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Soil enzyme responses to varying rainfall regimes in Chihuahuan Desert soils

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Abstract. Extracellular enzyme activities (EEAs) are indicators of both soil microbial activity and nutrient availability for plants. However, it is unclear how EEAs change over the growing season in desert grasslands. We examined whether EEAs changed in response to the size and frequency of rain events during the summer monsoon in the northern Chihuahuan Desert, and if the response varied between plant and interspace associated soils. Potential EEAs were measured within a rainfall manipulation experiment at the Sevilleta National Wildlife Refuge in central New Mexico, USA. Rainfall treatments included either three 10-mm events or one 30-mm rain event per month throughout the three month summer monsoon (July–September). EEAs were measured immediately before and within hours after experimental rain events under plants and in unvegetated interspaces. Throughout the season hydrolase activities were higher under vegetation than in interspace soils. Potential activities of hydrolytic enzymes were similar for the two rainfall regimes. Activities increased following early season rain, showed little response to mid-season rain, and decreased following late-season rain. Although enzyme activities did not differ between rainfall treatments, ratios between enzymes varied, indicating different nutrient limitations imposed by rain event size and frequency. Larger nitrogen and phosphorus limitations occurred in interspace soils that experienced large, frequent rain events. Many factors, including location relative to plants, seasonality, and rainfall size and frequency, influenced enzyme activities and nutrient availability in these Chihuahuan Desert soils throughout the monsoon season.

Key words: Chihuahuan Desert grassland; extracellular enzyme activity (EEA); precipitation regime; Sevilleta LTER.

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INTRODUCTION

Microbial communities control many biochemical processes in ecosystems worldwide. In dryland environments soil microbes, in particular, influence carbon cycling (Cable et al. 2008), potentially causing ecosystems to fluctuate between carbon sources and sinks based on event-scale and seasonal precipitation patterns (Huxman et al. 2004, Kurc and Small 2007, Anderson-Tiexeira et al. 2011). Soil organic matter decomposition rates are linked to microbial activity (Moorhead and Sinsabaugh 2000) and facilitate nutrient cycling and organic matter turnover in dryland environments. Soil microbes rely on a variety of extracellular enzymes for the breakdown of complex organic compounds into soluble energy and nutrient sources (Sinsabaugh

et al. 2002, Moorhead et al. 2012). During extended periods of drought, extracellular enzymes can degrade or stabilize on soil particles, potentially preserving the utility of these nutrient-generating agents until moisture returns (Stursova and Sinsabaugh 2008). Likewise, soil enzyme activities in many systems strongly respond to moisture fluctuations (Henry 2012) and enzyme activity has been suggested to increase following precipitation events (Munson et al. 2010).

Microbial activities in soils are strongly influenced by water availability (Huxman et al. 2004, Collins et al. 2008, 2014). Soil moisture stimulates plant productivity and microbial driven processes (Vargas et al. 2012). For example, timing and magnitude of rain events alter nitrogen mineralization, transformations of organic matter, and carbon loss from dryland soils (Austin et al. 2004, Belnap et al. 2005, Bell et al. 2008, Munson et al. 2010, Vargas et al. 2012). Therefore, small precipitation events may differentially influence plant and microbial activities by separating the timing of nutrient transformation and utilization (Austin et al. 2004, Huxman et al. 2004, Sponseller 2007, Collins et al. 2008). Although small, 5-mm rain events can activate plants (Sala and Laurenroth 1982, Thomey et al. 2011), a 10-mm rain event has been suggested to synchronize semiarid plant and microbial activity and maximize nutrient cycling efficiency (Dijkstra et al. 2012).

Soil resources and vegetation cover are heterogeneous in many aridland ecosystems (Schlesinger et al. 1990, 1996). These systems are characterized by patches of vegetation interspersed with unvegetated soils often occupied by biological soil crusts. Soil nutrients, organic matter, and soil moisture are generally greater (Schlesinger et al. 1990, Kieft et al. 1998, McCrackin et al. 2008) under plant canopies than beneath adjacent unvegetated soil patches (Bhark and Small 2003, Pockman and Small 2010). Assuming that soil resources, along with root exudates, influence the rate of microbial processes (e.g., Vargas et al. 2012, Collins et al. 2014), enzymatic activities are likely to be higher in soils beneath plant canopies than beneath unvegetated patches.

Precipitation in the Southwestern USA mainly occurs in small, pulsed events (Loik et al. 2004) and is predicted to become more variable in the future (Diffenbaugh et al. 2008, Gutzler and Robbins 2011). Given that dryland systems are sensitive to changes in precipitation (Heisler-White et al. 2009, Thomey et al. 2011, Sala et al. 2012, Collins et al. 2014) it is unclear how availability of soil resources, often made available via extracellular enzymes, will change under future patterns of precipitation. A study by Bell et al. (2009) in desert grassland found that EEA was similar at the beginning and end of the summer monsoon season, but enzyme dynamics following individual rain events across the season have not been determined. In this study, we experimentally altered the size and frequency of soil moisture inputs during the summer monsoon in a northern Chihuahuan Desert grassland and monitored extracellular enzyme potentials to examine how rainfall changes potential enzyme activities throughout the season.

Methods

Study site

Research was conducted on the Sevilleta National Wildlife Refuge (SNWR), in central New Mexico, USA (34.33° N, 106.83° W), also the location of the Sevilleta Long-Term Ecological Research (LTER) site. This research occurred in a mixed grassland which contained species from both Chihuahuan Desert and shortgrass steppe ecosystems. *Bouteloua eriopoda* and *Bouteloua gracilis* were the dominant grasses at the site and each plot contained equal amounts of each species. Soils are classified as a Typic Haplargid. Surface soils have a 3.0–7.5 cm deep sandy horizon composed of aeolian material and occur atop several argillic horizons. The course texture of surface soils allows relatively high infiltration to the argillic horizons, where water holding capacity is increased due to high montmorillonite content (Buxbaum and Vanderbilt 2007, Bryan-Ricketts 2012). A petrocalcic layer occurs 40–70 cm below the soil surface, which constrains root depth and moisture infiltration (Buxbaum and Vanderbilt 2007). Mean annual precipitation (MAP) over the past 22 years is 240 ± 14 mm, with ~60% of MAP occurring in larger, summer monsoon events from June to September (Gosz et al. 1995, Pennington and Collins 2007, Petrie et al.

2014). Plant production is aligned with precipitation and perennial grass production responds primarily to summer monsoon precipitation both locally and regionally (Muldavin et al. 2008, Notaro et al. 2010).

Experimental field study

From July to September 2010, potential soil enzyme activities were measured in a rainfall manipulation field study. Ten 2 m × 2 m complete rainout shelters were deployed in July 2010. Shelters had complete, clear polycarbonate roofs sloped from 1.2 to 0.9 m off the ground and were open along the sides therefore all precipitation was blocked but air easily mixed under the shelters. For complete control of precipitation in the field, natural rainfall was diverted from plots and water was experimentally applied using a hand-held garden wand during the monsoon season. Metal flashing was buried to 10 cm along the perimeter of each plot to prevent run-on. A one-time 30 mm rain event was added to all plots on 15 June 2010 to activate plants for the summer growing season. From July to September, plots were watered following one of two precipitation regimes. Five plots received one 30-mm rain event each month, and 5 plots received a 10-mm rain event every 10 days. Therefore over the course of the experiment plots received the same amount of water (120 mm) but precipitation regimes varied in frequency and magnitude of events. Soil moisture under shelters was measured in 15-min increments from soil moisture probes (ECH_2O EC-5 Decagon Devices, Pullman, WA, USA) at 5- and 15-cm depths within each plot.

To measure soil enzymatic response to precipitation variability, surface soils from 0 to 3 cm were collected one day before and within 4–6 h after the first experimental rain event of each month. Within each plot, soil samples were collected from unvegetated interspaces and plant-associated soils at the base of grasses (referred to as 'plant soils' hereafter) and analyzed separately. Both plants and microbes make extracellular enzymes, and our methods could not distinguish if plants or microbes produced the enzymes we measured. Because the majority of grass roots occur directly under aboveground biomass (Burnett et al. 2012), enzymes in the interspace were predominantly microbial-generated and presumably received considerably less exudate from plant roots. For each sample, four surface soil cores (1 cm diameter, 3 cm deep) were collected across each plot and combined for a representative assessment of soils within the plot. For plant soils, the four cores were split between the dominant grasses, and two soil cores were taken from under each of the two dominant grass species and homogenized for a single plant soil sample. Surface litter and an organic layer were absent within the plots and the entire 3 cm deep sample occurred within a soil horizon composed of unconsolidated aeolian deposits (Buxbaum and Vanderbilt 2007, Bryan-Ricketts 2012). Samples were refrigerated and processed within 48 h of collection to prevent enzyme degradation. Subsamples were weighed and dried at 60°C to calculate field soil moisture and then burned at 500°C for 4 h to determine percent organic matter. The potential enzyme activity levels of alkaline phosphatase (AP), beta-N-acetyl-glucosaminidase (NAG), leucine aminopeptidase (LAP), and beta-glucosidase (BG) were measured fluorometrically and phenol oxidase (PO) chlorometrically following methods of Stursova et al. (2006). AP removes phosphate groups from organic molecules. NAG degrades chitin, producing N-containing glucosamine for microbial consumption. LAP is an aminopeptidase that cleaves amino acids from proteins at the N-terminus. BG catalyzes the terminal step in cellulolysis, producing glucose from cellooligosaccharides. PO uses oxygen to oxidize phenolic compounds in more recalcitrant organic matter. Oxidative activity is high in arid mineral soils where oxygen is plentiful, pH is high, and organic matter content low (Sinsabaugh 2010). Potential activity levels for all enzymes were calculated as nmol of product created per hour per gram of OM (nmol h^{-1} g OM^{-1}). Activity levels of PO during August could not be assessed due to laboratory errors. Enzyme assays provide a measure of potential enzyme activity within the soil and tend to overestimate natural activity levels since natural substrates may be larger and more complex than the smaller, uniform test substrates. Although a possible overestimate of natural enzyme activities, enzyme potentials were uniformly measured throughout the experiment therefore our assessment of enzyme

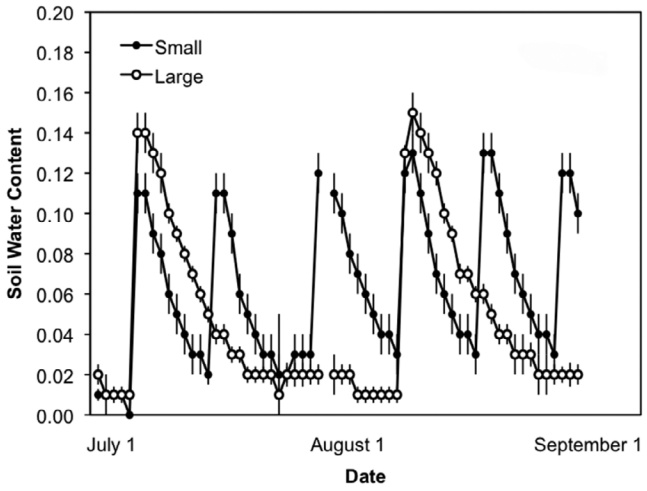

Fig. 1. Daily soil water content of large, infrequent (30 mm/month; open circles) and small, frequent (10 mm/10 d; black circles) rainfall treatments at 5-cm depth. Error bars indicate ±1 SE.

activities is comparable across treatments and over time.

Data analysis

We used analysis of variance (ANOVA) to test if soil organic matter content varied with regard to month, location of soil (plant or interspace), and rainfall treatment. Potential enzyme activity levels throughout the experiment were also compared with a separate ANOVA for each enzyme (AP, NAG, LAP, BG, PO). For each test, potential enzyme activity was compared to the main effects and all possible interactions of location (plant or interspace), month, timing (pre- or post-rain events), and rainfall treatment. The ratios between enzyme activities were also compared to examine nutrient limitations in the system (Sinsabaugh et al. 2008). BG activity relative to AP activity indicated changes in P availability, while BG activity relative to NAG plus LAP activity indicated N limitations. For both ratios, values below 1 suggested limitations in the associated nutrient, as more energy (C) was needed per unit of nutrient acquired (Sinsabaugh et al. 2008). Ratios were compared to the main effects and all possible interactions of location (plant or interspace), month, timing (pre- or post-rain events), and rainfall treatment, with a separate ANOVA for each ratio. All statistics were run in SAS v9.3 with an $\alpha = 0.05$.

Results

Rainfall manipulations altered soil water content throughout the season, and soil moisture persisted longer following large (30-mm) rain events when compared to the more frequent small (10-mm) rain events (Fig. 1; Thomey et al. 2014). Organic matter content statistically differed during the experiment ($p = 0.0008$, $F_{4,59} = 5.57$, $r^2 = 0.29$; Table 1), specifically with regard to month ($p = 0.004$, $F_{2,59} = 6.10$) and location ($p = 0.003$, $F_{1,59} = 9.43$) but not rainfall treatment ($p = 0.4$). Although, the change in OM was small (0.002 g OM/g soil), total OM in these soils is low and this difference was ~20% of total soil OM.

Table 1. Monthly soil organic matter content (g OM/g soil; mean ± 1 SE).

Location	Rainfall treatment	July	August	September	Seasonal mean
Plant	large, infrequent	0.011 ± 0.001	0.013 ± 0.0009	0.010 ± 0.0007	0.011 ± 0.0007
	small, frequent	0.012 ± 0.0004	0.012 ± 0.0005	0.011 ± 0.0004	0.012 ± 0.0006
Interspace	large, infrequent	0.009 ± 0.001	0.011 ± 0.0009	0.008 ± 0.0006	0.009 ± 0.0003
	small, frequent	0.011 ± 0.001	0.011 ± 0.0004	0.009 ± 0.0009	0.010 ± 0.0005

Table 2. Statistical results from separate ANOVAs for each enzyme. Only significant components ($p < 0.05$) of each model are included on the table.

Enzyme	Effect	R^2	F	df	p
AP	Model	0.50	7.56	14, 119	<0.0001
	Location		28.52	1. 119	<0.0001
	Month		15.28	2. 119	<0.0001
	Month × Timing		18.67	2, 119	<0.0001
BG	Model	0.52	8.05	14, 119	<0.0001
	Location		45.44	1, 119	<0.0001
	Month		14.54	2, 119	<0.0001
	Month × Timing		13.01	2, 119	<0.0001
LAP	Model	0.25	2.46	14, 119	0.005
	Month		6.98	2, 119	0.001
	Month × Timing		7.69	2, 119	0.0008
NAG	Model	0.43	5.71	14, 119	<0.0001
	Location		18.30	1, 119	<0.0001
	Month		12.53	2, 119	<0.0001
	Timing		4.17	1, 119	0.040
	Month × Timing		12.80	2, 119	<0.0001
PO	Model	0.29	2.76	10, 78	0.006
	Location		5.46	1, 78	0.020
	Month		9.85	1, 78	0.002
	Month × Timing		7.33	1, 78	0.009

Table 3. Statistical results from separate ANOVAs for each enzyme ratio. Only significant components ($p < 0.05$) of each model are included on the table.

Ratio	Effect	R^2	F	df	p
C:N	Model	0.62	12.28	14, 119	<0.0001
	Location		103.98	1, 119	<0.0001
	RainTrt		4.58	1, 119	0.03
	Month		13.98	2, 119	<0.0001
	Location × RainTrt		6.71	1, 119	0.01
	Location × Month		3.34	2, 119	0.04
	Month × Timing		6.58	2, 119	0.002
C:P	Model	0.65	14.21	14, 119	<0.0001
	Location		47.91	1, 119	<0.0001
	Month		58.31	2, 119	<0.0001
	Timing		6.02	1, 119	0.02
	Location × RainTrt		4.28	1, 119	0.04
	Location × Month		3.19	2, 119	0.04
	Month × RainTrt		4.56	2, 119	0.01

Activities of all enzymes statistically changed during the experiment (Table 2, Fig. 2). Activities were statistically higher under plants than in interspaces for all enzymes except LAP (Table 2, Fig. 2). Enzyme activity also was statistically different between months for all enzymes. Enzyme activity did not significantly vary between rainfall treatments for any enzyme (all $p > 0.05$), but the Month × Timing interaction was significant for all enzymes, which highlighted the decrease in enzyme activities following the September rain event (Table 2, Fig. 2). Enzyme ratios statistically varied with several aspects of the experiment (Table 3). C:N was higher under plants, varied between months, and was higher under small, frequent rain events in interspace soils (Table 3, Fig. 3). C:P was also higher under plants, varied between months, and was lowest in interspace soils which received large, infrequent rain events (Table 3, Fig. 3).

Discussion

Seasonal dynamics of enzyme activities should reflect the availability of their substrates (Hernández and Hobbie 2010), and our findings demonstrate that enzyme activities and nutrient availability varied with regard to rainfall throughout the season. Rain not only triggered microbial activity, but also presumably influenced nutrient availability via plant-microbe associations. Following the onset of monsoon watering, plants rapidly upregulated photosynthesis, peaking 4–5 days following a rain event (Thomey et al. 2014), and likely exuded labile compounds through roots and plant residue (Geisseler et al. 2011), which have been hypothesized to drive microbial activity in general (Fierer and Schimel 2003) and at our site (Vargas et al. 2012). Likewise, increases in labile compounds and soil moisture can stimulate microbes to produce enzymes (Dorodnikov et al. 2009, Gonzalez-Polo and Austin 2009), and enzyme activities increased shortly after early season rainfall. At the end of the season, soil nutrient resources presumably change as root production of the dominant grass decreases (Burnett et al. 2012), and enzyme activities greatly decreased following the final rain event.

Plants have a large influence on soil microbes, and activities of all hydrolytic enzymes were higher under plants than in unvegetated interspaces. The primary difference between plant and interspace soils was consistently higher hydrolase and lower oxidase activities under plants, presumably due to increased labile compounds under plants (Gonzalez-Polo and Austin 2009). Additionally, based on ratios between enzymes, N and P availability was lower within interspaces soils, particularly in the middle of the season. For our dominant grasses, roots generally do not extend past the aboveground canopy (Burnett et al. 2012) and plants utilize resources in interspace soils via

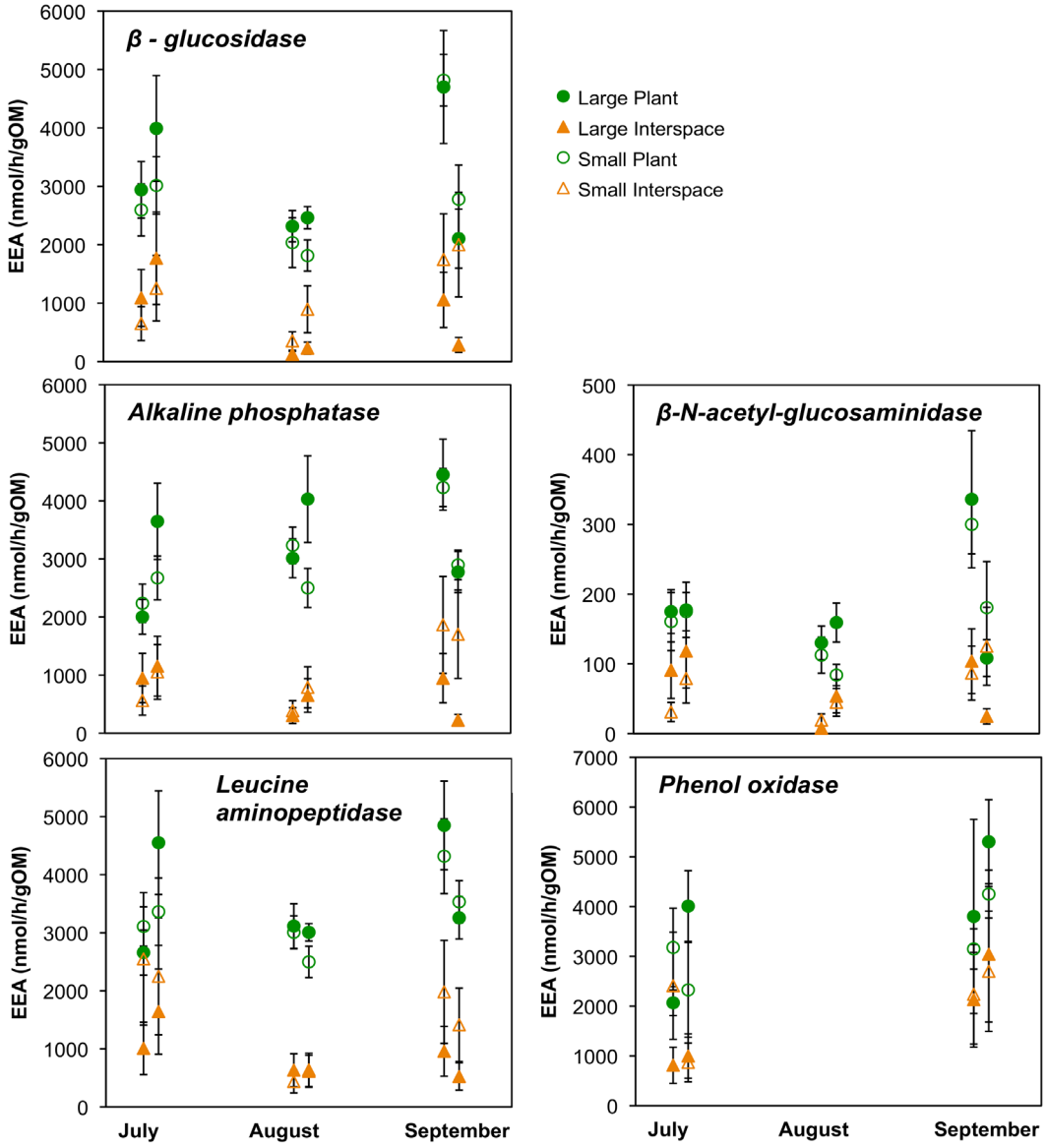

Fig. 2. Mean potential enzyme activities for each enzyme within plant (green circles) and interspace (orange triangles) soils following large, infrequent (closed) and small, frequent (open) precipitation events. The pair of enzyme activities associated with each month indicates activities before and after the rain events on the first of the month. Error bars represent ±1 SE. The scale of the vertical axis is different for the two graphs on the right.

fungal connections between interspaces to plant roots (Green et al. 2008, Marusenko et al. 2013). Although our methods cannot distinguish whether enzymes were created by plants or microbes, due to this spatial separation between plant roots and crust soils, interspace activities were primarily from microbial generated enzymes which received little to no root exudate. Plant-generated enzymes could also have increased total enzyme activity levels under plants, but the magnitude to which plants contribute to soil enzyme pools remains largely unknown.

Rainfall did not uniformly stimulate EEAs throughout the monsoon season. Several enzyme activities appeared to increase following the first rain event, but changes were small and variable

within replicates, and thus increases were not statistically significant. During the middle of the season, potential enzyme activities showed less response to rainfall and were not different before and after rain events. One interesting result was a net decrease in all hydrolytic enzyme activities following the final rain event in September, regardless of rainfall treatment. Several factors could have contributed to this decrease. Lower photosynthate availability late in the season may have reduced the rate of expression of new enzymes relative to the loss of activity from denaturing or consumption. Petrie et al. (2014) found that over a five-year period gross primary production in this grassland decreased precipitously each year in early September. Our assays could not determine if activities were from newly created or reused enzymes in the soil, therefore we could not directly test for this mechanism. Concurrent with the decrease in hydrolytic enzymes was an increase in non-specific oxidative enzymes. With reduced availability of labile organic matter at the end of the season, increased oxidative enzyme production could allow microbes to gather nutrients from any complex molecules in the soil, including hydrolytic enzymes. Therefore these oxidative enzymes could have directly contributed to lower hydrolytic enzyme activities following the last experimental rain event.

Potential enzyme activities followed similar temporal patterns in both rainfall treatments, but ratios between enzymes changed with regard to rainfall treatment, indicating that nutrient availability was influenced by rainfall regime. The greatest nutrient limitations for both N and P occurred within interspace soils that experienced large, infrequent rain events. Additionally, at the end of the season P was more limiting following larger, infrequent rainfall in both plant and interspace soils. The frequency and intensity of dry-rewetting cycles can influence nutrient availability and microbial function (Chowdhury et al. 2011). Long droughts can trap nutrients in SOM or on carbonate (Ippolito et al. 2010) and have created nutrient limitations at both wetter (Tiemann and Billings 2011) and drier (Yahdjian and Sala 2010) sites. Meanwhile frequent rain events increase nutrient availability in the soil (Fierer and Schimel 2003, Butterly et al. 2009). These dynamics likely occurred in our soils and contributed to larger nutrient limitations following large, infrequent rain events.

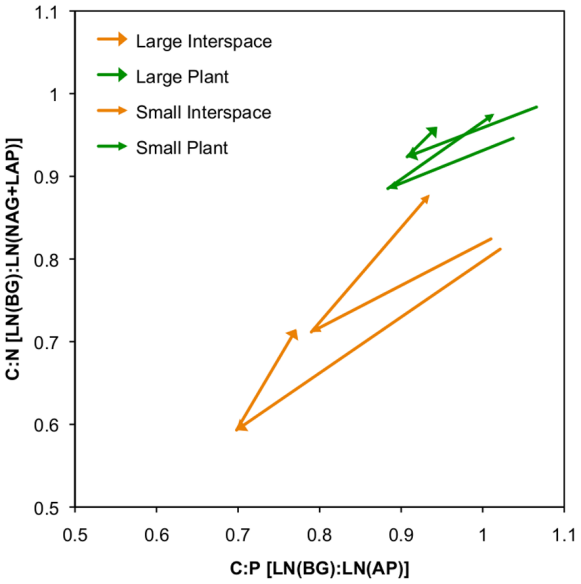

Fig. 3. Ratios of enzyme activities that represent C:P (horizontal axis) and C:N (vertical axis) through time for plant (green) and interspace (orange) soils. Mean monthly ratios are graphed with sequential months connected with arrows. Small arrowheads representing small, frequent rain events, and larger arrowheads represent large, infrequent rainfall.

Overall, enzyme activities were higher under plants and the response of extracellular enzyme activities to precipitation events changed throughout the season. Increased water availability following rain events stimulated hydrolytic enzyme activities early in the monsoon season, and as the season ended, enzyme activities decreased back to pre-season levels. Similar pre- and post-monsoon season enzyme activities have been observed elsewhere in the Chihuahuan Desert (Bell et al. 2009), but our enzyme measurements associated with individual rain events highlight how variable enzyme activities can be following rain events throughout the monsoon season. Changes in enzyme activities were similar following either large, infrequent or small, frequent precipitation regimes, but ratios between enzyme activities highlighted greater nutrient limitation following large, infrequent rain events.

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