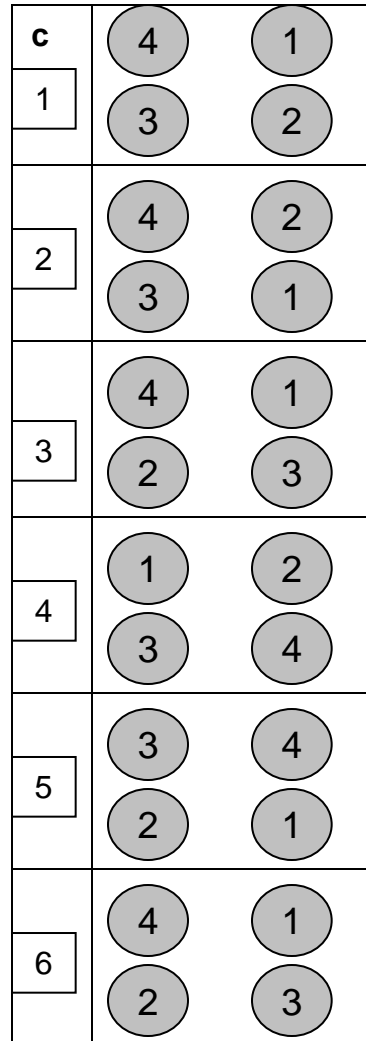
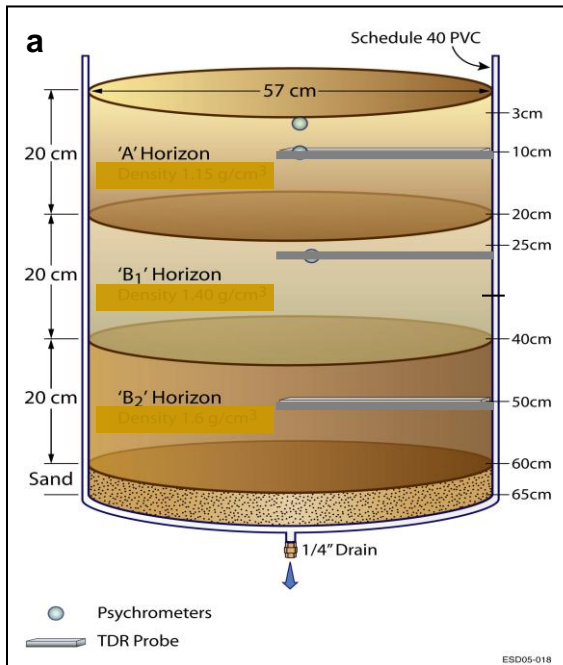
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Soil Type	Horizon	Bulk density (g/cm ³)	Porosity	Texture	pH	N (Total) %	C (Total) %
Hopland	A	1.15	0.56	Sandy loam	5.7	0.2	2.49
Hopland	B1	1.4	0.46	Sandy loam	5.5	0.05	0.21
Hopland	B2	1.6	0.38	Sandy loam	5.7	0.09	0.89
Sedgwick	A	1.36	0.48	Loam	5.6	0.14	0.73
Sedgwick	B1	1.32	0.49	Loam	6.1	0.13	0.32
Sedgwick	B2	1.33	0.49	Loam	6.1	0.12	0.15

Table 1. Texture and chemical attributes of the Hopland and Sedgwick soils.

Soil Type	Rainfall	Status	ET	PS	SP
Hopland	Low	Vegetated	95	-4	9
Hopland	Low	Bare	50	11	39
Hopland	High	Vegetated	23	4	74
Hopland	High	Bare	17	5	77
Sedgwick	Low	Vegetated	52	4	44
Sedgwick	Low	Bare	55	8	37
Sedgwick	High	Vegetated	4	4	92
Sedgwick	High	Bare	18	4	78

Table 2. Percentage of water from the high and low irrigation treatments that was allocated to evaporation and/or transpiration (ET), soil storage (PS) and seepage (SP) during the course of the growing season.



Treatment	Combination
1	Low rain and Hopland soil
2	High rain and Hopland soil
3	Low rain and Sedgwick soil
4	High rain and Sedgwick soil

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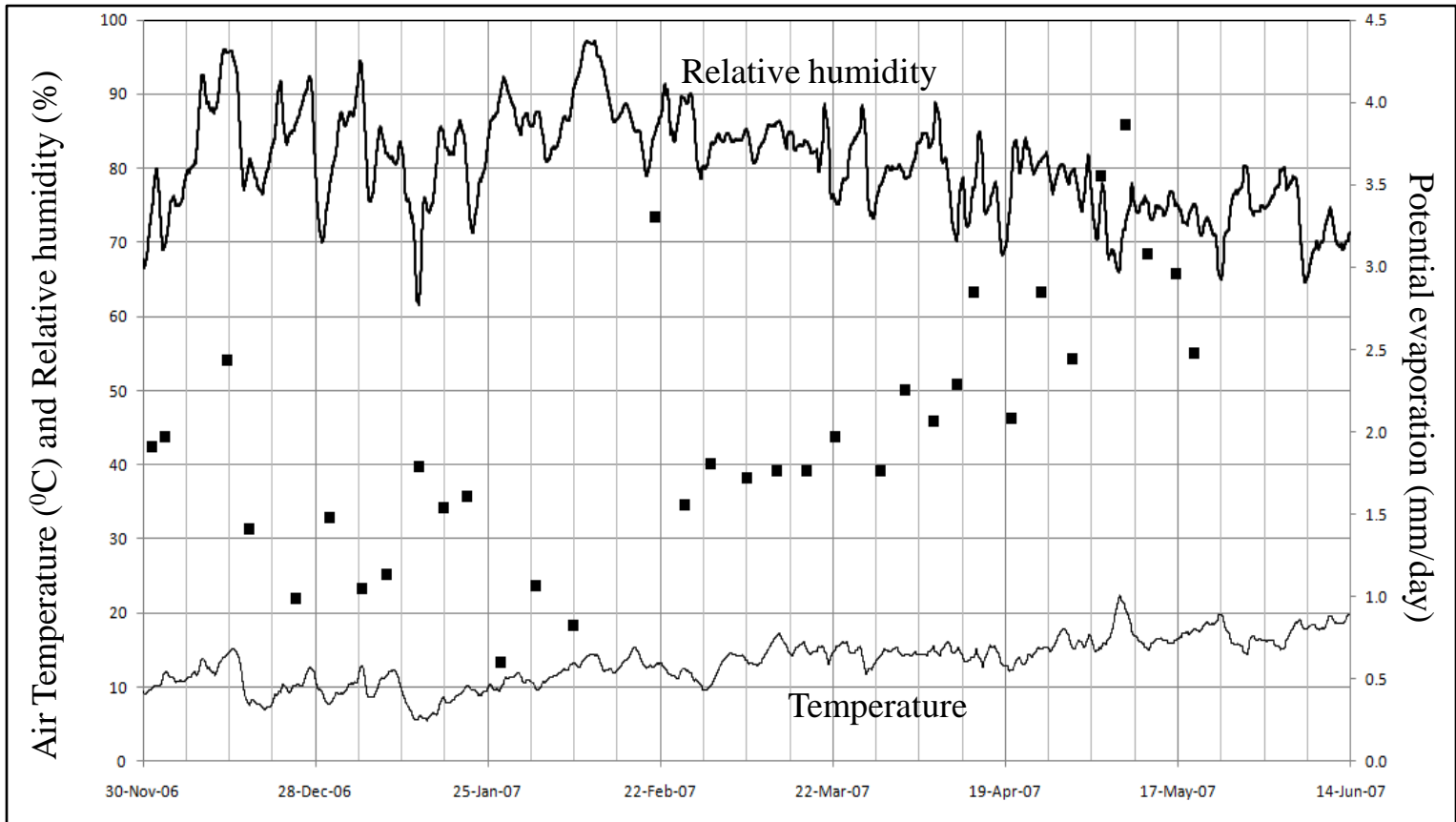


Figure 2. Air temperature, relative humidity and potential evaporation (in solid squares) measured in greenhouse.

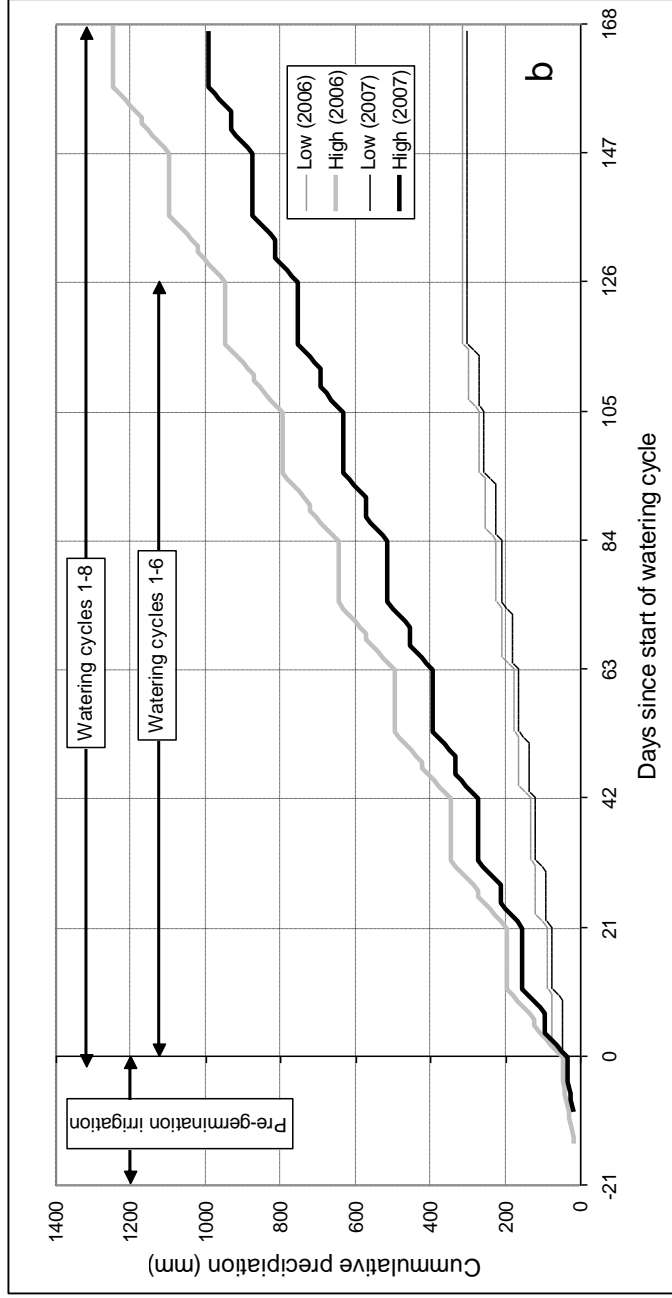
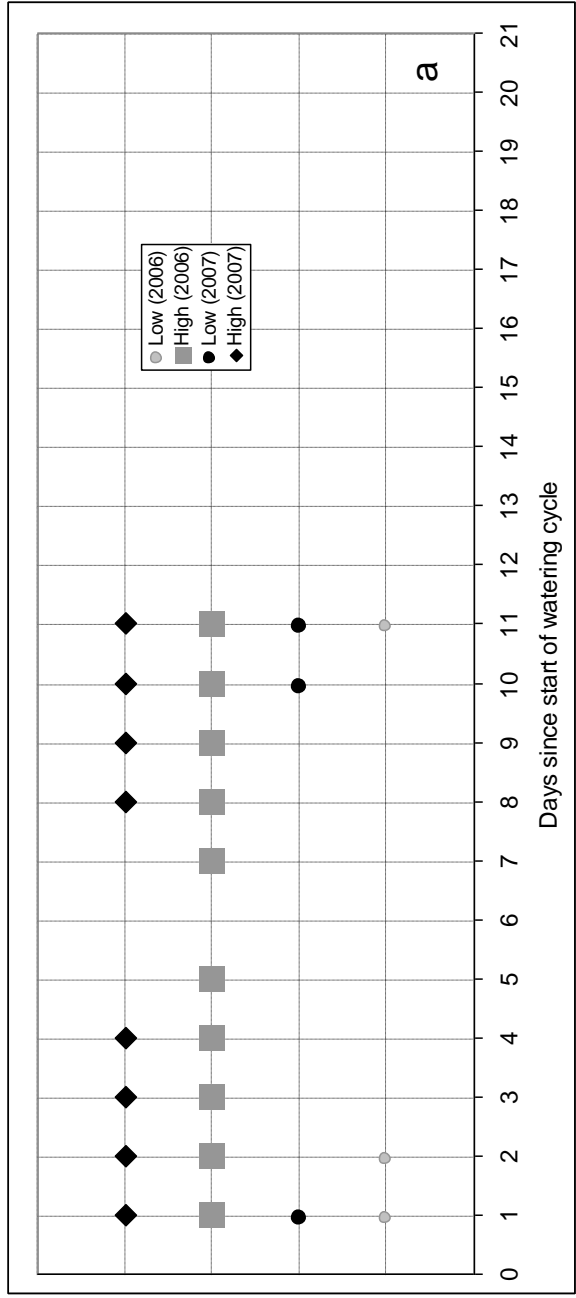


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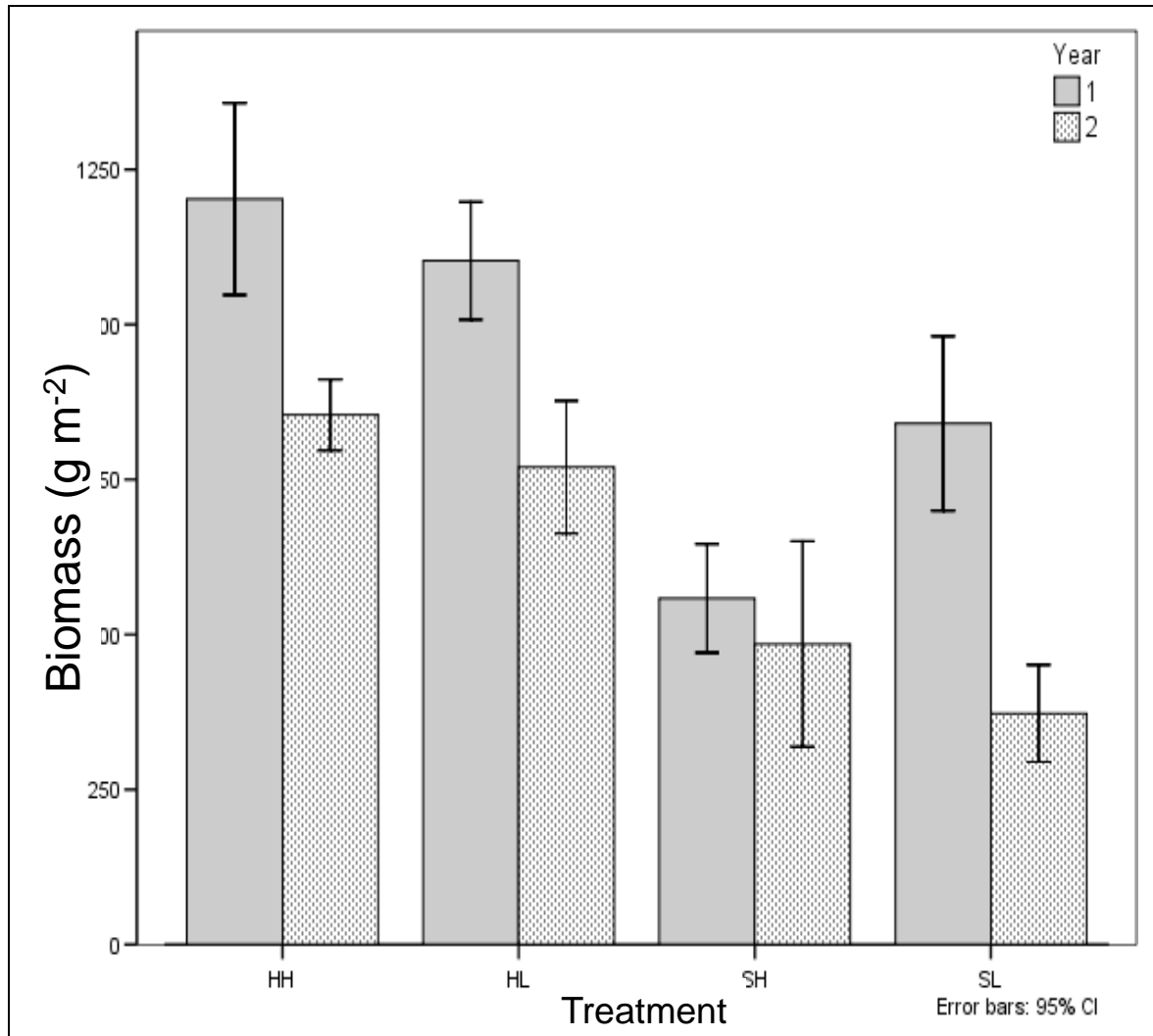


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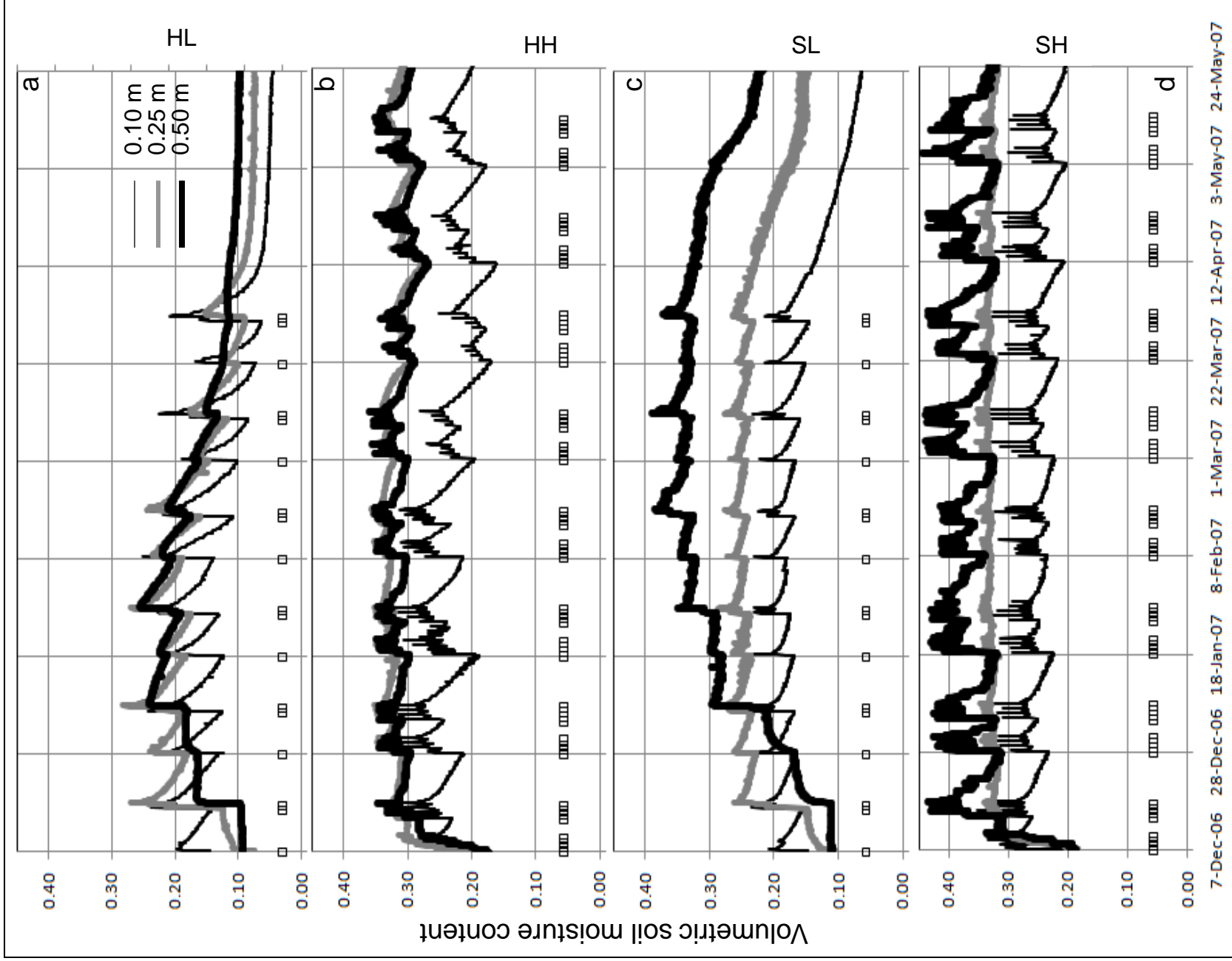


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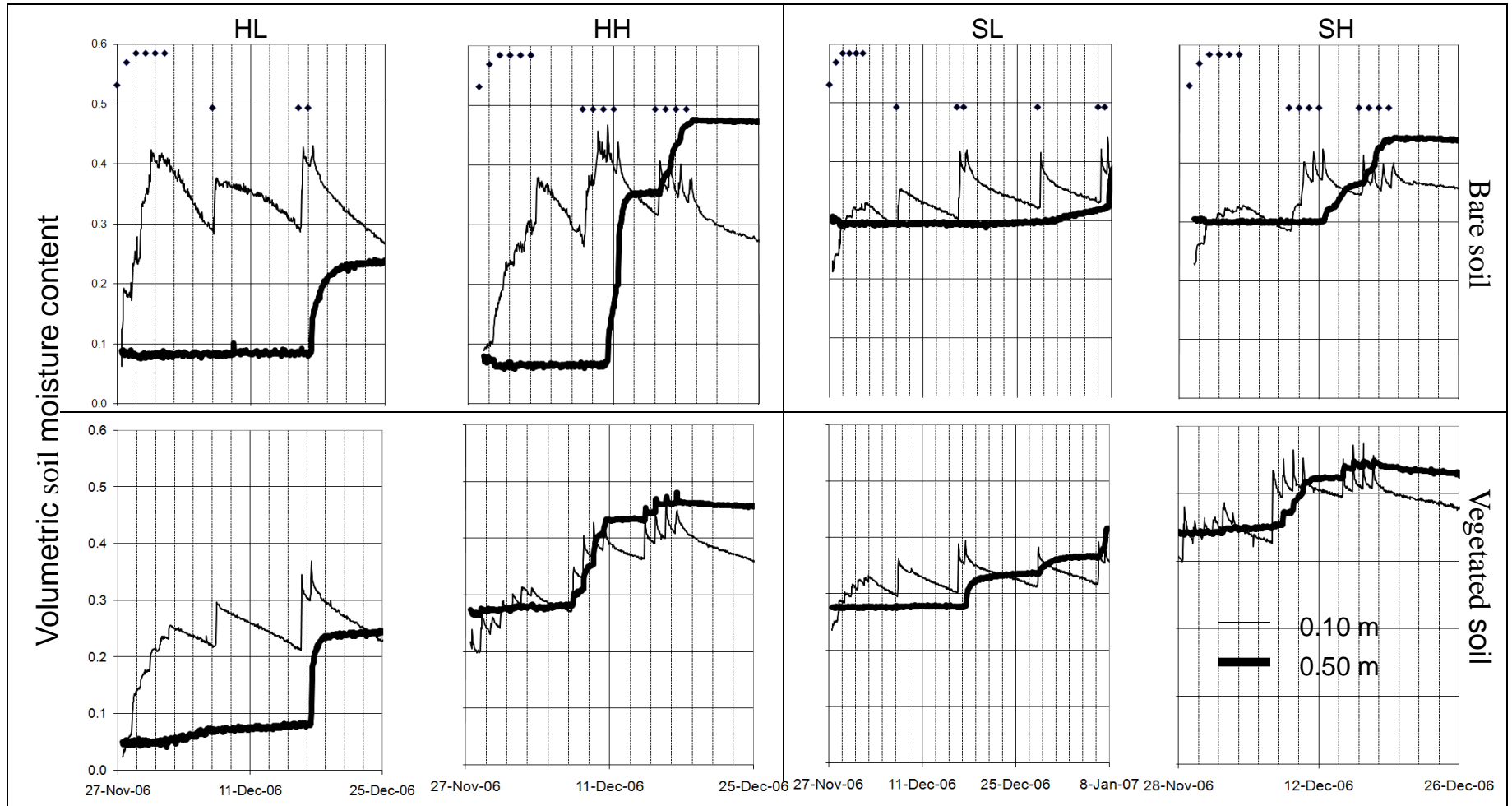


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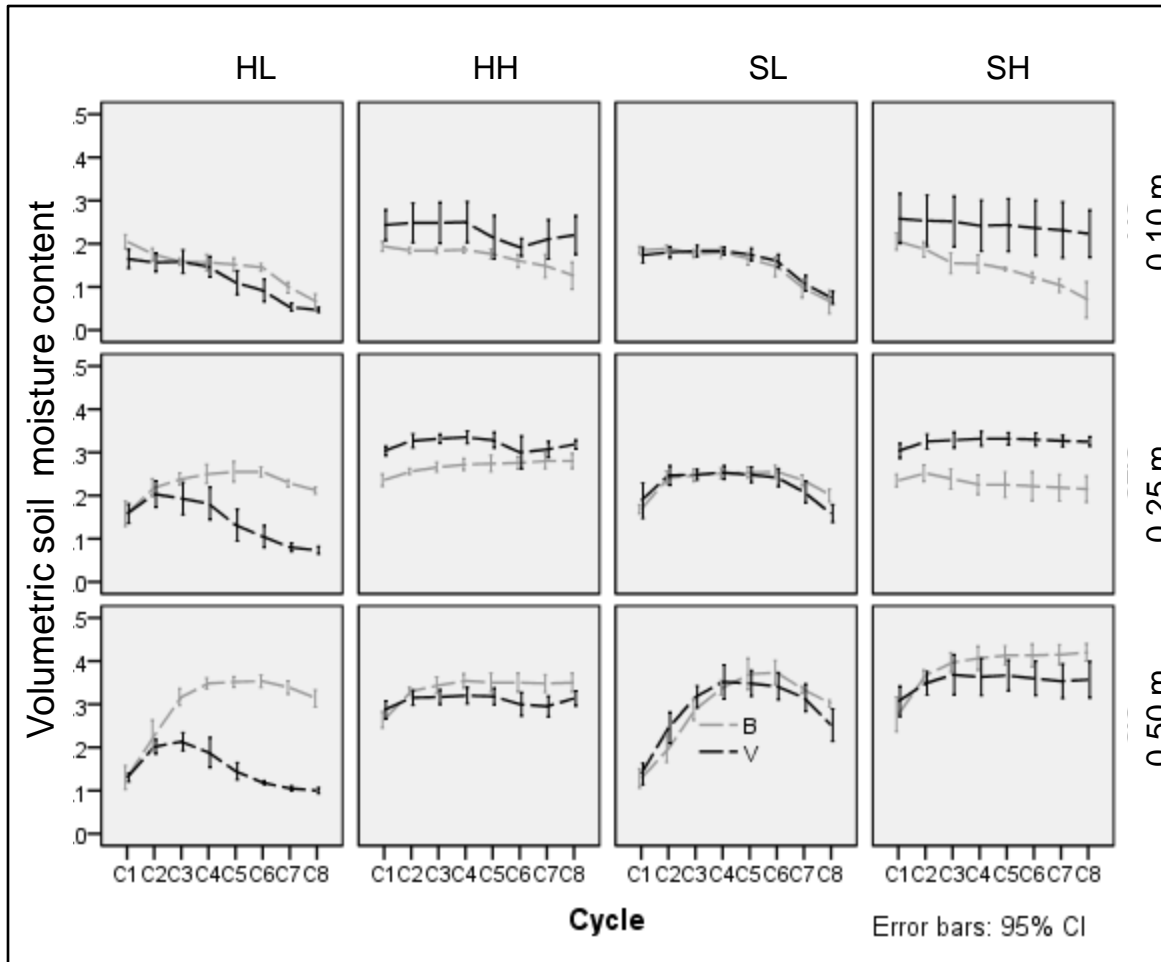


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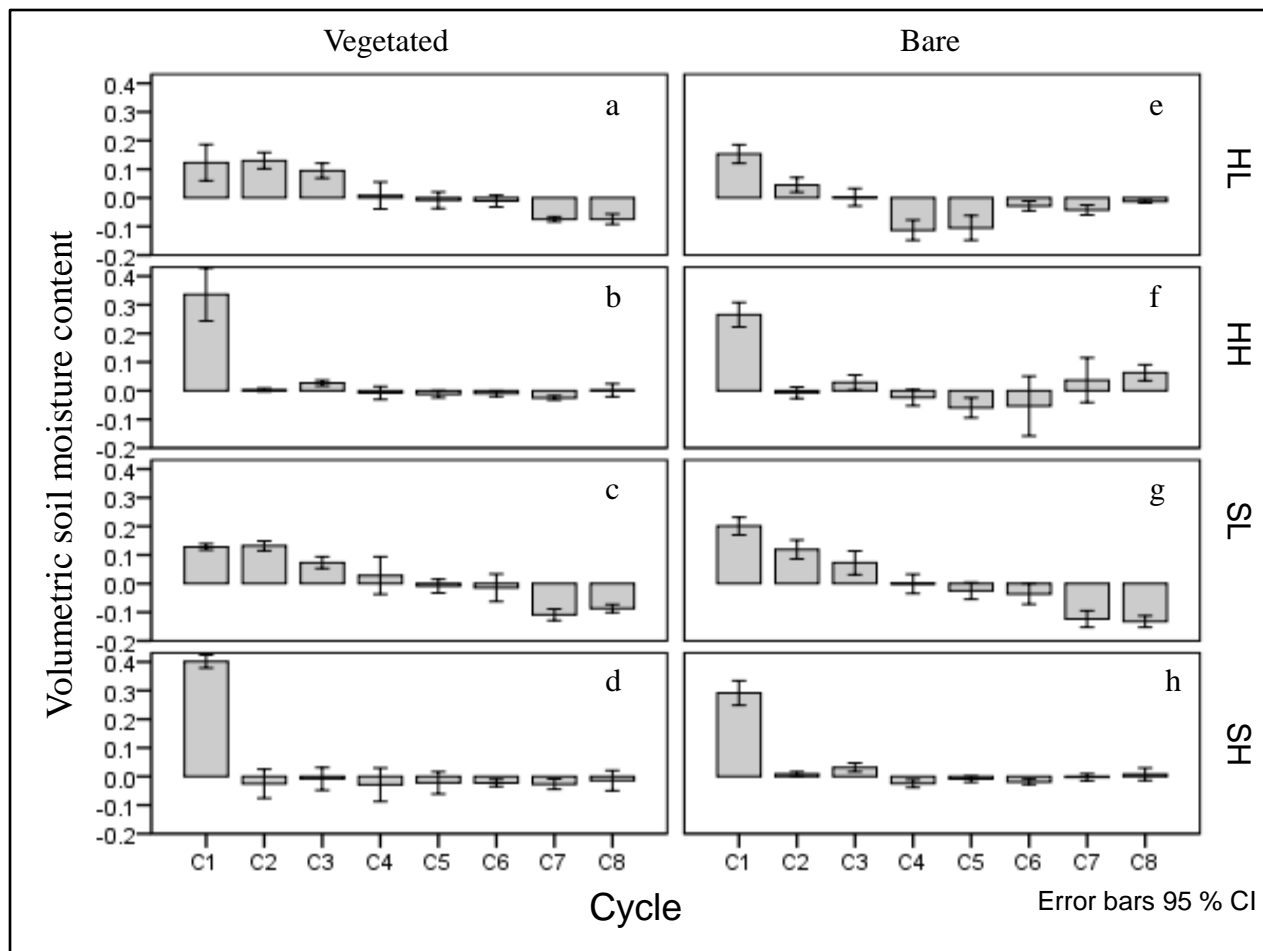


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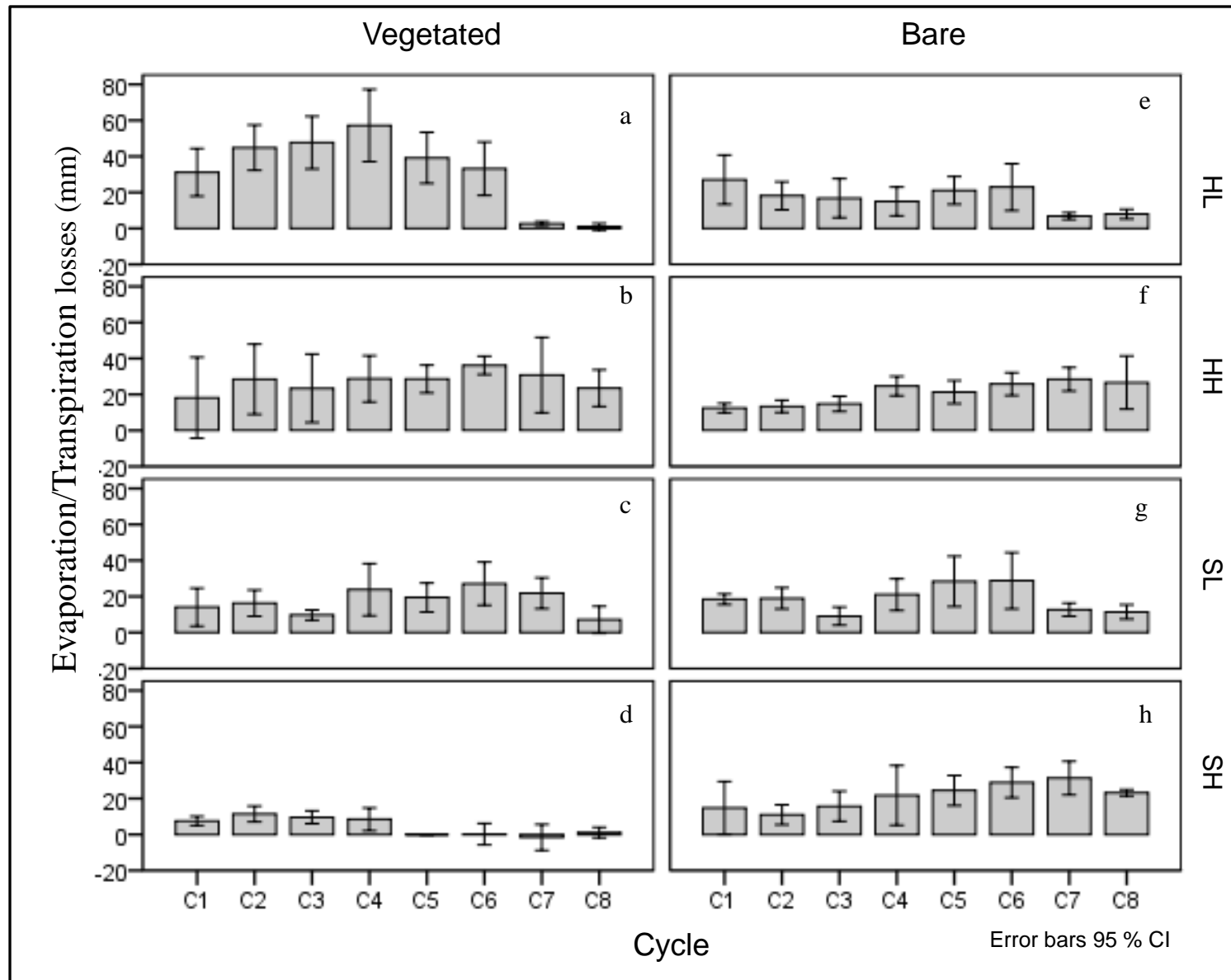


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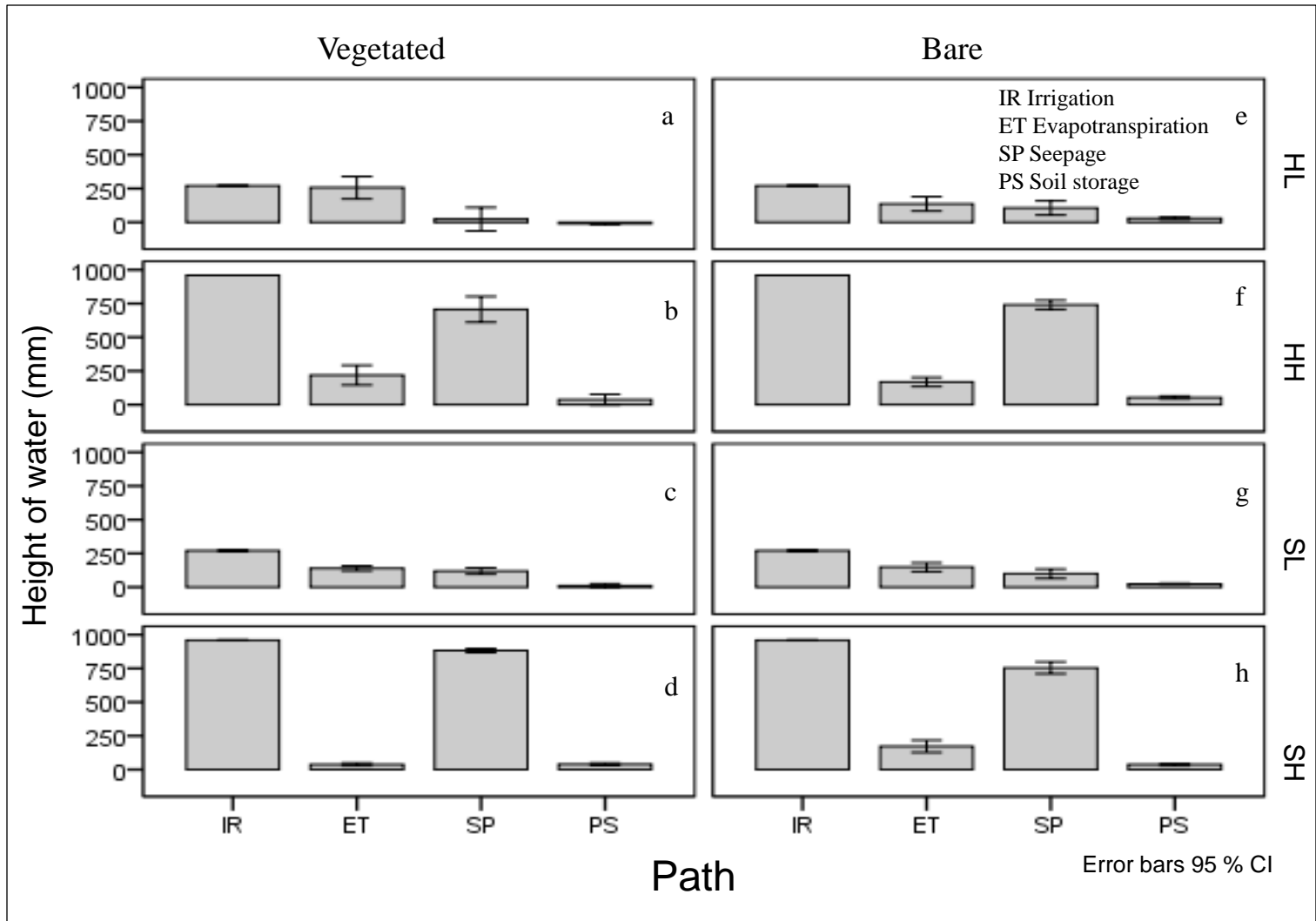


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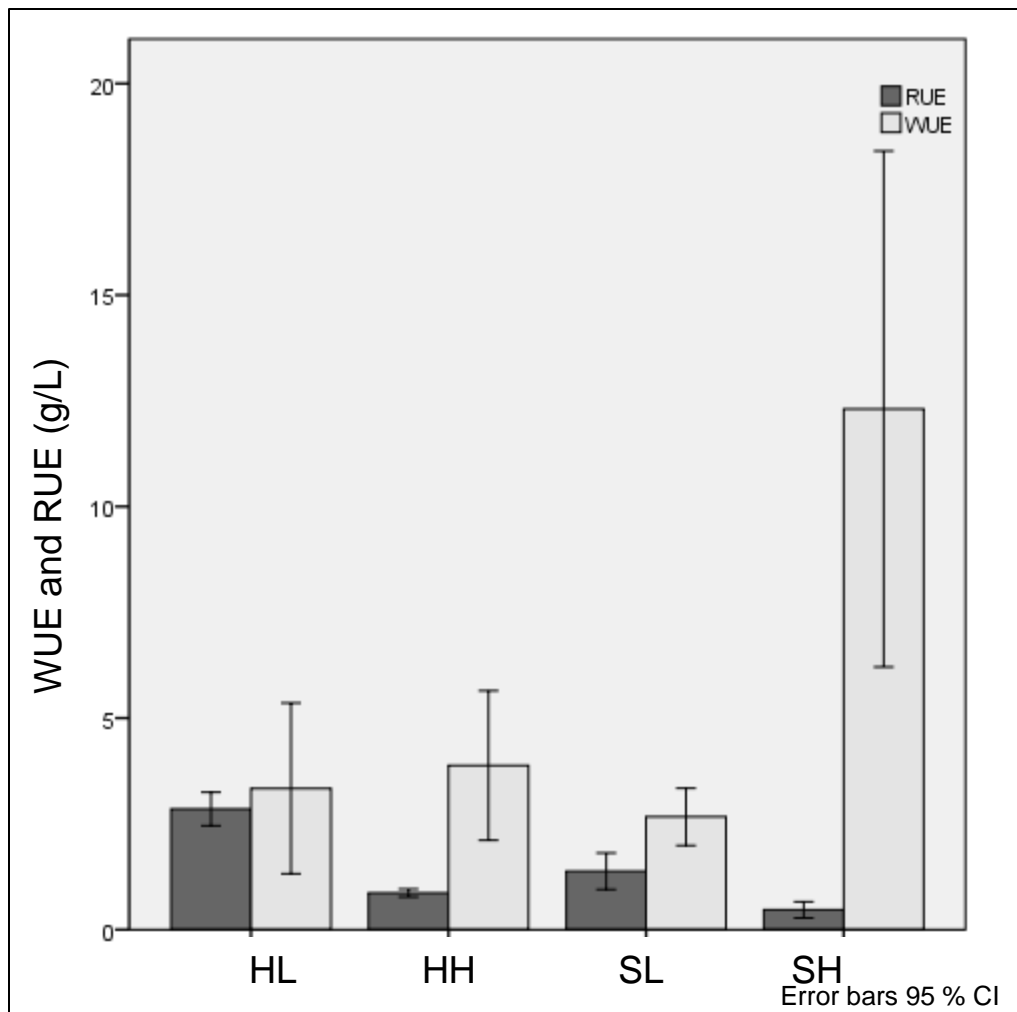


Figure 11. Water use efficiency (WUE) and Rain use efficiency (RUE) calculated from above ground biomass, ET and irrigation totals.

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