Enhanced precipitation variability decreases grass- and increases shrub-productivity

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Although projections of precipitation change indicate increases in variability, most studies of impacts of climate change on ecosystems focused on effects of changes in amount of precipitation, overlooking precipitation variability effects, especially at the interannual scale. Here, we present results from a 6-y field experiment, where we applied sequences of wet and dry years, increasing interannual precipitation coefficient of variation while maintaining a precipitation amount constant. Increased precipitation variability significantly reduced ecosystem primary production. Dominant plant-functional types showed opposite responses: perennial-grass productivity decreased by 81%, whereas shrub productivity increased by 67%. This pattern was explained by different nonlinear responses to precipitation. Grass productivity presented a saturating response to precipitation where dry years had a larger negative effect than the positive effects of wet years. In contrast, shrubs showed an increasing response to precipitation that resulted in an increase in average productivity with increasing precipitation variability. In addition, the effects of precipitation variation increased through time. We argue that the differential responses of grasses and shrubs to precipitation variability and the amplification of this phenomenon through time result from contrasting root distributions of grasses and shrubs and competitive interactions among plant types, confirmed by structural equation analysis. Under drought conditions, grasses reduce their abundance and their ability to absorb water that then is transferred to deep soil layers that are exclusively explored by shrubs. Our work addresses an understudied dimension of climate change that might lead to widespread shrub encroachment reducing the provisioning of ecosystem services to society.

ANPP | precipitation | interannual variability | plant-functional types | nonlinear response

Climate-change simulations project increases in precipitation variability as a result of global warming (1–3). The frequency of large precipitation events is expected to increase (3, 4), even in regions where precipitation will decrease (5). Similarly, the occurrence of wet days will decrease, resulting in a highly variable climate with enhanced probabilities of drought and heavy rainfall (5). Precipitation change will occur at intra-, interannual, and decadal scales. Mechanisms explaining such changes differ among temporal scales. At short-time scales, high precipitation variation results from the increased water-holding capacity of a warmer atmosphere that yields large rainfall events interspaced with droughts (6). At the interannual and decadal scales, climate change results in enhanced precipitation variability resulting from changes in atmospheric circulation that affect multiyear rainfall patterns (7).

Although precipitation variability changes are part of the public narrative (8) and motivated a special Intergovernmental Panel on Climate Change (IPCC) report on extreme events (9), our understanding of the effect of climate variability on the carbon cycle in grasslands is still weak (10). Aboveground net primary production (ANPP) is the main carbon fixation pathway, and even though its responses to changes in the amount of precipitation have been well studied, knowledge about the effect of precipitation variability on ANPP is rather poor, especially at the interannual to decadal time scales. A few short-term experiments focused on the effect of intra-annual precipitation variance and reported contrasting results, with null or positive effects in arid systems and negative effects in mesic systems (11–14). A modeling exercise found that increased interannual precipitation variability and temperature in the Tibetan Plateau led to productivity reduction in grasslands (15). Therefore, long-term manipulative experiments are needed to understand ecosystem responses to changes in resource amount and variability (16) at multiyear time scales.

Here, we aimed at assessing the effect interannual variability of precipitation on ecosystem functioning. Two hypotheses guided our work. (*i*) Increased interannual precipitation variation may increase, decrease, or have null effect on ANPP, depending on the shape of the productivity response to precipitation. Increased interannual precipitation variability implies sequences of relatively extreme dry and wet years. If the ANPP response to annual precipitation is linear, increased precipitation variance will result in a null effect on mean multiyear ANPP because the decline caused by dry years is compensated by ANPP increases in wet years. On the other hand, nonlinear responses result in either positive or negative effects of precipitation variation on ANPP (17). For example, an increasing ANPP response to annual precipitation leads to positive effects of precipitation variability because the ANPP decline caused by dry years is overcompensated by the nonlinear ANPP increase resulting from wet years. A decreasing response results in negative response to precipitation variability because the positive effect of wet years does not compensate dry-year ANPP decreases (18). (*ii*) The effect of enhanced interannual precipitation variation increases through time. The duration of increased precipitation variability periods may lead to hierarchical ecosystem responses (19). We expect that physiological responses

Significance

Although increased climatic variability resulting from climate change has been accepted by the scientific community and forms part of the public narrative, studies of the effect of climatic variability on ecosystems have received much less attention than effects of changes in the mean state of climate. Here, we report on a field experiment where we experimentally increased interannual variability of precipitation while maintaining average precipitation constant. Our results indicated that total productivity and that of grasses declined in response to increased precipitation variability, although shrubs benefited, suggesting a potential shift from grassland to shrubland in the future, with large consequences for the supply of ecosystem services. In addition, the effect of variability increased through time.

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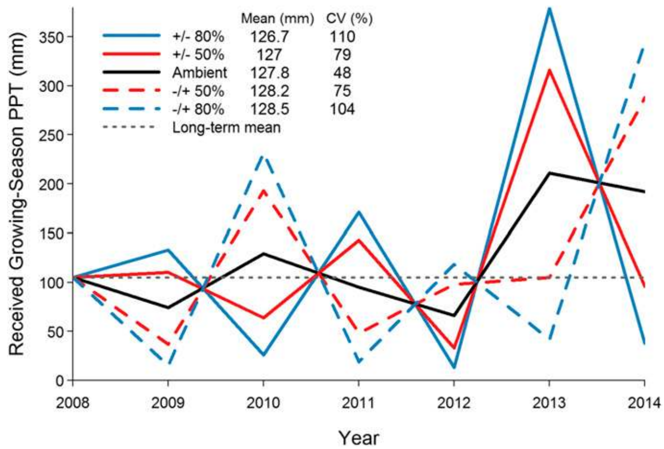


Fig. 1. Growing-season precipitation per treatment, including five different levels of precipitation manipulation: +80%, +50%, ambient, −50%, and −80%, all relative to ambient precipitation, resulting in five levels of precipitation variability. Treatments were switched every year from wet to dry and dry to wet. Colors indicate different precipitation variability enhancement: red corresponds to 50%, blue to 80%, and black to ambient precipitation. Solid lines indicate 50% and 80% treatments starting from irrigation, and dashed lines 50% and 80% treatments starting from drought. The gray dotted line indicates the long-term mean growing-season precipitation for reference. (*Inset*) The legend indicates mean and coefficient of variation for growing-season precipitation for each treatment received during the 6 y of the experiment, showing that precipitation mean stayed constant among treatments and the precipitation coefficient of variation varied from 48% to 110%.

to enhanced precipitation variability will occur sooner than changes in plant-community composition. As the duration of the enhanced precipitation-variability treatments increases, different mechanisms enter into play amplifying the ecosystem response. We envision that plants that share common physiological and ecological characteristics may, as a group, respond differently to enhanced precipitation variability than other groups; and that the ecosystem response corresponds to the abundance-weighed response of the individual groups. These groups of plant species, which in our case were defined based on their dominance, are dominant perennial grasses (i.e., *Bouteloua eriopoda*), shrubs (i.e., *Prosopis glandulosa*), and rare species, which include forb, annual-grass, and subshrub species. The rare-species group represents, on average, a very small fraction of the ANPP, although it hosts a large fraction of the plant diversity.

We used an automated rainfall manipulation system (20) to experimentally manipulate interannual coefficient of variation of precipitation while keeping average annual precipitation constant. We applied sequences of wet and dry years on 50 2.5-m × 2.5-m experimental plots during 6 y in a Chihuahuan Desert Grassland. The first year of the experiment started with five levels of rainfall manipulation, ranging from enhanced by irrigation (+80% and +50%, relative to ambient) to reduced rainfall by rainout shelters (−50% and −80%, also relative to ambient) plus a control (ambient). During the second year, plots that received water addition in the first year received a drought treatment of the same proportion, and plots that received drought during the first year received water addition treatment of the same proportion (−50% plots were inverted to +50%, +50% to −50%, −80% to +80%, and +80% plots to −80%). The third, fourth, fifth, and sixth years received alternations of first- and second-year manipulations (Fig. 1). These treatments significantly altered soil moisture patterns (Fig. S1) and precipitation coefficient of variation, but received virtually the same average precipitation during the 6-y period (Fig. 1, *Inset*). Our experimental design aimed at exploring the sensitivity of the ecosystem. Unlike studies of a specific climate-change scenario, our approach provides a response surface applicable to many projected changes in precipitation variance that might occur at different points in time.

Our results offered strong experimental evidence demonstrating that interannual precipitation coefficient of variation has a negative effect on ANPP (Fig. 2*A* and *SI Appendix, Statistical Analysis Description and Summary Output*). The precipitation variability effect on total ANPP resulted from a strong negative response of dominant grasses (Fig. 2*B*) that was not fully compensated by a weak positive response of shrubs (Fig. 2*C*) or the null response of rare species (Fig. 2*D*). The mechanism explaining the 6-y mean ANPP responses to the precipitation coefficient of variation resulted from the shape of the ANPP response to the precipitation amount. We assessed the shape of the relationship between growing-season precipitation and ANPP by fitting linear, second-order polynomial and quadratic models. We chose the best-model fit through Akaike's and Bayesian information criteria (*SI Appendix, Statistical Analysis Description and Summary Output*). Total ANPP presented a saturating response to precipitation where dry years had a larger negative effect on ANPP than the positive effect of wet years (Fig. 3*A*). Therefore, this 6-y-long sequence of wet and dry years reduced total ANPP. Furthermore, this ecosystem response resulted from the aggregation of responses of the individual plant groups (Fig. 3*B* and *SI Appendix, Statistical Analysis Description and Summary Output*). Dominant perennial grasses also showed a strongly decreasing response of ANPP to growing-season precipitation, where extremely dry years reduced productivity and wet years increased productivity but less than proportionally. Grass ANPP for the wettest growing season was of similar magnitude as ANPP of years that received precipitation amounts similar to the long-term average (105 mm) (Fig. 3*B*). In contrast, shrubs showed a weak increasing response to growing-season precipitation (Fig. 3*B*), indicating that dry years had a minor effect on shrub ANPP but wet years resulted in a relatively larger ANPP increase. This response may explain the positive but also weak effect of interannual precipitation variation on this plant-functional type. Finally, the rare-species group showed a strong linear relationship to growing season precipitation (Fig. 3*B*), explaining the nonsignificant response to the precipitation coefficient of variation because effects of dry years were offset by effects of wet years. During dry years, rare-species ANPP was close to zero, but during wet years this group of species produced large ANPP pulses that doubled that of shrubs. These results provide a mechanism of the ecosystem-level response to precipitation variability and highlight the differential response of the dominant group of plant species and the importance of functional diversity for ecosystem functioning.

Our results showed a significant amplification through time of the ecosystem response to interannual precipitation variability, supporting the second hypothesis (Fig. 4*A*). A single wet-to-dry or dry-to-wet transition did not show a significant effect on total ANPP, even to our most severe manipulation (Fig. 1). Results from the first 2 y, including a single transition for each treatment through years 2009 and 2010, agree with a previous experiment that showed that the negative effect of a previous-dry year on current-year ANPP was of the opposite sign but of the same magnitude as the positive effect of a previous-wet year on current-year ANPP (21). The effects of single dry-to-wet and wet-to-dry transitions cancelled each other and predicted null effects of interannual precipitation variation on average ANPP. The effects of these single-year transitions have been called "precipitation legacies" and represent the effect of an event after it has occurred (22). We discounted legacy effects from our results using the legacy quantifications calculated for this site (22) and reran our analyses. We obtained the same result of amplification of the variability effect through time (Fig. S2 and *SI Appendix,*

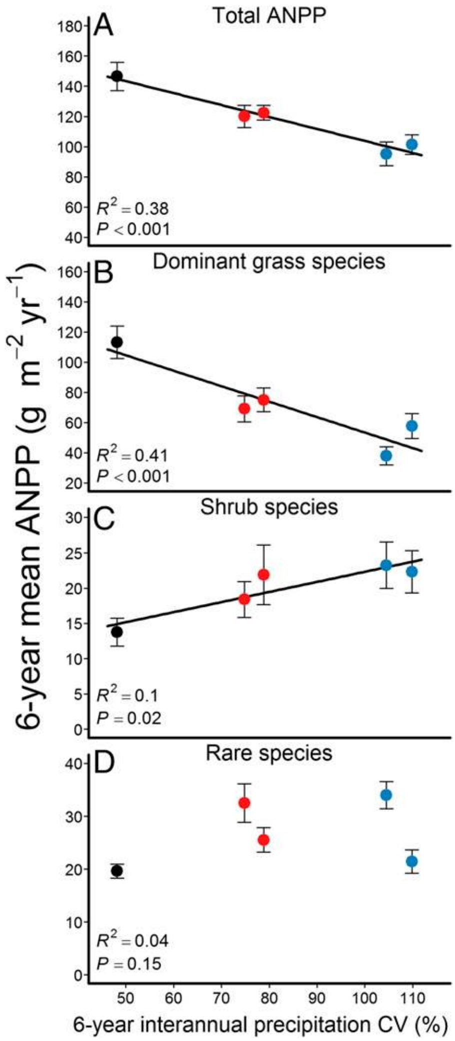


Fig. 2. Effects of interannual precipitation coefficient of variation on ANPP. Six-year mean ANPP as a function of precipitation coefficient of variation for (*A*) total, (*B*) dominant grass, (*C*) shrub, and (*D*) rare species ANPP. Points indicate mean values (±SE) for each treatment (n = 10). Different colors indicate treatments following Fig. 1.

Statistical Analysis Description and Summary Output). The amplification of ecosystem response through time resulted from chronic increased interannual precipitation variability not from the effect of the legacies of previous-year precipitation. Analyses of repeated measures resulted in significant time-by-treatment interaction, showing an increase in the effect of precipitation variability through time, even when annual precipitation was included as a covariate to account for the effect of differences in precipitation among years (*SI Appendix*, *Statistical Analysis Description and Summary Output*). A split analysis for the first and last 3 y of the experiment, which have different ambient annual-precipitation sequences, also supported our conclusion of amplified responses through time (*SI Appendix*, *Statistical Analysis Description and Summary Output*). In synthesis, our results provided strong evidence for amplifying ecosystem response to chronic increase in interannual precipitation variability.

The ANPP difference between the highest variability treatments and the ambient precipitation treatment increased from 16 $g \cdot m^{-2} \cdot yr^{-1}$ at the beginning of the experiment to 107 $g \cdot m^{-2} \cdot yr^{-1}$ at the end of 6 y of treatment. We hypothesize that the response of ANPP to increased interannual precipitation variability is amplified through time because of the gradual engagement of different hierarchical mechanisms (20). First, only physiological responses are involved, followed by changes in the abundance of organisms and finally changes in community composition. Existing work in arid ecosystems showed that increased intra-annual precipitation variability resulted in nonsignificant ANPP differences but significant physiological adjustments through changes in photosynthesis and leaf-water potential (12, 23). At a slightly larger temporal scale, responses to single-year precipitation variability had significant changes in meristem density (24). Our results complemented previous studies and showed novel responses at a multiyear time scale. We argue that the temporal scale of different climatic phenomena controls the type of ecological responses observed from plants and populations to communities and ecosystems.

The response through time to precipitation variability was different for grasses, shrubs, and rare species (Fig. 4 and *SI Appendix*, *Statistical Analysis Description and Summary Output*). Grasses showed a treatment effect consistently significant from

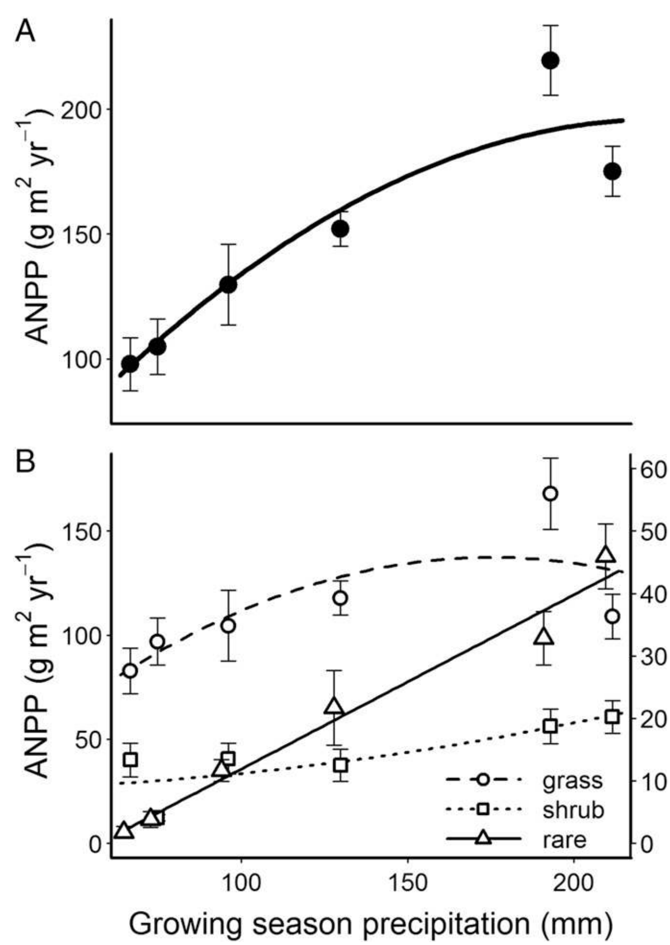


Fig. 3. Annual ANPP response to growing-season precipitation in ambient precipitation plots for different plant types. Symbols indicate annual mean (±SE, n = 10) for (*A*) total ANPP and (*B*) dominant grass, shrub, and rare (forb, annual grass, and subshrub species) species ANPP. Lines indicate best fit between ANPP and growing-season precipitation according to Akaike Information Criterion and Bayesian Information Criterion (*SI Appendix*, *Statistical Analysis Description and Summary Output*). In *A*, the solid line corresponds to total ANPP [total ANPP = (1.73 × PPT) − (0.004 × PPT2)]. In *B*, dashed line and open circles correspond to dominant grass ANPP [grass ANPP = (1.58 × PPT) − (0.004 × PPT2)], dotted line and open squares to shrubs [shrub ANPP = 8.51 + (0.0003 × PPT2)] and solid line and open triangles to rare species [rare ANPP = −16 + (0.28 × PPT)]. The right-hand side axis indicates ANPP for shrub and rare species.

ECOLOGY

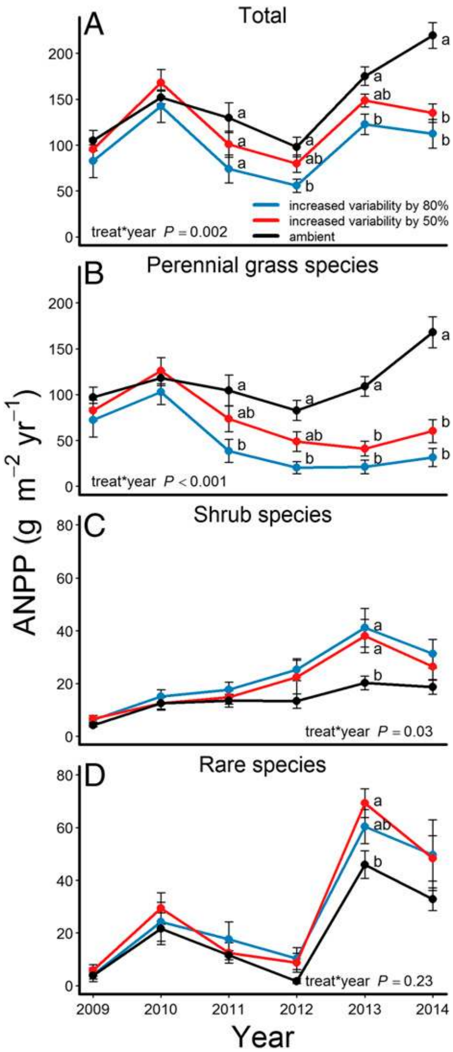
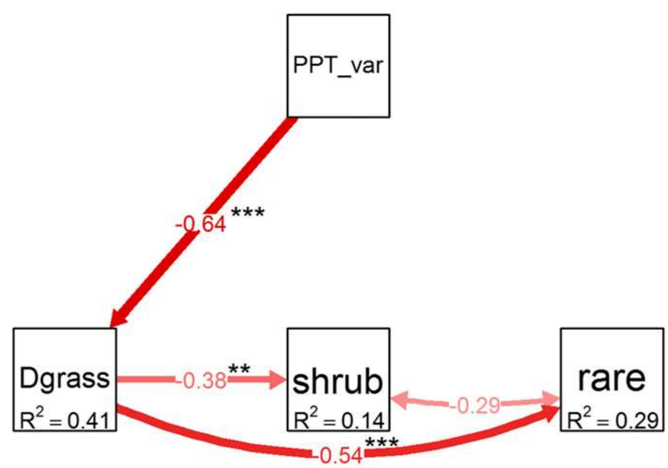


Fig. 4. Effect of precipitation variability on ANPP through time for: (*A*) total ANPP, (*B*) dominant-grass species ANPP, (*C*) shrub-species ANPP, and (*D*) rare-species ANPP. Points indicate mean values (±SE, $n = 10$) for each treatment; and different colors indicate different treatments. Different letters indicate significant differences among treatments within year. No letter means nonsignificant difference.

the third year until the end of the experiment (Fig. 4*B*). In contrast, shrub and rare species responses to increased precipitation-variation treatments were different from control only at the end of the experiment (Fig. 4 *C* and *D* and *SI Appendix*, *Statistical Analysis Description and Summary Output*).

We argue that the opposite responses of shrubs and grasses to precipitation variability result from contrasting root distributions and competitive interactions. Shrubs have deep roots (25) and use water stored in deep soil layers (26), whereas grasses have relatively shallow roots and use soil water located in upper layers of the soil (27). Therefore, changes in the location of available resources may determine the competitive balance between the two plant types (25). Increased precipitation variability has been shown to shift the soil profile downward (28), potentially explaining the positive effect on deep-rooted shrubs. In addition to the location of water sources, these contrasting rooting patterns determine the volume of soil explored by each plant type. Shrubs explore a relatively large volume of soil where water from wet years can be stored, whereas grasses not only explore a smaller volume of soil, but excess water percolating from top layers during wet years recharges the portion of the soil explored by shrubs. This mechanism explains why shrubs are benefited by increased variability but grasses are negatively affected. Low-to-modal precipitation years fill the top layer of the soil and have a positive effect on grass ANPP. Extremely wet years overcome the soil water-holding capacity of the top layer, explaining the plateau in the grass ANPP response, and percolate deeper into the soil profile, causing the increase in shrub ANPP (Fig. 3).

The mechanism explaining the observed amplification of the ecosystem response to enhanced precipitation variability through time is associated with biotic interactions among grasses, shrubs, and the rare-species. We ran a structural-equation model to specifically test the indirect effect of dominant-grass ANPP on the productivity of shrub and rare species (Fig. 5). The model showed positive indirect effects of precipitation variation on shrub and rare species through its negative effect on perennial-grass ANPP (*SI Appendix, Statistical Analysis Description and Summary Output*). This result supports the idea that shrubs and rare species benefit from the diminished dominance of perennial grasses under high precipitation variation and explain the delayed responses of shrub and rare species behind dominant grasses. During wet years following dry years, grasses do not hold enough structures to efficiently use available resources in the upper layers of the soil (24). Therefore, underused resources may percolate deep in the soil profile, increasing the pool of available resources in deep soil layers (29), enhancing shrub ANPP. The amplification results from each dry cycle reducing grass ability to capture resources that are transferred to shrubs. The longer the duration of the enhanced precipitation-variability conditions,



Indirect effect	Estimate	Std. error	Z value	P value
Dgrass on Shrub	0.109	0.042	2.616	0.009
Dgrass on Rare	0.148	0.041	3.593	<0.001

Fig. 5. Effect of precipitation coefficient of variation on 6-y mean dominant grass ANPP (Dgrass) and its indirect effects on 6-y-mean shrub and rare-species ANPP. The model includes the direct effect of precipitation coefficient of variation on dominant grasses and indirect effects through dominant grass ANPP on shrubs and rare species ANPP. Path coefficients are standardized by the mean so they are comparable to each other. Single-headed arrows mean direct negative effects. Double-headed arrows indicate noncausal correlation. Indirect effects result from the multiplication of two consecutive direct effects. (*Inset*) Table shows coefficients for indirect effects including estimates, SE, *z* scores, and *P* values. The model is well supported by our data ($\chi^2 = 2.47$, df = 2, $P = 0.29$). Other goodness-of-fit measures also support this model (standardized root mean square residual = 0.04, root mean square error = 0.07, comparative fit index = 0.974, Tucker–Lewis index = 0.973). Significance codes mean: ns, not significant, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$. For detailed description of analysis and output, see *SI Appendix*, *Statistical Analysis Description and Summary Output*.

the smaller the capacity of grasses to absorb water and the larger the transfer to deep soil layers where shrub have exclusive access. Rare species may benefit from reduced direct competition because of reduced abundance of the dominant grass.

The magnitude of the reduction in primary production because of increased precipitation variability is considerably large. ANPP in high precipitation-variability treatments decreased 49%; where grass ANPP decreased 81%, shrub ANPP increased 67%, and rare-species ANPP increased 50% compared with control ANPP in the sixth year of the experiment. We demonstrated here that ecosystem response to precipitation variability increased through time along the duration of our experiment. The effect of further ecosystem exposure to high interannual-precipitation variance is still uncertain. It may lead to a plateau if the precipitation variability effect is constrained by the water-holding capacity of deep soil layers. Alternatively, the positive feedback between the demise of grasses and the positive response of shrubs may lead the ecosystem into a nonlinear trajectory. If the decline of dominant grass species continues, the ecosystem may transition into a new state of shrub dominance with lower productivity (30, 31). Arid and semiarid ecosystems occupy a large fraction of the global terrestrial land so these drastic impacts of enhanced climate variability may have global consequences (32, 33).

Methods

Site Description. The experiment was carried out at the Jornada Basin Long-Term Ecological Research site (32.5°N, 106.8°W, 1,188 m above sea level) in New Mexico, United States. Long-term mean growing-season precipitation is 105 mm, with a coefficient of variation for a 6-y time window of 38% that ranges from 18% to 67%. The desert grassland under study is dominated by *Bouteloua eriopoda* (Torr.), with the presence of *Prosopis glandulosa* (Torr.). Soils are coarse-textured and present a petrocalcic horizon at depths ranging from 64 to 76 cm (34).

Experimental Design. We increased interannual precipitation variability by alternating rainfall interception and irrigation for 6 y, switching treatments every spring before the growing season started. Our treatments were designed to be relative to ambient precipitation, so we kept the number and timing of rainfall pulses under natural conditions and constant across treatments. The reasoning behind our design was to isolate the effect of precipitation variance from the effects of pulse number and timing studied elsewhere. With this design, we also kept constant among plots all other climatic factors. In fact, the product of natural rainfall and our treatments resulted in precipitation-variation treatments ranging from 48% to 110%; mean precipitation stayed almost the same among treatments, ranging from 126.7 mm to 128.5 mm. We used the automated rainfall manipulation system, ARMS (20), which consisted of rainout shelters (35) that collected either 50% or 80% of the incoming rainfall from exclusion plots and diverted it by means of a solar-powered pump to irrigation plots; control plots received ambient precipitation throughout the duration of the experiment. See refs. 20 and 35 for rainfall manipulation details.

Our experiment consisted of 10 replicates of 5 levels of precipitation interannual coefficient of variation, totaling 50 plots of 2.5 m by 2.5 m that were trenched down to 60 cm or to petrocalcic layer, and lined with 6-mL PVC film to prevent lateral movement of water and roots in or out of the plots. We ensured that all plots had the same starting conditions by picking 80 plots and keeping the 50 most similar in terms of plant-type cover and assigning treatments to each plot randomly.

Response Variables.

ANPP. Plant species were classified into plant types on the basis of their contribution to total productivity. Annual grasses, forbs, and subshrubs form the rare-species group and have low biomass, make small contribution to ANPP, and show episodic growth and reproduction. Dominant grasses represent the main component of the ecosystem productivity, are shallow-rooted and short-lived perennials. The shrub species present in our study is the second dominant, long-lived perennial species, and deep-rooted.

To avoid clipping effects in our multiyear experiment, we estimated ANPP using a nondestructive method that uses plant-species cover and shrub volume (36) as proxies for ANPP. We estimated herbaceous-species plant cover to a 1-cm precision on three 2.5-m permanent cover lines per plot; shrub volume was estimated by measuring two perpendicular diameters and height. ANPP was derived using allometric equations for each plant functional type developed on site. In the case of rare species, we did allometric calibrations for annual grasses, forbs, and subshrubs and estimated cover and harvested nine 20-cm by 40-cm quadrats of nine species (three annual grasses, three forbs, and three subshrubs), totaling 81 quadrats at peak biomass. Twenty 0.2-m by 1-m quadrats were double-sampled for perennial grasses. Biomass-cover regressions were run and slope estimates were used to transform species cover into ANPP. We also developed a shrub allometric equation harvesting one-quarter of 24 shrubs. We sorted for current-year biomass, dried and weighed the samples, and fit a regression model of measured ANPP values against shrub volume (Fig. S3). We are confident of our ANPP estimation method because it matches long-term measurements done with a different method at a similar site within the Jornada Long-Term Ecological Research. For example, in 2009 the mean ANPP for our control plots was 104.8 $g \cdot m^{-2} \cdot yr^{-1}$ and ANPP for the International Biological Programme Exclosure (IBPE) site (similar vegetation structure to our site) was 103.2 $g \cdot m^{-2} \cdot yr^{-1}$.

Soil moisture. We measured soil moisture in the top 30 cm of the soil profile every 30 min in four replicates of each treatment using Campbell Scientific CS625 probes and the data were logged onto CR200X data loggers during 3 y of the experiment (Fig. S1).

Statistical Analyses. We performed all analyses and created all figures using R v3.0.2 (37). For detailed description of statistical analyses and correspondent output, see *SI Appendix*, *Statistical Analysis Description and Summary Output*.

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