

Woody plant encroachment facilitated by increased precipitation intensity

Andrew Kulmatiski^{1*} and Karen H. Beard²

Global circulation models and empirical evidence suggest that precipitation events are likely to become more extreme across much of the globe^{1,2}. As most plant roots are in shallow soils^{3–5}, small but pervasive changes in precipitation intensity could be expected to cause large-scale shifts in plant growth, yet experimental tests of the effects of precipitation intensity are lacking^{6–9}. Here we show that, without changing the total amount of precipitation, small experimental increases in precipitation intensity can push soil water deeper into the soil, increase aboveground woody plant growth and decrease aboveground grass growth in a savannah system. These responses seemed to reflect the ability of woody plants to increase their rooting depths and competitively suppress grass growth. In many parts of the world, woody plant abundance has multiplied in the past 50–100 years, causing changes in fire, forage value, biodiversity and carbon cycling¹⁰. Factors such as fire, grazing and atmospheric CO₂ concentrations have become dominant explanations for this woody encroachment and semi-arid structure in general^{10–12}. Our results suggest that niche partitioning is also an important factor in tree-grass coexistence and that the woody plant encroachment observed over the past century may continue in the future should precipitation intensity increase.

Although global circulation models project that precipitation will increase in some parts of the world and decrease in others, a more widespread projection is that precipitation intensity will increase while annual precipitation will remain largely unchanged^{1,2}. Despite the pervasiveness of this projection, little is known about how plant communities respond to fewer, larger precipitation events^{6–8}. This is an important gap in understanding because in the coming decades terrestrial productivity, agricultural production, hydrologic cycles, fire regimes and feedbacks between the biosphere and atmosphere are likely to be determined, in part, by how plant communities respond to fewer, larger precipitation events^{6,13,14}.

Semi-arid systems, such as grasslands, shrublands and savannahs (that is, systems where the ratio of precipitation to potential evapotranspiration (P/PET) is less than ~0.5; Supplementary Table ST1), cover over 30% of Earth's surface, produce 30–35% of terrestrial annual net primary productivity (ANPP), and support 30% of human populations and most livestock^{8,13,15}. Observational data show that productivity in semi-arid systems has been highly sensitive to the timing and amount of annual precipitation^{8,15,16}. Semi-arid systems have also realized a pronounced change in composition with woody plant abundance multiplying two to ten times over the past 50 years in many areas^{10–12}. This woody plant encroachment has been attributed to increased fire suppression, increased

atmospheric CO₂ concentrations and increased grazing^{11,12,17,18}. Climate change, particularly changes in precipitation patterns, has also been suggested as a potential explanation for woody encroachment, but experimental tests are lacking^{11,12,17,18}.

Larger precipitation events can be expected to change semi-arid and arid plant communities in different ways depending on site conditions^{8,14,18,19}. In arid grasslands, very slight increases in precipitation intensity may benefit grasses if there is a decrease in the amount of water lost to interception and evaporation and an increase in shallow soil water availability (that is, 0–15 cm; refs 5,20). However, fewer, large precipitation events are also likely to increase the amount of time between events, creating drier surface soils^{1,2,8}. This is likely to decrease the growth of plants that rely on shallow soil water (for example, grasses)⁸. Furthermore, increasing precipitation intensity may push soil water to the slightly deeper depths (that is, below 15 cm) used by woody plants^{3–5,21,22}. As it is conceptually likely that increasing precipitation intensity will increase productivity in some sites (that is, arid sites and sites with woody plants) but decrease productivity other sites (that is, semi-arid sites and sites without woody plants), experimental tests are needed to understand how different systems will respond^{6–8}.

Many experiments have investigated how increases or decreases in mean annual precipitation affect herbaceous and woody ecosystems¹⁴. Only a small number of multi-year experiments have investigated how increases in precipitation intensity affect plant communities, and all of these studies have been conducted in one fairly mesic North American grassland^{6,8,23}. These studies found that large increases in precipitation intensity decrease shallow soil moisture and grassland ANPP (ref. 24). Single-season studies in more mesic European²⁵ and Canadian²⁶ grasslands have shown similar results. However, single-season studies in arid North American grasslands found that ANPP increased with precipitation intensity (Supplementary Table ST1)²⁰. Although results from this limited number of studies are consistent with our conceptual understanding of water use in arid and semi-arid grasslands, several recent articles have stressed the need for new experiments in sites outside North American temperate grasslands^{6–8}. Perhaps more importantly, these articles have also highlighted the need to test the effects of increasing precipitation intensity in woody ecosystems because these common ecosystems are likely to respond differently to changes in precipitation than grasslands^{6–8}.

We investigated the effect of three years of increased precipitation intensity on woody plant and grass growth using six large (8 m × 8 m) rainout shelters in a sub-tropical savannah ecosystem, Kruger National Park, South Africa. In contrast to previous studies that have intercepted all precipitation^{20,23}, we created a less extreme treatment²⁴ in which 50% of ambient precipitation fell on treated

¹Department of Plants, Soils and Climate and the Ecology Center, Utah State University, Logan, Utah 84322-4820, USA, ²Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322-5230, USA. *e-mail: andrewkulmatiski@hotmail.com

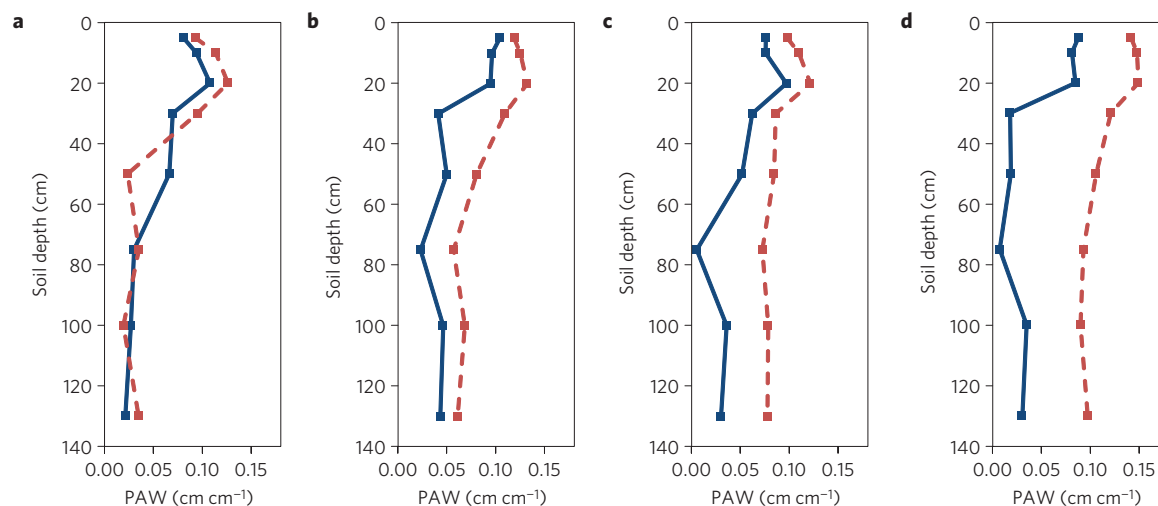


Figure 1 | Plant available water in control plots (blue symbols) and plots receiving fewer, larger precipitation events (treated; red symbols). **a–d.** Growing season plant available water (PAW) shown by soil depth before treatment installation (**a**) and during growing seasons ending in 2009 (**b**), 2010 (**c**) and 2011 (**d**). Soil water was assumed to be plant available when soil water potentials were greater than -2.5 MPa.

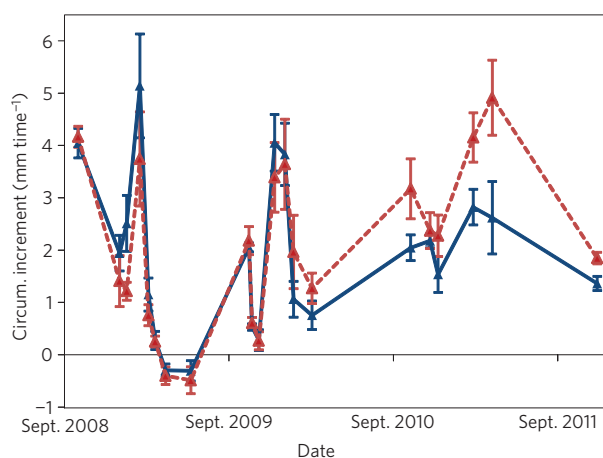


Figure 2 | Woody plant growth in control plots (blue symbols) and plots receiving fewer, larger precipitation events (red symbols). Values represent the circumference increment (Circum. increment) of woody plant stems since the last measurement in millimetres. Error bars are ± 1 s.e.m.

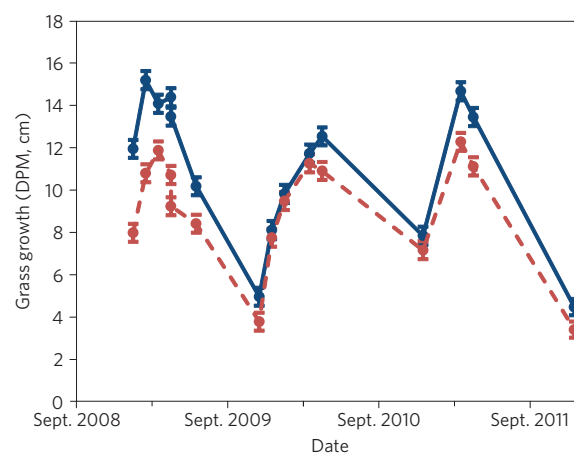


Figure 3 | Grass height in control plots (blue symbols) and plots receiving fewer, larger precipitation events (red symbols). Grass height was measured using a DPM. DPM measurements have been well correlated with grass biomass²⁹. Error bars are ± 1 s.e.m.

plots and the remaining 50% was collected with translucent roofing and released as moderately large 10-mm events (that is, 66% of daily precipitation values were <10 mm; Supplementary Figs S1 and S2). To be clear, treatments re-distributed ambient precipitation as large, intense precipitation events; treatments did not change the total amount of annual precipitation. Measurements made under these shelters were compared with measurements made in six control plots that received no treatment.

Ambient precipitation during the first, second and third years of the study was 94, 124 and 100% of the long-term mean annual precipitation (544 mm), respectively (Supplementary Fig. S3). The coefficient of variation of daily precipitation (CVDP) was used as a measure of precipitation variability and intensity²⁷. Between 1933 and 2005, the growing season (November to June) CVDP at the study site was 3.73 ± 0.96 (s.d.). During the 2008/2009, 2009/2010 and 2010/2011 growing seasons, treatments increased the CVDP from 3.10 to 3.40, 3.38 to 3.38 and 3.37–3.58, respectively. Treatment effects were greater in years when ambient precipitation occurred as many small events because precipitation from these small events was stored in tanks for release during a subsequent precipitation event, whereas precipitation from large events was

stored and released the same day as ambient precipitation. Treatment effects were small relative to historical variability and relative to previous studies that have increased the CVDP, for example, from 3.1 to over 4.5 (ref. 27).

Despite having relatively small effects on the CVDP, increased precipitation intensity quickly increased soil water availability and infiltration (Fig. 1). Recent research in Kruger National Park suggests that grasses and woody plants partition soil water resources over very short vertical distances, with grasses relying on soil water in the top 0–15 cm and woody plants relying on soil water in the 15–30 cm depths, with little uptake by any plants below 60 cm (refs 4,21). Soil moisture measurements, therefore, indicated that fewer, larger precipitation events pushed water through the very shallow soil depths that have been associated with grass root activity and into the deeper soil depths that have been associated with woody plant root activity^{4,21}. Consistent with results from these studies, woody plant growth was greater in plots with increased precipitation intensity (Fig. 2). There was no difference in the circumference increment of woody plants in treated and control plots at the beginning of the experiment ($F_{1,10} = 0.51$, $P = 0.49$). However, by the end of the three years, circumference

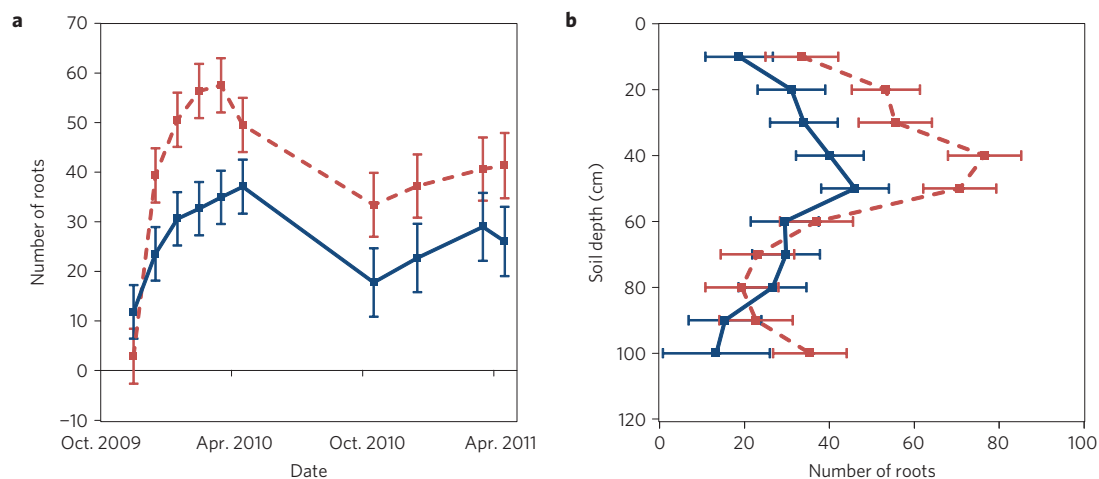


Figure 4 | The number of roots observed in control plots (blue symbols) and plots receiving fewer, larger precipitation events (red symbols). **a,b**, Root numbers shown over time (**a**) and across the top 100 cm of soil across all sampling periods (**b**). Error bars are ± 1 s.e.m.

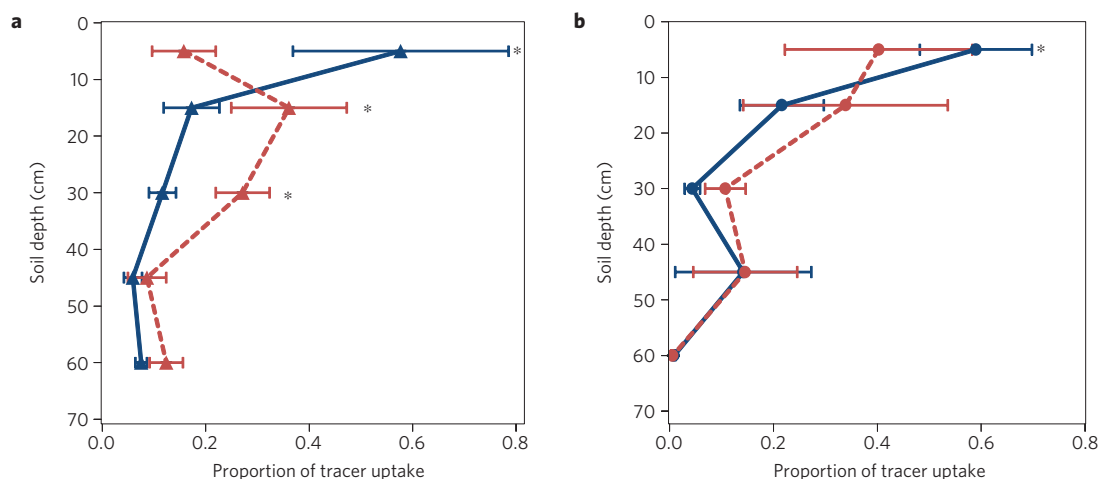


Figure 5 | Plant tracer uptake by depth in control plots (blue symbols) and plots receiving fewer, larger precipitation events (red symbols). Results shown for woody plants (**a**) and grasses (**b**). Asterisks indicate differences in the proportion of tracer uptake for a plant type at the indicated depth. Error bars are ± 1 s.e.m.

increments were greater with increased precipitation intensity (Fig. 2; treatment \times time interaction: $F_{19,181} = 1.72$, $P = 0.037$).

In contrast to woody plant growth, grass growth decreased with increased precipitation intensity. At the beginning of the experiment there was no difference in grass production (measured as grass height using a disc pasture meter (DPM)) between control (4.4 ± 0.2 cm) and increased precipitation intensity plots (4.2 ± 0.2 cm; $F_{1,10} = 0.59$, $P = 0.461$), but grass production was lower with increased precipitation intensity during the experiment (Fig. 3; treatment \times time: $F_{13,130} = 3.08$, $P < 0.001$). Measurements of grass biomass harvested at the end of the second and third growing seasons supported grass production measurements; there was less grass biomass with increased precipitation intensity (123 ± 10 g m $^{-2}$ in 2010 and 98 ± 4 g m $^{-2}$ in 2011) than in control plots (133 ± 10 g m $^{-2}$ in 2010 and 135 ± 9 g m $^{-2}$ in 2011; treatment: $F_{1,10} = 7.25$; $P = 0.023$; time and treatment \times time were not significant). Providing observational support for experimental results, grass production was lowest in the year with the most variable precipitation (that is, 2009/2010) even though total annual precipitation was greatest in that same year (Fig. 3). This suggested that grass growth was more sensitive to the variation in precipitation than to the total amount of precipitation during that year.

To try to explain why aboveground woody growth increased and aboveground grass growth decreased in response to increasing precipitation intensity, we measured root growth and root activity. At the beginning of the second season, the first season for which we have measurements, there was no difference in the number of roots at the beginning of the season but with increased precipitation intensity plants quickly produced more roots, especially in the 20–50 cm depths (Fig. 4; treatment \times time: $F_{9,630} = 8.61$, $P < 0.001$). This flush of deep roots was consistent with the deeper and more flexible rooting strategies observed in woody plants^{4,5}, but root images could not distinguish woody from grass roots. Similarly, root images could not be used to determine whether woody plants relied on an inherently deeper rooting strategy or whether they created deeper roots in response to treatments.

To distinguish woody from grass root activity, we measured woody plant and grass uptake of a hydrological tracer that was injected to five soil depths (5, 15, 30, 45 and 60 cm). As the tracer could be injected only to one depth in each plot and only six treated plots were available, results describe root activity in the treated and control plots and do not provide inference across the landscape. In response to increased precipitation intensity, woody plants decreased shallow (that is, 5 cm) tracer uptake and increased deeper (that is, 15 and 30 cm) tracer uptake whereas grasses, on the other

hand, did not increase deeper tracer uptake (Fig. 5; treatment \times depth: $F_{4,80} = 6.75$; $P < 0.001$, depth \times plant type: $F_{4,80} = 2.81$; $P = 0.031$). Woody plants, therefore, demonstrated a more flexible rooting strategy that allowed greater access to the deeper soil water that became available with greater rainfall intensity.

We found that small shifts towards fewer, larger precipitation events pushed soil water below narrow, shallow rooting zones used by grasses and into deeper soils that woody plants were better able to exploit^{4,5,22}. Our results suggest that increases in grass productivity in response to increasing precipitation intensity may not be as widespread as previously thought^{8,15,20} because where present, woody plants are likely to respond to increasing rainfall intensity by increasing rooting depth, accessing more soil water, increasing aboveground growth and competitively suppressing grass growth. Although factors such as fire, grazing and CO₂ fertilization have been incorporated into dynamic global vegetation models as primary factors determining woody abundance^{11,12,17}, our results demonstrate that root niche partitioning can be another important mechanism under present and changing climate conditions. The effects of woody plant encroachment can be quite variable but typical responses include increased carbon and nitrogen storage, increased evapotranspiration, decreased plant diversity and decreased land value for grazers, such as zebra or cattle¹⁰. The present research demonstrates how even small increases in precipitation intensity may encourage these changes in arid and semi-arid systems in the coming decades.

Methods

Experimental design. Research was conducted in the Cape Buffalo enclosure near the Satara rest camp, Kruger National Park, South Africa, which has been described elsewhere^{22,28}. Using 13.3-cm-wide strips of transparent polycarbonate roof²², six precipitation manipulation shelters (8 m \times 8 m \times 2.5 m tall) were installed at the end of the 2007/2008 growing season. Shelters collected half of ambient precipitation in four sealed, 200 l barrels. The barrels contained a tethered, floating outlet that collected water until the barrels were full, at which point the floating outlet would sink, and release a 1-cm precipitation event in about five minutes. This water was released through irrigation hoses that were suspended 1 m above ground.

Shelters were slightly warmer (25.5–25.7°C), drier (71.6–70.6% relative humidity) and received less light (25.9 versus 24.3 MJ m⁻² d⁻¹) than control plots. This resulted in a nominal decrease in evapotranspiration from 301 to 299 mm between December and April as estimated using a Penman–Monteith model (Supplementary Methods). Soil water potential (Campbell Scientific 229 heat dissipation sensors) was measured bi-hourly in one pair of shelter and control plots and values were converted to estimates of plant available water, assuming that soil water was plant available when water potentials were greater than –2.5 MPa (ref. 4).

Woody plants. Woody plant circumference was measured on 4–5 plants (2–7-cm diameter) in each plot using small-diameter dendrometer bands (Agricultural Electronics). Changes in circumference between sampling dates is reported as growth increment in millimetres. Species information is provided in the Supplementary Methods.

Grasses. DPM (ref. 29) measurements were made at each of 40 points in each treated and control plot (Supplementary Methods). At the end of each growing season, all grass in each plot was clipped and weighed in the field. A wet-to-dry weight conversion was determined by drying at least 10 grab samples (500–200 g) from each plot to constant weight at 60°C.

Roots. During each sampling period, 50 root images were taken from inside a 2-m-long, 5-cm-wide plastic tube that was installed at a 30° angle (that is, to a depth of about 1 m)³⁰ in each treated and control plot. Images were taken at $\times 15$ using a BTC-100x video microscope camera (Bartz Technology). Root number was measured by hand using Rootfly software (Birchfield and Wells, Clemson University).

D₂O tracer experiment. The proportion of water uptake by treatment, plant type and soil depth was determined using a hydrologic tracer (70% deuterium oxide) experiment^{4,5}. Into each point in a 15 cm \times 15 cm grid, tracer was injected to one of five depths (5, 15, 30, 45 and 60 cm)⁴ in 10 treatment and control plots. Two days later, five composited grass and five composited woody plant samples from

each treated or control plot were collected. Water from these samples was analysed for deuterium and ¹⁸O concentrations using a stable isotope analyser (Picarro Instruments) at the University of Alaska Anchorage^{4,5}.

Data analysis. A generalized linear mixed model was used to test for pre-treatment differences in abiotic factors, woody plant stem circumference increment growth and DPM measurements between shelter and control plots. After the start of the experiment, generalized linear mixed models were used to test for treatment effects through time on woody plants (dendrometer data, with a square-root transformation) and grasses (DPM and biomass). The effects of treatment at depth through time on summarized root data were assessed using a generalized linear mixed model. For analyses of the proportion of tracer uptake, a generalized linear mixed model with a beta distribution and logit link was used to evaluate treatment, depth, plant type, and their interactions. All models assumed compound symmetry covariance structures for repeated measures in time and/or depth. Post-hoc pairwise mean comparisons were made to detect differences by plant type, treatment and depth using the false discovery rate method to adjust *P* values for type I error. Descriptive statistic means ± 1 standard error are presented throughout. For more details, see Supplementary Methods.

Received 3 October 2012; accepted 17 April 2013 ; published online 26 May 2013

References

- Easterling, D. *et al.* Climate extremes: Observations, modeling, and impacts. *Science* **289**, 2068–2074 (2000).
- Frich, P. *et al.* Observed coherent changes in climatic extremes during the second half of the twentieth century. *Clim. Res.* **19**, 193–212 (2002).
- Schenk, H. J. & Jackson, R. B. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *J. Ecol.* **90**, 480–494 (2002).
- Kulmatiski, A. & Beard, K. H. Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia* **171**, 25–37 (2013).
- Kulmatiski, A., Beard, K. H., Verweij, R. J. T. & February, E. C. A depth-controlled tracer technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savanna. *New Phytol.* **188**, 199–209 (2010).
- Beier, C. *et al.* Precipitation manipulation experiments—challenges and recommendations for the future. *Ecol. Lett.* **15**, 899–911 (2012).
- Reyer, C. *et al.* A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability. *Glob. Change Biol.* **19**, 75–89 (2013).
- Knapp, A. K. *et al.* Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience* **58**, 811–821 (2008).
- Porporato, A., Daly, E. & Rodriguez-Iturbe, I. Soil water balance and ecosystem response to climate change. *Am. Nat.* **164**, 625–632 (2004).
- Eldridge, D. J. *et al.* Impacts of shrub encroachment on ecosystem structure and functioning: Towards a global synthesis. *Ecol. Lett.* **14**, 709–722 (2011).
- Buitenwerf, R., Bond, W. J., Stevens, N. & Trollope, W. S. W. Increased tree densities in South African savannas: >50 years of data suggests CO₂ as a driver. *Glob. Change Biol.* **18**, 675–684 (2012).
- Wigley, B. J., Bond, W. J. & Hoffman, M. T. Thicket expansion in a South African savanna under divergent land use: Local versus global drivers? *Glob. Change Biol.* **16**, 964–976 (2010).
- Grace, J., José, J. S., Meir, P., Miranda, H. S. & Montes, R. A. Productivity and carbon fluxes of tropical savannas. *J. Biogeogr.* **33**, 387–400 (2006).
- Wu, Z., Dijkstra, P., Koch, G. W., Pañuelas, J. & Hungate, B. A. Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Glob. Change Biol.* **17**, 927–942 (2011).
- Knapp, A. K. *et al.* Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* **298**, 2202–2205 (2002).
- Good, S. P. & Caylor, K. K. Climatological determinants of woody cover in Africa. *Proc. Natl Acad. Sci. USA* **108**, 4902–4907 (2011).
- Scheiter, S. & Higgins, S. I. Partitioning of root and shoot competition. *Am. Nat.* **170**, 587–601 (2007).
- Walker, B. H. & Noy-Meir, I. In *Tropical Savannas* (eds Huntley, B. J. & Walker, B. H.) 556–590 (Springer, 1982).
- Sala, O. E., Lauenroth, W. K. & Parton, W. J. Long-term soil water dynamics in the shortgrass steppe. *Ecology* **73**, 1175–1181 (1992).
- Heisler-White, J. L., Blair, J. M., Kelly, E. F., Harmon, K. & Knapp, A. K. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Glob. Change Biol.* **15**, 2894–2904 (2009).
- February, E. C. & Higgins, S. I. The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. *South Afr. J. Bot.* **76**, 517–523 (2010).
- February, E. C., Higgins, S. I., Bond, W. J. & Swemmer, L. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology* **94**, 1155–1164 (2013).

23. Fay, P. A. *et al.* Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. *Biogeosciences* **8**, 3053–3068 (2011).
24. Nippert, J. B., Knapp, A. K. & Briggs, J. M. Intra-annual rainfall variability and grassland productivity: Can the past predict the future? *Plant Ecol.* **184**, 65–74 (2006).
25. Walter, J. *et al.* Increased rainfall variability reduces biomass and forage quality of temperate grassland largely independent of mowing frequency. *Agr. Ecosyst. Environ.* **148**, 1–10 (2012).
26. Laporte, M., Duchesne, L. & Wetzal, S. Effect of rainfall patterns on soil surface CO₂ efflux, soil moisture, soil temperature and plant growth in a grassland ecosystem of northern Ontario, Canada: Implications for climate change. *BMC Ecology* **2**, 10 (2002).
27. Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M. & Collins, S. L. Productivity responses to altered rainfall patterns in a C-4-dominated grassland. *Oecologia* **137**, 245–251 (2003).
28. Venter, F. J., Scholes, R. J. & Eckhardt, H. C. in *The Kruger Experience* (eds du Toit, J., Rogers, K. & Biggs, H.) 83–129 (Island Press, 2003).
29. Zambatis, N., Zacharias, P. J. K., Morris, C. D. & Derry, J. F. Re-evaluation of the disc pasture meter calibration for the Kruger National Park. *Afr. J. Range For. Sci.* **23**, 85–97 (2006).
30. Hendricks, J. J. *et al.* Assessing the patterns and controls of fine root dynamics: An empirical test and methodological review. *J. Ecol.* **94**, 40–57 (2006).

Acknowledgements

We thank the Andrew Mellon Foundation, Alaska EPSCOR and the University of Alaska Anchorage's Environment and Natural Resources Institute for financial support, South African National Parks for allowing us to do this research in Kruger, and E. February, W. Bond and the University of Cape Town for the shelters. Field managers: M. Cooper, M. Mazzacavallo, M. Keretetsi, S. Heath and L. Hierl. Field/laboratory assistants: W. Sibuye, R. Mashele, V. Sibuye and M. Rogers. Statistical advice: S. Durham. Experiments complied with the present laws of the Republic of South Africa. This research was supported by the Utah Agricultural Experiment Station, Utah State University, and approved as journal paper number 8538.

Author contributions

A.K. and K.H.B. conceived the research, oversaw measurements, analysed data and contributed to the preparation of the manuscript.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to A.K.

Competing financial interests

The authors declare no competing financial interests.