Drought-induced forest decline: causes, scope and implications

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A large number of episodes of forest mortality associated with drought and heat stress have been detected worldwide in recent decades, suggesting that some of the world’s forested ecosystems may be already responding to climate change. Here, we summarize a special session titled ‘Drought-induced forest decline: causes, scope and implications’ within the 12th European Ecological Federation Congress, held in Ávila (Spain) from 25 to 29 September 2011. The session focused on the interacting causes and impacts of die-off episodes at the community and ecosystem levels, and highlighted recent events of drought- and heat-related tree decline, advances in understanding mechanisms and in predicting mortality events, and diverse consequences of forest decline. Talks and subsequent discussion noted a potentially important role of carbon that may be interrelated with plant hydraulics in the multi-faceted process leading to drought-induced mortality; a substantial and yet understudied capacity of many forests to cope with extreme climatic events; and the difficulty of separating climate effects from other anthropogenic changes currently shaping forest dynamics in many regions of the Earth. The need for standard protocols and multi-level monitoring programmes to track the spatio-temporal scope of forest decline globally was emphasized as critical for addressing this emerging environmental issue.

Keywords: climate change; drought; forest die-off; land-use changes; tree mortality

1. INTRODUCTION

Forests cover approximately 30 per cent of the land surface, and provide key services to ecological systems and society, including the regulation of climate and the hydrologic cycle, among many others [1]. Consequently, there is growing concern about how climate change may alter the distribution, composition and function of forests and the services they provide, particularly regarding the carbon cycle and feedbacks on climate forcing [2]. A recent assessment of tree mortality associated with drought and heat stress identified 88 well-documented episodes over the past 30 years worldwide [3]. Although attribution to changing climate is uncertain, the findings suggest that forests may be increasingly at risk, and that associated predictions of future mortality events are needed.

Our ability to predict which forests (and under which circumstances) are vulnerable to die-off is in large part constrained by our limited understanding of the physiological mechanisms leading to drought-induced tree mortality. A recent physiological review of drivers of tree mortality focused on the relative roles of hydraulic failure versus carbon starvation (owing to prolonged negative carbon balance) [4] and was followed by some studies highlighting a central role of C [5,6]. However, substantial debate ensued about the possibility of carbon starvation and the degree of detail needed to resolve the mechanism [7]. Subsequent updates highlight that hydraulic failure and carbon starvation are likely to be interrelated [8,9].

Collectively, this recent research activity set the stage for a special session on drought-induced forest decline within the 12th European Ecological Federation Congress ‘Responding to rapid environmental change’, held in Ávila (Spain) from 25 to 29 September 2011. Participants included scientists from Europe, North America and Australia working on a variety of ecological systems, scales and approaches.

2. RECENT ADVANCES

(a) Scope

Drought-related tree mortality is termed ‘die-off’ for events in which a large proportion of trees die in a population. It is a concept related to forest ‘decline’ or ‘die-back’, although the latter terms sometimes refer to partial mortality affecting only peripheral plant parts. An update of the aforementioned global review of drought- or heat-induced tree mortality [3], based on post-2009 publications and additional observations documented new episodes of forest mortality in all continents and an increasing number of scientific papers on the topic (Craig D. Allen, US Geological Survey). Numerous specific cases were highlighted, including Scots pine (Pinus sylvestris), one of the most widely distributed trees on Earth, which has exhibited extensive mortality in the Alps (Andreas Rigling, WSL, Switzerland). In Spain, a multi-decadal dataset from the European ICP Forest monitoring programme (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) and the Spanish National Forest Inventory enabled analysis of trends in forest condition that revealed increased crown defoliation associated with recent droughts, as well as widespread increases in standing tree mortality between 1989–1996 and 1997–2007 [10] (Marta Coll, CREAF, Spain). Additional drought-induced tree mortality events have been documented for Southern Australia, for which bioclimatic analysis indicates that long duration droughts of medium to high intensity are most likely to result in forest die-off. Both forests on shallow soils and on more mesic sites were vulnerable, suggesting that landscape patterns may be complex (Patrick Mitchell, CSIRO, Australia). Overall, much uncertainty remains regarding recent and past patterns of

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change, and a more global coordination of observations through an organized network is clearly needed (C. D. Allen).

(b) Causes
Given the emerging patterns of drought-induced forest die-off and projections of hotter drier conditions for much of the world, improved predictions of future mortality are needed [9]. However, the causes underlying tree mortality are complex and uncertain, potentially involving a plethora of biotic factors (insect pests, pathogens and mistletoes) predisposing, inciting or contributing to drought-induced mortality (A. Rigling). Scots pine is becoming a model species for the study of drought-induced decline, based on studies spanning multiple scales and approaches [11,12], including irrigation and thinning experiments (A. Rigling). Piñon pine (Pinus edulis) is another emerging model species for studying drought-induced tree mortality. Experimental evidence collected on this species was consistent with carbon starvation as a driving factor [4,5], with more recent work suggesting how carbohydrate availability in plants may interact with water transport and defence against biotic agents under severe drought [8,9] (David D. Breshears, University of Arizona, USA). Advances in the mechanistic modelling of the mortality process are also being made. The Castanea model was modified to include the various processes involved in carbon starvation and applied to recent Silver fir (Abies alba) decline in the Mount Ventoux area in Southern France (Hendrik Davi, INRA, France). These simulations were compared with measured series of radial growth, and highlighted the impact of juvenile growth rates on subsequent carbon allocation, the importance of leaf area regulation in limiting mortality and the key role of fine root dynamics. This latter aspect remains greatly understudied, despite the fact that it determines a fundamental link between the plant carbon and water balances. Additionally, radial growth patterns of now dead or declining trees were compared with those of coexisting healthy individuals, for both Douglas fir (Pseudotsuga menziesii; Anne-Sophie Sergent, INRA, France) and Scots pine (Juan Pedro Ferrio, University of Lleida, Spain). In both cases, less conservative growth was observed in declining trees, suggesting possible lower allocation to storage and resistance structures.

(c) Implications
Drought-induced tree mortality can potentially affect carbon, energy and water balances at large geographical scales, as well as modifying plant communities and populations dynamics. Such impacts are challenging, because they are likely to be big, fast and patchy, pervasively affecting ecosystem goods and services [13] (D. D. Breshears). For example, important implications of forest decline have been highlighted for the composition and functioning of soil communities in a long-declining Scots pine forest in northeast Spain. In this forest, Holm oak (Quercus ilex) seems to be progressively replacing pines as the dominant canopy species. Interestingly, soil respiration rates and the composition of soil microbial communities under dead pines differed from those under healthy pines and appeared to be more similar to those under nearby Holm oaks, even before any signs of local colonization of this species aboveground could be observed (Jorge Curiel Yuste, CREAF and CSIC, Spain). Importantly, some of the recent research highlights potential mitigation options through management (e.g. forest management may effectively reduce competition for water and thus improve tree condition in declining forests; A. Rigling, P. Mitchell), or adaptation options when mitigation is not feasible (D. D. Breshears).

3. SYNTHESIS AND OUTLOOK
The recent advances related to scope, causes and implications led to discussion organized around three main topics (Jordi Martinez-Vilalta, CREAF, Spain): (i) Is forest decline increasing? (ii) Can we predict which forests are more vulnerable? and (iii) What is the role of non-climatic drivers of global change in the observed decline?

It is important to note that studies that have shown consistent increases in tree mortality or defoliation with time are still rare [10,14]. There was an agreement on the need for global databases and widespread monitoring programmes using common protocols to detect mortality episodes and attribute causality. The diversity of definitions of drought, and the need to standardize the measurement of drought intensity to allow the separation of truly extraordinary episodes from those within the observed historical variability were identified as major challenges. Multi-level approaches combining different scales of measurement, from extensive networks of plot-level measures to remote sensing, seem best suited at present to establish the spatial and temporal scale of the events, as well as to detect the existence of trends.

Predicting which forests are more vulnerable to drought-induced die-off has proved a difficult task. Recent studies have shown that even tropical rainforests can be highly vulnerable to drought [15]. At the intraspecific level, things are not much easier, since it is not always clear that populations living in drier locations are more vulnerable [12]. Some progress has been made in characterizing the growth patterns of more vulnerable trees within a population. Trees that are about to die are frequently characterized by higher growth rates when they were young and by a sharp growth decline in the years immediately preceding death [11]. It remains to be established how juvenile growth relates to carbon allocation and storage. It is now emerging that hydraulic failure and carbon starvation are not independent mechanisms [9], and that an improved understanding of their role in tree mortality requires an integrated approach that takes into account: (i) the changes in the capacity to mobilize and transport stored carbohydrates under extreme drought (cf. [7]) and (ii) their involvement in the production of defence compounds and the refilling of embolized xylem [8].

Incorporating intraspecific variability into drought responses at different ecological scales in our conceptual and predictive models of vegetation dynamics remains an important challenge. Pre-adaptation to drought, phenotypic plasticity and intra-population variability have the potential to reduce mortality.
when trees are exposed to new conditions. At the same time, local adaptation may constrain the range of possible responses to unprecedented climatic conditions. Overall, the examples of well-documented vegetation shifts induced by drought are still relatively few, considering the magnitude of the climate change we have already experienced in most regions of the Earth. Although the possibility of threshold-type responses is real and should be taken into account, the resistance and the resilience of plant communities to changes in climate can also be substantial [16], and deserves further study.

If a common pattern emerges from the plethora of recent studies on drought-induced tree mortality is one of complexity, with multitude of causes and contributing factors, each of them frequently acting at different spatial and temporal scales. It is clear that drought and warmer temperatures, perhaps associated with recent climate change, are involved in many cases, but other factors also must be operating. Human influences on forests have been pervasive throughout the Holocene, and some of these impacts have built up over the last decades. It is impossible to understand the timing and the distribution of recorded mortality episodes without accounting for past changes in forest management and land use. In Western Europe, tree mortality seems to be associated with forest densification owing to widespread abandonment of intensive forest management [12]. In southwestern USA and other savannah systems around the world, recent vegetation dynamics seem to be explained, at least in part, by changes in patch-scale grazing and cascading effects through modifications in fire regimes [17,18]. Clearly, much of the recent drought-induced decline is interrelated with non-climatic components of human-induced forest change, and this interrelationship needs to be disentangled—a daunting challenge. More generally, drought-induced tree mortality and associated forest decline are an emerging and complex phenomenon with respect to patterns, mechanisms and impacts, all of which will need to be addressed as climate change progresses.

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