

## ALTERED RAINFALL PATTERNS, GAS EXCHANGE, AND GROWTH IN GRASSES AND FORBS

Philip A. Fay,<sup>1</sup> Jonathan D. Carlisle, Brett T. Danner,<sup>2</sup> Michelle S. Lett, James K. McCarron, Catherine Stewart,<sup>3</sup>  
Alan K. Knapp, John M. Blair, and Scott L. Collins

Division of Biology, Kansas State University, Manhattan, Kansas 66506-4901, U.S.A.

Although the potential for increased temperature is the primary and best-studied aspect of anthropogenic climate change, altered rainfall patterns, increased storm intensity, and more severe droughts are also predicted in most climate-change scenarios. We altered experimentally the rainfall regime in a native tallgrass prairie in northeastern Kansas and assessed leaf-level physiological activity and plant growth responses for C<sub>3</sub> and C<sub>4</sub> plant species. Our primary objective was to contrast the importance of reductions in rainfall quantity (30% smaller rain events, no change in rainfall pattern) with an altered, more extreme distribution of rainfall (no reduction in total growing-season quantity, 50% increased inter-rainfall dry intervals) for these dominant species from the two main plant functional groups (C<sub>4</sub> grasses, C<sub>3</sub> forbs) present in many grasslands. Leaf water potential ( $\psi_l$ ), net photosynthetic carbon gain ( $A_{CO_2}$ ), specific leaf mass, leaf C : N ratio, growth rate for *Andropogon gerardii* (C<sub>4</sub> grass) and *Solidago canadensis* (C<sub>3</sub> forb), vegetative and flowering stem densities, and canopy light penetration for grass and forb assemblages were intensively monitored during the 1999 growing season in a long-term rainfall manipulation study at the Konza Prairie Biological Station. Soil water content at 0–30 cm depth was more variable in response to the altered rainfall distribution compared to the reduced-quantity treatment. In *S. canadensis*,  $A_{CO_2}$ ,  $g_s$  (stomatal conductance),  $A : C_i$  (leaf stomatal [CO<sub>2</sub>]), and  $A : E$  (estimated leaf transpiration rate) were positively correlated with soil water content, but no relationship was seen for *A. gerardii*, indicating that even though this dominant grass species has most of its roots in the upper 30 cm of the soil, *A. gerardii* was buffered physiologically from increased resource variability. There were few significant responses in growth parameters in either grasses or forbs, but canopy light penetration increased with both rainfall treatments. We concluded (1) that the temporal variability in rainfall inputs can have as much impact on soil moisture as simple reductions in rainfall quantities with no change in temporal distribution, (2) that responses of *A. gerardii* and *S. canadensis* to altered rainfall distributions were not consistent with common views of soil resource partitioning between shallow-rooted grasses and deep-rooted forbs, and (3) that altered rainfall patterns may have the potential to offset elevated CO<sub>2</sub> impacts on grassland vegetation.

**Keywords:** grassland, climate change, rainfall, soil moisture, photosynthesis, water potential, *Andropogon gerardii*, *Solidago canadensis*.

### Introduction

Grassland biomes cover a major fraction of the earth's land surface (Bailey 1998) and are important ecosystems for biological diversity and as resources for native and domestic ungulate grazers (Samson and Knopf 1996; Williams and Diebel 1996). Seasonal water limitation of growth is common even in relatively mesic grasslands (Knapp et al. 2001), and intra- and interannual variability in rainfall drives patterns of diversity and productivity in these systems (Knapp et al. 1998a). For example, across the central Great Plains grasslands of

North America, long-term average annual rainfall varies four-fold (Borchert 1950), aboveground net primary productivity strongly increases with annual rainfall quantity (Sala et al. 1988), and species composition shifts from shortgrass to tallgrass prairies (Küchler 1974). Analogous patterns of precipitation, composition (Pyankov et al. 2000), and productivity (Shankar et al. 1993) occur across precipitation gradients in grassland regions worldwide.

Atmospheric general circulation models predict that altered rainfall patterns will accompany warming and other elements of anthropogenic climate-change scenarios (Houghton 1997; Easterling et al. 2000). For the Central Plains region, predicted changes include reduced total quantities of growing-season rainfall and an altered temporal distribution of rainfall. This altered distribution would result from a combination of increased intensity of convective rainfall events and longer dry intervals separating rainfalls, leading to lower overall soil moisture availability (Manabe et al. 1981; Gordon et al. 1992; Giorgi et al. 1994; Karl et al. 1996; Gregory et al. 1997; Watson et al. 1997). These predictions imply a reduction in

<sup>1</sup> Author for correspondence; telephone 785-532-6743; e-mail fay@ksu.edu.

<sup>2</sup> Current address: Burns and McDonnell Engineering Co., 9400 Ward Parkway, Kansas City, Missouri 64114, U.S.A.

<sup>3</sup> Current address: Department of Biology, Colorado College, 14 East Cache La Poudre Street, Colorado Springs, Colorado 80903-3298, U.S.A.

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the mean and an increase in the variability in growing-season rainfall patterns, potentially impacting the composition and productivity of these grasslands (Easterling et al. 2000).

Two functional groups comprise the bulk of many temperate grassland floras, warm season  $C_4$  grasses, and  $C_3$  forbs;  $C_4$  photosynthesis typically confers steeper light-response curves and higher light-saturated photosynthetic rates, water use efficiencies, and temperature optima compared to  $C_3$  photosynthesis (Percy and Ehleringer 1984; Knapp and Medina 1999). Grass and forb growth forms differ markedly in architecture, with grasses possessing traits consistent with drought tolerance, such as basal meristems, narrow, vertically oriented leaves, and a relatively shallow and fibrous root system, making grasses more reliant on water high in the soil profile. However, forbs have great diversity in leaf and meristem architecture and often produce a much deeper root system than grasses, thus accessing deeper, less varying water supplies (Weaver 1968; Sims et al. 1978; Knapp 1985). Assuming that shifts in rainfall patterns would most immediately affect shallow soil layers, stronger physiological and growth responses to altered rainfall patterns would be expected for  $C_4$  grass species, and weaker responses would be expected for forbs, based in these differences in physiology and root morphology. Previous studies have indicated that both leaf physiological activity and plant growth rates respond to rainfall distribution as well as quantity (Sala and Lauenroth 1982; Knapp 1984; Fisher et al. 1988; Gutierrez et al. 1988; Dougherty et al. 1996; Hamerlynck et al. 1997; Williams et al. 1998; BassiriRad et al. 1999; Ward et al. 1999), and differential responses to altered rainfall patterns among species may provide an underlying mechanism promoting shifts in plant species composition.

The objective of this study was to examine the leaf physiology and plant growth responses in a dominant tallgrass prairie  $C_4$  grass and a common  $C_3$  forb to two experimental alterations in rainfall patterns: (1) reduced rain event quantity, with no change in temporal distribution and (2) altered temporal distribution, specifically larger individual rain events, combined with increased interevent dry intervals, but no reduction in total quantity. Leaf-level physiological responses to rainfall patterns are important because they provide instantaneous indices of plant responses to resource variation; they are useful in models of plant growth, canopy gas exchange, vegetation distribution, and net primary productivity (Schulze et al. 1994; Luo et al. 2000); and they may indicate the potential of altered rainfall patterns to modify the impacts of global change phenomena such as warming or elevated  $CO_2$  concentrations on plant populations and communities (Walker et al. 1999).

Our research focused on the  $C_3$  forb *Solidago canadensis* and the warm-season  $C_4$  grass *Andropogon gerardii*, common members of their functional groups in the tallgrass prairie portion of the Central Plains grasslands. *Andropogon gerardii* dominates many tallgrass prairies in abundance and biomass, and many community and ecosystem responses are strongly influenced by this species (Knapp et al. 1998a). We measured plant water status, leaf gas exchange, and leaf C : N ratio as indicators of plant stress and physiological performance. Several indices of plant and canopy growth were also quantified as integrators of plant responses to altered rainfall patterns. The study was conducted in an ongoing long-term field ex-

periment, the Rainfall Manipulation Plots (RaMPs), where rainfall patterns have been manipulated since 1998 at the Konza Prairie Biological Station in northeastern Kansas (Fay et al. 2000).

## Material and Methods

### Study System

Konza Prairie is located in the Flint Hills (39°05'N, 96°35'W), the largest remaining area of unplowed native tallgrass prairie in North America (Küchler 1974). The vegetation of Konza Prairie consists of highly productive, matrix-forming, perennial warm-season  $C_4$  grasses, accompanied by a species-rich, but less productive, assemblage of  $C_3$  forbs in the Compositae, Fabaceae, Brassicaceae, and other families (Freeman 1998). Over 500 species representing >90 families have been recorded (Freeman and Hulbert 1985). Long-term records of climate, plant species composition, and productivity are available (Knapp et al. 1998b).

The Flint Hills experiences a temperate midcontinental climate, with a yearly mean temperature of 13°C (range: 6°–19°C), a January mean of –3 °C (range: –9° to 3°C), and a July mean of 27°C (range: 20°–33°C). Total precipitation at Konza Prairie averages 835 mm yr<sup>-1</sup>, with 75% falling during the growing season, May through September. Growing-season rainfall is bimodal, with high monthly rainfall totals during May and June, low rainfall and high temperatures in July and August, and a second, lesser rainy period in September. Variation from these general precipitation patterns is common, both in yearly totals and seasonal distribution (Hayden 1998).

### Overview of Rainfall Manipulation Plot Study

The RaMPs are a set of 12 undisturbed native prairie study plots each located beneath a fixed-location rainout shelter. The shelters serve to exclude natural rainfall inputs from the plots, to collect the excluded rainfall, and to reapply it in altered quantities and patterns. Each shelter has a clear polyethylene roof, two 4000-L reservoirs (equivalent to ca. 10 cm of rainfall) to collect and store rainfall off the roof, and an overhead grid of 13 irrigation nozzles to apply rainfall treatments. The shelters measure 14 × 9 m, covering a central 7.6 × 7.6-m experimental plot containing a 6 × 6-m sampling area. The experimental plots were surrounded by a 1.2-m-deep subsurface barrier to limit lateral water movement. Fay et al. (2000) provides further detail on shelter design and efficacy.

The RaMPS were located on a typical lowland Konza site in terms of soil, vegetative composition, productivity, and land management. Soils are Irwin silty clay loams. The dominant plant species in the plots include *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Sporobolus asper*, all warm-season  $C_4$  tallgrasses. Dominant forbs include *Solidago canadensis*, *Aster ericoides*, and *Solidago missouriensis*. Productivity has averaged 600 g m<sup>-2</sup> to date in the study plots. The plots and their surroundings have been burned each spring (late March).

In this study, we examined three rainfall manipulation treatments, each with three replicates.

*Ambient.* In these RaMPs, intercepted water was re-

applied to the plots each time a natural rainfall event occurred in the naturally occurring quantity.

**Reduced quantity.** Rainfall was again applied coincident with ambient rain events, but only 70% of the collected rainwater was applied to the plots. Only the quantity of each rain event, not the temporal distribution, was altered by this treatment.

**Altered distribution.** This treatment created a more extreme rainfall pattern, by lengthening the dry periods between rainfall events by 50%. All ambient precipitation falling during these increased dry periods was stored and applied in one large application. In this way, rainfall was redistributed into fewer, but larger, events with greater temporal separation, but the total quantity of precipitation applied over the growing season was not reduced.

In practice, these altered rainfall treatments affected the variability in rainfall inputs (on a per day basis) in addition to growing-season rainfall quantity, event size, and dry-interval length. The coefficients of variation (CV) for rainfall inputs ranged from 273 for the reduced-quantity treatment to 417 for the altered-distribution treatment. The ambient treatment CV (276) was comparable to the 15-yr CV in ambient rainfall inputs (286). See Williams et al. (1998) for a similar characterization of rainfall variability.

#### *Response Variables and Sampling Regime*

Soil water content, plant water stress, and leaf gas exchange parameters were measured weekly from May through October 1999. Soil water content was quantified using time domain reflectometry (Topp et al. 1980) at four locations per plot using 30-cm probes, integrating soil moisture conditions in the top 30 cm of the soil profile.

Plant water stress was assessed by determining midday leaf water potential ( $\psi_l$ ) with a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oreg.) on four leaves per species per plot. Healthy, fully expanded leaves were collected between 1200 and 1400 hours central daylight time, packaged and kept in the dark to prevent desiccation, and rapidly measured in the laboratory.

Leaf water potential samples were used to determine specific leaf mass ( $\text{mg dry mass cm}^{-2}$ ). The leaves were then pooled by plot, ground, and assayed for total C and N (% by weight) in an automated C:N analyzer (Carlo-Erba 1500C, Carlo Erba, Milan).

Leaf gas exchange was measured weekly with two cross-calibrated field-portable infrared gas analyzers (LI-COR 6200, Li-COR, Lincoln, Nebr.) on fully expanded upper canopy leaves, one leaf per plant, four plants per species per plot. Gas exchange measurements were conducted between 1030 and 1430 hours central daylight time, generally on cloud-free days. However, meeting a weekly sampling scheme sometimes required measurements on partly cloudy days. Samples were omitted from analysis if photosynthetic photon flux density (PPFD) was  $<500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and entire plots were omitted when plot mean PPFD was  $<1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Gas exchange parameters of interest in this study were net photosynthesis ( $A_{\text{CO}_2}$ ), stomatal conductance ( $g_s$ ), the ratio of  $A_{\text{CO}_2} : C_i$ , the

leaf substomatal [ $\text{CO}_2$ ], and the ratio of  $A_{\text{CO}_2} : E$ , the estimated leaf transpiration rate.

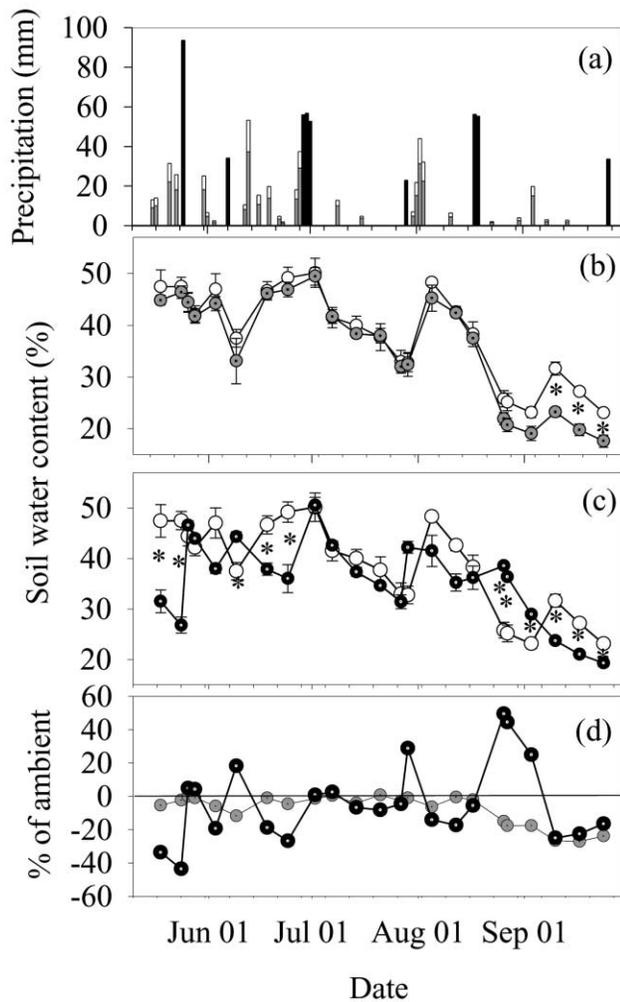
Whole-plant and canopy responses to rainfall manipulations were characterized in several ways. Relative growth rates for *A. gerardii* and *S. canadensis* were calculated from biweekly measurements of total leaf length (*A. gerardii*) and estimated total leaf area (*S. canadensis*) from 10 permanently marked plants per plot. Leaf areas for *S. canadensis* were estimated from allometric relationships between mean leaf length and total leaf area, determined from comparable plants growing outside the plots. New plants were marked when plants in the initial cohort were prematurely lost or senesced. Flowering stem density in three dominant grasses (*A. gerardii*, *S. nutans*, and *P. virgatum*) and vegetative stem densities of  $C_4$  grasses and forbs were censused during peak flowering (early September 1999). Canopy light extinction, measured as the height of 50% light attenuation, was measured biweekly at a fixed location in each plot, at 10-cm increments in the canopy using a 1-m ceptometer (Decagon, Pullman, Wash.).

#### *Statistical Analysis*

Each rainout shelter was an experimental unit, so sample date treatment and growing-season means ( $\pm 1$  SE) for soil water content,  $\psi_l$ ,  $A_{\text{CO}_2}$ ,  $g_s$ ,  $A : C_i$ ,  $A : E$ , leaf C : N, specific leaf mass, and relative growth rates were based on plot mean values. All responses were analyzed by mixed-model ANOVA (SAS Institute 2000), with rainfall treatments as fixed effects, sample date as a repeated measure, and covariance structure chosen based on Akaike's information criterion (Littell et al. 1996). Means separations were performed using *t*-tests of least squares means.

To gauge species differences in responses to soil water content variation induced by the treatments, sample date values of  $\psi_l$ ,  $A_{\text{CO}_2}$ ,  $g_s$ ,  $A : C_i$ , and  $A : E$  were regressed against soil water content. Preliminary analyses showed that soil water content and leaf physiological parameters tended to decline over the growing season, and the rainfall manipulations tended to cause the lowest soil water content late in the season. As a result, these seasonal patterns were confounded with treatment-induced soil water content variation. To factor out the seasonal patterns, we recalculated the gas exchange and  $\psi_l$  values as a percentage of the maximum (minimum for  $\psi_l$ ) observed on each sample date. Soil water content was used in regressions because in preliminary analyses it was a better predictor of leaf parameters than dry-interval length or rainfall quantity. Data from all three treatments were combined in this analysis to maximize the range of soil water content values. Soil water content and leaf responses were not always measured concurrently, so soil water content was calculated for leaf sampling dates from the most recent preceding soil water content determination using nonlinear relationships between soil water content, rainfall quantity, and dry-interval length derived from the 1999 data. See Fay et al. (2002) for similar relationships from previous sample years. This method successfully incorporated the nonlinear properties of soil moisture dynamics into the adjustments.

Stepwise multiple regressions were performed to compare the rainfall/soil moisture/leaf response relationships to other environmental influences on leaf physiological activity. For



**Fig. 1** Rainfall patterns and soil moisture profile for 1999 in the Rainfall Manipulation Plots field plots. *a*, Precipitation events. *b*, *c*, Soil water content values (mean  $\pm$  1 SE) by sample date. ANOVA results: date,  $F_{24,144} = 102.15$ ,  $P < 0.0001$ ; treatment  $\times$  date,  $F_{48,144} = 31.48$ ,  $P < 0.0001$ . Asterisks denote significant soil water content differences between (*b*) ambient and reduced quantity or (*c*) ambient and altered distribution on specific dates ( $\leq 0.05$ ). *d*, Soil water content deviations from ambient. Open circles = ambient quantity and interval; gray circles = reduced quantity; black circles = altered distribution.

$A_{CO_2}$  and  $g_s$ , these variables were PPFD, leaf temperature, and leaf-to-air vapor pressure deficit (VPD) from the gas exchange measurements and soil temperature at 15 cm during the measurement period from probes in the plots. For  $\psi_1$ , the variables were air and soil temperatures, net radiation, and VPD measured directly in the rainout shelters or at the Konza Prairie meteorological station, 0.5 km from the shelters. The predictor variables were initially submitted to principal component analysis, and the first two principal components (PCs) were used in the stepwise procedure along with soil water content. For  $A_{CO_2}$  and  $g_s$ , the first PC described temperatures and VPD ( $r^2 = 0.50$ ), and the second PC described PPFD ( $r^2 = 0.29$ ). PCs for  $\psi_1$  were similar to those for  $A_{CO_2}$ , with the first PC

describing temperatures and VPD ( $r^2 = 0.56$ ) and the second PC describing net radiation fluxes ( $r^2 = 0.25$ ).

## Results

### Rainfall Regime

Growing-season rainfall in 1999 totaled 753 mm, 14% above the 16-yr average. From May through September 1999, there were 28 ambient rainfall events, with 19 events  $>5$  mm (fig. 1*a*). The altered-distribution treatment resulted in six events (two applied over two or three consecutive days; fig. 1*a*). Mean event sizes in each treatment were  $15.85 \pm 0.49$  mm (ambient),  $11.38 \pm 0.35$  (reduced quantity), and  $51.21 \pm 2.76$  (altered distribution). The mean length of dry periods was  $6.2 \pm 1.7$  d for ambient intervals and  $15.5 \pm 4.9$  d for altered distribution. The  $>50\%$  difference in mean dry-interval length resulted from the numerous short intervals between ambient rain events during May and June.

### Soil Moisture Patterns

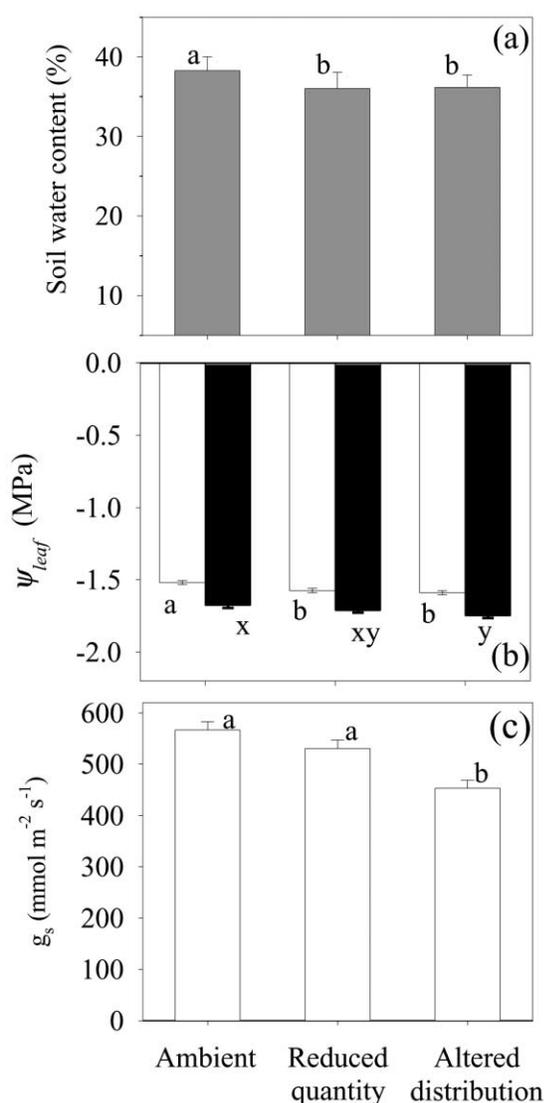
Frequent rainfall events caused high soil water content in the ambient and reduced-quantity treatments during May and June (fig. 1*b*). Soil water content declined through July, August, and September, interrupted by four consecutive days of rain in early August, totaling 105 mm, and later by a 20-mm rainfall early in September (fig. 1*a*). Soil water content in the reduced-quantity treatment closely tracked the ambient-quantity treatment until the end of the growing season (fig. 1*b*).

In the altered-distribution treatment, soil water content values fell significantly below ambient values during several of the experimentally increased dry intervals (fig. 1*c*). The mean deviation from ambient for this treatment was over 19% ( $\pm 2.9\%$ ), compared with 8% ( $\pm 1.9\%$ ) for the reduced-quantity treatment ( $t = 3.28$ ,  $P = 0.002$ ; fig. 1*d*), indicating that soil water content varied more strongly in response to the altered rainfall distribution. However, both the reduced-quantity and altered-distribution treatments reduced growing-season mean soil water content by similar amounts (fig. 2*a*).

### Plant Responses

**Leaf physiology.** The growing-season means for  $g_s$  and  $\psi_1$  in *Solidago canadensis* and for  $\psi_1$  in *Andropogon gerardii* were reduced by rainfall manipulations, with *S. canadensis*'s  $g_s$  strongly reduced by the altered-distribution treatment (fig. 2*b*, 2*c*). Multiple regressions of  $\psi_1$ ,  $A_{CO_2}$ , and  $g_s$  indicated that soil water content was the best predictor of  $\psi_1$  in both species and of  $g_s$  in *S. canadensis*. The PPFD principal component better predicted  $A_{CO_2}$  and  $g_s$  in *A. gerardii*, and the temperature/VPD principal component better predicted  $A_{CO_2}$  in *S. canadensis* (table 1).

Adjusted  $A_{CO_2}$  and  $g_s$  in *S. canadensis* were positively correlated with soil water content ( $R^2 = 0.30$ – $0.35$ ; fig. 3; table 2). In addition, *S. canadensis* photosynthetic efficiency increased with soil water content, as indicated by  $A : C_i$  and



**Fig. 2** a, Soil water content (0–30 cm); b, leaf water potential ( $\psi_l$ ); and c, stomatal conductance ( $g_s$ ) for *Andropogon gerardii* (black bars) and *Solidago canadensis* (white bars) in the Rainfall Manipulation Plot experiment. ANOVA results for (a)  $F_{2,6} = 10.92$ ,  $P = 0.0100$ ; b, *Andropogon*,  $F_{2,6} = 4.89$ ,  $P = .0549$ . *Solidago*,  $F_{2,6} = 6.51$ ,  $P = 0.0314$ ; c,  $F_{2,6} = 12.73$ ,  $P = 0.0069$ . Means sharing the same letter were not significantly different by *t*-tests of least squares means.

*A* : *E* ( $R^2 = 0.38$ – $0.40$ ; fig. 3; table 2). In contrast, *A* : *Ci* was the only physiological parameter correlated (negatively) with soil water content for *A. gerardii* ( $R^2 = 0.13$ ; fig. 3; table 2). Adjusted  $\psi_l$  was not related to soil water content for either species (table 2).

**Plant growth.** Most of the growth measures for these species were unresponsive to either rainfall manipulation treatment (table 3). Leaf C : N and specific leaf mass in *S. canadensis* were the exceptions, increasing in both the reduced-quantity and the altered-distribution treatments. Also, canopy structure was impacted by the rainfall manipulations, with light penetration into the canopy increased in both rainfall treatments (table 3).

## Discussion

### Treatment Impacts on Soil Moisture, Leaf Physiology, and Growth

Rainfall manipulations affected both the means and the temporal variability in soil moisture. The more extreme rainfall regime imposed in the altered-distribution treatment reduced the growing-season mean soil water content of the top 30 cm of the soil profile. This was a direct result of increased temporal variability in precipitation inputs since the altered rainfall distribution treatment received the full ambient quantity of rainfall over the growing season. Soil moisture dynamics in the upper soil profile are crucial for plant performance and other important aspects of ecosystem function because a large fraction of the root biomass, microbial biomass, decomposition, nutrient cycling, and carbon storage occurs there in tallgrass prairie and other terrestrial ecosystems (Jackson et al. 1996; Blair et al. 1998; Rice et al. 1998).

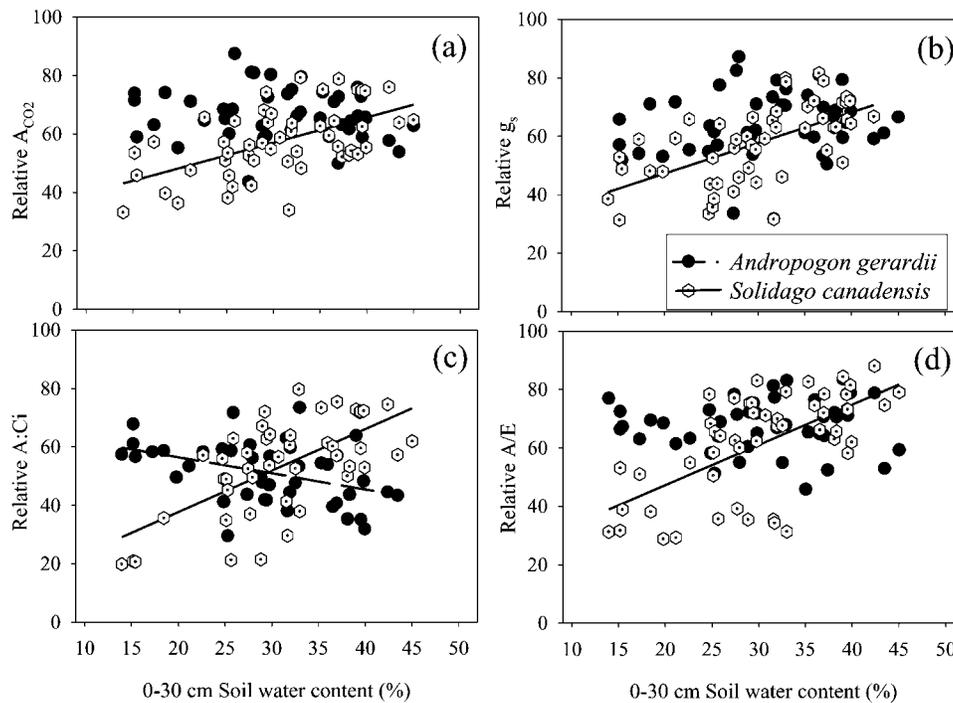
Soil moisture variability affected leaf-level physiological processes differently in these two species, although not in the way we initially expected. *Solidago canadensis* was more responsive

**Table 1**

**Stepwise Multiple Regression Analysis of *Andropogon gerardii* and *Solidago canadensis*  $\psi_l$ ,  $A_{CO_2}$  and  $g_s$**

Variable	Partial $R^2$	<i>F</i>	<i>P</i>
<i>A. gerardii</i> :			
$\psi_l$ :			
SWC	0.486	69.94	<0.0001
Temp/VPD	0.116	21.35	<0.0001
Netrad	0.018	3.40	0.0693
Total	0.620	39.19	<0.0001
$A_{CO_2}$ :			
PPFD	0.418	50.29	<0.0001
SWC	0.051	6.55	0.0127
Total	0.469	30.42	<0.0001
$g_s$ :			
PPFD	0.297	21.94	<0.0001
Total	0.297	21.94	<0.0001
<i>S. canadensis</i> :			
$\psi_l$ :			
SWC	0.279	28.69	<0.0001
Netrad	0.197	27.39	<0.0001
Temp/VPD	0.028	4.05	0.0479
Total	0.504	24.38	<0.0001
$A_{CO_2}$ :			
Temp/VPD	0.604	113.07	<0.0001
PPFD	0.076	17.37	<0.0001
SWC	0.015	3.65	0.0601
Total	0.696	54.91	<0.0001
$g_s$ :			
SWC	0.413	38.66	<0.0001
PPFD	0.069	7.18	0.0097
Total	0.482	25.10	<0.0001

Note. Analysis used soil water content (SWC) and two principal component analysis–derived variables, one combining air and soil temperatures (Temp) and vapor pressure deficit (VPD), the second primarily describing net radiation (Netrad;  $\psi_l$ ) or photosynthetic photon flux density (PPFD;  $A_{CO_2}$  and  $g_s$ ).



**Fig. 3** Relationships of (a) relative leaf photosynthesis ( $A_{CO_2}$ ), (b) relative stomatal conductance ( $g_s$ ), (c) relative photosynthetic carbon use efficiency ( $A_{CO_2} : Ci$ ), and (d) relative photosynthetic water use efficiency ( $A : E$ ) with 0–30 cm soil water content (c, d) for *Andropogon gerardii* and *Solidago canadensis*. Linear regression statistics in table 1.

than *Andropogon gerardii* to variability in 0–30-cm soil water content. Seasonally adjusted photosynthetic rates ( $A_{CO_2}$ ), stomatal conductance ( $g_s$ ), and photosynthetic efficiency ( $A : Ci$  and  $A : E$ ) increased with soil water content in *S. canadensis* but not in *A. gerardii*. The lack of response in *A. gerardii* was not expected from a putatively shallow, fibrous-rooted warm-season  $C_4$  grass, although Williams et al. (1998) reported similar results for an African  $C_4$  grass. The unresponsiveness of *A. gerardii* may have resulted from its inherently high water use efficiency and drought-tolerance mechanisms, which can buffer plant performance from soil moisture variability (Hayes 1985; Heckathorn and DeLucia 1994; Heckathorn et al. 1997; Knapp and Medina 1999). Moreover, in irrigation studies,  $\psi_1$  differed only slightly (0.17 MPa) between droughted and well-watered *A. gerardii*, despite large differences in productivity (Knapp et al. 2001), which is further evidence of the physio-

logical buffering capacity of this species. Previous studies found that leaf gas exchange and water status in *A. gerardii* responded less to soil moisture variation than another common  $C_4$  grass, *Sorghastrum nutans*, despite their frequent co-occurrence and similar life histories (Silletti and Knapp 2001). Thus, other warm-season  $C_4$  grasses may show stronger responses to soil moisture variability in both leaf activity and growth than *A. gerardii*.

*Solidago canadensis*'s photosynthetic responsiveness was not consistent with that of a deeply rooted  $C_3$  forb. Many of the predictions about  $C_3$  and  $C_4$  responses assume steady state conditions, and under conditions of resource variability imposed with our rainfall manipulations, these predictions may not apply (Knapp 1993). Patterns in soil water content below 30 cm may also provide an explanation. Typically, one would expect deep soil recharge and less temporal variability in deep

**Table 2**

**Linear Regression Parameters and Significance Tests for Relationships between  $A_{CO_2}$ ,  $g_s$ ,  $A : Ci$ ,  $A : E$ , and  $\psi_1$  versus Soil Water Content (SWC) in *Andropogon gerardii* and *Solidago canadensis***

	<i>A. gerardii</i>				<i>S. canadensis</i>			
	Slope	$R^2$	F	P	Slope	$R^2$	F	P
$A_{CO_2}$ vs. SWC	...	0.02	1.0	0.3227	86.6	0.30	23.0	<0.0001
$g_s$ vs. SWC	...	0.01	1.6	0.2141	104.9	0.35	28.1	<0.0001
$A_{CO_2}/Ci$ vs. SWC	-49.5	0.13	7.7	0.0084	142.1	0.40	31.4	<0.0001
$A_{CO_2}/E$ vs. SWC	...	0.02	0.1	0.8057	137.5	0.38	31.9	<0.0001
$\psi_1$ vs. SWC	...	0.02	2.0	0.1598	...	0.02	0.1	0.8487

Note. See figure 3.

Table 3

Plant Growth Responses in *Andropogon gerardii* and *Solidago canadensis* and Canopy Light Penetration (Means  $\pm$  1 SE) and ANOVA Statistics Resulting from Altered Rainfall Patterns in the Rainfall Manipulation Plot Experiment

	Ambient	Reduced quantity	Altered distribution	ANOVA	
				F	P
<i>A. gerardii</i> :					
Leaf C : N ratio (%)	38.8 $\pm$ 1.3	40.5 $\pm$ 1.3	38.9 $\pm$ 1.5	1.44	ns
Specific leaf mass (mg cm <sup>-2</sup> )	7.2 $\pm$ 0.3	7.2 $\pm$ 0.4	7.2 $\pm$ 0.3	0.01	ns
Total leaf length (cm)	288.7 $\pm$ 26.3	216.9 $\pm$ 20.4	205.4 $\pm$ 8.7	0.35	ns
Relative growth rate (cm cm <sup>-1</sup> d <sup>-1</sup> ) $\times$ 10 <sup>-2</sup>	2.11 $\pm$ 0.18	1.86 $\pm$ 0.18	2.16 $\pm$ 0.18	0.78	ns
<i>S. canadensis</i> :					
Relative growth rate (cm cm <sup>-1</sup> d <sup>-1</sup> ) $\times$ 10 <sup>-3</sup>	5.56 $\pm$ 0.68	5.70 $\pm$ 0.68	4.96 $\pm$ 0.68	0.34	ns
Leaf C : N ratio (%)	31.3 $\pm$ 0.8 <sup>A</sup>	33.3 $\pm$ 0.7 <sup>B</sup>	33.0 $\pm$ 0.8 <sup>B</sup>	5.53	0.0058
Specific leaf mass (mg cm <sup>-2</sup> )	9.9 $\pm$ 0.4 <sup>A</sup>	10.3 $\pm$ 0.4 <sup>B</sup>	11.9 $\pm$ 0.4 <sup>C</sup>	29.59	<0.0001
C <sub>4</sub> grass vegetative stem density (m <sup>-2</sup> )	1015.7 $\pm$ 36.6	1072.6 $\pm$ 79.8	1054.9 $\pm$ 90.4	0.11	ns
C <sub>4</sub> grass flowering stem density (m <sup>-2</sup> )	6.5 $\pm$ 2.3	6.9 $\pm$ 3.1	4.1 $\pm$ 1.6	0.63	ns
C <sub>3</sub> vegetative stem density (m <sup>-2</sup> )	230.1 $\pm$ 31.3	179.1 $\pm$ 64.4	111.8 $\pm$ 12.5	3.53	0.1308
Canopy light penetration (height at 50% of incident PPFD, cm)	47.1 $\pm$ 2.0 <sup>A</sup>	35.6 $\pm$ 2.5 <sup>B</sup>	41.7 $\pm$ 2.0 <sup>AB</sup>	6.56	0.0400

Note. Letters indicate significant differences between means. PPFD = photon flux density.

soil water content with large rain events, a pattern seen in other grassland systems (LeRoux and Bariac 1998). However, there may have been less deep soil recharge or greater temporal variation than expected, *S. canadensis* may be less deeply rooted than expected, or deeper soils had poor hydraulic properties. Questions of deep soil moisture patterns and species root activity profiles are among the most important issues for explaining plant performance and productivity under altered rainfall patterns. We currently have preliminary data suggesting an increased proportion of total biomass has been allocated belowground in the altered-distribution treatment, and we began neutron probe soil moisture sampling during the 2001 growing season.

The confounding of treatment-induced variation in soil moisture with seasonal patterns in soil moisture and its implications for leaf physiological activity require additional research. Adjusting the leaf-level responses to factor out the seasonal trend was important in our analysis because without the adjustment the species showed opposite reactions in gas exchange parameters, i.e., stronger relationships with soil moisture variability for *A. gerardii* than for *S. canadensis* and significant correlations for  $A_{CO_2}$  and  $\psi_l$ . These differences in patterns seen in the adjusted versus the unadjusted analysis imply that seasonal patterns were probably larger than treatment effects for *A. gerardii*; therefore, the seasonal variation in precipitation inputs and soil moisture may be more important for this and other C<sub>4</sub> grasses. In contrast, the within-season variability in precipitation and soil moisture, the focus of our manipulations, may be more important for *S. canadensis* and potentially for other forbs.

Soil moisture variability induced by rainfall manipulations caused few responses in the growth parameters of the two species measured in this study, a result also found by Gutierrez et al. (1988) in a desert grassland. A survey of 27 tallgrass prairie plant species, including all the dominant C<sub>4</sub> grasses and several abundant forbs, indicated that leaf-level photosynthesis was a good predictor of long-term success in tallgrass prairie but not necessarily of individual performance (Turner et al.

1995; McAllister et al. 1998). There may also have been offsetting effects of the rainfall manipulations on availability of other resources. For example, the increased canopy light penetration likely reduced light limitation for both species (Turner and Knapp 1996), potentially lessening the impacts on individual plant growth from lower, more variable soil water contents. Increased light penetration indicates lower total above-ground productivity, and we have documented that total productivity was reduced in both the reduced-quantity and the altered-distribution treatments (Fay et al. 2000). As a result, the impacts of lower, more variable soil water contents become more important at scales larger than individual plants. Increased canopy illumination with altered rainfall patterns may also have important consequences for species interactions and future species composition. C<sub>3</sub> and C<sub>4</sub> species differed in photosynthetic light response (Percy and Ehleringer 1984; Knapp and Medina 1999), a basis for species partitioning of the canopy light profile (Anten and Hirose 1999). Light regulates plant and leaf morphology (Skalova et al. 1999) and has been related to diversity in experimental assemblages (Spehn et al. 2000). Canopy illumination dynamics are thus likely to reflect both cause and effect in the long-term responses of this grassland to altered rainfall patterns.

#### Implications for Climate-Change Impacts on Grasslands

Alterations in rainfall patterns will be accompanied by elevated atmospheric CO<sub>2</sub> and other elements of climate change. Elevated CO<sub>2</sub> is expected to increase soil moisture availability in many ecosystems through improved plant water use efficiency (Townend 1993; Bazzaz 1996). Substantial increases in plant water status and carbon gain (up to 30%) have been reported in grassland systems in response to increased CO<sub>2</sub> concentrations (Knapp et al. 1996; Newton et al. 1996; Hamerlynck et al. 1997; Niklaus et al. 1998; Clark et al. 1999;

Ward et al. 1999; Volk et al. 2000). However, an implication of this study is that variability induced by altered rainfall patterns may offset elevated CO<sub>2</sub> effects on soil water content and leaf physiological activity, especially in species with C<sub>3</sub> photosynthesis. A comprehensive understanding of climate-change impacts on grassland species will also require addressing the role of projected atmospheric warming, which should reinforce the effects precipitation-induced soil-moisture variability on leaf and plant responses.

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