

Editorial

Amazonian rain forests and drought: response and vulnerability

Natural variation in moisture availability affects the productivity of tropical ecosystems more profoundly than any other climatic variable. As a result, drought is perhaps the most important climatic threat to tropical forests. Climate-change scenarios for the 21st century have suggested decreased soil-moisture availability in certain regions of the world (Bates *et al.*, 2008). Notably, the rain forests of Amazonia have been considered to be at particular risk, especially when possible climate impacts are examined alongside an increased incidence of land-use change (Scholze *et al.*, 2006; Soares-Filho *et al.*, 2006; Malhi *et al.*, 2008).

'... a growing body of data is showing that Amazonian rain forests are highly (and negatively) responsive to strong, and especially extended, soil-moisture deficit in terms of aboveground and belowground processes, net ecosystem production (NEP) and mortality.'

Amazonia is home to perhaps 25% of the world's terrestrial species (Dirzo & Raven, 2003), comprises a total biomass that is equivalent to > 10 times the current annual global CO₂ emissions to the atmosphere (IPCC, 2007) and performs *c.* 15% of global terrestrial photosynthesis (Field *et al.*, 1998). Substantial losses of Amazonian forests and the species diversity they house would impact climate at regional and intercontinental scales through changes in land-atmosphere energy exchange and precipitation (Werth & Avissar, 2002; Marengo, 2006), and globally through increased atmospheric CO₂ concentrations and changes to the global balance of other key greenhouse gases such as nitrous oxide and methane.

However, despite repeated modelled scenarios for Amazonia of 21st century warming, drought and the resultant dieback of rain forest (White *et al.*, 1999; Cox *et al.*, 2000; Betts *et al.*, 2004; Scholze *et al.*, 2006; Sitch *et al.*, 2008), our ability to understand the true vulnerability to loss of the region's forests has been hampered, first, by insufficient field data and, second, by a weak understanding of the predictive skill of the models themselves. This is especially so for land-surface processes where large differences in the estimates of global CO₂ emissions have been found using different dynamic global vegetation models (DGVMs) driven using the same climate data (Friedlingstein *et al.*, 2006; Meir *et al.*, 2006). In addition, climate scenarios vary substantially among global circulation models (GCMs; Friedlingstein *et al.*, 2006; Li *et al.*, 2006), even when the GCMs are driven forward from observed 20th century data using only the predicted anomalies from the mean. Clearly, the most reliable data for understanding the response by forests to drought are ground measurements, but these inevitably lack reach over space and time. Remote sensing offers a partial solution, especially in the context of assessing vulnerability in relation to changes in land use and to fire incidence (e.g. Aragao *et al.*, 2008), but any remote sensing-based assessment of ecological responses remains uncertain in the absence of good correlations with ground data.

In this issue of *New Phytologist*, a special feature on 'Amazonian rain forests and drought' provides important advances in all of these areas. First, it reports new data analyses on growth, mortality, physiological responses and deep-soil-moisture supply during multi-year experimental drought (da Costa *et al.*, pp. 579–591; Markewitz *et al.*, pp. 592–607; Metcalfe *et al.*, 2010b, pp. 608–621; Lima *et al.* pp. 622–630), also substantially extending recent important findings (Phillips *et al.*, 2009) on the observed impacts of natural drought across the Amazon (Phillips *et al.*, pp. 631–646). Second, it presents new modelling insights evaluating the accuracy of process-level drivers of modelled dieback in different DGVMs (Galbraith *et al.*, pp. 647–665), the possible influence on productivity of poorly modelled demographic processes, such as mortality (Fisher *et al.*, pp. 666–681), an examination of the quality of different GCM climate scenarios used to drive DGVMs (Jupp *et al.*, pp. 682–693) together with their consequences for modelled vegetation responses in one particular DGVM (Rammig *et al.*, pp. 694–706) and a novel, simplified model analysis of the combined response by vegetation to changes in lightning frequency, as well as climate (Hirota *et al.*,

pp. 707–719). This modelling analysis is complemented by Ray *et al.* (pp. 720–732) who use an experimental approach to develop an environmental model of fire risk, relevant where natural or anthropogenic ignition sources may be prevalent. Finally, and in a timely manner given recent disagreement in the literature (Saleska *et al.*, 2007; Samanta *et al.*, 2010), we include a review of the utility of remote sensing to understand drought impacts on Amazon forest processes (Asner & Alencar, pp. 569–578). One element in this review is examined in a second, independent, remote sensing study that uses ground data to suggest that perceived resilience in productivity to moisture deficit inferred from remotely sensed data is probably better explained by structural differences in the canopy that may be related to mortality (Anderson *et al.*, pp. 733–750).

Although only about half of the papers in this special feature are based on the analysis of new data, the need for appropriate ecological understanding derived from field-based measurements emerges strongly. As noted for remote sensing (Anderson *et al.*, pp. 733–750), the modelling analyses reported here highlight important weaknesses in the representation of the real world. Galbraith *et al.* (pp. 647–665) show that the mechanisms underlying the most basic processes in DGVMs, such as soil-water access, photosynthesis and respiration, all vary substantially among models. The outcome is that modelled forest dieback during drought appears – surprisingly – to result more from the modelled physiological response to temperature than from moisture deficit. Underscoring this outcome and the need for model improvement, all of the DGVMs considered by Galbraith *et al.* (pp. 647–665) (which includes a version of the model ‘LPJ’ also used in this issue by Rammig *et al.*, pp. 694–706) were largely insensitive to moisture deficit when compared against the results from two large-scale multi-year drought experiments (da Costa *et al.*, pp. 579–591; Brando *et al.*, 2008). Does this mean that some DGVMs simulate forest decline during climatic warming and drying, but for the wrong reasons? Accurate ecophysiological parameterization, for example to soil-moisture deficit and acclimation to temperature, clearly needs close attention in ongoing DGVM developments.

Natural or experimental droughts will help to guide these improvements in physiological representation, but they are less useful in helping us address the long-standing uncertainty over the decadal-scale response by tropical forests to the increasing concentration of CO₂ in the atmosphere (Long *et al.*, 1994; Lloyd & Farquhar, 2008). Increased CO₂, shown here by Rammig *et al.* (pp. 694–706), and previously (Hickler *et al.*, 2008; Lapola *et al.*, 2009), could ameliorate the negative impacts of moisture deficit on photosynthesis, especially at tropical temperatures. If the increased efficiency in water loss per unit of fixed carbon (that often occurs at higher CO₂ concentrations) is large and long-lived, then, in the absence of increased fire

incidence or land-use change, resilience over the long term to reduced soil moisture is implied, and perhaps also to phosphorus deficiency (Lloyd *et al.*, 2001). Not only is there uncertainty over the size and persistence of this ecophysiological ‘fertilization’ response to increased CO₂, but also over its possible impact on forest dynamics and species composition: both effects could counterbalance the gains from ‘CO₂ fertilization’ (Körner, 2004; Phillips *et al.*, 2004). Given the importance of this question and the size of the tropical forest biome, a free-air CO₂ enrichment experiment in the tropics could usefully complement existing field-scale drought experiments.

In addition to enabling better model validation, the measurements reported here also underline the importance of data for new understanding. Resource access by roots remains poorly understood (Silver *et al.*, 2005), as do the drought responses by respiring cells in vegetation and soil (Meir *et al.*, 2008), but both could have profound influences on forest ecosystem resilience to drought. Here, Markewitz *et al.* (pp. 592–607) suggest that deep-soil-water supply (where available) may only confer drought resistance for up to 1–2 yr, and that hydraulic redistribution processes probably transfer much less water to vegetation than recently supposed. Furthermore, Lima *et al.* (pp. 622–630) use an irrigation experiment at a site in eastern Para with relatively shallow soil to show strong root-growth responses to soil-moisture deficit (but not to reduced nutrient availability), whilst Metcalfe *et al.* (2010b, pp. 608–621) use multiple-component flux estimates to build on a recent finding of increased leaf dark respiration during experimental drought (Metcalfe *et al.*, 2010a). The outcome is that extended drought might cause increasing net CO₂ emissions from the forest to the atmosphere (Metcalfe *et al.*, 2010b, pp. 608–621). This result requires further careful testing, but may also have consequences for perhaps the most important ecological response to drought: increased mortality.

It is possible, although uncertain, that raised autotrophic respiration rates increase the risk of mortality in drought-impacted trees (McDowell *et al.*, 2008; Sala, 2009). The drought experiments referred to in this issue of *New Phytologist* provide an ideal platform to test such a hypothesis, but irrespective of the outcome, the impact of drought on mortality appears to be strong and relatively similar across Amazonia. The two Amazonian drought (‘throughfall-exclusion’) experiments in eastern Amazonia at Tapajós and Caxiuanã were performed on forests with different soils and probably different natural disturbance histories (Nepstad *et al.*, 2002; Meir & Grace, 2005; Fisher *et al.*, 2007). Yet, despite these differences, the responses to experimental drought were quantitatively similar in terms of increased mortality, the timing of increased mortality and the medium-term decline (5–8 yr) in carbon storage (da Costa *et al.*, pp. 579–591). Furthermore, when these

experimental results were placed in the context of a regional-to-global analysis of the impact of natural drought events on mortality in tropical rain forests (Phillips *et al.*, pp. 631–646), the response to soil-moisture deficit was surprisingly predictable for Amazonia, and in one analysis quite linear. Although we might expect important differences in the mortality responses to natural drought events and multi-year experimental reductions in soil moisture, these results hint at surprising generality. In a modelling analysis, Fisher *et al.* (pp. 666–681) show that when variability in modelled demographic processes, such as mortality, are incorporated in a new DGVM structure, large differences in biomass storage during the 21st century can be expected. Consistent with this, da Costa *et al.* (pp. 579–591) describe tantalizing evidence to show that distinct adult taxa differ widely in their vulnerability to drought. Conversely, the narrow range of mortality responses observed by da Costa *et al.* (pp. 579–591), Phillips *et al.* (pp. 631–646) and Brando *et al.* (2008) could helpfully constrain part of the theoretical uncertainty highlighted by Fisher *et al.* (pp. 666–681), although we caution strongly that the mortality/soil-moisture-deficit responses observed in Amazonia do not extend to other tropical regions, such as Borneo, where sensitivity to drought appears to be markedly higher.

How do the studies in this special feature advance our overall ability to estimate the vulnerability of Amazon rain forests to drought? The answer lies at the intersection of field data, and our understanding of model realism. On the one hand, the new analyses provide evidence for unexpected consistency in tree mortality and growth under drought. This points to high vulnerability in both eastern and western parts of Amazonia, in some areas at an annual time-scale, although where initial resistance to moisture deficit has been observed, this resistance also appears to break down following an imposed drought of 3 yr or longer (da Costa *et al.*, pp. 579–591; Phillips *et al.*, pp. 631–646). Certainly, the measured vulnerability in aboveground biomass storage to drought over a 5–8 yr period is substantially higher than is represented in at least three leading DGVMs (Galbraith *et al.*, pp. 647–665). On the other hand, in an analysis of multiple GCM-generated future climate scenarios weighted by their ability to reproduce observed 20th century precipitation (Jupp *et al.*, pp. 682–693), the variability in the strength and spatial occurrence of 21st century changes in precipitation places constraints on the (estimated) likelihood of declines in moisture availability across the region. This outcome reduces the perceived vulnerability to moisture deficit for some, but not all, regions of Amazonia, and must also be considered in the context of uncertainty in the long-term physiological response to increased atmospheric CO₂ concentration.

Overall, a growing body of data is showing that Amazonian rain forests are highly (and negatively)

responsive to strong, and especially extended, soil-moisture deficit in terms of aboveground and belowground processes, net ecosystem production (NEP) and mortality. The long-term consequences of extended drought for the carbon balance and forest species composition of these forests are therefore substantial. When assessing the future vulnerability to forest loss from soil-moisture deficit alone we remain limited by our ability to predict both future precipitation patterns and some physiological responses. Only long-term research can help us address these fundamental questions, pointing to the central importance of extending the observational and experimental climate and vegetation data sets that have already been developed for this region (e.g. Keller *et al.*, 2009). However, when expected feedbacks between vegetation and climate are combined with fire incidence and land-use change scenarios, we conclude that Amazon rain forests are highly vulnerable to loss during the coming decades. Yet this loss and its consequences are not inevitable: whether or not possible transitions to more depauperate vegetation types are sudden and caused by forest clearance and fire (Hirota *et al.*, pp. 707–719; Nepstad *et al.*, 2008), are strongly mediated by differences in soil fertility and neighbouring species assemblages (Meir & Pennington, 2010), or are constrained successfully through sustainable resource-management practices (Soares-Filho *et al.*, 2006; Nepstad *et al.*, 2008; Ricketts *et al.*, 2010), remain central questions for Amazonian ecosystem science and environmental governance.

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Patrick Meir

School of Geosciences, University of Edinburgh,
Edinburgh, UK
pmeir@ed.ac.uk

F. Ian Woodward

Editor-in-Chief, *New Phytologist*
f.i.woodward@sheffield.ac.uk

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Discovering biodiversity and its dynamics

The United Nations declared 2010 to be the International Year of Biodiversity in which everyone should play some part in safeguarding the Earth's diversity of living organisms. Individuals will have different visions of what constitutes the conservation of biodiversity, ranging from saving iconic species or small patches of species-rich habitat, to saving spatial scales of sufficient size from which the combined activities of the component species derive important ecosystem functions. All of these scales provide targets for conservation, and all can aim for the dual benefit of conserving species and at least some ecosystem characteristics. At large spatial scales there is often an interest in conserving virgin vegetation that has escaped human influences. Rackham (2008) points out, for woodlands at least, and even extending to the Amazon, that such virgin types probably do not exist in climates suitable for human habitation. The human footprint is ubiquitous and has many forms, from direct destruction to global-scale fumigation by oxides of nitrogen and CO₂ from industrial activities. These large-scale phenomena can drive changes in biodiversity (Xia & Wan, 2008) and, potentially, *in situ* evolution (Onoda *et al.*, 2009). The question of exactly what biodiversity should be conserved is difficult to answer, particularly when the biodiversity has rarely been quantified – anywhere.

The diversity of flowering plants is easy to see but this can only hint at a much higher belowground diversity. The application of molecular techniques for investigating fungal diversity has been a major boon to those working in soil. Recent work shows that under a temperate forest including oak and beech, as little as 4 g of soil may contain > 2000 species of fungi (Buée *et al.*, 2009; F. Martin pers. comm.), while just the leaves of bur oak may host one-third of this number of species (Jumpponen & Jones, 2009). Perhaps only 1% of this high species diversity dominates numerically, but the cut-off point for identifying important or useful species has no theoretical basis.

Global-scale travel of people and plants affects biodiversity by enhancing the geographical spread of many species, which become identified as alien species. Even buried species of ectomycorrhizal fungi hijack rides on plant roots to new locations (Vellinga *et al.*, 2009). These invasive plant species can exert large impacts on major ecosystem