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Precipitation thresholds for CO_2 uptake in grass and shrub plant communities on Walnut Gulch Experimental Watershed

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[1] In semiarid ecosystems, precipitation is the major driving force for carbon uptake and subsequent plant growth. The hypothesis for this study was that the timing, frequency, and precipitation amount would produce different precipitation thresholds for uptake of carbon dioxide in grass and shrub plant communities. Eight years of precipitation data were used to determine the amount needed for carbon dioxide uptake thresholds in spring and summer seasons. Bowen ratio energy balance systems were used to measure carbon dioxide and moisture fluxes. In spring at the shrub site, close to or above long-term average spring precipitation of 59 mm was required to produce an uptake response. At the grass site a minimum of 23 mm was needed to produce an uptake response, which was much less than the long-term precipitation average of 68 mm. At both sites, spring or multiple summer responses reduced the threshold values for a summer response. Summer threshold ranges for the shrub site were 57–94 mm with a spring response and 123–140 mm without. Grass site summer thresholds were 51–95 mm with a spring response and 80–148 mm without. Summer precipitation threshold values were higher than spring values relating to the high summer evapotranspiration demand. The influence and variability of precipitation timing and frequency on carbon dioxide uptake threshold values resulted in no definitive conclusions as to differences between the grass and shrub plant communities, except that the grass site had slightly lower thresholds. Precipitation timing and frequency influence on total carbon uptake in some situations were more important than total precipitation. The lower grass site threshold values, along with a shift in climate toward more frequent and smaller precipitation events, may give grass ecosystems a competitive growth advantage.

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1. Introduction

[2] The responses of arid and semiarid shrub and grass land ecosystems to a wide range of rainfall patterns associated with climate change are important ecological interactions that require investigation. Determining vegetation responses to the timing, duration, and frequency of rainfall events may help define their roles in these diverse plant communities. Current knowledge about the interaction of rainfall events and plant growth within semiarid grass and shrub ecosystems is limited. It is important to determine the effects of rainfall patterns within these ecosystems and use this knowledge to explore their interactions, especially the invasion of grasslands by shrub species, a frequent event in the southwestern U.S. deserts. Understanding the consequences of climate change associated with changes in rainfall patterns which impact soil water regimes may be critical in preserving these native grasslands.

[3] The highly random and variable precipitation patterns found in arid zones, along with the variation in timing and magnitude can produce unexpected plant growth responses (i.e., carbon uptake) [*Noy-Meir*, 1973] and can provide insights into climate change impacts on the ecosystems. *Noy-Meir* [1973] further points out that the organisms must adjust to this variability in order to grow and survive. *Reynolds et al.* [2004] used the patch arid lands simulation (PALS) model to identify biologically significant rainfall pulses, the relationship between rainfall pulses and soil moisture, and the ways that different plant types use soil moisture. Their results indicated that sequences of rainfall events are more important than individual events in terms of finding ecological responses to the rainfall pulses. They also found that from 1915 to 2000, in the Mojave, Sonoran, and Chihuahuan deserts, that 34–63% of individual rainfall events were trace amounts of <1 mm, and that the <5 mm group was the largest group. Depending on the status of the plants and antecedent soil moisture conditions, the time span between rainfall events could be extremely important in determining how plants might respond to the different levels of rainfall inputs. Small, random rainfall pulses or

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long dry periods would put the plants in a reduced physiological and morphological state of readiness to respond to the higher levels of rainfall. *Kurc and Small* [2004] evaluated the summer dynamics of ET in semiarid ecosystems and found that small rainfall events only influence the top 5 cm of soil and the moisture is depleted within 3 d. At higher levels of rainfall there would be a threshold level for an ecological response of carbon uptake in different plant communities.

[4] *Schwinning and Sala* [2004] outlined a hierarchy of soil moisture events and ecological responses to precipitation pulses of varying size and frequency. In the middle of this hierarchy is the ecosystem-wide growth response of carbon uptake. Precipitation threshold values for an ecosystem growth response are just beginning to be investigated [*Schwinning and Ehleringer*, 2001; *Huxman et al.*, 2004b]. *Schwinning et al.* [2003] hypothesized that grasses would be more efficient at using small precipitation events than shrubs and at larger event sizes lose their advantage. On a leaf area basis, cold desert grasses were able to take up more of the controlled pulse precipitation inputs than the shrubs, at all levels. Below a 9 mm summer event there was no significant response seen in any of the species to pulse inputs. In warm desert ecosystems there could be different rainfall levels at which the shrubs and grasses are able to respond. Looking at North American deserts, *Reynolds et al.* [2004] suggested that precipitation events should be considered as a group and not as a single event when investigating which events are biologically significant. The physiological and morphological state of the plant is a large determinant as to whether or not the plants can utilize the moisture they receive. Consequently, it is likely that there are some thresholds that must be reached before plants receive enough moisture to grow and thrive. These thresholds for carbon uptake would likely vary with season and prior soil moisture conditions [*Reynolds et al.*, 2004]. Additionally, precipitation events influence soil biogeochemical processes [*Austin et al.*, 2004]. The wet-dry cycles affect microbial processes which impact carbon and nitrogen mineralization and combine with the plant process to influence carbon fluxes critical to ecosystem function. *Sala and Lauenroth* [1982] examined the ability of shrubs and grasses to use large precipitation events on a short grass steppe in Colorado and concluded that small events have a larger effect on the ecosystem dynamics than larger events. Understanding how precipitation events influence ecosystem processes will shed light on ecosystem carbon exchange and how climate change with its associated shifts in timing, amount, and event size patterns may impact different ecosystems [*Weltzin et al.*, 2003; *Huxman et al.*, 2004c].

[5] This study analyzed eight years of precipitation pulse inputs and corresponding carbon dioxide and ET flux responses for a grass and shrub land community found on the Walnut Gulch Experimental Watershed. In semiarid ecosystems where water is limited, our hypothesis is that precipitation event size, frequency, and timing produce different precipitation thresholds for CO_2 uptake in grass and shrub plant communities. The objective was to determine precipitation threshold amounts associated with a CO_2 uptake response and associate the responses with the amounts, timing and frequency of precipitation, using seasonal groupings. The uptake of CO_2 was used as an indication of a response. Precipitation and ET fluxes were used as an indicator of soil moisture and to indicate when CO_2 uptake would be able to occur.

2. Materials and Methods

2.1. Experimental Site Descriptions

[6] Shrub and grass sites for this study were located on the Walnut Gulch Experimental Watershed in southeastern Arizona at the transition between the Chihuahuan and Sonoran deserts. The climate is semiarid with cool winters and warm summers and characterized by a bimodal precipitation pattern of summer precipitation occurring from July to September and winter between November and March. Average annual precipitation from 1963 to 2004 was 317 mm for the shrub site and 341 mm for the grass site, with a mean annual temperature of 17°C. Average seasonal precipitation from 1963 to 2004 at the shrub site is 59 mm for spring (day of year (DOY) 1–150), 201 mm for summer (DOY 151–273), and 64 mm for fall (DOY 274–365) and at the grass site average is 68 mm for spring precipitation, 213 mm for summer, and 71 mm for fall. The shrub site is known as Lucky Hills (110°3′5″W, 31°44′37″N, elevation 1372 m). The dominant shrubs are whitethorn Acacia (*Acacia constricta*), tarbush (*Flourensia Cernua*), creosotebush (*Larrea tridentata* (DC.) Cov.), and desert zinnia (*Zinnia pumila*) with some mariola (*Parthenium incanum*) and little leaf sumac (*Rhus microphylla*). The only grass species remaining at the site, which historically was a black grama (*Bouteloua eriopoda*) community, is bush muhly (*Muhlenbergia porteri*). The soil at this site is Luckyhills series (coarse-loamy, mixed, thermic Ustochreptic Calciorthids) with 3 to 8% slopes. Surface A horizon (0–6 cm) contained 650 g kg^{-1} sand, 290 g kg^{-1} silt, and 60 g kg^{-1} clay with 290 g kg^{-1} coarse fragments >2 mm, 8 g kg^{-1} organic carbon, and 21 g kg^{-1} inorganic carbon.

[7] The grass site is identified as Kendall (109°56′28″W, 31°44′10″N, elevation 1526 m). Dominant grasses are sideoats grama (*Bouteloua curtipendula*), black grama (*Bouteloua eriopoda*), hairy grama (*Bouteloua hirsuta*), tanglehead (*Heteropogon contortus*), sprucetop grama (*Navajita morada*), curly mesquite (*Hilaria bilangeri*), and lehmann lovegrass (*Eragrostis lehmanniana*) with a few existing shrubs of fairy duster (*Calliandra eriophylla*) and burroweed (*Haplopappus tenuisectus*). The soils at the site are a complex of Stronghold (coarse-loamy, mixed, thermic Ustollic Calciorthids), Elgin (fine, mixed, thermic, Ustollic Paleargids), and McAllister (fine-loamy, mixed, thermic, Ustollic Haplargids) soils, with Stronghold the dominant soil. Slopes range from 4 to 9%. The Stronghold surface A horizon (0–3 cm) contains 670 g kg^{-1} sand, 160 g kg^{-1} silt, and 170 g kg^{-1} clay with 790 g kg^{-1} coarse fragments >2 mm, 11 g kg^{-1} organic carbon, and 7 g kg^{-1} inorganic carbon.

2.2. Micrometeorological Measurements

[8] Continuous, 20 min average CO_2 and evapotranspiration (ET) flux measurements were made at both sites using Bowen ratio energy balance systems (BREB) (Model 023/CO_2 Campbell Scientific Inc., Logan, Utah, USA). (Note: Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA or the author and does not imply its approval to the exclusion of

other products that may also be suitable.) The systems were placed in locations with a fetch of 200+ m in all directions. The theory and procedures used to calculate the fluxes has been presented in detail by *Dugas* [1993] and *Dugas et al.* [1999]. Briefly, atmospheric gradients of air temperature, moisture, and CO_2 were measured every 2 seconds and averaged every 20 min. The 20 min averages were stored in a data logger (model 21X, Campbell Scientific Inc.). Kendall grass gradients were measured at 1 m and 2.5 m, and Lucky Hills shrub at 1.5 m and 3.0 m above the soil surface. Vegetation canopy height at the grass site ranged from 0.4 to 0.7 m during the growing season and at the shrub site at an almost constant 1 m height. Atmospheric carbon dioxide and moisture concentrations were measured with an infrared gas analyzer (IRGA) (LI-6262, LI-COR, Inc., Lincoln, Nebraska, USA). Simultaneously the following meteorological data were obtained; net radiation from a net radiometer (model Q*7 REBS, Seattle, Washington, USA), soil heat flux from five heat flux plates at 8 cm (model HFT3 REBS), soil temperature above each heat flux plate from averaging thermocouples, wind speed and direction from an anemometer/wind vane (model 03001 R.M. Young Wind Sentry Set R.M. Young Company, Traverse City, Michigan, USA), and air temperature and relative humidity from T/RH probe (model HMP35C Vaisala, Inc., Woburn, Massachusetts, USA). Net radiometers were calibrated yearly over a grass canopy. Carbon dioxide, water vapor, and energy fluxes were calculated from the 20 min average data. Temperature and water vapor gradients were used to calculate Bowen ratios. Bowen ratio, net radiation, soil heat flux, and soil temperature were used to calculate sensible heat flux. Eddy diffusivity was calculated from sensible heat fluxes and temperature gradients and assumed to be equal for heat, water vapor, and CO_2. Eddy diffusivity could not be calculated when sensible/latent heat flux was in the opposite direction of temperature/water vapor gradients, or when Bowen ratio approached -1.0 [*Ohmura*, 1982]. Under these conditions, eddy diffusivity was calculated by using wind speed, atmospheric stability, and canopy height [*Dugas et al.*, 1999]. This alternative method for calculating eddy diffusivity was used about 12% of the time, primarily at night when gradients and fluxes were small; hence any errors from the alternative method would have minimal impact on the calculated flux values. For short periods of time, usually at sunset and sunrise and when Bowen ratio was near -1.0, fluxes were estimated by linear interpolation with less than 5% of the data interpreted in this way. For longer time periods (i.e., days, usually associated with equipment failure) when there was a clear trend in the flux data, linear interpolation was used to estimate fluxes, otherwise no estimate was made. Normally, fluxes were calculated as the product of the eddy diffusivity and CO_2 gradient corrected for vapor density gradients at the two heights [*Webb et al.*, 1980]. Temperature corrections for the two heights were not applied as *Angell et al.* [2001] have shown the temperature differences to be insignificant as the air enters the IRGA for analysis. For this study, calculated negative CO_2 flux values were considered uptake of CO_2 by the ecosystem.

[9] The micrometeorological measurements of ET and CO_2 can also be done with Eddy covariance systems. The strengths and weakness of each method can be debated. For this work we chose to use the Bowen ration system because at the time this research was started, Bowen ratio systems were the only ones that could be installed and maintained in remote locations without extreme cost. *Lamaud and Irvine* [2006] have recently reported that Bowen ratio systems over estimate ET fluxes when compared with Eddy covariance systems. We agree with their findings, but an over estimation only became noticeable in our data on a long-term basis when precipitation and ET were compared annually. The impact on our results would be that the estimates of soil moisture by precipitation minus ET predicted dryer soil earlier than actually occurred. The time at which the Bowen ratio systems determined the ecosystem took up CO_2 should be relatively unaffected by an over ET estimate.

2.3. Data Analysis

[10] Precipitation, CO_2 and ET flux data were separated into seasons that related to the natural bimodal precipitation sequences and precipitation groupings found that occurred during the study. Spring was considered to be from DOY 1–150, summer was 151–273, and fall was 274–365. Total daily precipitation was defined as an event. The events were separated into size classes for evaluation of the number of events per class and the effect on CO_2 and ET fluxes. Total amount of precipitation from the start of a season to when CO_2 uptake started was determined along with the total amount of CO_2 uptake for the season. These values were used in the determination of threshold values for CO_2 uptake. Within seasons running totals of precipitation and ET were determined in order to estimate soil moisture availability for the potential of CO_2 uptake.

3. Results

3.1. Precipitation Characteristics

[11] The Lucky Hills shrub and Kendall grass sites for the study in most years had below average annual precipitation (Table 1) compared to long-term averages. The grass and shrub sites are located 13 km apart with the grass site receiving a total of 207 mm more precipitation during the study. The mean number of precipitation events within size classes was remarkably similar between sites. The 0–5 mm size class was by far the dominant size class (Table 1). *Reynolds et al.* [2004] found the same pattern in three different desert ecosystems. Yearly variability in total number of precipitation events and number of precipitation events within each size class was large. In 2004, both sites had the highest number of total and 0–5 mm size class events, despite the fact they had much less total precipitation than the highest year. The highest precipitation year was 2000, with the 0–5 mm size class being similar to the other years, but a large amount occurred in the fall (Tables 1, 2, and 3). The high precipitation amount in 2000 was related to the number of events in the larger size classes, especially for the grass site. Precipitation events in the largest size class were almost exclusively in the summer season.

3.2. Lucky Hills Shrub Site

[12] Spring precipitation at the shrub site ranged from 12 mm to 120 mm and occurred within a range of 7–135 d (Table 2). Only three years had CO_2 uptake during the spring season which was related to the timing of spring

Table 1. Lucky Hills Shrub and Kendall Grass Yearly Number of Precipitation Events by Size Class and Total Precipitation

Year	Size Class, mm 0–5	5–10	10–20	>20	Total	Total Precipitation, mm
			Shrub			
1997	47	11	5	3	66	331
1998	31	5	2	2	40	206
1999	31	6	5	4	46	314
2000	38	8	8	7	61	460
2001	35	9	8	1	53	279
2002	30	6	4	2	42	230
2003	44	5	6	2	57	248
2004	69	10	3	1	83	246
Mean	41	8	5	3	56	289
			Grass			
1997	45	9	6	2	62	337
1998	34	11	4	3	52	342
1999	28	8	6	4	46	323
2000	30	13	11	6	60	490
2001	37	7	5	3	52	282
2002	38	3	6	1	48	219
2003	44	8	3	1	56	196
2004	74	9	7	1	91	332
Mean	41	9	6	3	58	315

precipitation. Precipitation amounts that produced CO_2 uptake ranged from 50 mm to 73 mm. The next lower precipitation amount that did not produce a distinctive CO_2 uptake period was 39 mm, indicating that thresholds exists between 39 and 73 mm for CO_2 uptake to occur. The 39 mm received in 2003 did produce alternating days of CO_2 uptake and loss for about 20 d, indicating that it was on the verge of an uptake response. Since the 39 mm did not produce a definitive uptake period, this group of events was classified as no uptake response for the spring season. From these results, the low end of the threshold amount of precipitation for a CO_2 uptake response is estimated to be between 39 and 50 mm, with the high end at 73 mm. In 1997, the site received 59 mm of precipitation in the spring with no CO_2 uptake, but the precipitation was spread out over 135 d. The precipitation and ET running totals indicated that the precipitation was greater than ET only during the early part of the spring season. Soil moisture was depleted before the plants could respond. In 1998, the 56 mm of precipitation produced CO_2 uptake and occurred within 79 d with most events occurring loser together. This allowed soil moisture accumulation for plant growth.

[13] Generally, the summer season had the highest precipitation amounts ranging from a low of 94 mm to a high of 302 mm (Table 2) with the precipitation minus ET evaluations indicating all the spring precipitation was lost to ET by the start of the summer. Only one year, 1998, did not have CO_2 uptake for the summer season even with 132 mm of precipitation (Table 2). The timing of this summer precipitation was such that the running precipitation and ET totals indicated that precipitation was greater than ET for only a few days. The smallest amount of precipitation that produced CO_2 uptake was 48 mm for a second uptake period in 2002. This was the only year to have a second summer response. At the end of the first uptake period, precipitation minus ET calculations indicated they were close to being equal. The 48 mm of additional precipitation received within the following 20 d was enough to initiate the second ecosystem response of CO_2 uptake and illustrated the importance of an earlier response and precipitation timing.

[14] In years with a spring CO_2 uptake response or second summer response, the shrub site had summer ecosystem response thresholds of 48–94 mm (Table 2). The impact of a spring response on the total CO_2 uptake was seen in 2001, when a small amount of summer precipitation was received and site spring and summer uptake did not have adequate summer precipitation to produce a high summer CO_2 uptake. When there was no spring response, the summer still produced the highest CO_2 uptake of 550 g CO_2 m^{-2}. In 2004 another year with ecosystem response threshold ranged from 123 to 140 mm. The exception to this occurred in 2003 with uptake seen after 63 mm of precipitation. The 63 mm of precipitation came within a relatively short period of 21 d in 15 events and allowed for accumulation of soil moisture.

Table 2. Lucky Hills Shrub Site 8-Year Seasonal Precipitation, CO_2 Flux, and Precipitation Response Thresholds for CO_2 Uptake

	Spring (DOY 1–150)					Summer (DOY 151–273)					Fall
Year	Precip., DOY[a]	Precip., mm	Precip. to CO_2 Uptake, mm	Days of CO_2 Uptake, DOY	CO_2 Uptake, g CO_2 m^{-2}	Precip., DOY	Precip., mm	Precip. to CO_2 Uptake, mm	Days of CO_2 Uptake, DOY	CO_2 Uptake, g CO_2 m^{-2}	Precip., mm
1997	5–140	59	NU[b]	NU	+[c]	188–273	168	NA[d]	NA[d]–337	−9.0[d]	104[g]
1998	10–89	56	50	88–144	−38[e]	183–259	132	NU	NU	+	18
1999	75–94	12	NU	NU	+	175–266	302	140	208–289	−193	0[g]
2000	52–88	16	NU	NU	+	153–247	239	123	220–257	−96	205
2001	6–139	77	72	101–146	−103	173–257	184	57	194–329	−550	18[g]
2002	28–35	17	NU	NU	+	189–272	186	129, 48[f]	219–236, 256–271	−114, −42	27
2003	8–76	39	NU	NU	+	192–268	155	63	215–312	−200	54[g]
2004	1–102	120	73	82–146	−198	173–264	94	94	266–300	−46	32[g]

[a] DOY is days of year over which precipitation events occurred.

[b] NU means no CO_2 uptake.

[c] Plus represents a continuous loss of CO_2 during the season.

[d] NA means not available, equipment failure DOY 214–275, measured CO_2 uptake DOY 276–337, not complete uptake.

[e] Negative values are uptake of CO_2 during season.

[f] Values represent two separate summer uptake periods.

[g] Value is for fall periods with CO_2 uptake starting in the summer season.

Table 3. Kendall Grass Site 8-Year Seasonal Precipitation, CO_2 Flux, and Precipitation Response Thresholds for CO_2 Uptake

	Spring (DOY 1–150)					Summer (DOY 151–273)					Fall
Year	Precip., DOY[a]	Precip., mm	Precip. to CO_2 Uptake, mm	Days of CO_2 Uptake, DOY	CO_2 Uptake, g CO_2 m^{-2}	Precip., DOY	Precip., mm	Precip. to CO_2 Uptake, mm	Days of CO_2 Uptake, DOY	CO_2 Uptake, g CO_2 m^{-2}	Precip., mm
1997	6–140	66	NA[b]	NA	NA	188–273	179	106, 30	223–247, 258–274	−83, −59	92
1998	10–116	69	51	80–146	−57[c]	161–259	245	51	198–233	−44	28
1999	75–94	9	NU[d]	NU	+[e]	177–265	314	148	206–284	−548	0[g]
2000	53–82	10	NU	NU	+	160–270	252	80, 68	184–208, 228–256	−136, −39	228
2001	6–139	62	44	70–162	−345	170–273	190	NA[f]	NA	NA	30
2002	24–60	24	23	50–101	−16	189–255	162	78	210–294	−532	33[g]
2003	38–149	42	41	79–116	−6	160–268	110	95, 10, 16	245–263, 269–275, 286–297	−73, −9, −17	44[g]
2004	1–147	123	81	77–149	−312	173–269	171	64, 52	209–242, 266–298	−119, −119	38[g]

[a] DOY is days of year over which precipitation events occurred.

[b] NA means not available because of equipment failure in spring of 1997.

[c] Negative values are uptake of CO_2 during season.

[d] NU means no CO_2 uptake.

[e] Plus represents a continuous loss of CO_2 during season.

[f] NA means not available because of equipment failure from 2001, DOY 181 through 2002, DOY 35.

[g] Value is for fall periods with CO_2 uptake starting in the summer season.

[15] The influence of precipitation on the patterns of CO_2 flux can be seen in Figures 1 and 2. In years with low spring precipitation and no uptake response (Figure 1), there was a constant loss of CO_2 until the summer precipitation began. When the summer precipitation began, there were generally large increases in CO_2 loss before the summer uptake of CO_2 began. These same pulse releases of CO_2 have been observed with simulated precipitation pulses added to dry semiarid grassland plots [*Huxman et al.*, 2004a]. When a spring and summer response was observed, the large loss of CO_2 was not seen at the start of uptake (Figure 2). Spring uptake usually started between DOY 80 and 100 (Figure 2) depending on precipitation timing and coincided with rising air temperatures.

3.3. Kendall Grass Site

[16] Spring precipitation at the grass site ranged from 9 mm to 123 mm and occurred within 19 to 146 d (Table 3). Spring uptake of CO_2 occurred in all years except the two with the lowest precipitation. The threshold values of precipitation that produced a spring CO_2 ecosystem response ranged from 23 mm to 81 mm. The lowest precipitation threshold amount of 23 mm occurred in the shortest time period of 36 d, indicating the importance of precipitation timing and frequency. Precipitation for the other years that produced CO_2 uptake response all occurred over a period of more than 100 d. The range in precipitation threshold values for a spring ecosystem response was much

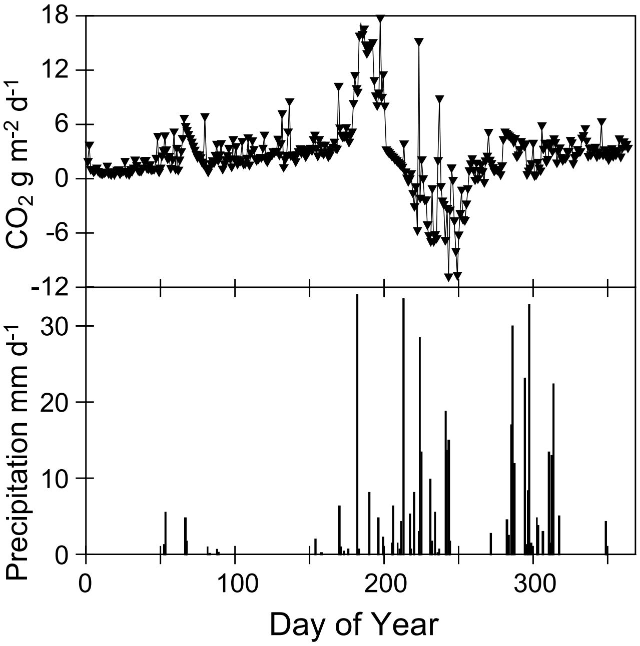

Figure 1. Lucky Hills shrub site, 2000 daily carbon dioxide flux and precipitation. Negative values indicate uptake.

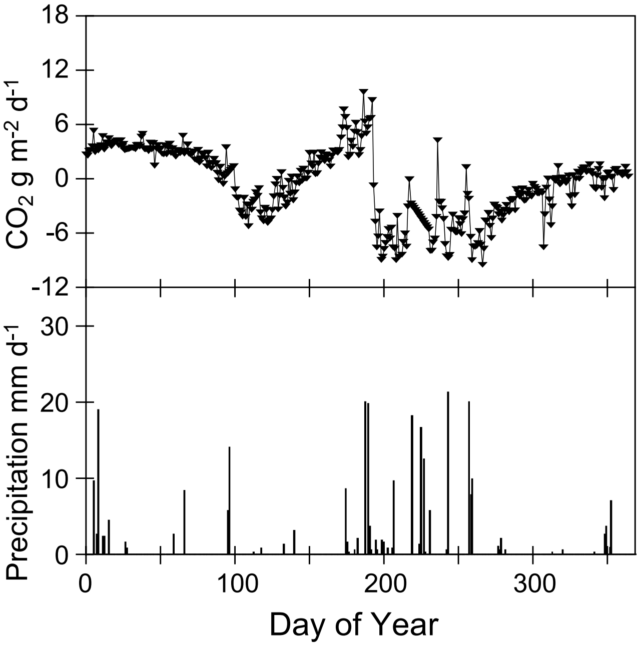

Figure 2. Lucky Hills shrub site, 2001 daily carbon dioxide flux and precipitation. Negative values indicate uptake.

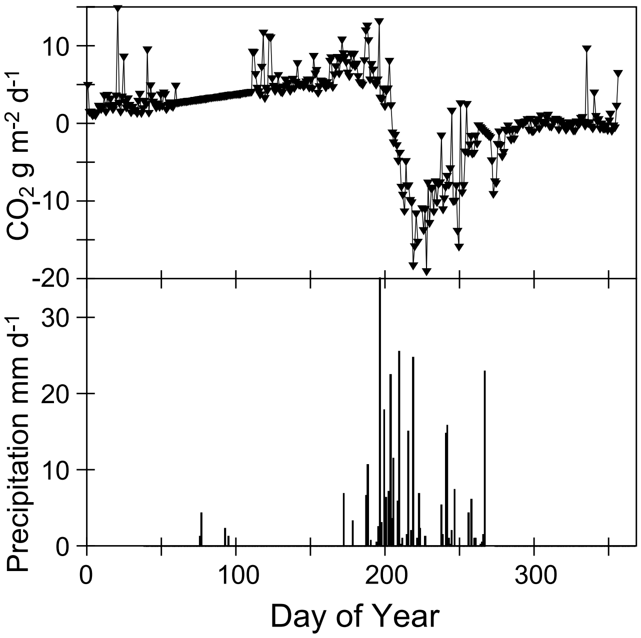

Figure 3. Kendall grass site, 1999 daily carbon dioxide flux and precipitation. Negative values indicate uptake.

larger for the grass site than the shrub site (Tables 2 and 3). The onset of spring CO_2 uptake was similar at both sites, around DOY 80.

[17] At the grass site running totals of precipitation minus ET indicated that all the precipitation was lost to ET by the start of the summer season. The summer season generally had the highest precipitation with a range of 110 mm to 314 mm and occurred within 66 to 110 d (Table 3). All the years had a CO_2 uptake response to summer precipitation. Four out of eight years had more than one ecosystem response of CO_2 uptake. The running totals of precipitation and ET indicated that soil moisture was depleted close to the end of the single and multiple CO_2 uptake responses.

[18] As with the shrub site, the influence of previous spring plant growth was evident on the summer threshold values. Therefore the precipitation thresholds for an ecosystem response of CO_2 uptake were separated into threshold ranges on the basis of three aspects: (1) when there was no spring uptake, (2) spring uptake with one summer uptake, and (3) spring uptake with two or more uptake periods. Years lacking spring uptake showed a summer ecosystem response threshold range of 80 mm to 148 mm of precipitation. When there was a spring response, the summer response threshold dropped to 51 mm to 95 mm. With two or more CO_2 uptake responses, the summer thresholds ranged from 10 mm to 68 mm. In 2002, a spring uptake response paired with a 78 mm summer threshold value reached within 21 d produced the second highest uptake of CO_2 at 532g CO_2 m^{-2} with the second-lowest summer precipitation received. The highest uptake of CO_2 occurred in 1999 with 314 mm of precipitation, 100 mm above the long-term average for summer precipitation.

[19] Precipitation timing, frequency, and amount produced two general patterns of CO_2 uptake. First, a dry spring with no CO_2 uptake and summer precipitation amounts that produced a single or multiple uptake periods (Figure 3). This pattern resulted in the larger ecosystem threshold response values for CO_2 uptake at both the grass and shrub sites (Tables 2 and 3). The second pattern of CO_2 uptake as seen in 2004, demonstrated a spring uptake with one or more summer uptake periods (Figure 4). As the number of summer uptake periods increased, the ecosystem threshold values for the second or third CO_2 uptake periods tended to decrease (Figure 4 and Table 3). The importance of spring uptake, precipitation timing, frequency, and small event size occurring in 2004 can clearly be seen on the CO_2 uptake (Table 1 and Figure 4). The spring plus summer uptake was the highest of any year and further more summer uptake was the third highest. Of further note, the site received one of the lowest summer precipitation totals at 171 mm (Table 3).

4. Discussion

4.1. Lucky Hills Shrub Site

[20] In semiarid ecosystems precipitation is the driving force for plant growth. Precipitation is bimodal with the majority of the precipitation occurring in the summer. These shrub and grass ecosystems are thought of as warm season plant growth communities because of summer soil moisture availability. The absence of a CO_2 uptake response was expected in the spring because of the generally lower precipitation amounts. Surprisingly, three out of eight years at the shrub site produced spring CO_2 uptake (Table 2). The years without spring uptake were dry, with below average spring precipitation or the precipitation occurred over a long period, preventing any accumulation of soil moisture for plant growth. These results indicate that the shrub site will likely have a CO_2 uptake response with close to or above the long-term average spring precipitation.

[21] Important factors for the unexpected spring uptake of CO_2 were related to spring precipitation timing, frequency, amount and the potential of previous year fall precipitation

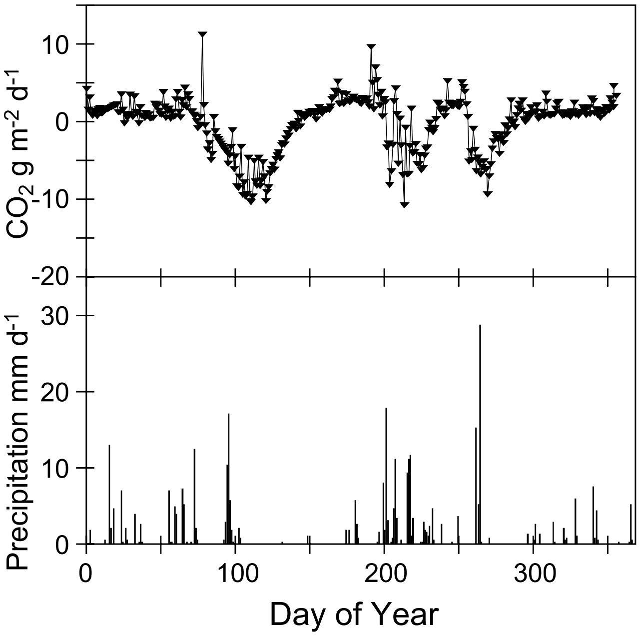

Figure 4. Kendall grass site, 2004 daily carbon dioxide flux and precipitation. Negative values indicate uptake.

soil moisture carryover. Close to or above the long-term average spring precipitation (i.e., 59 mm) was required for an ecosystem CO_2 uptake threshold value to be reached (Table 2). The years 1998 and 2001 had additional soil moisture that was carried over to the spring from the previous cool and low-ET fall period. This had the potential to lower the threshold values and increased the total CO_2 uptake [*Schwinning and Sala*, 2004]. The importance of timing, frequency, and amount of precipitation was again evident with the highest threshold value and largest CO_2 uptake seen, during the spring of 2004. This year had the highest number of total and small precipitation events (0–5 mm) requiring a longer period of time before enough soil moisture had accumulated for plant growth (Table 1). Once plant growth began the higher than average spring precipitation and numerous events allowed for additional plant growth with CO_2 uptake to occur before the soil moisture was depleted.

[22] In these semiarid ecosystems, summer precipitation supplies the majority of annual precipitation and soil moisture for most of the annual plant growth. The hot and dry period before the start of the summer precipitation depleted essentially all of the soil moisture previously received at both the shrub and grass sites. As a result, the summer threshold values were composed of summer precipitation moisture only. Even though summer precipitation is the highest, the potential ET is very high and the precipitation can be lost in short time periods [*Schwinning and Sala*, 2004]. An example of this was 1998 at the shrub site, with the lowest number of annual precipitation events, lowest annual precipitation and second-lowest summer precipitation (Tables 1 and 2). The small number of events and low precipitation amount did not allow for accumulation of enough soil moisture for plant growth to occur.

[23] The presence or absence of a spring ecosystem CO_2 uptake response had an impact on the summer threshold values. The years without a spring response had the higher summer threshold values. This was most likely the result of the physiological condition of the shrubs when the summer precipitation arrived [*Reynolds et al.*, 2004; *Potts et al.*, 2006]. The shrubs had not grown in a year and would likely be in a desiccated and dormant state which would require more soil moisture than usual and a longer time to recover before growth and CO_2 uptake could begin [*Yan et al.*, 2000]. Evidence of this was observed in the dry fall and into spring years when even the drought hardy creosote bushes had dropped most of their leaves. A relationship has been established between gross photosynthesis and leaf area index (LAI) [*Flanagan et al.*, 2002]. The spring CO_2 uptake responses would enable the plants to produce new leaf and root growth that would prime the shrubs for summer growth, producing the lower ecosystem threshold values. Further evidence of this effect was the second CO_2 uptake response in 2002 along with the smallest shrub ecosystem threshold value (Table 2). The shrubs experienced a depletion of soil moisture at the end first response. For the second response had to again become metabolically active again in order to take up CO_2 and were able to do this with 80 mm less precipitation than the first response.

[24] Additional insight into the importance of the spring response on summer ecosystem threshold values and the lack of importance of total summer precipitation on total carbon uptake was evident when 1999 and 2001 were examined. In 1999 there was no spring response and the highest summer threshold value was observed (Table 2). This year also had the highest summer and third-highest annual precipitation (Table 1), yet the summer carbon uptake was approximately one third of the highest seen in the 8 years. The physiological state of the shrubs at the start of the summer precipitation was most likely responsible for the high threshold value and low carbon uptake. Loss of roots due to cavitation, leaves to abscission, and lack of or low quantities of photosynthetic enzymes, all these factors are likely to be occurring at the end of the long dry period that occurred before the summer precipitation [*Yan et al.*, 2000; *Schwinning et al.*, 2003]. Year 2001 with a spring response had the lowest summer threshold value. The summer and annual precipitation was in the middle of the ranges observed, yet produced the highest summer and annual uptake of CO_2 with the longest uptake period. This clearly illustrates the importance of seasonal precipitation timing on ecosystem threshold values and questions the notion that more annual precipitation translates directly into more plant growth and CO_2 uptake.

[25] Another significant influence on ecosystem thresholds values and CO_2 uptake was precipitation timing and frequency interaction with precipitation event sizes and total amount. By far the highest number of annual precipitation events, number of small events, and lowest summer precipitation occurred in 2004 (Tables 1 and 2). These small events required a longer time to accumulate enough soil moisture, especially in the summer with the high ET potential, to allow for plant growth, even with the spring response that tended to shorten summer threshold values. This year had the highest summer threshold value with a spring response. The high number of total precipitation events and small size events with one of the lowest annual precipitation years combined to produce the second-highest spring plus summer CO_2 uptake. This was another illustration of how precipitation timing and frequency was more important than total precipitation on threshold values and CO_2 uptake. An additional aspect of the large number of small precipitation events is the associated wetting and drying cycles that tend to release nitrogen and phosphorus [*Austin et al.*, 2004; *Turner and Haygarth*, 2001]. This release of nutrient could stimulate plant growth and account for some of the increased CO_2 uptake.

[26] There was a relationship between the ecosystem threshold values and average long-term seasonal precipitation for the spring season, but not for the summer. The spring threshold values were close to the long-term average spring precipitation, while the summer values were much less than the long-term average summer precipitation. The lower summer threshold values in relation to the average summer precipitation is probably related to the shrubs being primarily warm season growth plants that would respond more to the summer precipitation. The generally higher summer precipitation threshold values compared to the spring were most likely related to the high summer potential ET requiring more precipitation to get enough accumulated soil moisture for plant growth. The deeper root systems of the shrubs would also require more precipitation to reach the roots [*Kurc and Small*, 2004; *Cox et al.*, 1986].

4.2. Kendall Grass Site

[27] Surprisingly, low spring precipitation was able to produce a CO_2 uptake response in most years, except in very dry years with <11 mm (Table 3). In most years the spring ecosystem threshold values were below the long-term average spring precipitation. The implication of these results is that in most years there will be spring and summer CO_2 uptake responses, contrary to the notion that warm season grasses have their growth period during the summer [*Culley*, 1943]. The bimodal spring precipitation pattern is some what similar to winter dominated precipitation pattern with spring growth of cool season grasses. The grasses are taking advantage of the winter/spring precipitation to have the two growth periods.

[28] The lowest threshold value in the spring of 2002 was the result of precipitation timing which allowed the small amount of precipitation to accumulate soil moisture for plant growth [*Schwinning et al.*, 2003]. The frequent and early in the year precipitation events allowed the CO_2 uptake response to occur earlier than in the other years. The grass plants have a large percentage of their biomass in a shallow root system [*Cox et al.*, 1986] enabling them to take advantage of even the small precipitation events for plant growth. The shallow and fine root systems of the grass plants could be partially responsible for the generally smaller threshold values in both seasons for the grass site when compared to the shrubs [*Cox et al.*, 1986]. The shrub plants have much less biomass in the root system and have deeper root profiles. The deeper root system probably required that there be close to average spring precipitation before the shrubs were able to respond.

[29] As with the shrub site, the grass site summer CO_2 uptake was in response to summer precipitation alone, as all the soil moisture was depleted by the start of the summer rains. Again, the impact of spring growth was evident in reducing the summer threshold values (Table 3). The spring growth enabled the grass plants to be in an enhanced physiological condition to better utilize summer precipitation. The shallow root system allowed the grass plants to take advantage of the initial summer soil moisture within a shorter period of time. These effects on the threshold values were clearly evident when there were multiple CO_2 uptake responses as with each response the threshold values tended to decrease.

[30] In the literature, it has been shown that annual precipitation is the dominant factor in net primary production (NPP) and gross primary production (GPP) in grassland ecosystems [*Sala et al.*, 1988; *Flanagan et al.*, 2002; *Khumalo and Holechek*, 2005]. The implication is that greater precipitation produces more NPP and GPP. In this semiarid grassland ecosystem, precipitation timing and frequency were able to greatly influence the threshold values and CO_2 uptake. An example of this was 2002, with the shortest summer precipitation duration and second-lowest summer precipitation producing a small threshold value and second-highest CO_2 uptake (Table 3). The spring uptake also allowed for the ecosystem to be in a better state for plant growth in the summer and to be able to take advantage of the summer precipitation timing and frequency. The influence of precipitation timing over the total precipitation amount on NPP and GPP has been observed in a Mediterranean grassland [*Xu and Baldocchi*, 2004]. They attributed the timing effect to a winter and spring growing season when ET would be low and moisture was not a limiting factor. In our semiarid grassland ecosystem, the summer ET is high and soil moisture can quickly become limiting. The precipitation timing and frequency were still dominating factors in both threshold values and CO_2 uptake. High summer precipitation alone can still dominate CO_2 uptake as was observed in 1999.

5. Summary and Conclusions

[31] Precipitation timing and frequency were found to be the major components in seasonal precipitation threshold values needed for a carbon uptake response at the shrub and grass sites. In some years, precipitation timing and frequency were more important for carbon uptake than total precipitation. Spring carbon uptake responses considerably decreased summer threshold values and could have an impact on seasonal as well as yearly carbon uptake. Threshold values for multiple uptake events decreased with each successive one. The influence of precipitation timing and frequency and the variability in precipitation timing and frequency prevented definitive conclusions to be drawn on differences in threshold values between sites. The grass site tended to have lower threshold values, especially in the spring, and greater overall carbon uptake. If a shift in climate occurs toward more frequent and smaller precipitation events, as was observed in 2004, the grass ecosystems may have a competitive advantage for carbon uptake because its shallower root system is better able to utilize the soil moisture [*Kurc and Small*, 2004].

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