sequence data sets for *S. paradoxus* versus other mammals, for *S. paradoxus* versus *S. cubanus*, and for *Cricosaura typica* versus other xantusiid lizards.

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Correspondence and requests for materials should be addressed to A.L.R. (roca@ncifcrf.gov), S.J.O'B. (obrien@ncifcrf.gov) or W.J.M. (murphywi@ncifcrf.gov). The sequences reported in this study are deposited under GenBank accession numbers AY530066–AY530088.

Convergence across biomes to a common rain-use efficiency

Travis E. Huxman[1]*, **Melinda D. Smith**[2,3]*, **Philip A. Fay**[4], **Alan K. Knapp**[5], **M. Rebecca Shaw**[6], **Michael E. Loik**[7], **Stanley D. Smith**[8], **David T. Tissue**[9], **John C. Zak**[9], **Jake F. Weltzin**[10], **William T. Pockman**[11], **Osvaldo E. Sala**[12], **Brent M. Haddad**[7], **John Harte**[13], **George W. Koch**[14], **Susan Schwinning**[15], **Eric E. Small**[16] **& David G. Williams**[17]

[1] *Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA*
[2] *National Center for Ecological Analysis and Synthesis, Santa Barbara, California 93101, USA*
[3] *Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06511, USA*
[4] *Natural Resources Research Institute, Duluth, Minnesota 55811, USA*
[5] *Department of Biology, Colorado State University, Fort Collins, Colorado 80523, USA*
[6] *Department of Global Ecology, Carnegie Institution of Washington, Stanford, California 94305, USA*
[7] *Department of Environmental Studies, University of California, Santa Cruz, California 95064, USA*
[8] *Department of Biological Sciences, University of Nevada, Las Vegas, Nevada 89154, USA*
[9] *Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409, USA*
[10] *Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37919, USA*
[11] *Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, USA*
[12] *Department of Ecology and IFEVA, Faculty of Agronomy, University of Buenos Aires, Buenos Aires C1417DSE, Argentina*
[13] *Energy and Resources Group, University of California, Berkeley, California 94720, USA*
[14] *Biological Sciences and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, Arizona 86011, USA*
[15] *Biosphere 2 Center, Columbia University, Oracle, Arizona 85623, USA*
[16] *Department of Geological Sciences, University of Colorado, Boulder, Colorado 80309, USA*
[17] *Renewable Resources and Botany, University of Wyoming, Laramie, Wyoming 82071, USA*

* These authors contributed equally to this work

Water availability limits plant growth and production in almost all terrestrial ecosystems[1–5]. However, biomes differ substantially in sensitivity of aboveground net primary production (ANPP) to between-year variation in precipitation[6–8]. Average rain-use efficiency (RUE; ANPP/precipitation) also varies between biomes, supposedly because of differences in vegetation structure and/or biogeochemical constraints[8]. Here we show that RUE decreases across biomes as mean annual precipitation increases. However, during the driest years at each site, there is convergence to a common maximum RUE ($\mathrm{RUE_{max}}$) that is typical of arid ecosystems. $\mathrm{RUE_{max}}$ was also identified by experimentally altering the degree of limitation by water and other resources. Thus, in years when water is most limiting, deserts, grasslands and forests all exhibit the same rate of biomass production per unit rainfall, despite differences in physiognomy and site-level RUE. Global climate models[9,10] predict increased between-year variability in precipitation, more frequent extreme drought events, and changes in temperature. Forecasts of future ecosystem behaviour should take into account this convergent feature of terrestrial biomes.

There is a compelling need to understand how terrestrial ecosystems respond to precipitation and other external drivers to permit the forecasting of potential biosphere feedback to natural and anthropogenic changes in the climate system[11]. This is especially important given historical trends and future models of greenhouse gases, global temperature and precipitation regimes[9]. Water is a primary resource limiting terrestrial biological activity[1–5], particularly in arid and semi-arid regions[12], and its availability mediates the responsiveness of communities and ecosystems to global changes[13,14]. Indeed, ANPP, a key ecosystem process, has been shown to increase across biomes with increasing mean annual precipitation (MAP)[2,3,7,15]. However, variability in ANPP within ecosystems does not exhibit such a clear pattern, because variability often peaks at intermediate precipitation[6,7]. This suggests differential sensitivities of ANPP to inter-annual variability in precipitation across biomes.

Life history and biogeochemical mechanisms can interact to influence the production response of terrestrial ecosystems to precipitation[6–8]. The evolutionary history and ecological attributes of species present in the vegetation assemblage can influence production potential as a result of constraints on growth rate imposed by trade-offs with traits for stress tolerance[16]. For example, primary production in arid regions is constrained by generally lower plant densities and the relatively high frequency of slow-growing stress-tolerant species that are delayed in reaching their maximum growth rates until resources become abundant[17]. Production can also be constrained by an interaction between climatic and biogeochemical conditions, changing the relative importance of limiting resources (for example, water, soil nitrogen, soil phosphorus or light). In this case, for sites with high production potential in years with greater than average precipitation, soil nitrogen or other limiting resources might transiently limit biological activity[18]. These two mechanisms are likely to operate differentially across a water availability gradient, producing the following patterns: first, water-limited regions with low production potential should be relatively insensitive to inter-annual variation in precipitation[6,17]; second, water-limited regions with relatively high production potential should be very sensitive to variation in water availability[7]; and last, mesic sites with high production potential should exhibit relatively low sensitivity to inter-annual variability in precipitation[19].

We evaluated relationships between ANPP and precipitation (both annual values for certain years and MAP) for 14 terrestrial ecosystems in nine biomes located throughout North and South America (Supplementary Information) to quantify the sensitivity (change in ANPP divided by change in precipitation) of different ecosystems to variation in precipitation. We chose ecosystems varying by an order of magnitude in annual rainfall, spanning xeric to mesic biomes, in which the relative importance of precipitation as a limiting variable might change through time. The selected data sets were additionally limited to locations where sufficient, inter-annual records of precipitation (PTT) and ANPP could be obtained. We contrasted ANPP/precipitation relationships across and within biomes to identify potential mechanisms underlying variation in ecosystem sensitivity to precipitation, and to build on our mechanistic knowledge of precipitation effects on ecosystem processes.

When evaluated across all sites and years, ANPP increased with PTT (Fig. 1a). However, there was substantial variation in sensitivity relationships between sites. In general, the greatest slopes of ANPP and precipitation occurred at the driest sites (JRN, KNZ, RV, SEV and SGS; see Methods for site abbreviations), and the lowest (or even negative) slopes occurred at the most mesic sites (AND, BCI, HBR and HFR; Fig. 1a). To some degree, this varying sensitivity reflects differences in climatic controls on ANPP between xeric and mesic biomes. Indeed, stepwise multiple regression analysis of ANPP using annual precipitation, growing season maximum temperature ($T_{\max}$), precipitation coefficient of variance and seasonality, and ANPP in the previous year indicated that ANPP at the most productive sites (more than $800\,\mathrm{g\,m^{-2}\,yr^{-1}}$) was more strongly correlated with $T_{\max}$ and production in the previous year than with annual precipitation, whereas annual precipitation remained the best correlate of ANPP at the least productive sites (less than $500\,\mathrm{g\,m^{-2}\,y^{-1}}$; see Supplementary Information).

The variation in the sensitivities of ANPP to precipitation with low to high MAP across the range of biomes is consistent with the hypotheses that life history and biogeochemical mechanisms can explain how ecological systems are affected by water availability. Life history (that is, vegetation) constraints influence the impact of precipitation on biological activity in a manner that can decrease with increasing precipitation, whereas biogeochemical constraints (limitation of activity by resources other than water) can increase with increasing precipitation[7,8]. At the sites with lowest MAP, high efficiency of water use associated with individual plant growth rate is translated to high efficiency of water use at the ecosystem level. In contrast, at sites with high MAP, selection has favoured plants with high growth rates and competitive abilities for other resources rather than high efficiency of water use. The result is less effective water use by mesic vegetation; consequently, other resources such as nitrogen and light will influence ANPP more strongly. However, both in locations with high MAP and in those with low MAP, water availability is tightly linked to biogeochemical constraints through mineralization processes and leaching[20]. Precipitation affects both nutrient availability through its effects on microbial activity and

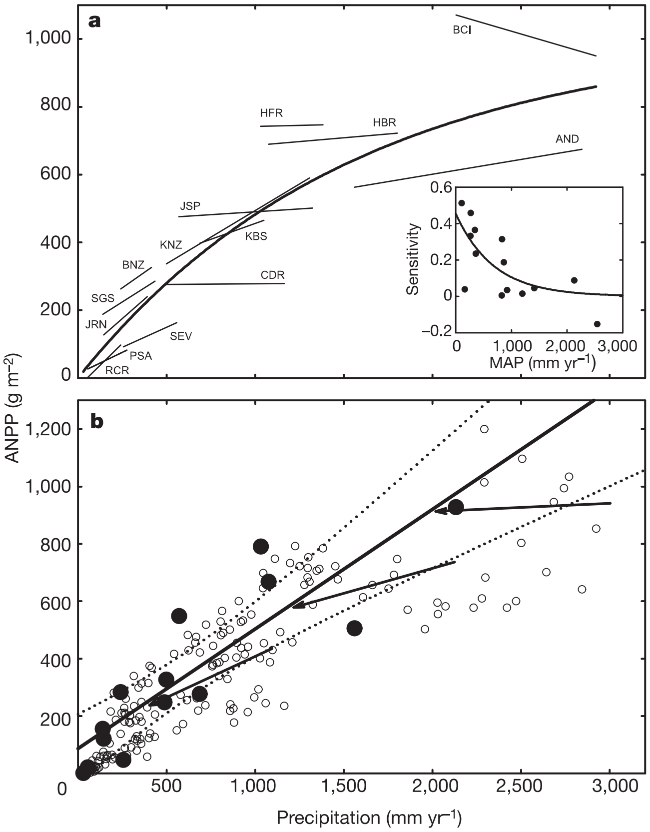

Figure 1 Between-year variation in production across a precipitation gradient and a maximum rain-use efficiency. **a**, Plot of ANPP against PPT for 14 sites (see Methods for abbreviations). Multi-year data give site-specific relationships by using linear regression (see Supplementary Information). The overall relationship (bold line) derives from data from all sites: $\mathrm{ANPP} = 1011.7 \times (1 - \exp(-0.0006 \times \mathrm{precipitation}))$; $r^2 = 0.77$; $P < 0.001$. The inset shows the site-level slopes (ANPP plotted against precipitation) as a function of MAP: $\mathrm{ANPP} = 0.388 \times (1 - \exp(-0.0022 \times \mathrm{precipitation}))$; $r^2 = 0.51$; $P < 0.001$. **b**, An overall $\mathrm{RUE}_{\max}$ derived from the slope of the minimum precipitation and the corresponding ANPP for all sites (solid line): $\mathrm{ANPP} = 86.1 + 0.42 \times \mathrm{PTT}_{\min}$. Closed circles, minima; open circles, remaining data; dotted lines, 95% confidence intervals. Arrows show average slopes for sites with low, medium and high precipitation.

nutrient extraction from soils through its effects on plant growth and nutrient demand.

Variable sensitivity of ANPP to precipitation from low-production to high-production biomes reflects differences in site-level mean RUE. However, when ANPP from years with the historic minimum precipitation were combined for all sites, a positive linear relationship emerged (Fig. 1b). Thus, when water limitations on ANPP were greatest, a common $\mathrm{RUE}_{\mathrm{max}}$, estimated by the slope of the historic minimum ANPP/precipitation relationship, was found for all biomes. Sites (mostly deserts) with low production potential had a mean RUE (based on all years) close to $\mathrm{RUE}_{\mathrm{max}}$, whereas high-productivity sites were characterized by mean RUE that deviated significantly from $\mathrm{RUE}_{\mathrm{max}}$. Consistent with earlier analyses[7] was our observation that intermediate sites (mostly grasslands) were more variable in yearly patterns of RUE. These sites also converged to a common $\mathrm{RUE}_{\mathrm{max}}$ when water was the primary limiting resource.

Two predictions (Fig. 2a) arise from the existence of a common $\mathrm{RUE}_{\mathrm{max}}$: first, if climate change drives precipitation below a historic minimum, ANPP will be more strongly affected than predicted from site-level (mean) RUE; and second, the removal of other resource limitations so that precipitation becomes the primary limiting resource will result in an increase in site-level RUE that approaches $\mathrm{RUE}_{\mathrm{max}}$. Thus, $\mathrm{RUE}_{\mathrm{max}}$ should act as a boundary by which site-level ANPP or RUE are constrained. Existing global change manipulations in a tallgrass prairie[21] and a Mediterranean grassland[14] support these two predictions (Fig. 2). First, reductions in ANPP with the exclusion of growing season precipitation (May to October) resulted in a substantial deviation from the predicted ANPP based on the site-level mean ANPP/precipitation relationship in tallgrass prairie. In this case, ANPP was decreased to that predicted from $\mathrm{RUE}_{\mathrm{max}}$ rather than from mean RUE (Fig. 2b). Second, with the alleviation of limiting resources other than water (soil nitrogen, and soil nitrogen plus CO_2) in Mediterranean grassland, RUE increased to a value equivalent to the overall $\mathrm{RUE}_{\mathrm{max}}$ (Fig. 2c). These results indicate that ANPP in terrestrial ecosystems might be fundamentally and equivalently constrained when water is most limiting, despite differences in vegetation.

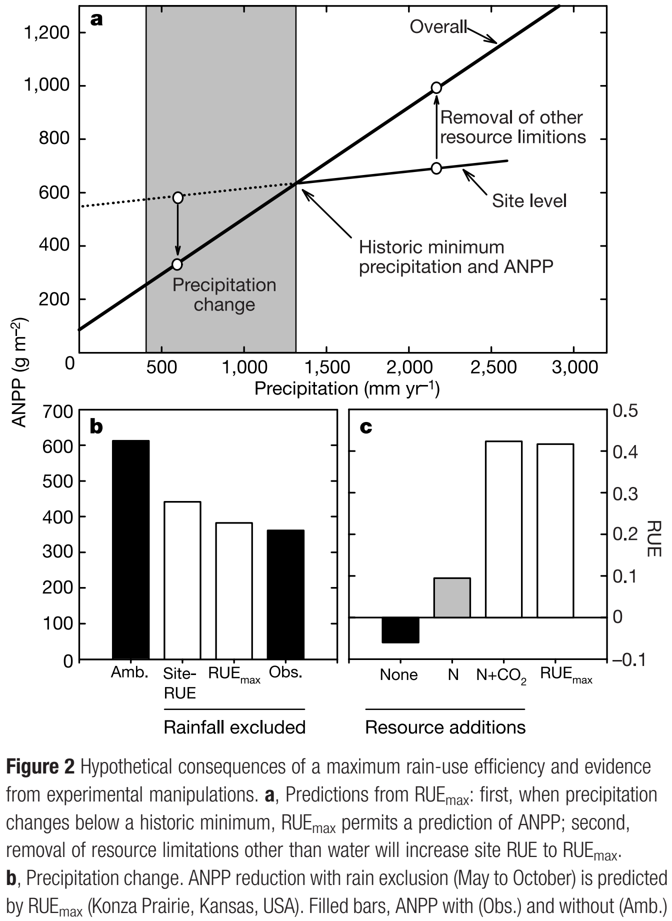

Figure 2 Hypothetical consequences of a maximum rain-use efficiency and evidence from experimental manipulations. **a**, Predictions from $\mathrm{RUE}_{\mathrm{max}}$: first, when precipitation changes below a historic minimum, $\mathrm{RUE}_{\mathrm{max}}$ permits a prediction of ANPP; second, removal of resource limitations other than water will increase site RUE to $\mathrm{RUE}_{\mathrm{max}}$. **b**, Precipitation change. ANPP reduction with rain exclusion (May to October) is predicted by $\mathrm{RUE}_{\mathrm{max}}$ (Konza Prairie, Kansas, USA). Filled bars, ANPP with (Obs.) and without (Amb.) rain exclusion; open bars, ANPP predicted from site-level RUE and $\mathrm{RUE}_{\mathrm{max}}$. **c**, Removal of resource limitations. The addition of resources other than water increases RUE to $\mathrm{RUE}_{\mathrm{max}}$ (Jasper Ridge, California, USA). Here RUE is calculated as the change in ANPP from plots with ambient precipitation to those with water addition, for (1) no 'other' resource addition (black bar), (2) addition of soil nitrogen (N) (grey bar) and (3) addition of soil nitrogen plus CO_2 (open bar).

The presence of a common $\mathrm{RUE}_{\mathrm{max}}$ is not consistent with a simple life-history hypothesis for the control of ANPP by precipitation. Differences between species—a function of trade-offs between water-use efficiency (WUE) and growth rate—are compounded by other ecological processes at the community level; this produces divergent relationships of biomass production with water availability between the individual scale and the community scale. As a result, abiotic–biotic interactions, such as the relationship between plant-based WUE and the ecosystem transpiration/evaporation ratio, might be important in producing a common $\mathrm{RUE}_{\mathrm{max}}$ rather than species traits alone. For example, at sites with low precipitation, individual plants might have higher WUE but more total precipitation might be lost to soil evaporation than to plant transpiration, decreasing system RUE below the plant-based value. In sites with higher precipitation, individual plants might have lower WUE but a greater fraction of water might move through plant transpiration, resulting in a greater balance between plant-level WUE and ecosystem RUE. The most parsimonious explanation of the divergence of local sites from the overall mean (for example, site-specific sensitivity of ANPP to precipitation) is the increasing importance of other resource limitations, and not the water-use characteristics of individual species. Because water availability has an overriding effect on all aspects of element cycling in arid lands[22], nitrogen or other resources might limit production only during anomalous wet periods[23]. This is not true of grasslands and forests, in which multiple factors can limit production to varying degrees[24].

Variation in the abundance and seasonal distribution of water availability is often used as the causal explanation for global differences in ecosystem structure and function[25]. Here we show, through a cross-site comparison together with an examination of local processes, that the relative control of water on ANPP is a function of an overall $\mathrm{RUE}_{\mathrm{max}}$ coupled with the dynamic nature of multiple limiting resources. Shifts in the timing, magnitude or variability of precipitation should have impacts on evolutionary and ecological processes that underlie this interaction between plant function, community composition and biogeochemistry[12,26,27]. This highlights the need to understand not only the overall relationship between precipitation and biological activity but also how inter-annual variation in precipitation can affect ecosystem structure and function[28].

Our analysis suggests that water limitation can impose a common constraint on ANPP across diverse biomes, and that ecosystems have the same potential $\mathrm{RUE}_{\mathrm{max}}$ despite differences in sensitivities of ANPP to precipitation, physiognomy, climatic history, hydrology and phylogenetic origin of representative flora. We show that differential sensitivity occurs as a result of local sites deviating from an overall $\mathrm{RUE}_{\mathrm{max}}$ with the increasing influence of other resource limitations on ecological processes as precipitation increases. This suggests that biogeochemistry, rather than attributes of individual species alone, constrains community level ANPP in response to precipitation across biomes[8]. As a result, potential responses of the biosphere to changes in precipitation must be bounded by these underlying ecological constraints. Increased inter-annual variability and extreme droughts are major predictions of global climate models[9,10]. Thus, there might be a greater frequency of transition between ANPP limitation by water and by other limiting resources. A key result would be reductions in ANPP that were greater than expected, as well as greater variability, than that predicted by site-level models alone—even in biomes previously considered insensitive (for example, forests)—in response to future climate. □

Methods

We searched for data from a variety of sources, but included only those data sets with at least six years of concurrent measures of annual precipitation and ANPP. We assembled data from 14 sites that met these criteria, including ten US Long-Term Ecological Research (LTER) Network sites[7], and sites in Rock Valley (RCR; desert), Nevada[29], Jasper Ridge Biological Preserve (JR; Mediterranean grassland), California[14], Patagonia Steppe (PSA; grass/shrub steppe), Argentina[30], and Barro Colorado Island (BCI; tropical forest), Republic of Panama. These sites represent a broad gradient of precipitation in North and South America (105–2,542 mm MAP). The LTER sites are listed in ref. 7, and include Bonanza Creek, Alaska (BNZ), Cedar Creek, Minnesota (CDR), Harvard Forest, Massachusetts (HFR), Hubbard Brook, New Hampshire (HBF), Jornada, New Mexico (JRN), Kellogg, Michigan (KBS), Konza Prairie, Kansas (KNZ), Sevilleta, New Mexico (SEV), and Shortgrass Steppe, Colorado (SGS). We added the H.J. Andrews Experimental Forest, Oregon (AND), to this LTER data set. Data for BCI were obtained from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC at http://www-eodis.ornl.gov/npp/npp_home.html).

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Correspondence and requests for materials should be addressed to T.E.H. (huxman@email.arizona.edu) or M.D.S. (melinda.smith@yale.edu).

Harmonic-hopping in Wallacea's bats

Tigga Kingston[1]* **& Stephen J. Rossiter**[2,3]*

[1] *Department of Geography, Boston University, Massachusetts 02215, USA*
[2] *School of Biological Sciences, Queen Mary, University of London, London E1 4NS, UK*
[3] *School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK*

* These authors contributed equally to this work

Evolutionary divergence between species is facilitated by ecological shifts, and divergence is particularly rapid when such shifts also promote assortative mating[1–3]. Horseshoe bats are a diverse Old World family (Rhinolophidae) that have undergone a rapid radiation in the past 5 million years[4]. These insectivorous bats use a predominantly pure-tone echolocation call matched to an auditory fovea (an over-representation of the pure-tone frequency in the cochlea and inferior colliculus[5,6]) to detect the minute changes in echo amplitude and frequency generated when an insect flutters its wings[7]. The emitted signal is the accentuated second harmonic of a series in which the fundamental and remaining harmonics are filtered out[8]. Here we show that three distinct, sympatric size morphs of the large-eared horseshoe bat (*Rhinolophus philippinensis*) echolocate at different harmonics of the same fundamental frequency. These morphs have undergone recent genetic divergence, and this process has occurred in parallel more than once[9]. We suggest that switching harmonics creates a discontinuity in the bats' perception of available prey that can initiate disruptive selection[1]. Moreover, because call frequency in horseshoe bats has a dual function in resource acquisition and communication, ecological selection on frequency might lead to assortative mating and ultimately reproductive isolation and speciation, regardless of external barriers to gene flow[1–3].

The large-eared horseshoe bat (*Rhinolophus philippinensis*) is a rare species found from the Wallacea region of southeast Asia to northeast Australia. Observed variation in body size across its range has led to suggestions that more than one species might be present, currently recognized as subspecies[10]. A previous study of two size forms from Queensland, calling at 40 and 28 kHz, revealed a polyphyletic origin[11]. We used acoustic and genetic analyses to determine the basis of phenotypic variation in this species. Bats were captured on Buton Island, southeast Sulawesi, with an additional individual from neighbouring Kabaena Island. Intensive trapping over four summers revealed low numbers of three discrete size morphs ($n = 24$) (Fig. 1).