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Climate warming and precipitation redistribution modify tree–grass interactions and tree species establishment in a warm-temperate savanna

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Abstract

Savanna tree–grass interactions may be particularly sensitive to climate change. Establishment of two tree canopy dominants, post oak *(Quercus stellata*) and eastern redcedar (*Juniperus virginiana),* grown with the dominant C_4 perennial grass (*Schizachyrium scoparium*) in southern oak savanna of the United States were evaluated under four climatic scenarios for 6 years. Tree–grass interactions were examined with and without warming (+1.5 °C) in combination with a long-term mean rainfall treatment and a modified rainfall regime that redistributed 40% of summer rainfall to spring and fall, intensifying summer drought. The aim was to determine: (1) the relative growth response of these species, (2) potential shifts in the balance of tree–grass interactions, and (3) the trajectory of juniper encroachment into savannas, under these anticipated climatic conditions. Precipitation redistribution reduced relative growth rate (RGR) of trees grown with grass. Warming increased growth of *J. virginiana* and strongly reduced *Q. stellata* survival. Tiller numbers of *S. scoparium* plants were unaffected by warming, but the number of reproductive tillers was increasingly suppressed by intensified drought each year. Growth rates of *J. virginiana* and *Q. stellata* were suppressed by grass presence early, but in subsequent years were higher when grown with grass. *Quercus stellata* had overall reduced RGR, but enhanced survival when grown with grass, while survival of *J. virginiana* remained near 100% in all treatments. Once trees surpassed a threshold height of 1.1 m, both tiller number and survival of *S. scoparium* plants were drastically reduced by the presence of *J. virginiana*, but not *Q. stellata*. *Juniperus virginiana* was the only savanna dominant in which neither survival nor final aboveground mass were adversely affected by the climate scenario of warming and intensified summer drought. These responses indicate that climate warming and altered precipitation patterns will further accelerate juniper encroachment and woody thickening in a warm-temperate oak savanna.

Keywords: climate change, competition, plant growth, precipitation patterns, savanna, tree–grass dynamics

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Introduction

Mid-latitude grasslands and savannas of North America are predicted to experience a combination of atmospheric warming (1.5–4.5 °C) and modified precipitation regimes characterized by a reduced number of larger events, a shift from summer to spring distribution, and a modest increase in mean annual amount during this century (Manabe & Wetherald, 1986; Easterling *et al.*, 2000; Meehl *et al.*, 2007). The occurrence of warmer temperatures and greater evapotranspiration coupled with a decrease in summer precipitation and increased intervals between rainfall events will collectively intensify summer drought (Wetherald & Manabe, 1995; Pope *et al.*, 2000; MacCracken *et al.*, 2003). Intra-annual rainfall variability strongly affects grassland productivity (Fay *et al.*, 2003; Nippert *et al.*, 2006). For example, fewer, larger precipitation events decreased productivity in mesic grasslands, but increased it in semiarid grasslands (Heisler-White *et al.*, 2008). Modifications to the amount and seasonal availability of soil water have the potential to alter the function, growth, and distribution of various plant functional groups as well as the outcome of resource competition among species (Hungate *et al.*, 2002; Knapp *et al.*, 2008a,b).

Tree–grass interactions in savannas may be particularly sensitive to the effects of climate warming and rainfall modification because of the contrasting leaf traits and physiological tolerances among growth forms that could disrupt the competitive balance, especially during tree establishment, when tree–grass competition for resources and abiotic stresses are thought to be magnified (Jeltsch *et al.*, 1996; Dunnett & Grime, 1999;

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Rodriguez-Iturbe *et al.*, 1999; Zimmermann *et al.*, 2008). Differences in leaf habit, xylem structure, and hydraulic conductivity as well as differences in belowground traits such as root architecture, root density, and rooting depth will determine how these species respond to intensified drought (Reich *et al.*, 2003; Tjoelker *et al.*, 2005; Beerling & Osborne, 2006). Physiological responses to drought in trees generally progress in severity from initial growth reductions (reduced cell expansion) to reduced photosynthesis and eventually to hydraulic failure and xylem cavitation (McDowell *et al.*, 2008, 2011). The risk of mortality increases as plants experience (1) a rate of xylem embolism that exceeds repair and refilling, and/or (2) carbon starvation where carbon uptake is severely suppressed by stomatal closure and potential metabolic injury (McDowell *et al.*, 2011). For example, *Juniperus virginiana* exhibited low but steady rates of net gas exchange throughout the summer season while *Quercus stellata* and *Schizachyrium scoparium* maintained high rates of gas exchange when water was available, but significantly reduced rates of gas exchange as water supply became limited and drought intensified (Volder *et al.*, 2010). This latter drought-avoidance response may predispose plants to carbon starvation and potential mortality during prolonged drought and climate warming.

The post oak savanna region occupies about three million hectares in south central Texas and eastern Oklahoma and represents the southernmost extent of a continental-scale ecotone separating the eastern deciduous forest and Great Plains of North America. Post oak (*Q. stellata*) and eastern redcedar (*J. virginiana*) are the major canopy tree dominants and little bluestem (*S. scoparium)* is the major perennial grass dominant (Ward & Nixon, 1992). This savanna, like many ecosystems along a grassland–forest continuum, has undergone a transition from a tree–grass dominated savanna toward a closed canopy oak and oak-juniper woodland over the last century (Scholes & Archer, 1997; Coppedge *et al.*, 2001; Breshears, 2006). The invasive nature and rapid growth rate of juniper enables it to attain sufficient size and density to suppress both oak regeneration and grass density in the absence of fire (Rykiel & Cook, 1986; Briggs & Gibson, 1992; Briggs *et al.*, 2002b). Climate change is often implicated as a causal agent in woody plant encroachment of savannas and grasslands (Polley *et al.*, 1997; Morgan *et al.*, 2007; Kgope *et al.*, 2010), in addition to fire suppression and intensive grazing (Briggs *et al.*, 2005), yet conclusive evidence of climate change effects on tree encroachment is limited (Van Auken, 2000; Knapp *et al.*, 2008b).

Warming may induce either positive or negative effects on plant growth in various ecosystems (Llorens *et al.* 2004, Dermody *et al.* 2007). This is a consequence of specific thermal limits among various plant species and variation in ambient thermal conditions. Warming may enable plants to remain physiologically active for longer periods (i.e. shortening the winter season, (Norby *et al.*, 2003; Zhang *et al.*, 2004)) by removing low-temperature limitations on physiological processes (Gunderson *et al.*, 2000, 2010). In contrast, warming may decrease growth by elevating leaf temperatures beyond their physiological optimum, reducing soil water content through increased evapotranspiration (Wan *et al.*, 2002; Hovenden *et al.* 2008) or by enhancing leaf dark respiration rates although this response is generally tempered by acclimation (Atkin & Tjoelker, 2003; Gifford, 2003).

Competitive interactions that affect plant establishment and growth have recently been recognized as an important process by which climatic drivers can mediate community and ecosystem responses. In savannas, the competitive advantage shifts from grasses to trees along gradients of increasing precipitation (Sankaran *et al.*, 2005). Increasing atmospheric CO_2 may have shifted the competitive advantage from C_4 grasses to C_3 trees, enhancing tree growth rates following fire (Bond *et al.*, 2003). Substantial uncertainty exists in both the magnitude and direction of competitive effects in response to climatic drivers (Tylianakis *et al.*, 2008), including tree–grass interactions during establishment that may underpin potential tipping points in ecosystem state changes with climatic change (Higgins & Scheiter, 2012).

The overarching aim of this experiment was to determine the effects of climate warming and altered precipitation patterns on growth of the most abundant C_4 perennial grass, canopy dominant oak, and encroaching juniper species of the southern oak savanna to answer the following three questions: (1) what is the relative growth response of these dominant species to climate change drivers? (2) how may climate change drivers affect the balance of tree–grass interactions in savanna systems?, and (3) can juniper encroachment into grasslands and savannas be accelerated under future, warmer climatic conditions? Answers to these questions have important implications for our understanding of tree–grass interactions and the composition and structure of southern oak savanna in future climates.

Methods

Site and experiment description

The Texas warming and rainfall manipulation experiment is located on a remnant post oak savanna site (N 30°34″ W 96° 21″) near Texas A&M University, College Station, Texas. The site has a mean annual temperature of 20.4 °C. The facility was constructed in March 2004 to investigate the combined effects of altered precipitation distribution and warming, both independently and in combination. The experiment is comprised of five planted species combinations grown under a factorial combination of two precipitation and two warming treatments for a total of 20 treatment combinations with four replicates (Fig. S1). The research 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, while effectively excluding precipitation (Fay *et al*., 2000; Weltzin & McPherson, 2000). A fine mesh, neutral density shade cloth, matching the radiation attenuation of the film (70% transmittance), excludes wind-blown precipitation from entering the two open ends on each shelter. Sheet metal flashing 40 cm in height was inserted 30 cm into the soil penetrating the clay hard pan (ca. 20 cm depth) to isolate each shelter from surface and subsurface water flow. Ten 2 × 2 m plots, with five species combinations, were located beneath each shelter in the native soil. An overhead irrigation system (17 pressure-regulated spray nozzles per shelter) simulated precipitation regimes by supplying reverse osmosis water to each shelter, drawing from four 11 500 L holding tanks. Infrared lamps (Kalglo Electronics, Bethlehem, PA, USA; model MRM-1208L) suspended over individual plots (at 1.5 m height) simulate warming (Harte & Shaw, 1995; Wan *et al*., 2002; Kimball, 2005).

Solar radiation (total and PAR), air temperature, and relative humidity were monitored hourly in each shelter and outside the shelters (Hobo U12; Onset Computer Corp., Bourne, MA, USA). Soil moisture data were collected 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 including the entire sandy loam upper soil profile, which is generally the zone where the majority of fine roots are located (Jackson *et al*., 1996; Schenk & Jackson, 2002). We began collection of soil water content data in each plot beginning in March 2004 using both portable and permanent probes. From December 2004 onward all 80 plots were instrumented with permanent TDR probes for the duration of the 6-year study. Soil temperature at two depths (3 cm, a surface measure, and 10 cm, the midpoint of the upper 20-cm soil profile) was measured hourly in 20 representative plots (n = 1 per treatment combination) using Hobo dataloggers (Hobo U12; Onset Computer Corp.). The shelter design preserves natural variation in the microenvironment that is, for the most part, similar to ambient conditions (Fay *et al*., 2000). Mean daily air temperatures in the shelters were on average 0.3 °C higher, RH values 2% lower, and PAR levels 30% lower than outside the shelters.

Plant species combinations

Five species combinations were replicated twice within each of the ten 2 × 2 m plots beneath each of the rainout shelters (Fig. S1). Each individual plot was planted with 25 plants on a 0.4 m spacing in May 2003. Post oak (*Quercus stellata* Wangenh.), juniper (*Juniperus virginiana* L.), and little bluestem [*Schizachyrium scoparium* (Michx. Nash)] were each planted in monoculture with a density of 25 plants per plot. In addition, each tree species was planted in a combination with *S. scoparium* in separate plots of 13 trees and 12 grasses. Grass densities were representative of local native grasslands (Butler & Briske, 1988). Plots were established in 2003, 1 year prior to experimental treatment from local transplants of *S. scoparium* and greenhouse-grown, 1-year-old, bare-root *Q. stellata* and containerized 18-month-old *J. virginiana* seedlings. Twelve trees were harvested from the *J. virginiana* and *Q. stellata* monoculture plots in December 2007 to the same number as tree–grass plots as the trees had maximized available growing space. Plots were maintained by hand weeding and selective spraying with the herbicide, glyphosate (Roundup, Monsanto, St. Louis, MO, USA).

Precipitation and warming treatments

The 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 (Fig. 1). A long-term (50 year) precipitation pattern with annual total, and frequency and intensity (amount) of individual precipitation events characteristic of the region was replicated within four of the shelters. In the precipitation redistribution treatment imposed beneath the other four shelters, summer (May–September, dry phase) precipitation was reduced by 40% by subtracting this amount from each event

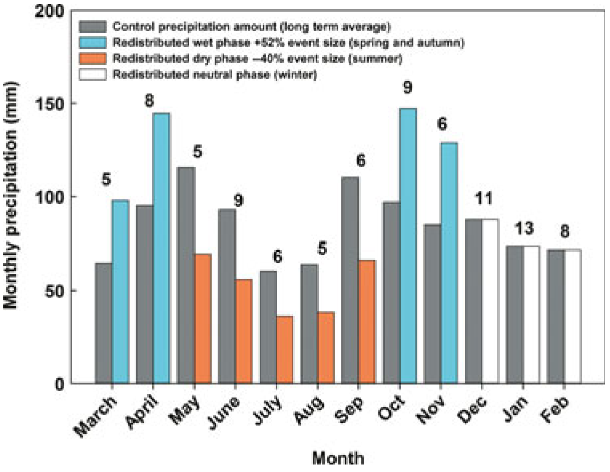

Fig. 1 Monthly precipitation totals applied each year for six successive years (2004–2009). Numbers indicate the number of precipitation events in each month. Summer (May–September) events were 40% smaller in the redistributed precipitation pattern while spring (March, April) and autumn (October, November) events were 52% larger in the redistributed precipitation pattern. The total annual amount (1018 mm) and number of events (91) as well as stochastic features of size (0.3–36.7 mm) and timing (0–20 days between events) were determined from the long-term (50 year) climatic record and was the same for both the control and redistribution treatments.

and evenly redistributing it to rainfall events in the two preceding spring (March and April, wet phase) and two subsequent autumn (October and November, wet phase) months of each year. Plant growth metrics were calculated using the beginning and end point growth measures corresponding to each of the four annual precipitation-treatment intervals, as defined in our study (spring: March–April; summer: May–September; autumn: October–November; winter: December–February) (Fig. 1). This precipitation treatment design enabled us to expose the plots with a high degree of consistency for six consecutive years to document tree–grass interactions under four climate change scenarios throughout the tree establishment phase.

One plot of each of the five species combinations was subjected to continuous (24 h day^{-1}) warming and an unwarmed control in each shelter (Fig. S1) for a total of four warmed and four control plots among the four replicate shelters of each precipitation treatment. The warmed plots were heated with overhead infrared lamps (Kalglo Electronics Co.) that output 400 W of radiant energy from a height of 1.5 m above the soil, while the control plots were fitted with dummy lamps constructed of bent sheet metal of the same size and shape as the lamp housing. In February 2008, infrared heater height was raised to 2.0 m above the soil and output was increased to 800 W as tree height surpassed 1.5 m. Tests of the heater height and output and *in situ* field measures of foliage temperature (and standardized surface targets in each plot) with infrared thermometry throughout the study revealed a comparable magnitude of warming (ca. 1.5 °C at mid-canopy height) compared with the ambient unheated controls. Warming of 1.5 °C represents the lower level of climate warming expected within the southern plains of the US during this century (IPPC 2007).

Measurements

We collected stem diameter measurements on trees with calipers at 1 cm above the soil four to six times per year for the same five trees nearest to the center of both the monoculture and combination plots (Fig. S1). Allometric relationships were developed for both tree species in each of the treatments following one harvest in December 2007 when monocultures were thinned from 25 to 13 trees and in a final harvest at the end of the experiment (October 2009) when the five trees that were measured throughout the experiment were harvested as well as the largest and smallest trees in each plot. The allometric relationships related base stem diameter to total aboveground dry mass (data not shown), and were used to convert diameter measurements to total aboveground dry mass. At the start of the treatments (March 2004), estimated mean aboveground dry mass per *J. virginana* tree was 63 g with a height of 414 mm, while mean estimated aboveground dry mass for *Q. stellata* was 0.4 g per tree with a height of 125 mm.

Tiller number and basal area occupied per plant (measured with a diameter tape) were measured on two of the central four grass plants within each plot containing *S. scoparium* (Fig. S1). Tiller numbers of individual *S. scoparium* plants were counted at least four times per year by dividing individual clones of this bunchgrass in either halves or quarters, counting all the tillers within a section, and extrapolating these values to a whole plant basis. The proportion of tillers that had become reproductive each year were recorded for the same plants from May to December by evaluating culm (stem) elongation and inflorescence emergence. Senescent biomass was removed from *S. scoparium* plants to a height of 35 cm every January to prevent excess litter accumulation in the plots.

Statistical analysis

The factorial experimental design where each species mixture × warming × precipitation distribution treatment was replicated four times (Fig. S1) enabled an evaluation of plant response to altered precipitation patterns and warming both independently and in combination. The same five center trees were sampled per plot through time (Fig. S1). Treatment effects on changes in the natural logarithm of mass through the entire 6-year period of study were tested using ANOVA and a restricted maximum likelihood procedure (JMP 10.0 Pro; SAS Institute, Cary, NC, USA). Precipitation treatment constituted the whole-block factor ($n = 4$), while warming and species combinations were assigned as within-plot factors while time was used as a covariate. Significant interactions with time denote a significant effect of treatment on relative growth rate (RGR) (Poorter & Lewis, 1986). For mean seasonal RGR, mean RGR was calculated for each plot for each season and year first by fitting a curve through the ln transformed mass of all trees per plot at the beginning and end point of each time interval ($n = 5$ trees) and using the slope of the line as mean RGR per plot. Differences in RGR as affected by season, year, and treatment were then further analyzed with ANOVA using a restricted maximum likelihood procedure (JMP 10.0 Pro; SAS Institute). *Quercus stellata* exhibited considerable mortality throughout the experiment. For each interval, we only included mass of trees that were alive at both the start and the end of the interval.

Results

Direct and indirect driver effects

Precipitation redistribution resulted in reductions in volumetric soil water content in summer and increases in spring and in autumn throughout the 6-year study (Fig. 2a). Annual patterns of soil water content as well as minimum and maximum air temperatures were comparable throughout the experimental period (Fig. 2b and c). Soil water content and soil surface warming showed a slight decreasing trend as the experiment progressed (Fig. S2).

Tree growth, survival, and response to grass

Saplings of *J. virginiana* and *Q. stellata* exhibited rapid rates of aboveground growth throughout the 6-year experiment (Figs S3 and S4). Over the entire 6-year period, mean RGR of *J. virginiana* was reduced by

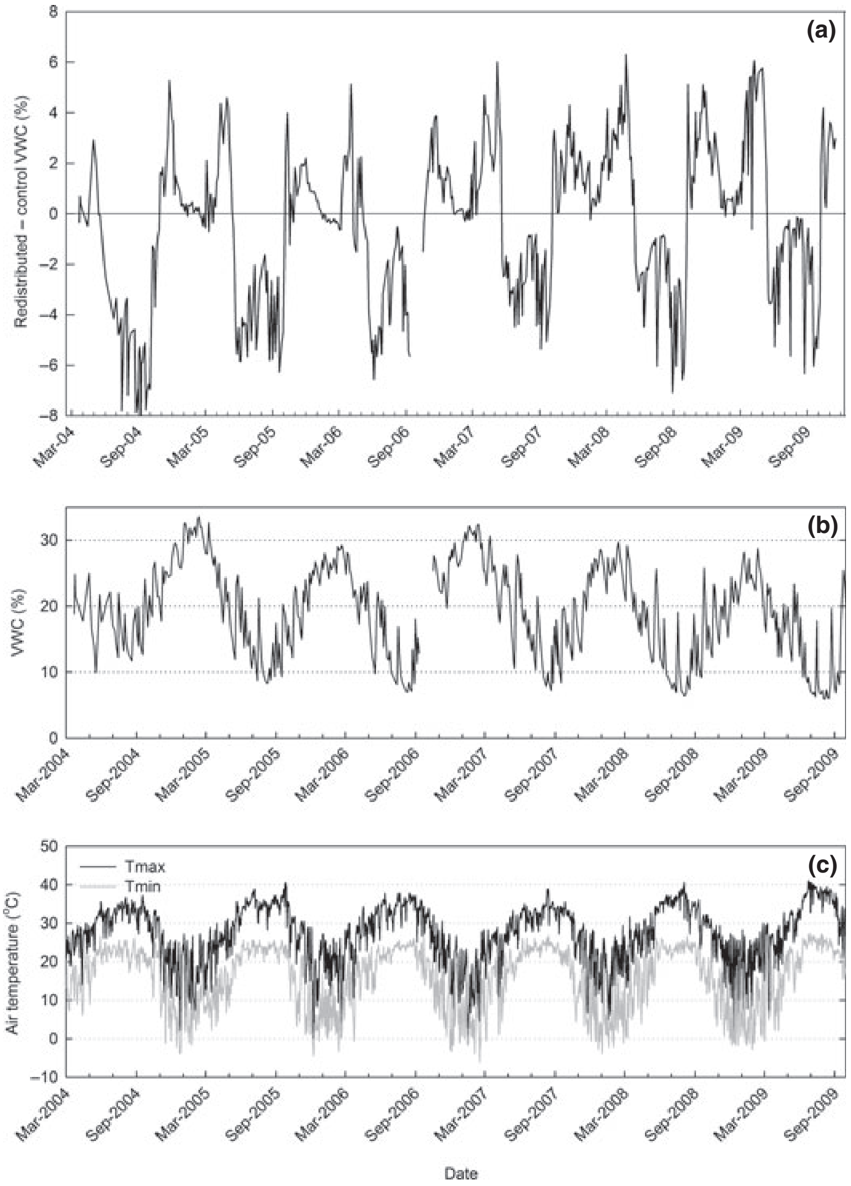

Fig. 2 (a) Absolute difference in mean soil volumetric water content between redistributed precipitation plots and control precipitation plots (0–20 cm depth). Precipitation treatments are as described in Fig. 1. (b) Soil volumetric water content in the control precipitation treatment. There is a gap in October 2006 due to instrument failure. (c) Daily maximum and minimum air temperatures at Easterwood airport in College Station (<0.5 km from the site) during the experimental period.

precipitation redistribution and increased by warming, but importantly, the combined effects of warming and precipitation treatment on growth were modified by grass presence (Table 1). The positive effect of warming on RGR disappeared in the redistributed precipitation treatment in *J. virginiana* grown with *S. scoparium*. Overall, RGR was 26% greater for *J. virginiana* grown with *S. scoparium* (1.29 mg g^{-1} day^{-1}) than when grown in monoculture (1.02 mg g^{-1} day^{-1}; Fig. 3; Table 1). However, there was a clear shift in tree–grass interactions during this 6-year study. In each of the first 2 years of the experiment (2004 and 2005), mean RGR of *J. virginiana* grown in monocultures was greater than that for trees grown with *S. scoparium*; however, in the third and fourth year (2006 and 2007), RGR of trees grown with *S. scoparium* exceeded those grown in monocultures. Overall, RGR of *J. virginiana* grown in monocultures showed a declining trend from 2004 until 2007 prior to thinning (Fig. 3a–d) as trees grew larger in monoculture than with grass, while there was no such decline in RGR of trees grown with grass.

For *Q. stellata*, precipitation and warming treatment effects on mean RGR over the 6-year study were interactive and the effect of precipitation distribution

Table 1 Precipitation redistribution (P), warming (W), and grass competition (SC) effects on relative growth rate (RGR) of *Juniperus virginiana* and *Quercus stellata* trees during a 6-year period (2004–2009). Standing mass of individual trees through time was ln transformed and ANOVA was used to test treatment effects. RGR is the slope of ln mass plotted against time and thus significant interactions with time (T) denote significant treatment effects on RGR (Poorter & Lewis, 1986). Data are plotted in Figs 3 and 4. *P*-values <0.05 are printed in bold. Model fit; *J. virginiana*: $r^2 = 0.498$, RMSE = 0.824, $P < 0.001$, *Q. stellata* $r^2 = 0.722$, RMSE = 1.259, $P < 0.001$

	J. virginiana		*Q. stellata*	
Effect	*F* Ratio	*P*	*F* Ratio	*P*
P × T	3.88	**0.049**	0.94	0.333
W × T	6.81	**0.009**	0.01	0.916
P × W × T	0.21	0.650	9.60	**0.002**
SC × T	34.3	**<0.001**	5.93	**0.015**
P × SC × T	3.11	0.078	6.55	**0.011**
W × SC × T	6.23	**0.013**	1.77	0.183
P × W × SC × T	5.35	**0.021**	0.00	0.978

was modified by the presence of grass ($P_{\text{precipitation} \times \text{warming} \times \text{time}} = 0.002$, $P_{\text{precip} \times \text{species combination} \times \text{time}} = 0.011$, Fig. 4f). Precipitation redistribution reduced *Q. stellata* RGR when grown with grass (from 2.5 mg g^{-1} day^{-1} to 2.2 mg g^{-1} day^{-1}), but not in monocultures (from 2.8 mg g^{-1} day^{-1} to 2.9 mg g^{-1} day^{-1}). Likewise, warming did not affect RGR in *Q. stellata* monocultures (2.7 mg g^{-1} day^{-1} in each treatment), but reduced RGR when grown with grass (from 2.5 mg g^{-1} day^{-1} to 2.2 mg g^{-1} day^{-1}). At the end of the study, surviving trees were larger on average in monocultures than in mixtures (406 g vs. 68 g, $P = 0.033$). Among individual years, there was a negative effect of *S. scoparium* on RGR of *Q. stellata* in 2004 when the oaks were still small.

By the end of the study, *Q. stellata* had experienced considerable mortality while only a single *J. virginiana* died during the experiment. Mortality of *Q. stellata* was much greater when grown in monoculture than when grown with *S. scoparium* (Fig. 5a and b, $P < 0.001$). On average, only 25% of *Q. stellata* saplings in the monocultures survived to the end of the 6-year study compared with 71% of those grown with *S. scoparium*. Warming further reduced survival of *Q. stellata* grown in monocultures ($P_{\text{warming} \times \text{species combination}} = 0.089$), while precipitation treatment had no effect on mortality, although the redistributed and warmed plots had the lowest survivorship overall.

Throughout the 6-year study, the presence of *S. scoparium* positively affected RGR of *J. virginiana* in the spring, particularly in the control precipitation treatment (Fig. 6a, $P_{\text{species combination}} = 0.012$, $P_{\text{precip} \times \text{species combination}} = 0.070$). Despite the evergreen leaf habit of *J. virginiana*, we found no evidence that warming enhanced *J. virginiana* RGR more during the cooler seasons than during the summer (Fig. 6). In the summer, in the redistributed (dry) precipitation treatment, warming resulted in increased RGR of *J. virginiana* in monoculture, but this was not the case when juniper was grown with grass ($P_{\text{species combination} \times \text{precipitation} \times \text{warming}} = 0.087$, Fig. 6b). In autumn, *J. virginiana* RGR was lowest in the monocultures in the control precipitation treatment, regardless of warming, while RGR was highest in monocultures in the redistributed (wet) precipitation treatment, but warming strongly reduced RGR in monocultures in the redistributed treatment ($P_{\text{species combination} \times \text{precipitation} \times \text{warming}} = 0.065$, Fig. 6c). In contrast with *J. virginiana*, *Q. stellata* showed no effect of treatments on seasonal RGR.

Grass growth, survival, and response to trees

Mean tiller number of individual *S. scoparium* plants attained a maximum in April of each year and then declined as the growing season progressed (Fig. 7). Mean tiller number per plant increased initially; however, during the third year of treatment (June 2006), there was a long-term decrease in tiller numbers for *S. scoparium* plants grown with *J. virginiana*. Total tiller number declined to the greatest extent when *S. scoparium* was grown in combination with *J. virginiana*, regardless of precipitation treatment (Fig. 7c). Peak tiller numbers in spring of the final 2 years of study were reduced in *S. scoparium* grown with *J. virginiana* ($P_{\text{species combination}} < 0.001$); however, declines in peak tiller numbers were mitigated in redistributed precipitation treatment ($P_{\text{species combination} \times \text{precipitation}} < 0.05$), where additional springtime precipitation enhanced tiller production. In contrast, the presence of *Q. stellata* either increased peak tiller number (2005 and 2007, $P \leq 0.011$) or had no effect on tiller number or seasonal dynamics compared with the grass monoculture (Fig. 7e).

Precipitation redistribution delayed the proportion of tillers that became reproductive in every year and reduced the peak proportion of tillers that became reproductive in 2005 and 2008 ($P \leq 0.031$). The proportion of reproductive tillers decreased sharply in 2008 when *S. scoparium* was grown with *J. virginiana* ($P = 0.008$) and no reproductive tillers were produced in 2009 when *S. scoparium* was grown with *J. virginiana* in either precipitation treatment (Fig. 7d).

After 6 years of exposure to these climate scenarios, survival of *S. scoparium* plants was 89% and 92% for plants grown in monoculture and those grown with

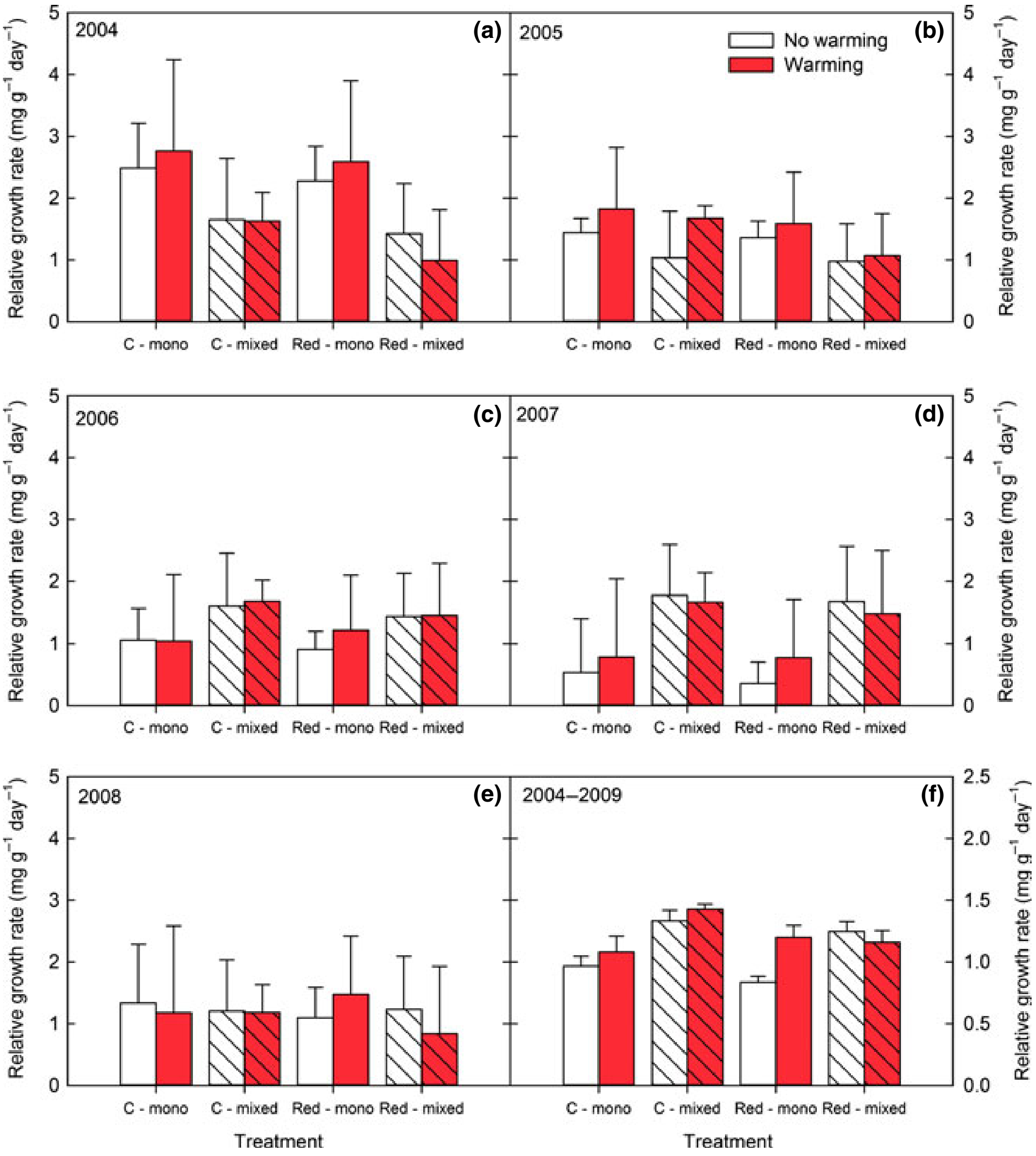

Fig. 3 (a–e) Mean annual relative growth rate (RGR) for aboveground dry mass of *Juniperus virginiana* as affected by precipitation distribution [control (C), redistributed (Red)], warming (closed bars), and species mixture (monoculture: open bars; combination with *Schizachyrium scoparium*: hatched bars). (f) Mean RGR over the entire 6-year experiment. Each treatment year ran from March 1 to March 1. In 2009, measures ended September 30. Monocultures had 25 trees until December 2007 when tree density per plot was reduced to 13 trees, tree–grass mixed plots had 13 trees throughout. Thin bars are standard errors. Statistics: 2004: $P_{\text{species combination}} = 0.006$; 2005: n.s.; 2006: n.s.; 2007: $P_{\text{species combination}} = 0.019$; 2008: n.s. Thin bars are standard error. Statistical analyses for 2004–2009 are shown in Table 1.

Q. stellata, respectively, but only 27% when grown in combination with *J. virginiana* (Fig. 5c). Survival of *S. scoparium* plants grown with *J. virginiana* declined rapidly after March 2007 during the third year of treatment, when mean height of *J. virginiana* trees grown in the mixed plots reached 1100 mm (and an aboveground dry mass equivalent of 480 g, Fig. 5d) exceeding mean height of the grass canopy.

Discussion

Tree responses to climatic drivers

We had expected that all species, but especially trees, in our experiment would have shown a reduction in aboveground RGR and/or survival in response to summer warming, when soil water is the most limiting,

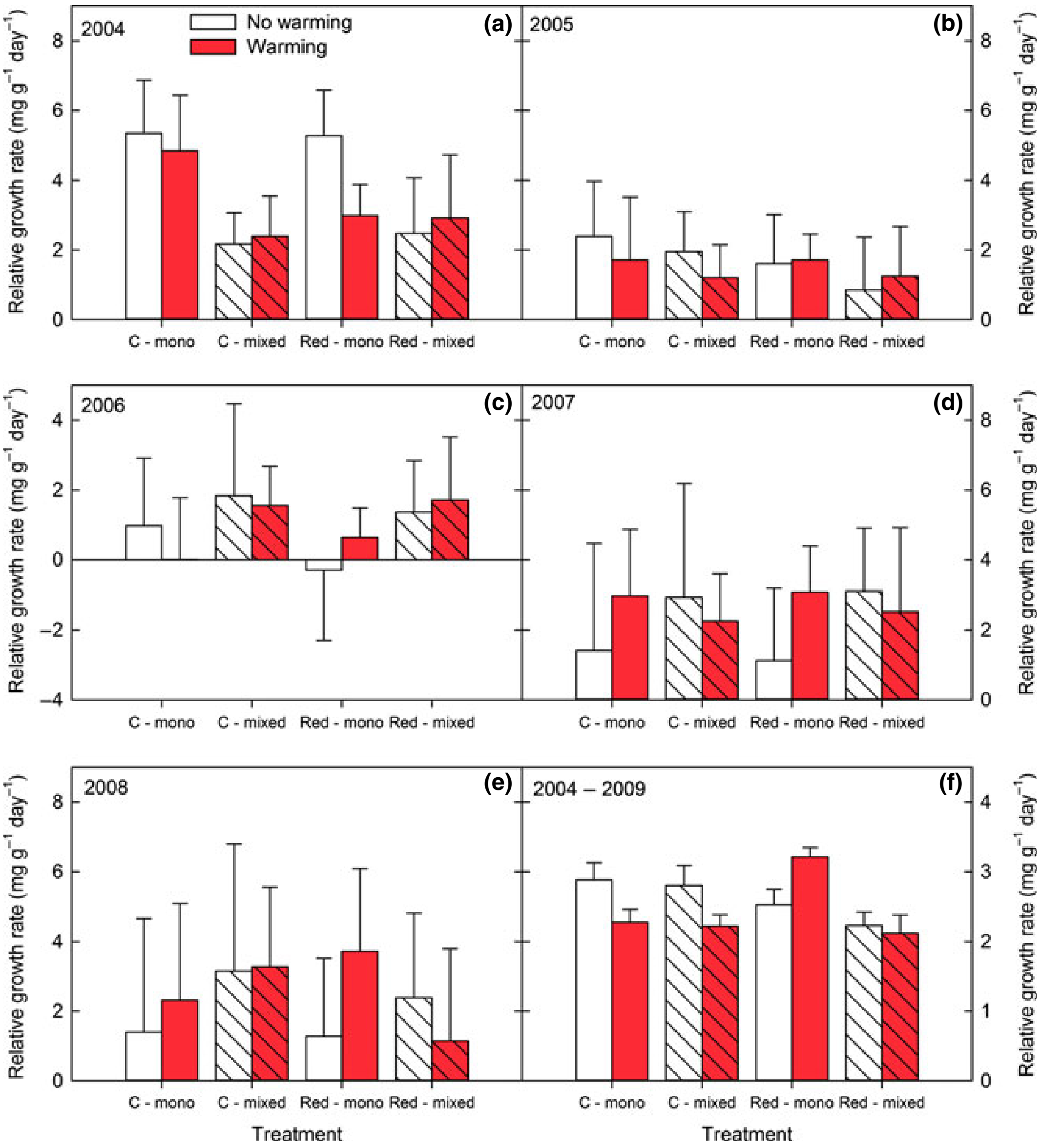

Fig. 4 (a–e) Mean annual relative growth rate (RGR) for aboveground biomass of *Quercus stellata* as affected by precipitation distribution [control (C), redistributed (Red)], warming (closed bars) and species mixture (monoculture: open bars; combination with *Schizachyrium scoparium*: hatched bars). (f) Mean RGR over the entire 6-year experiment. Each treatment year ran from March 1 to March 1. In 2009 measures ended September 30. Statistics: 2004: $P_{\text{species combination}} < 0.001$; 2005: n.s.; 2006: n.s.; 2007: n.s.; 2008: n.s. Thin bars are standard errors. Statistical analyses for 2004–2009 are shown in Table 1.

particularly in the redistributed precipitation treatment where summer precipitation (from May to September) was reduced 40% compared with the long-term mean in each of six successive years. We ascribe the absence of direct precipitation treatment effects on plant growth to the well-developed drought tolerance of all three species (Ni & Pallardy, 1991; Axmann & Knapp, 1993; Pallardy & Rhoads, 1993) and the already severe summer water limitation that is characteristic of this region (July and August are the warmest and driest months; Fig. 1). Although the absence of a significant effect of intensified drought on RGR of *Q. stellata* provides evidence of its drought tolerance (Parker & Pallardy, 1988; Ward & Nixon, 1992), the high mortality of *Q. stellata* plants in response to the combined warming and redistribution treatment indicates that it was less drought tolerant than *J. virginiana,* which exhibited no drought-related mortality. Similarly, *J. monosperma* has been shown to survive a historic drought in the southwestern USA due to its ability to maintain hydraulic

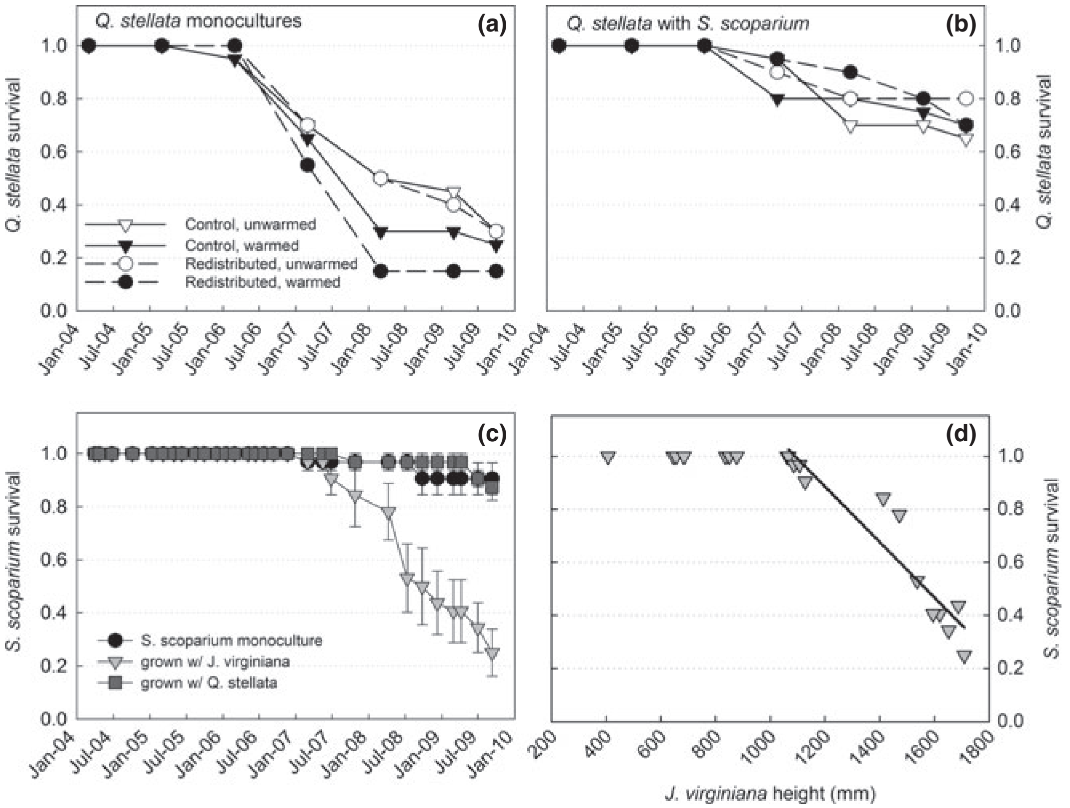

Fig. 5 (a) Survival of *Quercus stellata* seedlings grown in monoculture or (b) in a mixture with *Schizachyrium scoparium*. Triangles are *Q. stellata* subjected to a control precipitation pattern while circles are *Q. stellata* subjected to a redistributed precipitation pattern. Open symbols are *Q. stellata* growing in unwarmed plots while closed symbols are *Q. stellata* growing in warmed plots (n = 20 trees). (c) Survival of *S. scoparium* grown in monoculture or with *Juniperus virginiana* or *Q. stellata*, Means (±SE) across warming and precipitation distribution treatments are shown (n = 32 plants). $P_{\text{species combination}} < 0.001$, using a parametric survival test ($\chi^2 = 45.4$). (d) Survival of *S. scoparium* plants grown with *J. virginiana* in relation to *J. virginiana* height.

conductivity while tolerating very negative xylem pressures (Breshears *et al.*, 2005). This enabled *J. monosperma* to continue to extract some soil water during the severe drought, retain partial stomatal opening, and maintain a positive carbon balance. Data on leaf gas exchange and water potential collected on our site by Volder *et al.* (2010) suggest that *J. virginiana* may exhibit a similar physiological tolerance to drought as described for *J. monosperma*.

Warming induced substantial oak mortality while juniper saplings showed no mortality and positive growth responses to warming suggesting that warming will benefit *J. virginiana* growth and establishment. Increased mortality of *Q. stellata* in response to warming could be associated with enhanced tissue respiration rates, supraoptimal temperatures for photosynthesis, and direct damage to thermo-sensitive cellular components (Sage & Kubien, 2007). Another explanation for oak mortality could be that warming enhanced transpiration rates and water stress that caused stomatal closure which may have led to drought-induced mortality due to carbon starvation (McDowell *et al.*, 2011). Although warming induced substantial oak mortality in our experiment, future increases in atmospheric CO_2 concentration may partially alleviate negative summer responses to warming by enhancing water-use efficiency and prolonging soil water availability to promote plant growth (Albert *et al.*, 2011).

Tree–grass interactions were dynamic throughout the investigation, even though our experiment minimized variability in both intra- and interannual precipitation. We anticipated that the abiotic environment of both trees and grasses would be modified in response to increasing tree height and canopy volume as tree growth progressed. For example, over the course of the 6-year study, the already low soil water contents during summer exhibited a declining trend in the controls (Fig. 2). Increased tree canopy size likely led to increased transpiration and/or canopy interception, resulting in drier soil and perhaps intensifying competition for water. At the same time, increasing tree height

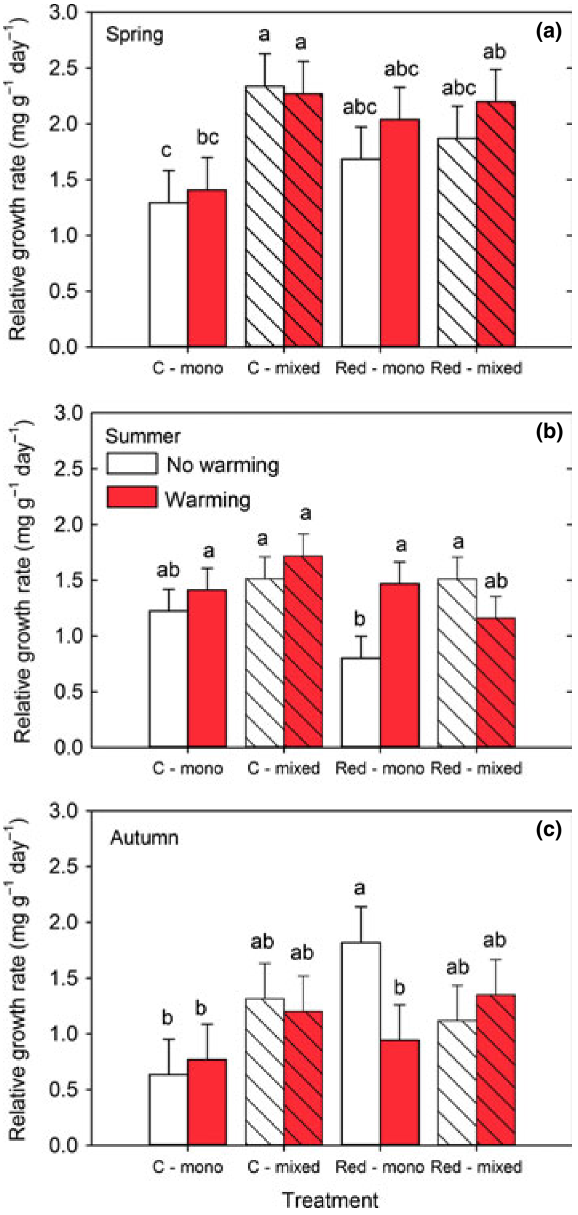

Fig. 6 Seasonal relative growth rate averaged across 6 years for *Juniperus virginiana* as affected by precipitation distribution [control (C), redistributed (Red)], warming (closed bars) and species mixture (monoculture: open bars; combination with *Schizachyrium scoparium*: hatched bars). (a) Spring, (b) Summer, and (c) Autumn. Winter RGR was generally not different from zero or affected by treatment or species mixture and is not shown for brevity. Note that in spring and autumn, trees grown in the redistributed treatment received 52% more precipitation, while in summer they received 40% less precipitation. Statistical tests: (a) $P_{\text{species combination}} = 0.012$, $P_{\text{precip} \times \text{species combination}} = 0.070$, (b) $P_{\text{species combination}} = 0.098$, $P_{\text{species combination} \times \text{warming}} = 0.095$, $P_{\text{species combination} \times \text{precipitation} \times \text{warming}} = 0.087$, (c) $P_{\text{precip} \times \text{species combination}} = 0.057$, $P_{\text{species combination} \times \text{precipitation} \times \text{warming}} = 0.065$. Presented are least-square means and SEM. Different letters indicate significant differences between means at $P < 0.05$ as indicated by a Student's *t*-test.

also elevated tree canopy position and modified the radiative environment of the grass. Consequently, increased canopy cover and drier soils are likely reflected in the declining trend in soil surface warming (but not canopy warming) through time (Fig. S2). This indicates that precipitation redistribution had the greatest effect on soil water availability in the early years of the experiment and diminished thereafter. In addition, younger trees may respond differently to water limitation or drought than older trees (Donovan & Ehleringer, 1991; He *et al*., 2005).

Grass responses to climatic drivers

New tiller production possessed sufficient plasticity to track shifts to early season (March–April) precipitation in the redistribution treatments. Growth of new tillers is more responsive to changes in resource availability than either tiller height, mass, or density, as has been demonstrated with this grass species (Butler & Briske, 1988; Derner & Briske, 1999). The proportion of reproductive tillers decreased by a minimum of 13% in response to precipitation redistribution in all years except 2007. We anticipate that this direct response to precipitation occurred because *S. scoparium* is a long-day plant that initiates inflorescence development during mid-summer (late June–early July at low latitudes) which is coincident with intensification of summer drought in the precipitation redistribution treatment.

Delivery of comparable amounts of annual precipitation as fewer, but larger events reduced soil water availability to reduce aboveground production, particularly of the subdominant C_4 grass species, in a mesic grassland in Kansas (Knapp *et al.*, 2002; Fay *et al.*, 2003, Heisler-White *et al*., 2008). The number of reproductive tillers of the dominant C_4 grass, *Andropogon gerardii*, was not reduced during a drought year receiving only 60% of the long-term mean precipitation. However, in the same drought year, the number of reproductive tillers in the subdominant C_4 grass *Sorghastrum nutans* was reduced by approximately 20% compared with years with normal rainfall, regardless of rainfall pattern (Fay *et al*., 2003). This reduction in reproductive output is similar to the reduction that we observed for *S. scoparium*. Although intensified summer drought suppressed sexual reproduction in *S. scoparium*, the perenniality of long-lived grasses originates from the annual production of new tillers from axillary buds of existing tillers (Briske & Butler, 1989; Welker & Briske, 1992; Dalgleish & Hartnett, 2006). The phenotypic plasticity of new tiller development in *S. scoparium* coupled with considerable drought tolerance of meristematic tissues (Hendrickson & Briske,

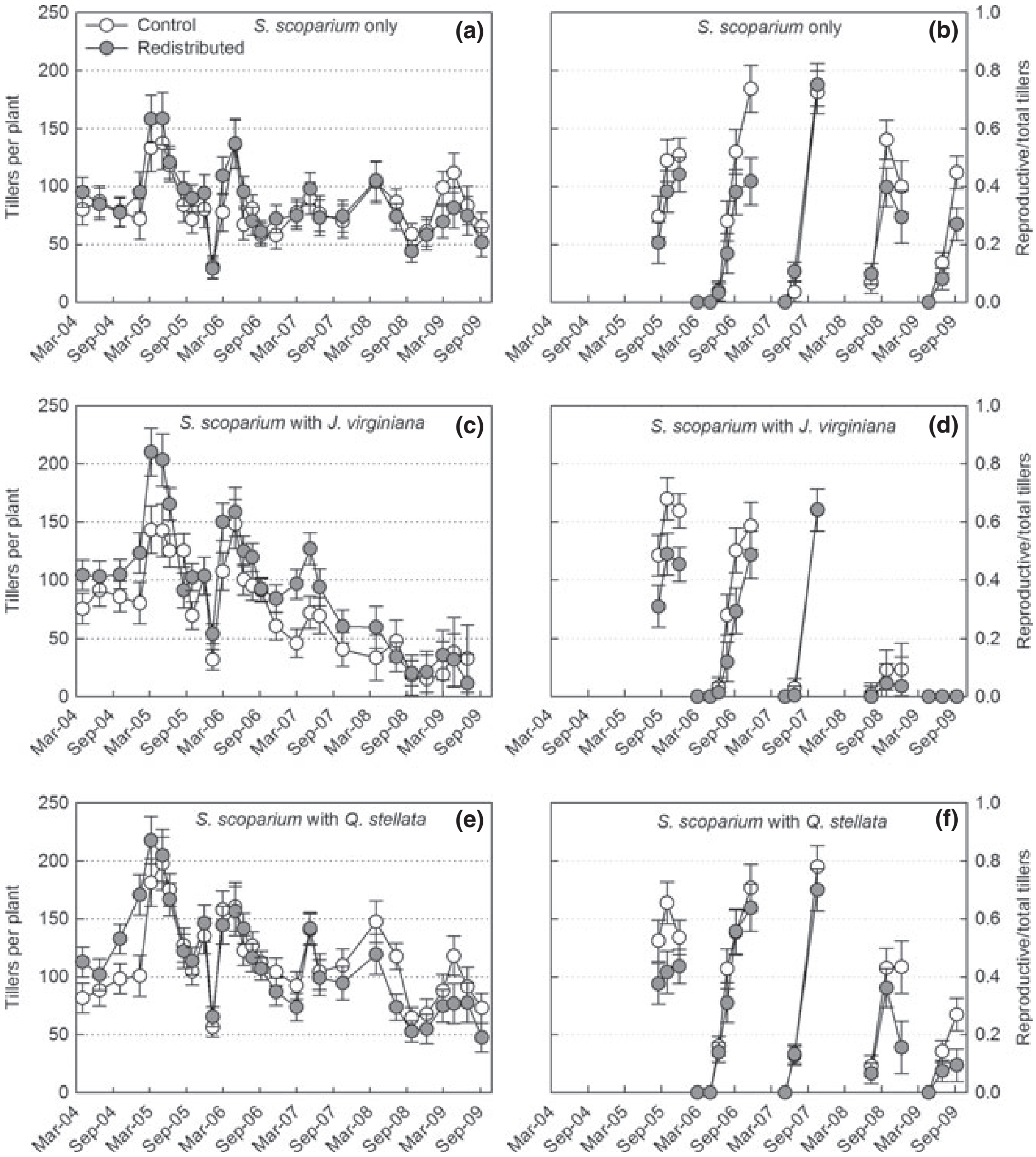

Fig. 7 Mean number of tillers (a, c, e) and proportion of reproductive tillers (b, d, f) per *Schizachyrium scoparium* plant throughout the 6-year experiment as affected by plot species composition and precipitation distribution. Open symbols are control precipitation pattern while closed symbols indicate the redistributed precipitation pattern. (a, b) *Schizachyrium scoparium* monoculture; (c, d) mix with *Juniperus virginiana*; (e, f) mix with *Quercus stellata*. Data are averaged across warming treatments, means ± SE, *n* = 4.

1997) forms the basis for the persistence of this grass species in warm climates with dry summers. Therefore, a decrease in seed production, even on a frequent basis, may not adversely affect persistence of these grass populations in the short term (Gatsuk *et al*., 1980; Welker & Briske, 1992). However, severe multiyear drought can induce mortality of both grass tillers and plants to reduce net primary production and potentially contribute to modified species composition (Knapp & Smith 2002; Dalgleish & Hartnett, 2006; Yahdjian & Sala 2006.)

Tree–grass interactions

Schizachyrium scoparium live tiller count and survival were strongly reduced in the presence of *J. virginiana*. At the end of the experiment, *S. scoparium* survival was approximately 90% when grown in monoculture or in combination with *Q. stellata*, but it declined to 27% when grown with *J. virginiana*. The proportion of reproductive tillers was higher when *S. scoparium* was grown with either tree species rather than in monoculture for the initial 4 years, especially in the redistributed precipitation treatment, but it then decreased rapidly when grown with either tree species the final 2 years. The intensification of both above- and belowground competition for light, nutrients, and physical space with increasing tree size contributed to the dramatic suppression of the grass when grown with *J. virginiana.* Given that the climate change treatments were imposed after a 1-year period and that the *J. virginiana* seedlings were 1.5 years old when planted, a period of approximately 5 years was required for *J. virginiana* to attain a competitive advantage and suppress *S. scoparium*. A comparable time period was required for *Prosopsis glandulosa* to attain a competitive advantage in native grasslands of central Texas (Brown & Archer, 1999; Jurena & Archer, 2003) and *Q. emoryi* was observed to require more than 3 years to escape the competitive effect of native grasses in oak woodlands of Arizona (Weltzin & McPherson, 2000). These data suggest that a warmer climate with intensified summer drought will accelerate the rate at which juniper will attain a competitive advantage over the grass. After 6 years of treatment, the final aboveground biomass of *J. virginiana* was 21% higher at 940 g for trees grown in the warmed, redistributed precipitation treatment compared with 780 g for trees grown under ambient temperatures and the control precipitation distribution.

Collectively, these results substantiate the importance of competitive interactions in mediating climate change drivers (Gilman *et al.*, 2010; Jeffers *et al.*, 2011), the occurrence of substantial temporal dynamics in these interactions (Leuzinger *et al.*, 2011), and the potential for unique responses by individual plant species to the same climate drivers (Chapin, 2003; Poorter & Navas, 2003; Evans *et al.*, 2011). For example, tree–grass interactions had much greater effects on tree survival and growth than did the direct effects of warming and precipitation redistribution. In cases where the climate change drivers did have significant direct effects, they varied temporally as tree growth modified the outcome of competitive interactions with the grass. Tiller number per grass plant was relatively unaffected by warming and intensified summer drought, but sexual reproduction of this grass was substantially reduced by the precipitation redistribution treatment. These results identify the magnitude and temporal patterns of tree–grass interactions in savanna systems and thereby support the overriding importance of competitive interactions and shifts in functional composition (Hoeppner & Dukes, 2012) in mediating climate change effects (Brooker, 2006; Tylianakis *et al.*, 2008; Gilman *et al.*, 2010) These temporal dynamics provide another potential mechanism for the occurrence of 'effect size dampening' with increasing treatment duration and complexity of climate change experiments (Leuzinger *et al.*, 2011).

Implications for southern oak savanna

How may a future climate characterized by warmer temperatures and intensified summer drought affect the composition and structure of southern oak savanna? The most striking result from this investigation is the ability of *J. virginiana* to tolerate both warming and intensified drought, both in monoculture and when grown with grass. This will likely provide juniper with a substantial competitive advantage in projected future climates relative to both the grass and oak. Nevertheless, the dominant grass *S. scoparium* will initially persist in a warmer climate with intensified summer drought, albeit with less aboveground production and reproductive output, because of its ability to shift tiller production to earlier seasons of the year in these low latitude savannas. However, as *J. virginiana* establishment and density in savannas increases, it is clear that *S. scoparium* will be quickly outcompeted by *J. virginiana* and its dominance will decline. The persistence of a C_4 grass component is critical to the integrity of this oak savanna ecosystem for two distinct reasons. First, our data show that grass has an important role in facilitating oak survival, growth, and establishment during the first several years of growth. In turn, grass survival is higher when grown with oak than with juniper presumably because it experiences a reduced intensity of interspecific competition when grown with the oak, even when heights of established trees surpass that of the grass canopy. Therefore, a reduction in either oak or grass abundance will likely feedback to further reduce abundance of the other species and enhance juniper establishment and dominance. In contrast, the presence of grass did not adversely affect juniper survival and only reduced juniper growth in the first 2 years after which juniper growth was enhanced when grown with grass. Second, grasses provide the fine fuel necessary to carry fires that have the capacity to kill *J. virginiana*, especially when the trees are less than 2 m high (7-years growth in this experiment) and when fine fuel loads exceed 3000 kg ha^{-1} (Briggs & Gibson, 1992; Ortmann *et al.*, 1998; Briggs *et al.*, 2002b). In addition, an increasing incidence of wildfire may suppress this fire-sensitive juniper species as the climate becomes both warmer and drier (Pechony & Shindell, 2010). The size and frequency of wildfires are most strongly correlated with existing drought condition (i.e., Palmer drought severity index) and with wetter than normal conditions in May and August of the previous year (Westerling *et al.*, 2006).

These data strongly suggest that *J. virginiana* will attain a competitive advantage over the two current codominant species in a warmer climate characterized by a precipitation shift from summer to spring and fall.

Consequently, juniper invasion will very likely increase in the southern oak savanna under these projected future climatic conditions. Although juniper–oak competition was not investigated in this experiment, evidence does exist to suggest that juniper has the ability to overtop and outcompete established oaks in the absence of fire (Rykiel & Cook, 1986; Briggs *et al*., 2002b; DeSantis *et al*., 2011). This clearly emphasizes that the reintroduction of frequent fire regimes is a critical determinant of the continued existence of southern oak savannas in future climatic scenarios (Peterson & Reich, 2001; Briggs *et al*., 2002a,b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. (a) Plot (2 × 2 m) layout within an individual rainout shelter. Warming treatments [control (gray) and heated (red)] were randomly assigned within each shelter to each of five planted species combinations (*Quercus stellata* monoculture, *Juniperus virginiana* monoculture, grass monoculture and both tree-*Schizachyrium scoparium* combinations, data not shown). Four shelters received the control precipitation distribution treatment, while four shelters received a redistributed precipitation pattern (see Materials and Methods). (b) Configuration and spacing of the plants within each 2 × 2 m plot. Each species monoculture had 25 individuals, while the two tree–grass plots had 12 *S. scoparium* (white circles) and 13 trees (black circles). (c) Aerial view of the eight experimental shelters.

Figure S2. (a) Soil temperature at 3 cm depth over time, gray line = control, red line = warmed plots. (b) Mean difference in soil surface temperature (3 cm depth) between warmed and control plots. The effect of warming was averaged over five species combinations and two precipitation treatments in a subset of instrumented plots ($n = 10$). Red regression line indicates an overall declining trend in soil surface warming over the course of the 6-year study: Response to warming = 0.48 − 0.00027 × number of days, $r^2 = 0.137$, $P < 0.001$.

Figure S3. Aboveground dry mass growth of *Juniperus virginiana* through time in response to precipitation redistribution or warming in monoculture (a, c) and when grown with *Schizachyrium scoparium* (b, d). Least-square means of natural log transformed masses ±SE are shown averaged across either warming (a, b, $n = 4$ plots) or precipitation (c, d) treatments ($n = 8$ plots).

Figure S4. Aboveground dry mass growth of *Quercus stellata* through time in response to precipitation redistribution or warming in monoculture (a, c) and when grown with *Schizachyrium scoparium* (b, d). Least-square means of natural log transformed masses ±SE are shown averaged across either warming (a, b, $n = 4$ plots) or precipitation (c, d) treatments ($n = 8$ plots) for surviving plants at the end of study.