# Commentary

## Nonlinear responses of land ecosystems to variation in precipitation

### The double asymmetry model

As global change induces more and more extreme climate events (Field *et al.*, 2012), temporal variability in precipitation is likely becoming larger than ever. How land ecosystems respond to the stronger temporal variability in precipitation is a new frontier research area for ecologists (Reichstein *et al.*, 2013; Niu *et al.*, 2014). In this issue of *New Phytologist* Knapp *et al.* (pp. 41–47) frame a new conceptual model to understand responses of aboveground net primary production (ANPP) to stronger temporal variability in precipitation.

*'... which provides a crucial step to improving our understanding of how rainfall gradients impact on productivity of ecosystems across the world.'*

Ecologists have extensively studied ecosystem responses to temporal and spatial variations in precipitation (Huxman *et al.*, 2004). Over a broad spatial scale, ANPP usually responds to precipitation nonlinearly; that is, ANPP linearly increases with increasing precipitation in its low range, but levels off in its high range. At a given location, however, ANPP has been usually found to respond in a linear manner to year-to-year variations in precipitation. Knapp *et al.* hypothesize a double asymmetric model: a positive asymmetric response of ANPP to nominal levels of interannual variability in precipitation and a negative asymmetric ANPP response to extremely low precipitation. The positive asymmetry shows a higher percentage in ANPP change in response to increasing than decreasing precipitation. The negative asymmetry describes negative impacts of extreme dry periods on ANPP as being much greater than positive effects of extreme wet periods.

### Other ecosystem processes in response to extreme precipitation variability

The double asymmetry model is proposed to characterize responses of ANPP to temporal variability in precipitation. Other ecosystem processes likely respond quite differently from ANPP to extreme precipitation variability due to different mechanisms. For example, increased precipitation stimulated belowground net primary production (BNPP) to a much lesser extent than ANPP, as shown by meta-analyses of results from manipulative experiments (Wu *et al.*, 2011; Zhou *et al.*, 2016). Oddly, both decreased precipitation (i.e. drought) and higher rainfall slightly increased soil organic carbon (SOC) as revealed in a meta-analysis by Zhou *et al.* (2016). The various responses of BNPP and SOC to precipitation among different ecosystems may be partly due to antecedent precipitation, manipulative magnitudes, and the vegetation types. By contrast, a transect study along a precipitation gradient from 340 to 1100 mm found that BNPP and soil carbon (C) content were largely constant (Fig. 1; Zhou *et al.*, 2009).

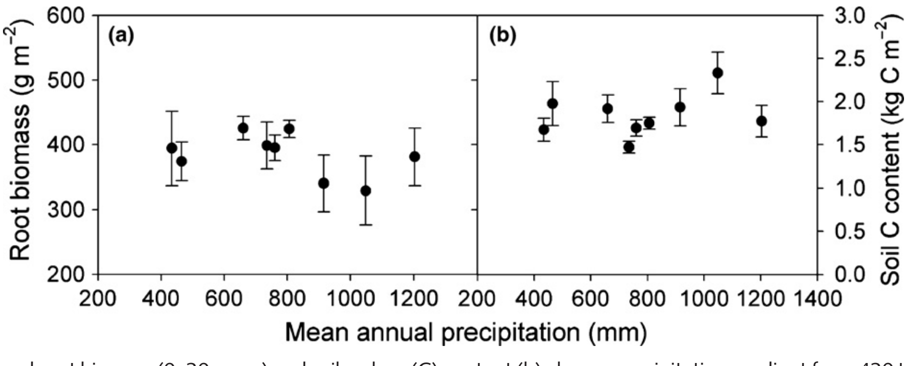


**Fig. 1** Patterns of belowground root biomass (0–30 cm, a) and soil carbon (C) content (b) along a precipitation gradient from 430 to 1200 mm in the southern Great Plains, USA. Data are presented with mean ± standard error (SE) from five replicates. The study was conducted at nine grassland sites to represent three grassland types that differ in physiognomy: short-grass steppe, mixed-grass prairie, and tallgrass prairie. The sites had a minimum amount of disturbance and land-use impact. While mean annual precipitation (MAP) across these sites varied from 430 mm in northwestern Oklahoma to 1200 mm in southeastern Oklahoma, mean annual temperature (MAT) changed relatively little, ranging from 13.0 to 16.5°C. Data from Zhou *et al.* (2009).

This article is a Commentary on Knapp *et al.*, **214**: 41–47.



**Fig. 2** Pictures of gradient precipitation experiments in the southern Great Plains, USA (a) and eastern Qinghai-Tibet Plateau, China (b). (a) The gradient precipitation experiment in the southern Great Plains was set up in a tallgrass prairie near Washington, OK, USA (34°58′54″N, 97°31′14″W) and started running in April 2016 to study responses of prairie ecosystems to altered precipitation. There are seven levels of precipitation treatment: 0%, 20%, 40%, 60%, 80%, 100% and 150% of ambient precipitation. The altered precipitation is achieved by constructing a roof above each of the 3.6 m × 3.6 m plots. For 0% of ambient precipitation treatment, corrugated clear plastic sheets are used to exclude all precipitation and for the rest of the six treatments, the same number of 'U'-shaped clear plastic tubes are placed in different directions to intercept precipitation. (b) A manipulative experiment was set up in an alpine meadow in the eastern Qinghai-Tibet Plateau in 2015 to simulate a precipitation gradient. The experiment has five 2 m × 3 m plots for each of eight levels of precipitation (0, 1/12, 1/4, 1/2, 3/4, 1 and 5/4 times ambient, which equals 30, 140, 280, 420, 560, 700 and 840 mm, respectively, in average year). The varying levels of precipitation are achieved using combinations of water catchment and rainout shelters. The rainout shelter is used to reduce precipitation. The fixed-location shelter, with a roof consisting of curved, transparent acrylic bands, blocks different amounts of rainfall. Fiberglass plates are inserted down to a depth of 40 cm in the soil surrounding the plots to cut off lateral movement of soil water. The devices help achieve the goal of a free-air controlled experiment with minimal site disturbance.

Responses of BNPP and soil C content to precipitation are regulated by a suite of mechanisms, such as C allocation to the root vs the shoot, root turnover time, and species composition. When soil-water resource changes over seasons due to altered precipitation, plants usually adjust C allocation to balance aboveground and belowground functions, resulting in changes in root : shoot ratios. When precipitation changes over longer time scales (i.e. years or decades) root turnover time (or longevity) and plant species composition may change, leading to different patterns of changes in BNPP and soil C content from that for ANPP. Thus, it is critical to understand adjustments in root : shoot ratios, root turnover time, and species composition as key mechanisms underlying responses of belowground C processes to changes in precipitation.

Microbial community structure and long-term ecosystem processes (e.g. mineral assemblage, soil development, soil texture, aggregate stability) may also regulate response patterns of belowground C processes to changing precipitation. For example, along a precipitation gradient from 430 to 1200 mm, soil respiration from grasslands increased linearly with mean annual precipitation (MAP) in the Great Plains, USA (Zhou *et al.*, 2009). Moreover, across 24 arid and semi-arid ecosystem sites along a precipitation gradient from 100 to 400 mm in the Mongolian Plateau, China, microbial biomass, fungal biomass, bacterial biomass, and actinomycete biomass all increased with MAP (Chen *et al.*, 2015). Soil bacterial abundance decreased with the precipitation gradient while bacterial diversity was independent of the precipitation gradient from 100 to 400 mm in a Mediterranean ecosystem (Bachar *et al.*, 2010). Collectively, these observations highlight the importance of precipitation for a range of belowground processes central to ecosystem function.

## Manipulative experiments to test the double asymmetry and other hypotheses

The positive asymmetry outlined in Knapp *et al.* is based primarily on the response ratio of ANPP under increased or decreased precipitation compared with that under control conditions (Knapp & Smith, 2001; Wu *et al.*, 2011; Unger & Jongen, 2015). When observed ANPP is regressed against precipitation over years, the positive asymmetry is not very obvious. By contrast, the negative asymmetry is primarily derived from spatial analysis or modeling (Luo *et al.*, 2008; Zhou *et al.*, 2008; Zscheischler *et al.*, 2014) due to the rare natural occurrence in extreme drought years. To gain empirical evidence on ecosystem responses to large variations in precipitation, it is imperative to conduct field-gradient experiments, with multiple levels of precipitation, in different types of ecosystems around the world (Fig. 2). These multi-level precipitation experiments are complementary to the existing experiments that mostly have two or three levels of precipitation treatment.

Such field experiments may offer opportunities to investigate a suite of critical issues related to the double asymmetry hypothesis and other hypotheses. Examples are:

**1.** How best can we detect the positive asymmetry within the nominal variability in precipitation?

**2.** How soon can we detect the negative asymmetry once the extreme precipitation treatments are imposed?

**3.** At what levels of precipitation would the thresholds occur for the positive and negative asymmetries?

**4.** Would the thresholds shift as the experiments proceed?
**5.** Would the asymmetrical responses occur for any of the belowground processes, such as BNPP, soil respiration, microbial biomass, and soil C dynamics?
**6.** How would other global change factors, such as warming, rising atmospheric $CO_2$ concentration, and nitrogen deposition, interactively influence the asymmetrical responses of ANPP to precipitation?

During long-term precipitation experiments, plant and microbial species compositions, and other plant and soil properties, likely change with time. Those biotic and abiotic changes during the course of long-term experiments prompt other questions, such as:
**7.** How would changes in species composition regulate the asymmetrical responses of ANPP to precipitation?
**8.** Would the availability of nutrients be significantly affected by changes in precipitation and then indirectly influence ANPP?
**9.** At what level of precipitation can the ecosystem recover after the cessation of the treatments?

To test the earlier mentioned hypotheses, multi-level precipitation experiments may have to be supported by modeling and other experiments (Luo *et al.*, 2011). Results from these experiments will likely reveal emergent properties of ecosystems as precipitation is shifting to extremely variable regimes. The emergent patterns will become exceptionally valuable for benchmarking models. Future advances in this research area will, at least partially, be underpinned by the double asymmetry model proposed by Knapp *et al.*, which provides a crucial step to improving our understanding of how rainfall gradients impact on the productivity of ecosystems across the world.

**Yiqi Luo[1,2]*, Lifen Jiang[2], Shuli Niu[3] and Xuhui Zhou[4]**

[1]Department of Earth System Science, Tsinghua University, Beijing 100084, China;
[2]Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, USA;
[3]Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China;
[4]School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China
(*Author for correspondence: tel +86 183 1062 8167; email luoyiqi@mail.Tsinghua.edu.cn)

## References

**Bachar A, Al-Ashhab A, Soares MIM, Sklarz MY, Angel R, Ungar ED, Gillor E. 2010.** Soil microbial abundance and diversity along low precipitation gradient. *Microbial Ecology* **60**: 453–461.

**Chen D, Mi J, Chu P, Cheng J, Zhang L, Pan Q, Xie Y, Bai Y. 2015.** Patterns and drivers of soil microbial communities along a precipitation gradient on the Mongolian Plateau. *Landscape Ecology* **30**: 1669–1682.

**Field CB, Barros V, Stocker TF, Qin D, Dokken DJ, Ebi KL, Mastrandrea MD, Mach KJ, Plattner GK, Allen SK *et al.*, eds. 2012.** *Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change*. Cambridge, UK, and New York, NY, USA: Cambridge University Press.

**Huxman TE, Smith MD, Fay PA, Knapp AK, Shaw MR, Loik ME, Smith SD, Tissue DT, Zak JC, Weltzin JF *et al.* 2004.** Convergence across biomes to a common rain-use efficiency. *Nature* **429**: 651–654.

**Knapp AK, Smith MD. 2001.** Variation among biomes in temporal dynamics of aboveground primary production. *Science* **291**: 481–484.

**Knapp AK, Ciais P, Smith MD. 2017.** Reconciling inconsistencies in precipitation–productivity relationships: implications for climate change. *New Phytologist* **214**: 41–47.

**Luo Y, Gerten D, Le Maire G, Parton WJ, Weng E, Zhou X, Keough C, Beier C, Ciais P, Cramer W *et al.* 2008.** Modeled interactive effects of precipitation, temperature, and $CO_2$ on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* **14**: 1986–1999.

**Luo YQ, Melillo J, Niu SL, Beier C, Clark JS, Classen AT, Davidson E, Dukes JS, Evans RD, Field CB *et al.* 2011.** Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology* **17**: 843–854.

**Niu SL, Luo YQ, Li DJ, Cao SH, Xia XY, Li JW. 2014.** Plant growth and mortality under climatic extremes: an overview. *Environmental and Experimental Botany* **98**: 13–19.

**Reichstein M, Bahn M, Ciais P, Frank D, Mahecha MD, Seneviratne SI, Zscheischler J, Beer C, Buchmann N, Frank DC *et al.* 2013.** Climate extremes and the carbon cycle. *Nature* **500**: 287–295.

**Unger S, Jongen M. 2015.** Consequences of changing precipitation patterns for ecosystem functioning in grasslands: a review. In: Lüttge U, Beyschlag W, eds. *Progress in botany 76*. Cham, Switzerland: Springer International, 347–393.

**Wu Z, Dijkstra P, Koch GW, Penuelas J, Hungate BA. 2011.** Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology* **17**: 927–942.

**Zhou X, Talley M, Luo Y. 2009.** Biomass, litter, and soil respiration along a precipitation gradient in southern Great Plains, USA. *Ecosystems* **12**: 1369–1380.

**Zhou X, Weng E, Luo Y. 2008.** Modeling patterns of nonlinearity in ecosystem responses to temperature, $CO_2$, and precipitation changes. *Ecological Applications* **18**: 453–466.

**Zhou X, Zhou L, Du Z, Nie Y, Fu Y, Zheng Z, Wang X. 2016.** Regulation of carbon allocation in the responses of soil carbon storage to both drought and irrigation: a meta-analysis. *Agriculture, Ecosystems and Environment* **228**: 70–81.

**Zscheischler J, Reichstein M, Harmeling S, Rammig A, Tomelleri E, Mahecha MD. 2014.** Extreme events in gross primary production: a characterization across continents. *Biogeosciences* **11**: 2909–2924.

**Key words:** aboveground net primary production (ANPP), belowground net primary production (BNPP), double asymmetry model, ecosystem processes, manipulative experiments, precipitation, soil carbon content, temporal variability.