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Reconciling inconsistencies in precipitation–productivity relationships: implications for climate change

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Contents

Summary	41	V. Conclusions	45
I. Introduction	41	Acknowledgements	46
II. The PPT–ANPP relationship: spatial vs temporal models	42	References	46
III. Inconsistencies with a linear temporal model	43		
IV. Revision of the temporal PPT–ANPP model to better forecast climate change impacts	44		

Summary

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Precipitation (PPT) is a primary climatic determinant of plant growth and aboveground net primary production (ANPP) over much of the globe. Thus, PPT–ANPP relationships are important both ecologically and to land–atmosphere models that couple terrestrial vegetation to the global carbon cycle. Empirical PPT–ANPP relationships derived from long-term site-based data are almost always portrayed as linear, but recent evidence has accumulated that is inconsistent with an underlying linear relationship. We review, and then reconcile, these inconsistencies with a nonlinear model that incorporates observed asymmetries in PPT–ANPP relationships. Although data are currently lacking for parameterization, this new model highlights research needs that, when met, will improve our understanding of carbon cycle dynamics, as well as forecasts of ecosystem responses to climate change.

I. Introduction

Terrestrial ecosystems cover less than one-third of the Earth's surface, yet account for approximately two-thirds of global net primary production (NPP), with the carbon (C) resident in terrestrial plant biomass equivalent to *c.* 70% of that in the atmosphere (Houghton, 2007). The aboveground fraction of NPP (ANPP) is particularly important both as an integrator of terrestrial ecosystem function (Fahey & Knapp, 2007), and because humans depend on ANPP for food, fiber and fuel (Haberl *et al.*, 2007). Thus, in this era of unprecedented climate change, an

understanding of the primary controls of ANPP is important from climatological, ecological and socioeconomic perspectives. There is a rich history of foundational studies documenting water availability as a key determinant of spatial and temporal patterns of ANPP (e.g. Rosenzweig, 1968; Webb *et al.*, 1978), and more recent analyses have confirmed that precipitation (PPT) inputs, or alternative measures of water availability, limit or co-limit ANPP, as well as gross primary production (GPP), over much of the globe (Fig. 1; Nemani *et al.*, 2003; Garbulsky *et al.*, 2010; Ahlström *et al.*, 2015; Seddon *et al.*, 2016). Of course, some biomes are more strongly limited by water than others (Fig. 1) but, even in cold or

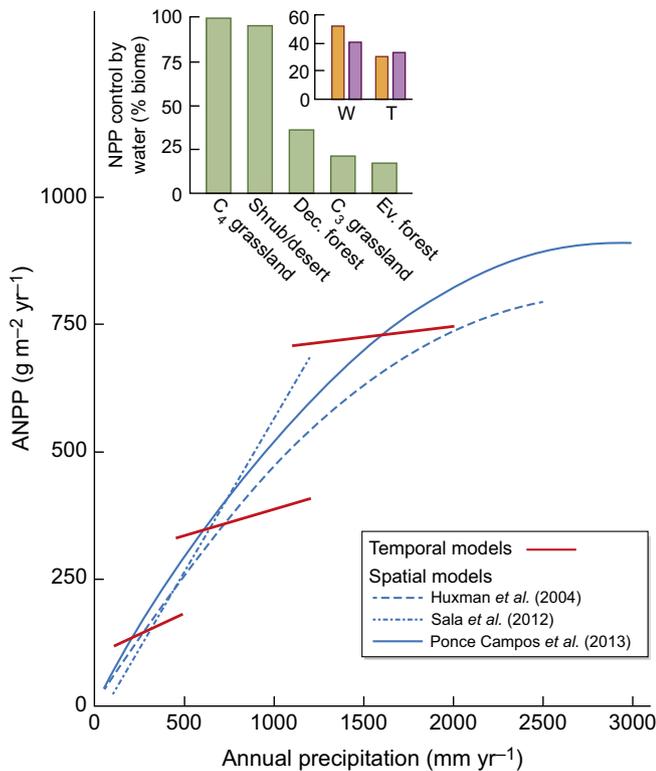


Fig. 1 Precipitation is the predominant climatic factor controlling the rates and patterns of primary production in terrestrial ecosystems globally. Relationships between aboveground net primary production (ANPP) and precipitation (PPT) are derived from multi-year observations in two ways. Temporal models (red lines) are site based and relate interannual variability in PPT to interannual variability in ANPP. Spatial models (blue lines) relate mean annual PPT to mean ANPP across multiple sites. The temporal models depicted are idealized, but illustrate the oft-observed inverse relationship between the slope of the ANPP–PPT relationship with precipitation amount (Huxman *et al.*, 2004). The spatial models shown are based on globally extensive datasets which include multiple biomes (deserts to tropical forests; Huxman *et al.*, 2004; Ponce-Campos *et al.*, 2013) or a single biome (grasslands) sampled across precipitation gradients on three continents (Sala *et al.*, 2012). Inset: proportion of major global biomes in which water is the predominant climatic factor limiting productivity (Dec., deciduous; Ev., evergreen, from Churkina & Running, 1998). Globally, estimates of the proportion of land area in which productivity is primarily limited by water (W) vary from 40 to >50%. For comparison, temperature (T) is the primary limiting climatic factor for c. 30% of the global land area. Estimates from Churkina & Running (1998; orange bars) and Nemani *et al.* (2003; purple bars).

humid regions, in which temperature or other factors are expected to more strongly limit ANPP, ecosystems are surprisingly sensitive to variations in water availability, directly or indirectly (Schuur, 2003; Vicente-Serrano *et al.*, 2013; Winkler *et al.*, 2016). Thus, forecast changes in PPT are predicted to have significant impacts on ANPP from local scales that extend to the global C cycle (Reichstein *et al.*, 2013).

While a warming atmosphere is the most certain climatic change occurring, the global hydrological cycle has been forecast to intensify as well (IPCC, 2012). This intensification may be manifest in many ways, including increased interannual PPT variability, more frequent extreme PPT years (wet and dry) and alterations in annual PPT amount, with some regions expected to

become wetter and others drier (Lau *et al.*, 2013; Polade *et al.*, 2014). Recent climatological trends have supported these predictions (Huntington, 2006; Fischer & Knutti, 2014; Hubbart *et al.*, 2016). Thus, forecasting how future ecosystem structure and function will respond to changing PPT regimes requires a robust understanding of the relationship between PPT and ANPP. Key to such forecasts is the presumption that the contemporary form of the PPT–ANPP relationship is appropriate for the prediction of responses to climate change. In the last two decades, ecologists have conducted scores of analyses of long-term ANPP datasets, and modeling and experimental studies, to provide insights into how ANPP (and other C cycle components) will respond to future PPT regimes. Although much has been learned, this body of research includes a number of results that are inconsistent with one another and our current understanding of the PPT–ANPP relationship. This lack of clarity with regard to how ANPP responds to a primary climatic control suggests that the PPT–ANPP relationship needs to be revisited.

Below, we summarize recent research results with an emphasis on discrepancies between what has been observed vs expected based on our contemporary understanding of the PPT–ANPP relationship. We then reconcile these inconsistencies with a new conceptual model for the PPT–ANPP relationship, one which highlights research needs that, when addressed, will improve forecasts of C cycle responses to future changes in PPT.

II. The PPT–ANPP relationship: spatial vs temporal models

The PPT–ANPP relationship is typically derived from multi-year measurements of PPT and ANPP, and is viewed through either a spatial or temporal lens. This has led to two distinct models: *spatial models* based on ANPP data combined from many sites arrayed along PPT gradients, and *temporal models* derived from individual sites in which PPT and ANPP have varied over time (Fig. 1). These two models are often related because spatial models are usually based on mean values from site-based temporal models (Huxman *et al.*, 2004). Statistical relationships for spatial models are usually nonlinear (concave down or saturating, Fig. 1) when they span large gradients in PPT, although these can be linear when models are restricted to a single biome (Fig. 1, e.g. grasslands – Sala *et al.*, 2012). Temporal PPT–ANPP relationships from long-term site-level data are almost always portrayed as linear regardless of the ecosystem type (Fig. 1). Although more complex nonlinear statistical models have been fitted to some PPT–ANPP relationships, in most cases, linear and nonlinear models explain equal amounts of variation, nonlinearities tend to be weak, and support for nonlinear over linear models is minimal (Hsu *et al.*, 2012; Hsu & Adler, 2014).

Spatial and temporal models often share the same data, but the slopes of spatial relationships are usually much steeper than those of temporal models (Fig. 1). Thus, temporal models predict that ANPP will be less sensitive to future changes in PPT than do spatial models (Estiarte *et al.*, 2016). Several mechanisms have been posited to explain why spatial models predict greater sensitivity of ANPP to PPT. The most likely is that spatial models include both vegetation *and* PPT change along gradients of PPT, whereas

vegetation does not change appreciably over time in temporal models. This places a ‘vegetation constraint’ (Lauenroth & Sala, 1992) on ANPP responses to PPT at the site level. For example, plants in arid ecosystems tend to be smaller, with inherently slower absolute growth rates and reduced plant and meristem densities relative to those in more mesic ecosystems (Knapp & Smith, 2001; Huxman *et al.*, 2004; La Pierre *et al.*, 2016). As a result, ANPP responses to wet years in arid ecosystems are constrained by these plant community characteristics. Indeed, Gaitan *et al.* (2014) estimated that two-thirds of the increase in ANPP along regional PPT gradients in Patagonia could be attributed to changes in plant communities and not to direct responses to increased PPT. In addition, Sala *et al.* (2012) argued that ‘legacy effects’ of previous year’s PPT on current year’s ANPP are widespread. In this case, previous wet or dry years can dampen ANPP responses in subsequent years and reduce the slope of site-based PPT–ANPP relationships. Despite differences in sensitivity to PPT, both models predict that the sensitivity of ANPP to PPT decreases from dry to wet ecosystems, as a result of increasing biogeochemical limitations of ANPP as ecosystems get wetter (Huxman *et al.*, 2004).

Although climate change is expected to affect plant community and biogeochemical constraints on ANPP, both of which are implicitly incorporated into empirically derived spatial models, there is little evidence that spatial models are superior to temporal models for the prediction of ANPP responses to future changes in

PPT (Estiarte *et al.*, 2016; Wilcox *et al.*, 2016). For example, when predictions from temporal vs spatial models were compared with results from multiyear PPT manipulation experiments, temporal models performed consistently better (Estiarte *et al.*, 2016). This is probably because substantial changes in plant communities (turnover of dominant life-forms) and corresponding alterations in soil biogeochemistry only occur over very long time scales (decades to centuries; Smith *et al.*, 2009; Wilcox *et al.*, 2016). However, even over long time scales, the novelty of future climates and interactions with other global change drivers are expected to lead to communities that do not match current climate–vegetation patterns (Zarnetske *et al.*, 2012). Thus, at least for near to mid-term (decade to century) forecasts of climate change effects on ANPP, temporal models are preferred over spatial models (Estiarte *et al.*, 2016). These temporal models are the focus of the remainder of this review.

III. Inconsistencies with a linear temporal model

Evidence for positive asymmetry

Despite the near-universal use of linear models to describe the temporal relationship between PPT and ANPP (Fig. 1), results from a number of recent studies are inconsistent with an underlying linear relationship (Fig. 2). For example, when long-term PPT–ANPP relationships from multiple biomes were assessed,

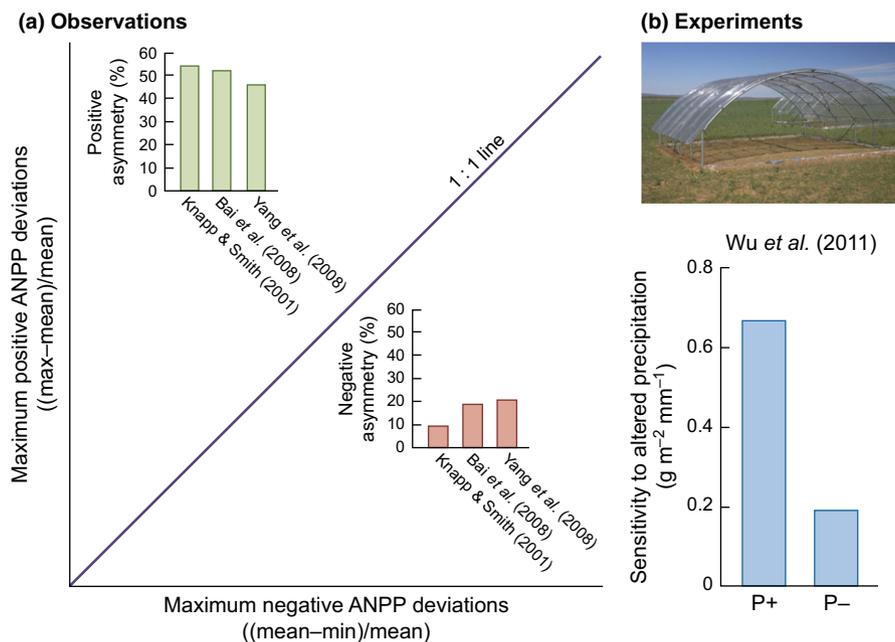


Fig. 2 Results from both observational and experimental studies are inconsistent with linear temporal relationships between aboveground net primary production (ANPP) and precipitation (PPT). (a) Three independent analyses of long-term PPT–ANPP datasets all display similar patterns of asymmetric responses to wet vs dry years (Knapp & Smith, 2001: 11 sites spanning a 300–1400-mm PPT gradient and multiple biomes; Bai *et al.*, 2008: 21 sites spanning a 100–500-mm PPT gradient and desert and steppe biomes; Yang *et al.*, 2008: 118 sites spanning a 100–1500-mm PPT gradient and multiple grassland types globally). Across these sites, the maximum positive deviations from mean ANPP were compared with the maximum negative deviations observed in long-term records. Sites with *positive asymmetry* (positive ANPP deviations > negative) were much more numerous (2–5-fold) than those with *negative asymmetry* (negative deviations > positive) or with symmetrical ANPP responses. (b) Consistent with this analysis of long-term observational data, Wu *et al.* (2011) synthesized results from 28 manipulative experiments that increased (P+) or decreased (P–) PPT, and found that sensitivity to alterations in PPT also displayed positive asymmetry, with responses of ANPP to increased PPT (g m⁻² mm⁻¹) more than threefold greater than ANPP sensitivity to reduced PPT. Photograph: a precipitation reduction experiment in Inner Mongolia, China (photograph credit: A. K. Knapp).

maximum ANPP values in response to high PPT years deviated more from the long-term mean than did minimum ANPP values in low PPT years (Knapp & Smith, 2001). This *positive asymmetry* in maximum vs minimum ANPP responses to PPT could not be explained by corresponding asymmetry in PPT, and suggests that ANPP in these ecosystems responded more to wet than dry years. Subsequent analyses of long-term data from > 100 additional sites revealed similar patterns of asymmetry worldwide (Fig. 2). Experimental manipulations of PPT offer further support for positive asymmetry in ANPP responses to PPT. Wu *et al.* (2011) synthesized results from 28 experiments and reported that ANPP was much more sensitive to increased than decreased PPT (Fig. 2). Unger & Jongen (2015) reported similar patterns from an even larger number of experiments. Further, they noted that positive asymmetry in ANPP responses to PPT was particularly pronounced in arid and semi-arid regions, as did Knapp & Smith (2001). Ahlström *et al.* (2015) reported positive asymmetries in GPP in semi-arid ecosystems as well. Taken together, these observational and experimental analyses are inconsistent with an underlying linear model describing the PPT–ANPP relationship.

Mechanisms that may lead to positive asymmetric responses in ANPP to PPT are varied. These include maintenance of ANPP during dry years as a result of the carry-over of soil water from previous years (Sala *et al.*, 2012), as well as plants increasing water use efficiency during drought years (Gutschick & BassiriRad, 2003; Huxman *et al.*, 2004). In wet years, other resources (e.g. soil nutrients) may be increased in concert with PPT, leading to higher than expected ANPP (Seastedt & Knapp, 1993). In addition, wet years are characterized by more numerous large PPT events compared with average and dry years (Knapp *et al.*, 2015), and these large events can have disproportionate positive impacts on ANPP, particularly in more arid ecosystems (Heisler-White *et al.*, 2008; Raz-Yaseef *et al.*, 2010).

Evidence for negative asymmetry

In contrast with the positive asymmetry in ANPP observed under conditions of nominal (baseline or contemporary) variability in PPT, there is mounting evidence that extreme PPT anomalies, which, by definition, are statistically rare (Smith, 2011), can lead to *negative asymmetry* in ANPP responses to PPT. Recent analyses of global satellite estimates of GPP spanning 30 yr, as well as model intercomparisons (Zscheischler *et al.*, 2014a,b) have revealed that negative impacts of extreme dry periods on GPP are much greater than positive effects of extreme wet periods. Consistent with this analysis, Luo *et al.* (2008) simulated NPP responses to extreme changes in annual PPT (doubling or halving) in multiple ecosystems, and reported that production responded much more strongly when PPT was reduced than when increased.

At the site level, empirical support for negative asymmetry is uncommon because extreme years are, by definition, rare (Smith, 2011), and are seldom encountered in long-term ANPP datasets. To overcome this, we extended a long-term PPT–ANPP relationship for a central US grassland to include experimentally imposed extreme wet and dry years (Hoover *et al.*, 2014; Wilcox *et al.*, 2016). When these PPT extremes are included, evidence of

negative asymmetry emerges at the site level as well (Fig. 3). This suggests that a nonlinear concave-down relationship between PPT and ANPP is more appropriate than a linear model when including extreme PPT years. Such a model predicts that ANPP responses to PPT will saturate in extreme wet years (Zhou *et al.*, 2008; Flombaum *et al.*, 2016), whereas a collapse in ecosystem function (perhaps driven by plant mortality; McDowell *et al.*, 2008) occurs with extreme drought.

IV. Revision of the temporal PPT–ANPP model to better forecast climate change impacts

With abundant evidence for positive asymmetry in ANPP responses to nominal interannual variability in PPT (Fig. 2) and negative asymmetry in ANPP when contrasting extreme wet and dry years (Fig. 3), why are linear rather than nonlinear models fitted to temporal PPT–ANPP relationships? As noted above, nonlinear models were fitted by Hsu *et al.* (2012) to long-term PPT–ANPP datasets and, consistent with these opposing types of asymmetry, they found some support for both concave-up and concave-down models. Overall, however, support for nonlinear over linear models

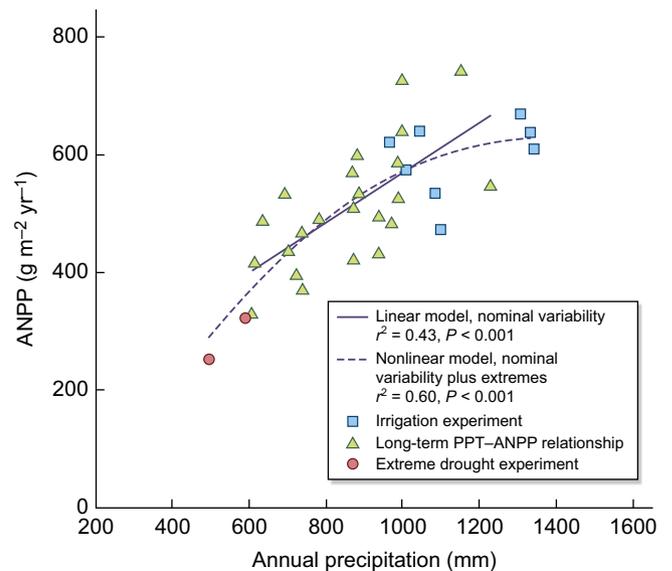


Fig. 3 Bending a linear temporal aboveground net primary production (ANPP)–precipitation (PPT) relationship by including extreme levels of PPT. Similar to long-term PPT–ANPP relationships in almost all terrestrial ecosystems, a linear model best fits this relationship in mesic grasslands of the central USA (green triangles, Konza Prairie Long-Term Ecological Research (LTER) data, 1991–2013). However, when ANPP responses to experimentally increased PPT (blue squares) and to experimentally imposed extreme drought (red circles) are included, a nonlinear model provides the best fit. Note that the asymmetry induced by pushing PPT to amounts beyond those found in the observational record is negative (reductions in ANPP mm^{-1} PPT are greater than increases in ANPP mm^{-1} PPT) and opposite to that observed under nominal conditions (Fig. 2). Responses of ANPP to increased PPT are from the initial 8 yr of an irrigation experiment (water added during growing season dry periods, from Wilcox *et al.*, 2016). Extreme dry years were imposed by removing 66% of growing season rainfall with infrastructure similar to the photograph in Fig. 2 (data from Hoover *et al.*, 2014). Linear model, ANPP = $144.9 + 0.42 \times \text{PPT}$; nonlinear model, ANPP = $648.8 / (1 + \exp(-(PPT - 544.4) / 228.2))$.

was weak and equivocal, and is probably a result of two key data limitations. First, even among years with similar levels of PPT, variability in ANPP can be quite high (Fig. 3), because ANPP is influenced by many factors in addition to PPT (Fahey & Knapp, 2007). Thus, the detection of relatively low magnitude nonlinearities in observational data is challenging. This is underscored by the much stronger evidence for positive asymmetry in experiments in which only PPT is manipulated (Fig. 2). Second, as noted earlier, extreme wet and dry years are rare (Smith, 2011) and PPT–ANPP relationships that include multiple extreme years are uncommon. Thus, the derivation of empirical models of the curvature of the PPT–ANPP relationship may require new experiments, with treatments that include multiple levels of increased and decreased PPT, as well as extreme PPT anomalies (Fig. 3). Results from such experiments would be invaluable for the parameterization of models, particularly if experimental data and models are integrated through data assimilation approaches (Luo *et al.*, 2011). An assessment of the impacts of longer duration PPT anomalies (multi-year droughts and wet periods) vs short-term (single-year) extremes on the PPT–ANPP relationship would also be valuable, although Hoover & Rogers (2016) argued that short-term extremes are likely to have the largest C cycle consequences. Regardless, it is clear that, given forecasts of increased PPT variability *and* extremes (IPCC, 2012), temporal PPT–ANPP relationships must be revised to better represent these dynamics.

We propose that a nonlinear ‘double asymmetry’ model (Fig. 4) will forecast climate impacts on ANPP much better than linear models. This new model includes both positive (slight concave-up)

asymmetry under conditions of nominal PPT variability and negative (strong concave-down) asymmetry when extended to extreme PPT years (Fig. 4). Although data are lacking to parameterize this (or other) nonlinear models for most ecosystems, this conceptual perspective highlights several important knowledge gaps. For example, the PPT level at which the PPT–ANPP relationship saturates, the maximum levels of ANPP with no water limitation and the PPT level beyond which ANPP declines (Schoor, 2003; Hubbart *et al.*, 2016; Fig. 4) are unknown for most biomes. Similarly, PPT thresholds below which ecosystem function (ANPP) strongly declines or collapses (Fig. 4) are largely unknown (Estiarte *et al.*, 2016). Yet, for global land models to simulate the C cycle consequences of an intensified hydrological cycle (Reichstein *et al.*, 2013), knowledge of these thresholds is critical. Indeed, recent calls for the evaluation of land models have identified accurate representations of PPT–productivity relationships as a benchmark for the assessment of model performance (Luo *et al.*, 2012).

V. Conclusions

Despite the widespread use of linear models to describe temporal PPT–ANPP relationships, evidence has accumulated that these fail to capture both the oft-observed positive asymmetric response in ANPP under nominal levels of interannual PPT variability (Fig. 2), as well as the much stronger negative asymmetric ANPP response expected when extreme PPT years occur (Fig. 4). Because both interannual PPT variability and extreme PPT years are forecast to

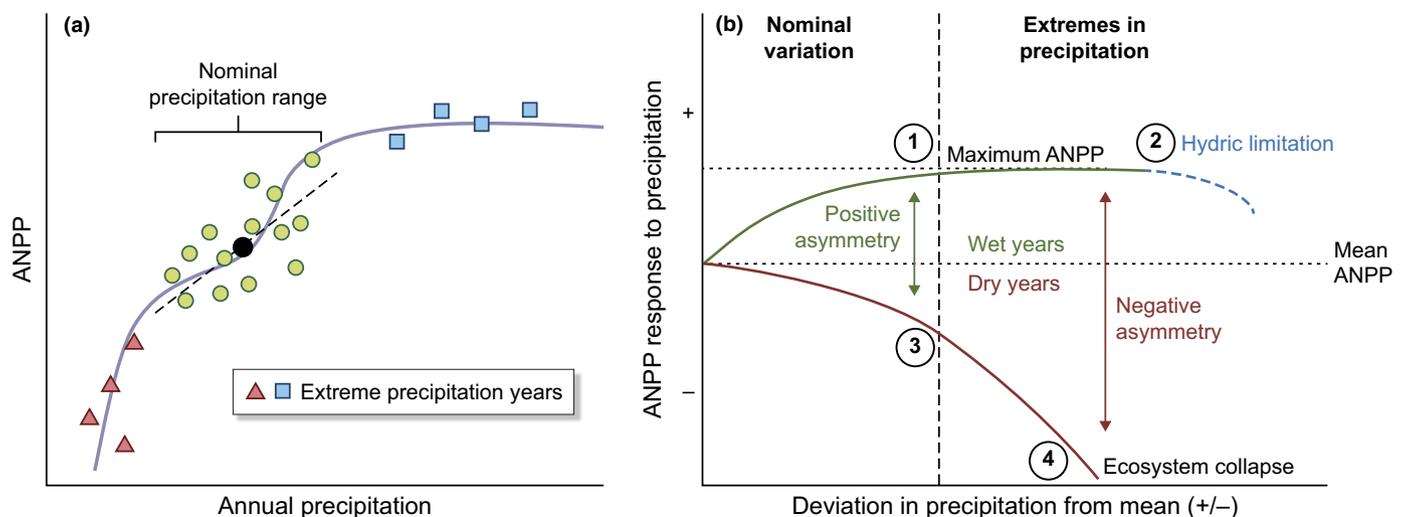


Fig. 4 Conceptual model depicting proposed nonlinear temporal relationships between aboveground net primary production (ANPP) and precipitation (PPT). (a) PPT–ANPP relationship displaying positive ANPP asymmetry under conditions of nominal variation in PPT (maximum ANPP deviates more strongly from the mean (black circle) than does minimum ANPP), but negative asymmetry at extreme precipitation levels (ANPP saturates in extreme wet years, but declines strongly in extreme dry years). This *double asymmetry* model is more consistent with results from experiments and long-term observations (Figs 2, 3) than are linear temporal PPT–ANPP models. Positive asymmetry in the PPT–ANPP relationship is difficult to detect with a regression approach under conditions of nominal variability in PPT because of high interannual variability in ANPP (green circles) in most ecosystems. Thus, a linear model (dashed regression line) usually provides the best statistical fit. (b) Double asymmetry model re-drawn to emphasize the comparative magnitudes of positive vs negative asymmetry in ANPP. This depiction also highlights four critical PPT thresholds (circles) in PPT–ANPP relationships that are unknown for most terrestrial ecosystems. These key knowledge gaps are: (1) the level of PPT required to maximize (saturate) ANPP; (2) the level of PPT that causes ANPP to decrease as a result of hydric limitations (direct or indirect effects of anoxia and pathogens: Schoor, 2003; Knapp *et al.*, 2008; Hubbart *et al.*, 2016); (3) the inflection point at which decreases in PPT lead to reductions in ANPP that deviate substantially from those expected from nominal variation in PPT; and, finally, (4) the reduction in PPT that leads to significant mortality, potential ecosystem collapse and possible ecosystem state change.

increase with climate change, a nonlinear form of the temporal PPT–ANPP relationship will almost certainly better predict responses of ANPP to changing PPT regimes (Fig. 4). Indeed, recent evidence suggests that several other key C cycle processes will probably respond asymmetrically to changing PPT regimes as well (Haverd *et al.*, 2016; Liu *et al.*, 2016). The use of an underlying double asymmetric model may be particularly important in semi-arid regions, in which positive asymmetries in ANPP are expressed most strongly (Unger & Jongen, 2015; Haverd *et al.*, 2016), because these ecosystems appear to play a disproportionate role in the global C cycle (Ahlström *et al.*, 2015). However, even for those terrestrial ecosystems in which positive asymmetries are less evident, temporal PPT–ANPP models should be extended to include extreme annual PPT values (Estiarte *et al.*, 2016). This will facilitate the identification of critical thresholds which, if crossed, can abruptly change the functioning of the world's major terrestrial ecosystems (Fig. 4), as well as greatly increase our ability to forecast the C cycle consequences of climate change.

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