Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements


Global climate change is projected to produce warmer, longer, and more frequent droughts, referred to here as “global change-type droughts”, which have the potential to trigger widespread tree die-off. However, drought-induced tree mortality cannot be predicted with confidence, because long-term field observations of plant water stress prior to, and culminating in, mortality are rare, precluding the development and testing of mechanisms. Here, we document plant water stress in two widely distributed, co-occurring species, piñon pine (Pinus edulis) and juniper (Juniperus monosperma), over more than a decade, leading up to regional-scale die-off of piñon pine trees in response to global change-related drought. Piñon leaf water potentials remained substantially below their zero carbon assimilation point for at least 10 months prior to dying, in contrast to those of juniper, which rarely dropped below their zero-assimilation point. These data suggest that piñon mortality was driven by protracted water stress, leading to carbon starvation and associated increases in susceptibility to other disturbances (eg bark beetles), a finding that should help to improve predictions of mortality during drought.

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designated as the zero assimilation point (Lajtha and Barnes 1991), can be estimated from leaf-level measurements of gas exchange over a range of water potentials. If plant water potential remains at or below the zero assimilation point for a protracted period, metabolic depletion of carbon reserves should eventually lead to tree mortality (McDowell et al. 2008), even though stomatal closure has prevented transport failure.

As described above, our understanding of the mechanistic basis of tree mortality is limited by the availability of long-term water potential measurements that describe pre-drought variability and drought response of trees, particularly of species that exhibit differential mortality responses. Here, we report monthly, pre-dawn water potential in piñon and juniper individuals over more than a decade, a period that culminated in a severe drought across the southwestern US in 2000–2003. This drought was characterized by higher temperatures than a previous, severe drought event in the region during the 1950s, thereby representing a global change-type drought (Breshears et al. 2005). It also resulted in extensive mortality of a widely distributed tree species, piñon pine (Pinus edulis), while individuals of the co-occurring juniper species (Juniperus monosperma) largely survived (Breshears et al. 2005; Figure 1). The resultant mortality was of sufficient magnitude to transform landscapes (Figure 2) and highlights how the impacts of climate change may be driven by changes associated with events rather than by trends (Jentsch et al. 2007). We discuss insights revealed by the long-term plant water potential data and relate them to ongoing development of more mechanistic models for assessing vegetation die-off (McDowell et al. 2008).

Methods

The study was conducted at the Mesita del Buey site at Los Alamos National Laboratory, near Los Alamos, NM (35.85° N, 106.27° W; Breshears 2008). The site is at an elevation of 2140 m and has an annual precipitation of ~ 400 mm, mainly in the form of winter snowfall and late-summer precipitation. Mean ambient air temperature is ~ 9°C, and ranges from –2°C in January to 21°C in June, and soil depth varies between 33 to 125 cm. Tree canopy cover prior to the mortality event was ~ 50%, divided roughly equally between J monosperma and P edulis (Breshears 2008). More than 90% of the piñons across the site died between 2002 and 2003, in response to the severe drought, whereas nearly all the junipers at the site survived (Breshears et al. 2005). Several species-specific physiological relationships (Lajtha and Barnes 1991) and patterns of root and foliar water uptake (Breshears et al. 1997; Breshears et al. 2008) have been quantified at this site, which aids in interpreting and extrapolating site observations (see references in Breshears 2008).

Pre-dawn plant water potentials were measured on five trees of each species, using standard methods (Breshears et al. 1997), approximately every 4 weeks from 1992 through the 2000–2003 drought, until after the death of all measured piñon trees. Measurements continued through mortality of piñon individuals, which occurred over a period of 11 months, beginning in August 2002 and ending in July 2003. After the initiation of the drought, individual piñon trees were evaluated every month, concurrently with plant water potential measurements, for signs of infestation by bark beetles (eg bore holes).

Results

Prior to the onset of the drought (March 1992–September 2001), long-term mean pre-dawn water potential for individual piñons averaged ~1.38 MPa (mega-Pascals; individuals ranged from ~1.33 to ~1.43 MPa; Figure 3). During periods of severe drought (October 2001–December 2003), mean piñon water potential decreased to ~2.35 MPa (with individual means ranging from ~2.11 to ~2.66 MPa) and all measured piñons died after pre-dawn water potential remained below the zero assimilation point (Lajtha and Barnes 1991) continuously for at least 10 months (Figure 3). In contrast, all juniper trees studied survived the drought, with plant water potential only

Figure 1. A semi-arid piñon–juniper woodland near Los Alamos, NM, after an unusually warm drought – a global change-type drought – resulted in mortality of piñon pine trees (Pinus edulis), while junipers (Juniperus monosperma) survived.

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species limit transpiration to maintain relatively constant mid-day leaf water potential, which severely constrains carbon assimilation (Williams and Ehleringer 2000; McDowell et al. 2008). The widespread mortality observed after the water potential of the piñon trees dropped below their zero carbon assimilation value for more than 10 months contrasted with the recovery observed after 0–4-month periods of similar stress, and brackets the duration of drought that probably can be tolerated by piñon, potentially reflecting the longevity of stored energy resources.

Although juniper water potentials were frequently lower than those for piñon, juniper exhibits anisohydric behavior, allowing leaf water potential to decrease as soil water potential decreases. This stomatal behavior resulted in shorter periods where water potential was below the species-specific zero assimilation threshold for juniper. Juniper appears to be more drought tolerant than piñon, based on numerous physiological and morphological characteristics, including cavitation relationships (eg 100% stem cavitation occurs at about –11 MPa for juniper but at only about –7 MPa for piñon; Pockman et al. 1995; Linton et al. 1998; West et al. 2007). In addition, junipers are more drought tolerant with respect to transpiration and photosynthesis responses (Lajtha and Barnes 1991) and are even able to substantially reduce water stress through foliar absorption of intercepted rain (Breshears et al. 2008). The piñon mortality associated with protracted water stress was probably driven by carbon starvation (McDowell et al. 2008), although increased vulnerability to cavitation in xylem previously cavitated and refilled (so-called “cavitation fatigue”; Hacke et al. 2001) might also have contributed to mortality. The reported species-specific zero assimilation points, which were based on controlled phytotron (controlled growth chamber) experiments, are approximate but appear to be broadly applicable for both species on the basis of three other sets of observations. First, field mea-
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References


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