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Contrasting physiological responsiveness of establishing trees and a C_4 grass to rainfall events, intensified summer drought, and warming in oak savanna

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Abstract

Climate warming and drought may alter tree establishment in savannas through differential responses of tree seedlings and grass to intermittent rainfall events. We investigated leaf gas exchange responses of dominant post oak savanna tree (*Quercus stellata* and *Juniperus virginiana*) and grass (*Schizachyrium scoparium*, C_4 grass) species to summer rainfall events under an ambient and intensified summer drought scenario in factorial combination with warming (ambient, +1.5 °C) in both monoculture and tree-grass mixtures. The three species differed in drought resistance and response of leaf gas exchange to rainfall events throughout the summer. *S. scoparium* experienced the greatest decrease in A_{area} (−56% and −66% under normal and intensified drought, respectively) over the summer, followed by *Q. stellata* (−44%, −64%), while *J. virginiana* showed increased A_{area} under normal drought (+13%) and a small decrease in A_{area} when exposed to intensified summer drought (−10%). Following individual rainfall events, mean increases in A_{area} were 90% for *S. scoparium*, 26% for *J. virginiana* and 22% for *Q. stellata*. The responsiveness of A_{area} of *S. scoparium* to rainfall events initially increased with the onset of drought, but decreased dramatically as summer drought progressed. For *Q. stellata*, A_{area} recovery decreased as drought progressed and with warming. In contrast, *J. virginiana* showed minimal fluctuations in A_{area} following rainfall events, in spite of declining water potential, and warming enhanced recovery. *J. virginiana* will likely gain an advantage over *Q. stellata* during establishment under future climatic scenarios. Additionally, the competitive advantage of C_4 grasses may be reduced relative to trees, because grasses will likely exist below a critical water stress threshold more often in a warmer, drier climate. Recognition of unique species responses to critical global change drivers in the presence of competition will improve predictions of grass–tree interactions and tree establishment in savannas in response to climate change.

Keywords: climate change, competition, drought, gas exchange, *Juniperus virginiana*, plant functional types, *Quercus stellata*, *Schizachyrium scoparium*, tree–grass interactions

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Introduction

An increase in globally averaged surface temperatures from 1.1 to 6.4 °C within the next century is predicted to result in fewer, but larger precipitation events and a greater proportion of these events may occur during the cooler seasons of the year (Bates *et al*., 2008). Elevated global air temperatures have been associated with a 10% increase in annual precipitation in the contiguous US over the past century and this increase is primarily expressed as an intensification of precipitation events (Karl & Knight, 1998; Groisman & Knight, 2008). However, ecosystem water balance may be reduced by the occurrence of more intense storms that will generate runoff from saturated soils, as well as greater evaporation in response to warmer atmospheric temperatures that will likely increase the frequency, duration, and intensity of droughts (Wetherald & Manabe, 1995; Fay *et al*., 2003). Rising atmospheric CO_2 levels improve plant water-use efficiency (WUE) and may partially alleviate drought through water-savings effects (Owensby *et al*., 1993; Polley *et al*., 2008). However, changes in rainfall event size and distribution coupled with climate warming may have equal or larger impacts on plant performance and productivity than the effects of elevated CO_2 in grassland ecosystems (Knapp *et al*., 2002; Dukes *et al*., 2005; Luo *et al*., 2008). In addition, stimulatory effects of elevated atmospheric CO_2 on photosynthesis and growth differ among plant func-

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tional types and can be limited by other plant resources, especially water availability, and photosynthetic acclimation (Lee *et al*., 2001; Reich *et al*., 2001b; Shaw *et al*., 2002). Collectively, modifications to ecosystem water balance will very likely have numerous impacts on ecosystem processes and services (Baer *et al*., 2005; Briggs *et al*., 2005; Harper *et al*., 2005; Knapp *et al*., 2008a, b).

In North America, oak savanna occupies a transitional area between the central plains and eastern deciduous forests, ranging from Minnesota to central Texas, where longitudinal boundaries are strongly tied to precipitation gradients (Ward & Nixon, 1992; Rebertus & Burns, 1997). Post-oak savanna in central Texas and Oklahoma, encompassing the warm, southern and dry, western geographic range limit of the deciduous forest biome, may be especially sensitive to climate warming. The dominant tree and grass species in this area possess contrasting leaf traits arising from differing photosynthetic pathways and leaf habits (e.g., evergreen and deciduous). Historically, the deciduous tree *Quercus stellata* (post oak) and the C_4 grass *Schizachyrium scoparium* (little bluestem) were the dominant species. However, in the absence of fire, the invasive evergreen tree *Juniperus virginiana* (Eastern redcedar) has become increasingly abundant in post-oak savanna during the past century (Briggs & Gibson, 1992).

We hypothesize that these contrasting functional types may uniquely affect the response of savanna dominants to climate warming and intensified summer drought (Reich *et al*., 2001a; Tjoelker *et al*., 2005). All three of the dominant savanna species possess a high degree of drought resistance (Bifoss, 1947; Pallardy & Rhoads, 1993; Awada *et al*., 2002; Kikuta *et al*., 2003), but their potential for physiological recovery following transient precipitation events during prolonged seasonal drought is largely unknown. The ability to respond to intermittent rainfall events may be especially important for survival, growth, and competitive ability during tree seedling establishment. *Q. stellata* is among the most drought-tolerant oaks and it is typically found on xeric sites (Ni & Pallardy, 1991, 1992; Pallardy & Rhoads, 1993), whereas *J. virginiana* is tolerant to a wide range of soils and water availabilities (Bifoss, 1947; Axmann & Knapp, 1993; Kikuta *et al*., 2003; Eggemeyer *et al*., 2006). In contrast, *S. scoparium* is a C_4 grass known for its high photosynthetic temperature optimum and two to fourfold greater WUE compared with C_3 plants and for its drought-avoidance traits (Polley *et al*., 1992, 1996; LeCain & Morgan, 1998; Espeleta *et al*., 2004; Eggemeyer *et al*., 2006). Thus, we would expect *S. scoparium* to be better able to maintain photosynthetic capacity in future climates characterized by warmer and drier summers than the two C_3 woody species.

To successfully cope with periods of intense summer drought, plants must possess sufficient resistance mechanisms to survive prolonged drought and maintain some degree of physiological responsiveness to take advantage of intermittent precipitation events during these drought periods (e.g., Schwinning *et al*., 2002). The rate and magnitude of physiological recovery following transient precipitation events during summer drought may also determine species success in coping with intensified drought associated with a shift to fewer, larger precipitation events in a warmer climate (Groisman *et al*., 2005; Knapp *et al*., 2008b). Species that are extremely drought resistant, but unresponsive in terms of photosynthetic recovery to intermittent precipitation events during drought, may incur a competitive disadvantage compared with more responsive species. Physiologically responsive species would be able to capture more resources and exhibit greater growth during periods of transient water availability. The timing of precipitation events, in addition to event size, can also have a strong influence on the species responsiveness (Ignace *et al*., 2007; Knapp *et al*., 2008a; Resco *et al*., 2008).

Our objective in the present study was to determine the magnitude of water stress alleviation and leaf-level photosynthetic response of three dominant savanna species in response to intermittent summer rainfall events as affected by intensified summer drought, warming, tree–grass competition and timing of rainfall events. This study represents one component of a comprehensive climate change project designed to evaluate the effects of altered precipitation distribution and warming on tree–grass interactions in southern oak savanna. We collected data on predawn water potential, mid-day water potential, and leaf gas exchange both before and after intermittent rainfall events on four dates throughout the summer drought period (May–September). The goal was to quantify the responsiveness of both water potential and gas exchange to alleviation of drought stress as drought progressed throughout the summer in monocultures of all three species and in both tree–grass mixtures. We hypothesized that: (1) recovery of xylem pressure potential following rainfall events would be closely coupled to increased photosynthetic rates and that the magnitude of recovery would differ among tree and grass species, (2) rates of leaf photosynthetic gas exchange of the C_4 warm-season grass, *S. scoparium* would be least affected by summer drought because of its high WUE and high temperature tolerance, and, (3) the capacity to photosynthetically respond to rainfall events would decrease with intensification of drought, warming, and interspecific competition.

Materials and methods

Experimental site and project infrastructure

The Texas warming and rainfall manipulation experiment (Texas WaRM Experiment) is located on a remnant post oak savanna site (30°34″N 96°21″W) in College Station, Texas. The infrastructure includes eight permanent 18 × 9 × 4.5 m (L × W × H) rainout shelters covered with clear polypropylene film. The sidewalls below 1.5 m are open to maintain microclimatic conditions as near ambient as possible, but effectively exclude precipitation (Fay *et al*., 2000; Weltzin & McPherson, 2000). A fine mesh, neutral density shade cloth, matching the radiation attenuation of the film (70% transmittance), precludes wind-blown precipitation from entering the two 4.5 m high open ends on each shelter. Sheet metal flashing 40 cm in width was inserted 30 cm into the soil penetrating the clay hard pan to isolate each shelter from surface and subsurface water flow.

Ten 2 × 2 m plots, with five species combinations (described below), are located beneath each shelter in native soil. Soils consist of a shallow layer ($\leq$20 cm) of Booneville fine sandy loam underlain by a thick claypan, characteristic of the claypan prairies and savannas in the region. An overhead irrigation system (17 pressure-regulated spray nozzles per shelter) drawing from four 11 500 L holding tanks simulated precipitation regimes in each shelter, supplying groundwater treated by reverse osmosis to remove excessive sodium. A weather station (EZ Mount GroWeather, Davis Instruments, Hayward, CA, US) on site recorded precipitation, air temperature and humidity, while solar radiation (total and PPFD), air temperature and relative humidity were continuously monitored in each shelter and the control plots using dataloggers (Hobo U12, Onset Computer Corp., Bourne, MA, USA). Soil water content was measured twice-weekly for each plot using permanently installed time domain reflectometry (TDR) probes (Soil Moisture Corp., Santa Barbara, CA, USA) that were inserted vertically to give an integrated measure of volumetric soil water content in the top 20 cm. The rainout shelter design preserves natural variation in the microenvironment that is, for the most part, similar to ambient conditions (Fay *et al*., 2000). Mean daily temperatures in the shelters were on average 0.3 °C higher, RH values 2% lower and PPFD levels 30% lower than ambient.

Simulated precipitation regimes included two patterns that varied in seasonal distribution and event size, but not in total annual precipitation (1018 mm) or total number of events. The long-term (50 years) mean precipitation pattern characteristic of the region was simulated from the long-term precipitation record and included both the frequency and amounts of individual precipitation events. In the precipitation redistribution regime, summer (May–September) precipitation was reduced by 40% by subtracting from each event and evenly redistributing the withheld amount to the events occurring in the two preceding spring (March and April) and two subsequent autumn (October and November) months. Each precipitation regime was replicated within each of four rainout shelters. Precipitation regimes were initiated in March 2004, with same event size and frequency applied during each subsequent year.

One-half of the experimental plots beneath each shelter were continuously warmed (24 h per day) with overhead infrared heaters (model MRM-1208L, Kalglo Electronics, Bethlehem, PA, USA) that output 100 W m^{-2} of radiant energy from a height of 1.5 m above the soil. This warming protocol, including type of heater used, suspension height, and energy output was similar to that used by Wan *et al*. (2002) in Oklahoma grasslands as modified from Harte *et al*. (1995) and Shaw and Harte (2001). Laboratory warming tests using a standardized surface (2 × 2 m painted plywood) revealed that the lamp radiant output increased average surface temperatures by 2.7 °C at 0.75 m and by 1.6 °C at 1.5 m, the distance from the lamp to the soil surface in the field. This likely was the maximum amount of warming that could be achieved in the field as actual rates of canopy and soil warming would be strongly reduced wind and canopy shade (Kimball, 2005; Kimball *et al*., 2008). Field measures of canopy temperatures using an infrared thermometer confirmed canopy warming of 1.5–3.0 °C at approximately 75 cm from the lamp on a windless morning. Mean soil surface warming at 3 cm depth during summer was 0.20 °C, but mean values of soil surface temperatures ranged from 0.90 °C cooler to 0.97 °C warmer than the control, depending upon canopy cover and soil water content changes through the summer. Although warming reduced soil water content overall, especially during the wetter months (data not shown), warming treatments did not differ in mean soil water content during the length of the present study (June–September 2005).

Five species combinations were grown in 2 × 2 m plots beneath each of the eight rainout shelters and two unsheltered controls. Within each of the rainout shelters, the five species combinations were subjected to a warming and control treatment (one replicate each per shelter). Little bluestem [*S. scoparium* (Michx.) Nash], post oak (*Q. stellata Wangenh.*), and eastern redcedar (*J. virginiana L.*) were each grown in monoculture (25 plants per plot). In addition, each of the tree species was grown with the grass in separate mixed species plots (13 trees, 12 grasses). The plots were established in 2003 1 year before experimental treatment from local transplants of little bluestem, 1-year-old containerized post oak and eastern redcedar seedlings grown from native, regional seed sources. Mean tree height at the end of the this study in the summer of 2005, when the trees were 3-years old, was 0.27 m for *Q. stellata* and 0.87 m for *J. virginana*, while grass canopy generally remained below 0.60 m (not including flowering stalks).

Experimental protocol

Leaf level gas exchange and predawn and mid-day water potential measurements were taken 1 or 2 days before and 1–3 days after each of four selected rainfall events during summer 2005 (Fig. 1). The pre-event measurements were all collected at a minimum 6 days (6–11 days) following the last substantial (>2 mm) rainfall event and soil water content had declined (Fig. 1). Leaf level gas exchange and water potential were collected for one plant of each species per plot in all treatment combinations within the overall project design.

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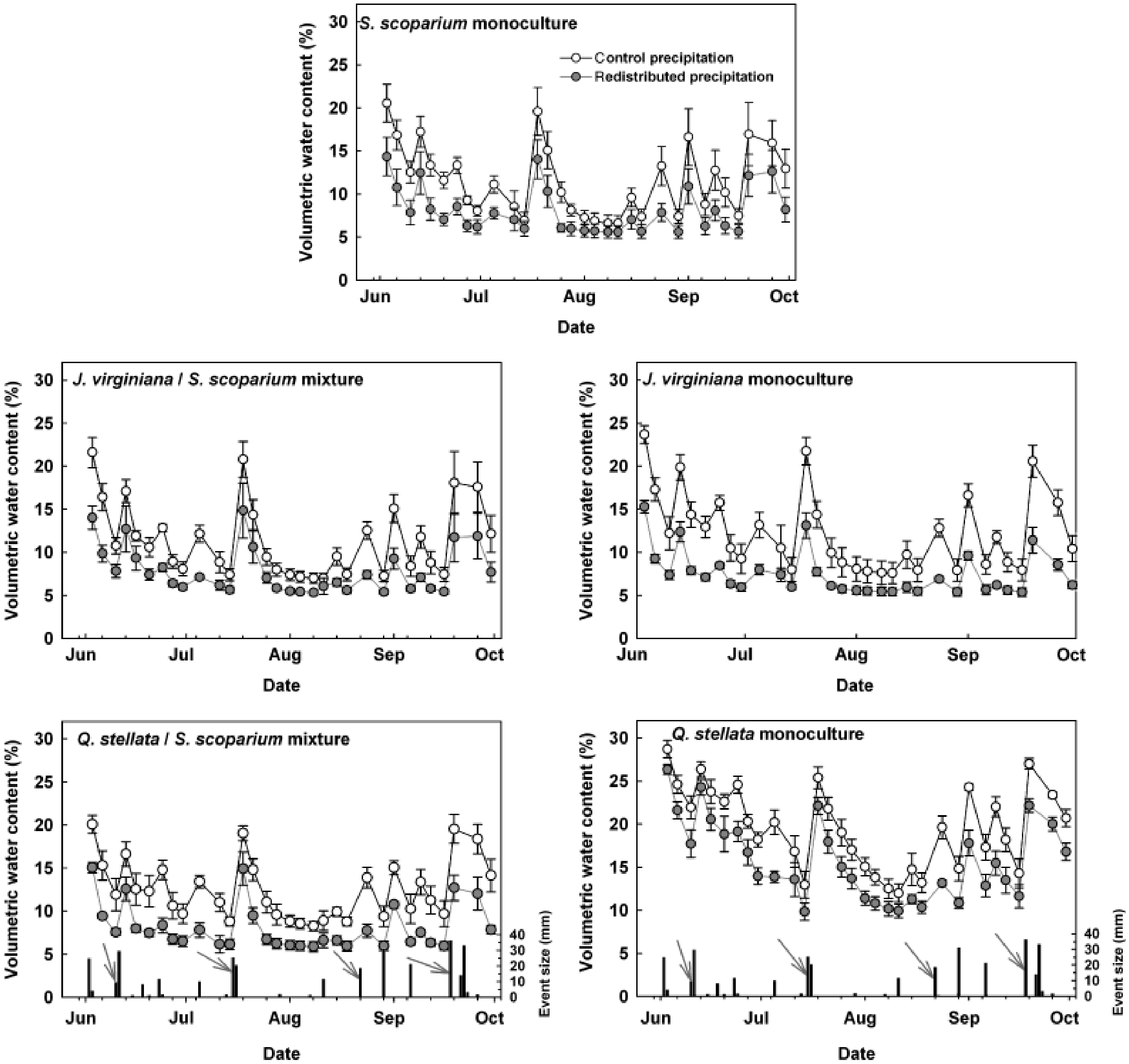

Fig. 1 Effect of species mixture, rainfall events, and event size on volumetric soil water content during the summer of 2005. Open symbols and black lines are plots subjected to the control precipitation pattern, grey symbols and grey lines are plots subjected to a redistributed rainfall pattern (−40% event size). Data were averaged for the warming treatments within each shelter, and then averaged by precipitation treatment ($n = 4$). Black bars indicate the distribution and size of the 24 individual rainfall events (control precipitation) and arrows indicate the four events used for the pre- and post rainfall event comparisons.

These include the five species combinations and two warming and two precipitation treatments ($n = 4$ per treatment combination). For the first measurement date, in June, an additional set of measurements was collected 5 days after the rainfall event occurred. Light-saturated rates of leaf-level net photosynthesis (A_{area}, $\mu\text{mol m}^{-2}\,\text{s}^{-1}$) were measured using a portable photosynthesis system (LiCOR 6400, LiCOR Inc., Lincoln, NE, USA) with the reference CO_2 level set at $380\,\mu\text{mol mol}^{-1}$, PPFD controlled at $1600\,\mu\text{mol m}^{-2}\,\text{s}^{-1}$ (using the LiCOR red/blue LED light source and standard 2×3 cm chamber), measurement temperature controlled at either 30 °C (June, August, September) or 33 °C (July) and ambient humidity levels. Measurements were taken between 10:00 and 15:00 hours using two identical, calibrated photosynthesis systems, with each unit assigned randomly to two shelters of each precipitation regime. Edge plants and the center plant were not used for gas exchange and water potential measurements. Gas exchange rates and stomatal conductance (g_s, $\text{mol m}^{-2}\,\text{s}^{-1}$) were measured on fully expanded, full sun exposed external canopy leaves, produced during the current growing season for all three species, one measurement per species per plot, for a total of four measurements per treatment combination. Tree leaves

Table 1 Probability values (*P*-values) determined using repeated measures ANOVA for the absolute changes in pre-dawn water potential ($\Delta\Psi_{PD}$), mid-day water potential ($\Delta\Psi_{MD}$) and post/pre watering event ratios of A_{area} and g_s due to summer rainfall events on four summer dates in June, July, August, and September of 2005

	Schizachyrium scoparium				*Juniperus virginiana*				*Quercus stellata*			
Treatment	$\Delta\Psi_{\mathbf{PD}}$	$\Delta\Psi s_{\mathbf{MD}}$	g_s ratio	A_{area} ratio	$\Delta\Psi_{\mathbf{PD}}$	$\Delta\Psi_{\mathbf{MD}}$	g_s ratio	A_{area}ratio	$\Delta\Psi_{\mathbf{PD}}$	$\Delta\Psi_{\mathbf{MD}}$	g_s ratio	A_{area}ratio
Precip (P)	**0.004**	**0.023**	0.656	0.495	0.198	0.598	0.988	0.574	0.145	0.470	0.959	0.793
Warming (W)	0.129	0.386	0.494	0.492	0.509	0.781	0.233	0.779	**0.008**	0.971	**0.024**	**0.024**
W × P	0.213	0.898	0.695	0.861	0.192	0.914	0.880	0.319	**0.008**	0.765	0.225	0.147
Mixture (M)	0.106	0.193	0.326	0.369	**0.001**	**0.026**	0.120	0.795	<**0.001**	0.493	<**0.001**	0.181
P × M	0.120	**0.031**	0.620	0.828	0.531	0.676	0.600	0.756	**0.074**	0.480	0.206	0.194
W × M	0.453	0.215	0.479	**0.075**	0.332	**0.003**	0.212	**0.086**	0.358	0.339	0.354	0.402
P × W × M	0.305	**0.082**	0.555	0.847	0.195	0.166	0.866	0.132	0.779	0.289	0.844	0.973
Date (D)	<**0.001**	<**0.001**	<**0.001**	<**0.001**	<**0.001**	<**0.001**	<**0.001**	**0.022**	**0.002**	<**0.001**	<**0.001**	**0.056**
P × D	<**0.001**	**0.001**	**0.001**	0.250	**0.002**	**0.008**	0.582	0.166	**0.026**	0.134	0.709	0.407
W × D	0.521	0.886	0.458	0.854	0.926	0.873	0.858	0.751	0.133	0.480	0.224	0.145
P × W × D	0.546	0.700	0.705	0.663	0.193	0.994	0.711	**0.017**	**0.091**	0.675	0.195	0.380
M × D	0.253	0.461	0.196	0.770	0.167	0.476	0.335	0.631	**0.001**	0.240	**0.040**	0.309
P × M × D	0.532	0.719	0.492	0.974	0.927	0.986	0.520	0.747	**0.006**	0.588	0.169	0.315
W × M × D	0.559	0.353	0.307	0.441	0.858	0.462	**0.084**	0.421	0.338	0.953	0.267	0.416
P × W × M × D	0.533	0.845	**0.100**	0.415	0.162	0.782	0.622	0.283	0.199	0.633	0.575	**0.069**

P-values ≤ 0.10 are printed in bold.

were selected from a comparable canopy height across dates to the extent possible and, physiological measurements were collected on progressively older leaves throughout the summer for all three species because few new leaves were formed after June 2005. We observed a visual decline in leaf quality for *S. scoparium* and *Q. stellata*, but not *J. virginiana*, as the summer progressed. In the warmed plots, leaves were selected on the side of the plant that faced the infrared heater. After each gas exchange measurement, leaves were removed from the plants to measure projected leaf area using a flatbed scanner (WINRHIZO software, Regent Instruments Inc., Quebec, Canada) and then ovendried (70 °C) to determine dry mass. Predawn (Ψ_{PD}) and mid-day (Ψ_{MD}) water potentials of the same plants as used for the gas exchange measurements were determined using a pressure chamber (Soil Moisture Corp., Santa Barbara, CA, USA) on leaves (*S. scoparium* and *Q. stellata*) and small branches (*J. virginiana*) of all three species within minutes of separating the leaves from the plants.

Precipitation regime, warming treatment, and species mixture were arranged as a split-plot factorial in a completely randomized design. Precipitation regimes constituted the whole-plot factor (with four replications), while the warming and species combinations were assigned as within-plot factors. Absolute increases in water potential (postevent – pre-event) and log-transformed A_{area} and g_s response ratio data (postevent/pre-event) were analyzed for each species separately using repeated-measures ANOVA. Precipitation effects were tested over the 'between shelter' error, and warming and species mixture effects and treatment interactions were tested over the residual error. All analyses were conducted with statistical analysis software (JMP 7.01, SAS Institute, Cary, NC, USA).

Results

Precipitation treatment and warming effects on soil water content

On average, the redistributed summer precipitation treatment produced a lower average volumetric soil water content (−3.9% VWC), intensifying the summer drought (precipitation effect, $P = 0.003$, Fig. 1). Volumetric soil water content increased following each of the four rainfall events used to evaluate the responsiveness of plant water potential and gas exchange (Fig. 1). Warming did not affect soil water content during the dry summer season (warming effect, $P = 0.530$, warming interactions with other treatments, $P \geq 0.269$; data not shown). Consequently, indirect warming effects mediated through reduced soil water content were expected to be minor.

Recovery of predawn water potentials following rainfall events

The recovery of predawn water potential ($\Delta\Psi_{PD}$) to intermittent rainfall events during summer drought differed among the species, and in tree seedlings, differed between plants in monoculture and tree–grass mixtures. Averaged over the four events, species mixture effects on $\Delta\Psi_{PD}$ were evident for *Q. stellata* and *J. virginiana* ($P \leq 0.001$; Table 1, Fig. 2), but not

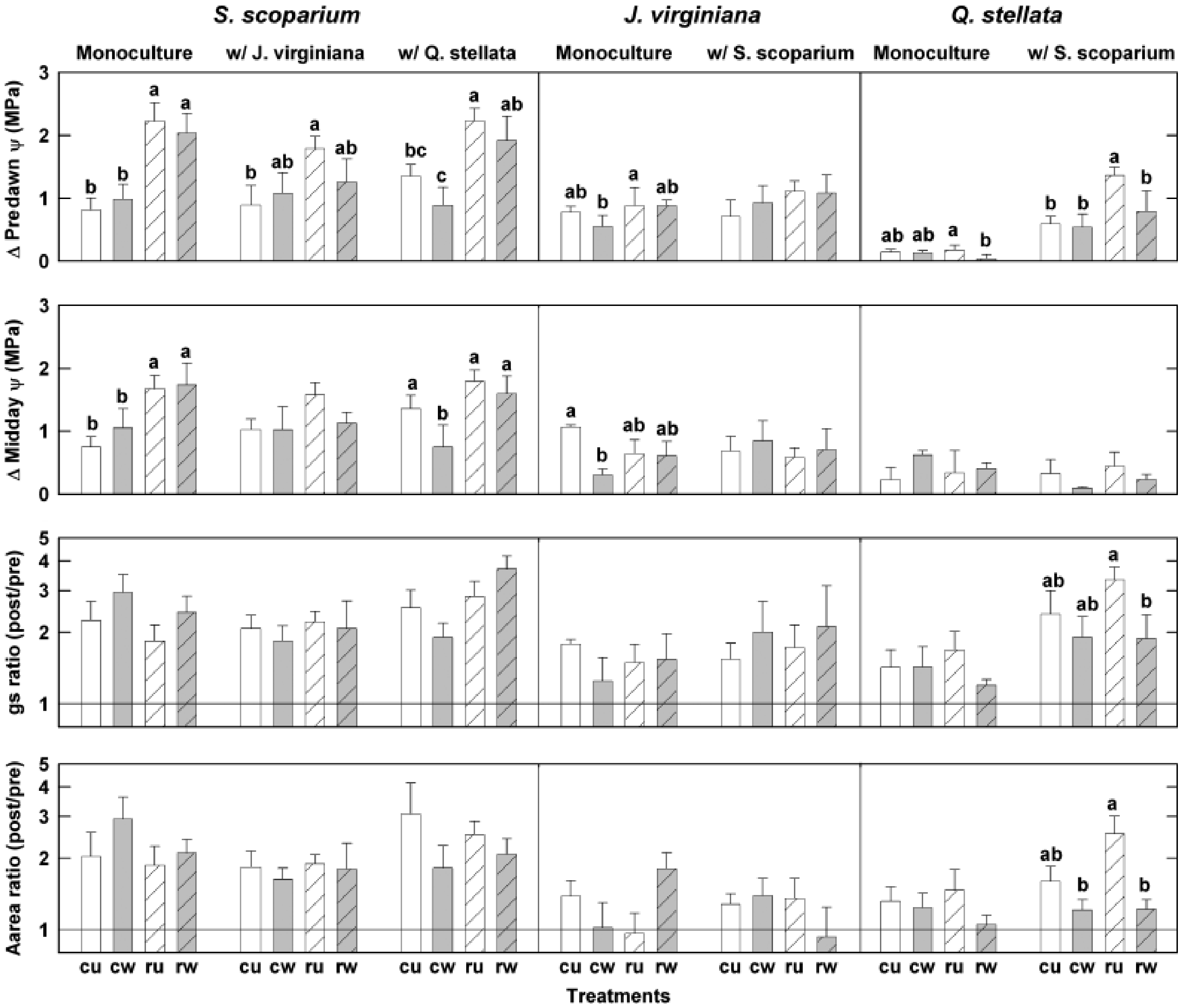

Fig. 2 Mean (±SE) response of predawn water potential, mid-day water potential, stomatal conductance (g_s) and net photosynthesis (A_{area}) to summer rainfall events, averaged over the four dates. Water potential values reflect the absolute increase in water potential (MPa) as a result the precipitation events, while changes in g_s and A_{area} are plotted as post rainfall event/pre rainfall event. Note the log scale for the ratio values. Open bars are normal summer precipitation (c-), while hatched bars are intensified summer drought (r-). White bars are unwarmed (-u), while grey bars are warmed plants (-w). Solid lines reflect the expected values if there was no response. Different letters above the bars indicate significant ($P < 0.05$) differences in response for a species within a species mixture.

S. scoparium. In general, tree seedlings had a more negative Ψ_{PD} before the rainfall events when grown with grass (Fig. 3). Thus, as Ψ_{PD} increased to similar values after a rainfall event, trees growing with *S. scoparium* exhibited a greater $\Delta\Psi_{PD}$ than their counterparts grown in monoculture (Fig. 2).

The effect of precipitation treatment on recovery of Ψ_{PD} to rainfall events differed among species. Averaged over the four dates, *S. scoparium* had larger $\Delta\Psi_{PD}$ in the intensified drought treatment than normal precipitation regime ($P = 0.004$, Fig. 2). For *Q. stellata*, the effect of precipitation regime on $\Delta\Psi_{PD}$ was evident when grown with *S. scoparium*, but not in monoculture (precipitation × mixture effect, $P = 0.074$; Fig. 2, Table 1). The average pre-event Ψ_{PD} of the oaks growing in monocultures was −0.61 MPa (normal precipitation regime) and −0.74 MPa (intensified drought), while in the mixtures these values were much lower (−1.09 and −1.84 MPa, respectively) (precipitation × mixture effect, $P = 0.004$, Fig. 3). After the rainfall events, the average Ψ_{PD} of the oaks was much higher (−0.44 and −0.50 MPa in the monocultures, and −0.54 and −0.84 MPa in the mixtures) and although the Ψ_{PD} was still more negative for the oaks growing in mixtures with intensified

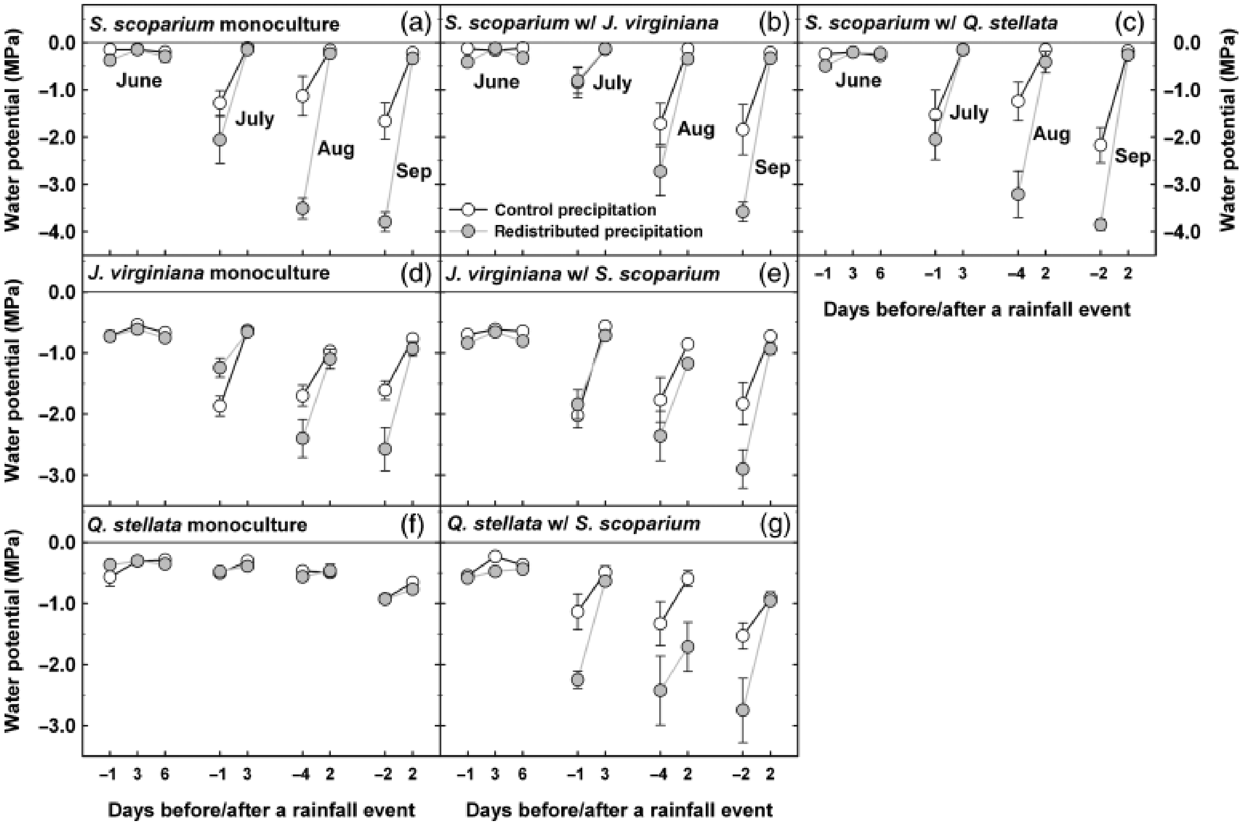

Fig. 3 Predawn water potential values (MPa) of (a) *Schizachyrium scoparium* in a monoculture, (b) *S. scoparium* grown with *Juniperus virginiana*; (c) *S. scoparium* grown with *Quercus stellata;* (d) *J. virginiana* in a monoculture; (e) *J. virginiana* grown with *S. scoparium;* (f) *Q. stellata* in a monoculture; and (g) *Q. stellata* grown with *S. scoparium*, before and after summer rainfall events. Filled symbols are plants in the long-term rainfall treatment and open symbols are plants in the intensified summer drought treatment (40% less water per rainfall event). Mean values (±SE) are shown averaged across warming treatments ($n = 4$).

drought (precipitation × mixture effect, $P = 0.003$), the difference was not nearly as large as before the rainfall event, thus explaining the greater $\Delta\Psi_{PD}$ for these plants (Fig. 2, Table 1).

Warming treatment effects on Ψ_{PD} and its response to rainfall events were evident only for *Q. stellata*. Warming reduced $\Delta\Psi_{PD}$ of *Q. stellata* in the intensified summer drought treatment in both monoculture and mixture (Fig. 2, warming × precipitation effect, $P < 0.008$). Surprisingly, this was due to the fact that, when averaged over the four events, pre-event Ψ_{PD} was more negative in the unwarmed than warmed plots in the intensified drought treatment (−1.56 vs. −1.02 MPa). There was no pre-event warming effect on Ψ_{PD} in the control precipitation treatment.

Predawn water potential responses ($\Delta\Psi_{PD}$) to rainfall events varied across dates ($P \leq 0.002$, Table 1). For *S. scoparium* and *J. virginiana*, $\Delta\Psi_{PD}$ increased throughout the summer drought, as pre-event Ψ_{PD} became increasingly negative as the summer progressed (Fig. 3). There was a date × precipitation regime interaction on $\Delta\Psi_{PD}$ for all three species ($P \leq 0.026$; Table 1) with precipitation treatment effects becoming more pronounced later in the summer. For *S. scoparium*, intensified summer drought increased $\Delta\Psi_{PD}$ in August and September compared with the normal precipitation regime, while the only significant effect of intensified summer drought on $\Delta\Psi_{PD}$ for *J. virginiana* and *Q. stellata* was in September.

Recovery of midday water potentials following rainfall events

Species also differed in recovery of midday water potentials ($\Delta\Psi_{MD}$) and several treatment effects were evident in *S. scoparium* and *J. virginiana*. Averaged over the four rainfall events, *S. scoparium* $\Delta\Psi_{MD}$ differed among the species mixtures, and was greater in monoculture and *Q. stellata* mixture plots than *J. virginiana* mixture plots (precipitation × mixture effect, $P = 0.031$; Fig. 2, Table 1). Both tree species exhibited more negative Ψ_{MD} than *S. scoparium* following the rainfall events. The warming treatment reduced $\Delta\Psi_{MD}$ averaged over

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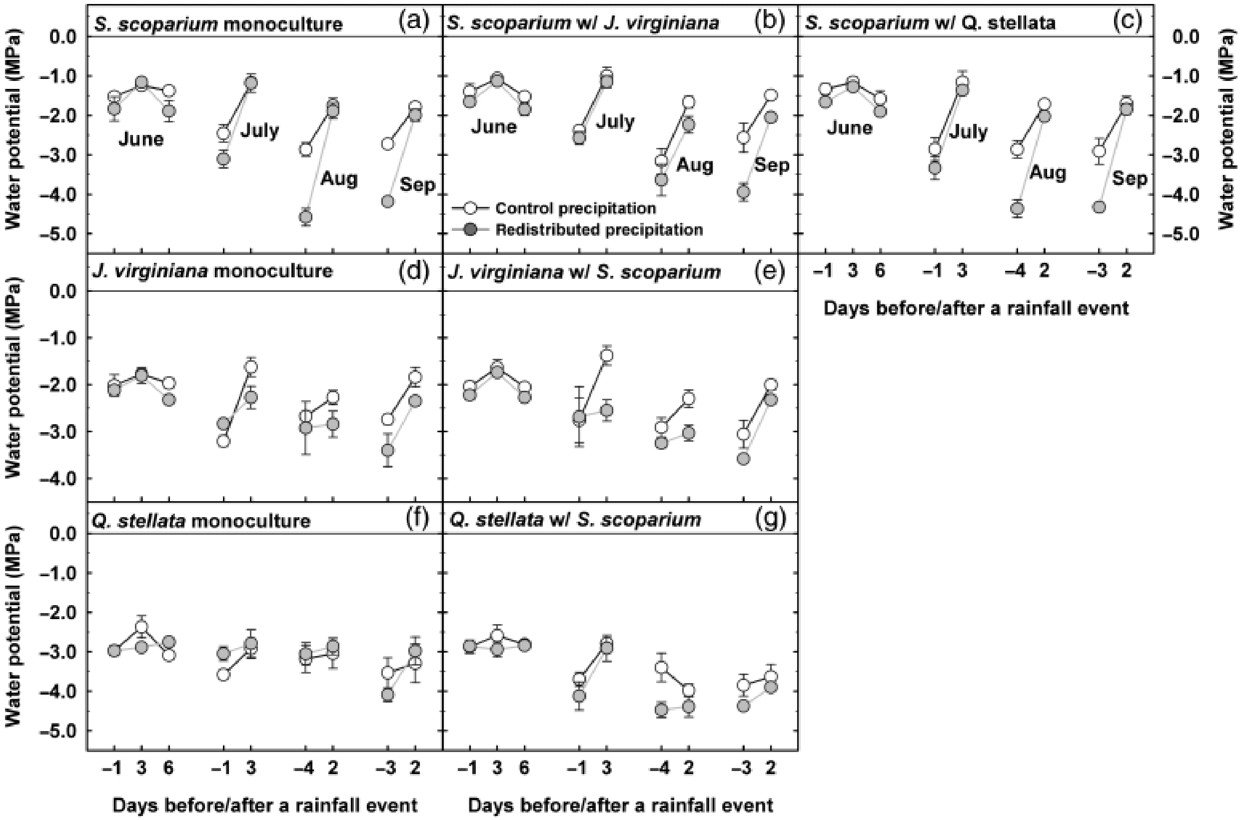

Fig. 4 Mid-day water potential values (MPa) of (a) *Schizachyrium scoparium* in a monoculture, (b) *S. scoparium* grown with *Juniperus virginiana* (evergreen tree); (c) *S. scoparium* grown with *Quercus stellata;* (d) *J. virginiana* in a monoculture; (e) *J. virginiana* grown with *S. scoparium;* (f) *Q. stellata* in a monoculture; and (g) *Q. stellata* grown with *S. scoparium*, before and after summer rainfall events. Filled symbols are plants in the long-term rainfall treatment and open symbols are plants in the intensified summer drought treatment (40% less water per rainfall event). Mean values (±SE) are shown averaged across warming treatments ($n = 4$).

the four dates for *J. virginiana* monocultures, but not mixtures (warming × mixture effect, $P = 0.003$, Fig. 4, Table 1). The average pre-event *J. virginiana* Ψ_{MD} was least negative in the warmed monocultures (−2.74 MPa) among the four treatment combinations, and most negative in the warmed mixtures with *S. scoparium* (−3.30 MPa). After the rainfall events, Ψ_{MD} was least negative in the unwarmed monocultures (−1.98 MPa), and significantly more negative in the warmed plots of both monocultures and mixtures (−2.22 and −2.24 MPa, respectively). Thus, warming reduced $\Delta\Psi_{MD}$ of *J. virginiana* monocultures through the combined effects of reduced (less negative) pre-event Ψ_{MD} and increased postevent Ψ_{MD} in warmed compared with unwarmed plots. Warming reduced $\Delta\Psi_{MD}$ of *S. scoparium* grown with *Q. stellata* in the control precipitation treatment only (precipitation treatment × warming × mixture effect, $P = 0.082$; Fig. 2, Table 1).

Intensified summer drought resulted in more negative Ψ_{MD} both before, and following individual rainfall events, when compared with the long-term average precipitation regime (Fig. 4). For *S. scoparium*, the recovery of mid-day water potentials ($\Delta\Psi_{MD}$) was greater in July (1.55 MPa), August (1.70 MPa) and September (1.63 MPa) than in June (0.39 MPa, date effect, $P < 0.001$, Table 1). Furthermore, $\Delta\Psi_{MD}$ was larger in the intensified drought treatment compared with the normal rainfall treatment in August (2.15 vs. 1.25 MPa) and September (2.20 vs. 1.07 MPa) than in the earlier two sampling periods, reflecting a precipitation treatment × date effect ($P < 0.001$; Table 1). This was mainly due to very negative pre-event Ψ_{MD} in the intensified drought treatment compared with the control treatment in August (−4.29 vs. −2.96 MPa) and September (−4.15 vs. −2.73 MPa). By comparison, postevent differences in Ψ_{MD} between precipitation treatments were smaller in August (−2.15 vs. −1.71 MPa) and September (−1.96 vs. −1.66 MPa, intensified vs. normal drought treatment).

For both tree species, the postevent recovery in mid-day water potential of seedlings increased strongly across dates, as pre-event Ψ_{MD} declined more so than postevent Ψ_{MD} over the course of the summer drought.

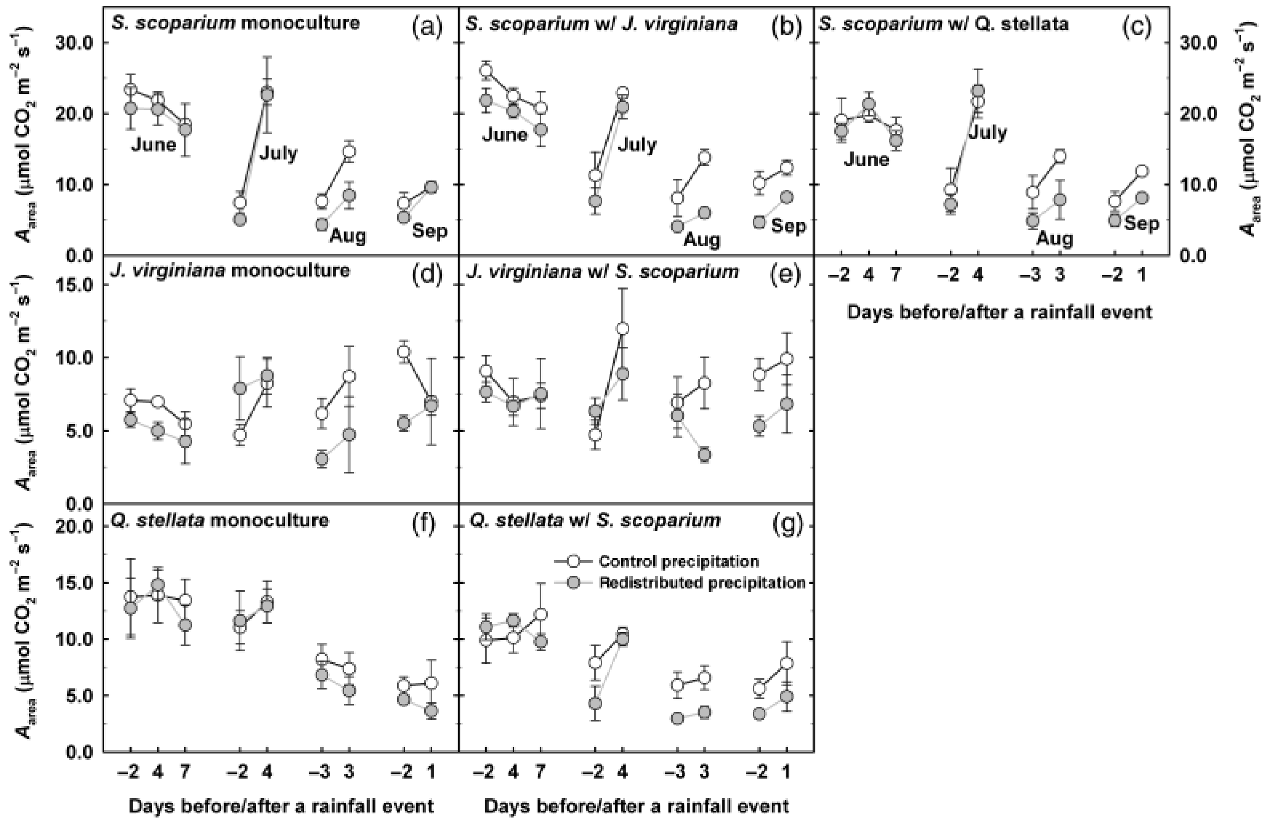

Fig. 5 Net photosynthesis rates (A_{area}, μmol CO$_2$ m^{-2} s^{-1}) of (a) *Schizachyrium scoparium* in a monoculture, (b) *S. scoparium* grown with *Juniperus virginiana* (evergreen tree); (c) *S. scoparium* grown with *Quercus stellata;* (d) *J. virginiana* in a monoculture; (e) *J. virginiana* grown with *S. scoparium;* (f) *Q. stellata* in a monoculture; and (g) *Q. stellata* grown with *S. scoparium*, before and after summer rainfall events. Filled symbols are plants in the long-term rainfall treatment and open symbols are plants in the intensified summer drought treatment (40% less water per rainfall event). Mean values (±SE) are shown averaged across warming treatments ($n = 4$).

For *J. virginiana*, the effect of precipitation treatment on $\Delta\Psi_{\mathrm{MD}}$ was inconsistent across rainfall events (precipitation treatment × date, $P = 0.008$), owing to changes in both pre and postrainfall event Ψ_{MD} among dates (Fig. 4).

Response of net photosynthesis rates and stomatal conductance to rainfall events

Averaged over all four events, the response of area-based rates of light-saturated net photosynthesis (A_{area}) and g_{s} decreased with warming for *Q. stellata* (warming effect, $P = 0.024$; Table 1, Fig 2). Although there were no statistically significant main effects of warming ($P \geq 0.601$, not shown) on pre-event and postevent A_{area} and g_{s} of *Q. stellata*, small changes in these variables did result in significant warming effects on postevent/pre-event A_{area} and g_{s} ratios. Pre-event A_{area} and g_{s} were, on average, 5% higher in the warmed plots than in the unwarmed plots. Postevent A_{area} and g_{s} were 2% and 1% lower in the warmed plots than in the unwarmed plots. There was a weak warming × species mixture effect ($P = 0.075$, Table 1; Fig. 2) for *S. scoparium*, where warming enhanced the A_{area} response to rainfall events in monoculture, but reduced A_{area} response in the grass–tree mixtures. By comparison, warming enhanced the A_{area} response of *J. virginiana* when grown with *S. scoparium* ($P = 0.086$). Averaged across all dates, treatments and species mixtures, A_{area} of individual plants in response to rainfall events increased by 90% for *S. scoparium*, and only by 26% for *J. virginiana* and 22% for *Q. stellata*, in spite of near complete recovery of Ψ_{PD} for all species.

A_{area} at the start of the summer were greatest for *S. scoparium* and lowest for *J. virginiana* (Fig. 5). Both *S. scoparium* and *Q. stellata* exhibited decreasing pre-event A_{area} as the summer progressed, while for *J. virginiana*, A_{area} was comparatively stable throughout the summer (Fig. 5). A_{area} of *S. scoparium* was generally higher in the long-term average precipitation treatment than the intensified summer drought treatment, whereas A_{area} of the tree species did not consistently differ between the precipitation treatments. The increase of A_{area} in response to rainfall events varied

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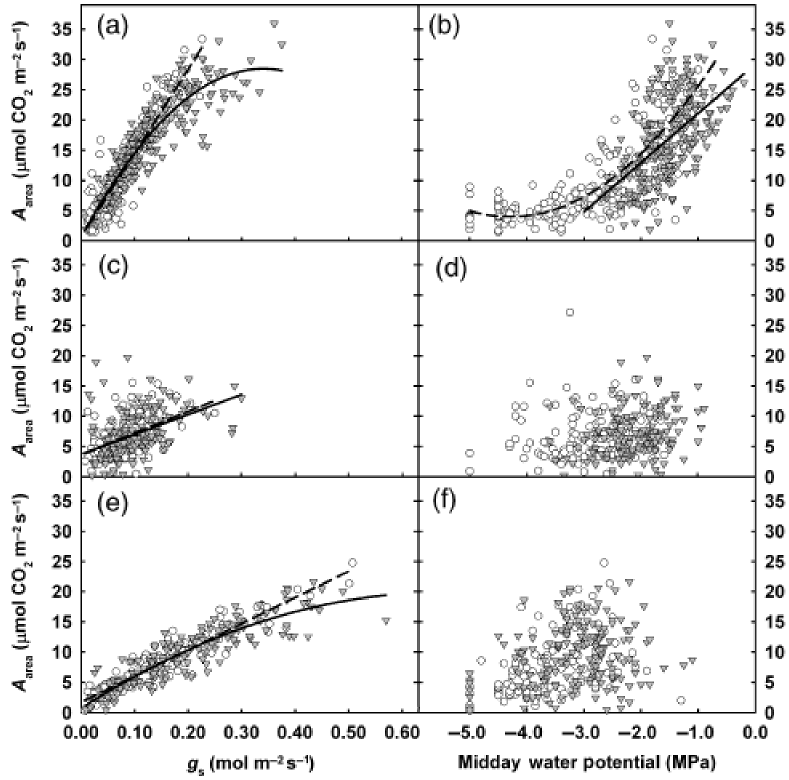

Fig. 6 Relationship among stomatal conductance (g_s, mol m^{-2} s^{-1}), A_{area} (μmol CO$_2$ m^{-2} s^{-1}), and mid-day water potential (MPa) for the three species. Shown are values for each plant in each treatment combination measured before (open circles) and following (grey triangles) the summer rainfall events. Lines depict statistically significant regression relationships for pre rainfall event (dashed lines) and post rainfall event (solid lines) measurements. (a) and (b) *Schizachyrium scoparium*, (c) and (d) *Juniperus virginiana*, (e) and (f) *Quercus stellata*. For *S. scoparium* pre event: $A_{area} = 0.499 + 139.4 \times g_s$, $r^2 = 0.863$, $P < 0.001$, and $A_{area} = 29.2 + 8.15 \times \Psi_{MD}$, $r^2 = 0.323$, $P < 0.001$; post event: $A_{area} = 4.559 + 101.7 \times g_s - 240.5 \times (g_s - 0.129)^2$, $r^2 = 0.812$, $P < 0.001$ and $A_{area} = 24.4 + 5.71 \times \Psi_{MD} + 1.99 \times (\Psi_{MD} + 2.86)^2$, $r^2 = 0.672$, $P < 0.001$. For *J. virginiana* pre event: $A_{area} = 3.69 + 35.5 \times g_s$, $r^2 = 0.189$, $P < 0.001$ and ns for Ψ_{MD};post event: $A_{area} = 3.68 + 32.9 \times g_s$, $r^2 = 0.203$, $P < 0.001$ and ns for Ψ_{MD}. For *Q. stellata* pre event: $A_{area} = 1.70 + 43.3 \times g_s$, $r^2 = 0.881$, $P < 0.001$ and ns for Ψ_{MD}; post event: $A_{area} = 2.29 + 40.2 \times g_s - 41.6 \times (g_s - 0.197)^2$, $r^2 = 0.818$, $P < 0.001$ and ns for Ψ_{MD}. a + b = *S. scoparium*, c + d = *J. virginiana*, e + f = *Q. stellata*.

among dates for all three species (date effect, $P \leq 0.056$; Table 1, Fig. 5). *S. scoparium* exhibited a large response to the July rainfall event, with postevent rates approaching those of June values (Fig. 5). August and September rainfall events also stimulated A_{area}, but to a lesser degree compared with the July event (Fig. 5).

Relationships between soil water content, midday water potential and gas exchange

In contrast to *J. virginiana*, both *S. scoparium* and *Q. stellata* exhibited a strong relationship between A_{area} and g_s (Fig. 6). Overall, the slope of the regression line (i.e., the A_{area}: g_s ratio) of all pooled pre-event observations was much steeper for *S. scoparium* (139.4 μmol CO$_2$ mol^{-1} H$_2$O) than for either tree species (35.5 and 43.3 μmol CO$_2$ mol^{-1} H$_2$O for *J. virginiana* and *Q. stellata*, respectively). All three species showed a declining WUE at higher postevent values of g_s (> 0.2 mol H$_2$O m^{-2} s^{-1}). There was a strong relationship between Ψ_{MD} and A_{area} for *S. scoparium*, but not for either tree species (Fig. 6).

Ψ_{PD} and Ψ_{MD} decreased exponentially for all three species when volumetric soil water content fell below 10% (data not shown). When A_{area} was regressed against cumulative number of days with volumetric soil water content below 10%, *S. scoparium* exhibited a declining ability to respond to watering events as chronic summer drought progressed (Fig. 7). Postevent A_{area} declined rapidly after 80 cumulative drought days and the ability to positively respond to watering events disappeared completely after 100 cumulative drought days. In contrast, pre-event A_{area} of *J. virginiana*, did not decline significantly with increasing drought days, and postevent A_{area} declined only very gradually (Fig. 7b). There was no statistical difference between the pre-event and post event slope or intercept. Similarly, for *Q. stellata* there also was no difference in the pre-event and post-event relationship, however, A_{area} declined by 51% as cumulative drought days increased (Fig. 7c).

Discussion

All three southern oak savanna species possessed sufficient drought resistance to survive intensified summer drought characterized by a 40% reduction in total rainfall over a 5-month period. This pattern of rainfall redistribution simulated an intensified summer drought comparable to the driest 10% of summers recorded in the past 50 years in the region. As the summer progressed, leaf gas exchange continued, albeit at reduced rates for *S. scoparium* and *Q. stellata*, but *J. virginiana* was largely unaffected. Physiological responses were unique for each species both before and following rainfall events (Figs 6 and 7). A_{area} was more closely coupled to water stress and its alleviation by rainfall events in *S. scoparium* than in either of the two tree species. *J. virginiana* in particular showed minimal fluctuations in A_{area} throughout the summer, in spite of substantial changes in both Ψ and soil water availability. The absence of a significant relationship between mid-day water potential and A_{area} (Fig. 6d) indicates that plant water status had little effect on net photosynthesis of *J. virginiana* during the summer. *J. osteosperma* has also been shown to be unresponsive to small rainfall events during the summer (West *et al.*, 2007). In that study, low plant hydraulic conductivity and deep rooting depth were offered as potential explanations.

Q. stellata is known for its drought tolerance (Abrams, 1990). Even though *Q. stellata* exhibits a wide range of water potential values in the field, its xylem anatomy is such that it allows for rapid water movement when water is available, yet also is capable of moving water at very negative water potentials when large vessels may undergo cavitation (Abrams, 1990). The deep root system and xylem vessel anatomy of *Q. stellata* allow for gas exchange to continue even at very negative water potentials (Abrams, 1990, 1996; Pallardy & Rhoads, 1993). The 3-year-old *Q. stellata* trees grown in monocultures in this study had very low predawn leaf water potentials (Fig. 3) and did not experience very low soil water availability in either precipitation treatment (Fig. 1), suggesting that these trees did not experience great water stress. However, even these trees showed a marked decline in A_{area} as the season progressed. It is likely that the decline in photosynthetic capacity may have been more linked to leaf aging than an actual response to cumulative effects of summer drought. This is underscored by the lack of a relationship between midday water potential and A_{area} (Fig. 6).

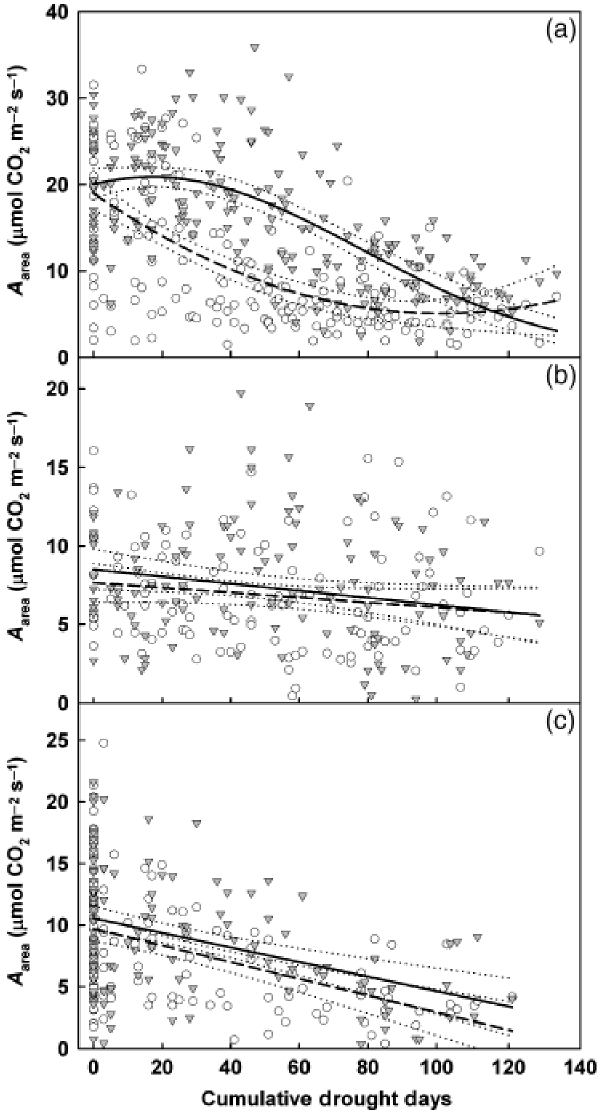

Fig. 7 Relationship between A_{area} (μmol CO$_2$ m^{-2} s^{-1}), and cumulative drought days (days with soil VWC $<$ 10%) for the three species. Shown are values measured for each plant in each treatment combination before (open circles) and following (grey triangles) the summer rainfall events. Lines depict statistically significant regression relationships for pre rainfall event (dashed lines) and post rainfall event (solid lines) measurements. Dotted lines are 95% confidence intervals. (a) *Schizachyrium scoparium*, pre-event $A_{\mathrm{area}} = 18.96 - 0.274 \times \mathrm{VWC} + 0.0014 \times \mathrm{VWC}^2$, $r^2 = 0.394$, $P < 0.001$; post event $A_{\mathrm{area}} = 20.87 \times \exp^{[-0.5 \times ((\mathrm{VWC} - 17.11)/60.20)2]}$; $r^2 = 0.436$, $P < 0.001$ (b) *Juniperus virginiana*, pre-event $A_{\mathrm{area}} = 7.64 - 0.0158 \times \mathrm{VWC}$, $r^2 = 0.141$, intercept $P < 0.001$, slope ns; post event $A_{\mathrm{area}} = 8.49 - 0.0225 \times \mathrm{VWC}$, $r^2 = 0.191$, intercept $P < 0.001$, slope $P = 0.033$; (c) *Quercus stellata*, pre-event $A_{\mathrm{area}} = 9.70 - 0.068 \times \mathrm{VWC}$, $r^2 = 0.214$, $P < 0.001$; post event $A_{\mathrm{area}} = 10.55 - 0.059 \times \mathrm{VWC}$, $r^2 = 0.170$, $P < 0.001$.

The greater physiological responsiveness of the grass to intermittent rainfall events corroborates previous interpretations that C_4 grasses possess an opportunistic photosynthetic strategy that enables them to assimilate large amounts of carbon when soil water is available, but that this capacity rapidly decreases as soil water content decreases and plants become increasingly drought stressed (Ghannoum *et al.*, 2003; Swemmer *et al.*, 2006). This interpretation is also consistent with the hypothesis that C_4 grasses may possess a drought stress threshold beyond which they lose their advantage to C_3 plants in spite of their high WUE when soil water is available (Ripley *et al.*, 2007; Ibrahim *et al.*, 2008). Mechanisms associated with this water stress threshold have yet to be determined, but reductions in electron transport rate and photochemical efficiency suggest that they are likely associated with light harvesting mechanisms. However, enzyme activities and metabolite concentrations specific to the CO_2 pump have also be shown to be adversely effected by severe water stress (ContourAnsel *et al.*, 1996).

The tight coupling of A_{area} with Ψ in *S. scoparium* decreased during the latter half of the summer, indicating the potential occurrence of nonstomatal drought injury with severe water stress. Nonstomatal injury has been shown to constrain ATP production in chloroplasts (Tezara *et al.*, 1999; Galmes *et al.*, 2007) or impose other limitations to rubisco activity and light-harvesting. Nonstomatal effects have been related to the suppression of $A_{\max}$ and quantum yield in four tropical C_4 grasses exposed to a gradual decrease in soil water content (Ghannoum *et al.*, 2003). In terms of phenotypic appearance, the grass showed reduced green leaf area and increasing leaf senescence as the summer progressed. Drought-induced canopy senescence in C_4 grasses is associated with N reallocation from leaves to belowground structures which may further delay photosynthetic recovery following drought (Heckathorn *et al.*, 1997). Grasses replace leaf canopy following severe drought by the production of new leaves and tillers from apical meristems and axillary buds near the soil surface when favorable growth conditions resume (Welker & Briske, 1992; Hendrickson & Briske, 1997; Dalgleish & Hartnett, 2006). Under a climatic scenario of warmer and drier summers, the ability to resume growth from drought-resistant meristems near the soil surface may confer this C_4 grass with the ability to maintain dominance, albeit with a reduced level of production and competitive ability. Under future climate conditions, the adverse effects of intensified drought may also be partially alleviated by increasing atmospheric CO_2 concentration that are known to increase WUE even in C_4 grasses, especially during drought conditions (Owensby *et al.*, 1993; Ghannoum *et al.*, 2000).

The lower responsiveness of A_{area} to rainfall events in either tree species over the course of the summer raises the question, 'why was A_{area} of the tree species not more strongly related to Ψ_{plant} as in the case of the C_4 grass'? Contrasting leaf traits among these three species resulted in considerable variation in the dynamics of Ψ_{plant} as indicated by interspecific variation in Ψ_{PD} and Ψ_{MD}. *Q. stellata* experienced favorable Ψ_{PD}, but much more negative Ψ_{MD}, even under conditions of high soil water availability when grown in monoculture (Fig. 3). This was likely a function of high g_s and transpiration as well as the ability to more effectively rehydrate during the night as indicated by the least negative Ψ_{PD} potentials of the three species at low soil water content. For *Q. stellata*, g_s remained high even when Ψ_{MD} became very negative (Fig. 6). An earlier study also found that g_s did not change significantly with increasing water stress, or after rewatering in containerized *Q. stellata* plants (Ni & Pallardy, 1992). Stomatal conductance of *J. virginiana* showed a much narrower range and remained relatively low (max. $0.30\,\mathrm{mol\,m^{-2}\,s^{-1}}$) compared with those of *Q. stellata* (max. $0.58\,\mathrm{mol\,m^{-2}\,s^{-1}}$), even when soil water was readily available.

Although *S. scoparium* was most responsive to water stress alleviation, it also experienced a greater decrease (−61%) in average A_{area} between June and September (from 21.2 to $8.3\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) than *Q. stellata* (−55%; from 12.3 to $5.6\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$), while *J. virginiana* showed no temporal decrease in A_{area} throughout the summer ($7.4\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$). Consequently, integrated foliar carbon gain would be reduced by intensified summer drought more so in *S. scoparium* and *Q. stellata* than *J. virginiana*. Thus, of the three species studied, *S. scoparium* has the greatest ability to respond to intermittent rainfall events during drought, while also being the least resistant to chronic drought.

The ability of *J. virginiana* to maintain moderate, but remarkably constant rates of photosynthesis over a wide range of soil water content and Ψ_{plant} was unexpected and is difficult to interpret in spite of the well documented drought resistance of juniper species (Axmann & Knapp, 1993). Drought resistance mechanisms of *Juniperus* spp. include low g_s for a C_3 species (Bahari *et al.*, 1985) and a xylem anatomy well adapted to severe water stress, including low tracheid diameters that convey reduced vulnerability to xylem cavitation (McElrone *et al.*, 2004; West *et al.*, 2007). Comparisons of *J. ashei* with *Q. fusiformis* and *Q. sinuata* also documented substantially lower xylem conduit diameters, hydraulic conductivities and cavitation thresholds in the juniper compared with either of the oak species (McElrone *et al.*, 2004). Neither tree species in our study showed a threshold level of drought injury indicating that the most negative Ψ_{PD} (<4.0–$4.5\,\mathrm{MPa}$) did not exceed a cavitation threshold. Drought tolerance could be manifested through turgor maintenance mechanisms of osmotic adjustment and modulus of elasticity that would not be reflected in Ψ_{plant} measurements (Castro-Díez & Navarro, 2007), but they were not evaluated in this investigation.

Significant differences in species performance between monocultures and grass–tree seedling mixtures likely originated from preemptive soil water use by grass in the plots. This is particularly true for *Q. stellata*, where soil water content rarely fell below 10% in monocultures while in oak–grass mixtures it often fell below 10%. Consequently, water potentials were substantially more negative when *Q. stellata* was growing with grass, indicating that competitive interactions may have a substantial role in mediating responses to global change drivers (Fig. 4).

Modified rainfall patterns in southern oak savanna through reduced total amounts, reduced effectiveness due to higher atmospheric temperatures and greater evapotranspiration, or the occurrence of fewer, larger events associated with prolonged intervening drought, may have unique affects on grass-tree competitive interactions that may potentially modify grassland-woodland boundaries (Knapp *et al.*, 2001; Sankaran *et al.*, 2004; Sankaran *et al.*, 2005). Our data suggest that the competitive advantage of C_4 grasses may be reduced relative to that of the woody dominants during tree establishment because grasses will likely exist below a critical water stress threshold more often under future than under current climatic regimes (Briggs *et al.*, 2005; Fay *et al.*, 2008; Knapp *et al.*, 2008b). This could indirectly promote seedling establishment and growth of both *J. virginiana* and *Q. stellata* by reducing the negative effects of grass competition for soil water, especially during intensified summer drought. *J. virginiana* will likely attain a greater advantage than *Q. stellata* under future climatic scenarios because A_{area} was least affected by intensified drought (Axmann & Knapp, 1993) and this invasive evergreen species has the potential to conduct photosynthesis throughout the entire year in these low latitude savannas and woodlands. In addition, warming further reduced the responsiveness of A_{area} to rainfall events in *Q. stellata* and enhanced the response of A_{area} in *J. virginiana*. Disparate interspecific abilities to maintain or rapidly recover physiological activity during prolonged drought and climate warming may uniquely modify water and carbon fluxes and subsequently the structure of savanna ecosystems (Nippert *et al.*, 2006). Recognition of these unique species responses to modified precipitation regimes, and their potential modification by competitive interactions, will further refine simulation models emphasizing global change scenarios that include grass–tree interactions.

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