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

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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 (e.g., 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). 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...
rarely falling below the zero assimilation point of –4.5 MPa (Lajtha and Barnes 1991), and never for longer than 4 months (Figure 3).

Several conditions characterized the lead-up to piñon mortality. In the decade prior to the onset of the drought, piñon trees recovered on nine separate occasions from a drop in water potential to below the species-specific zero assimilation point; these periods accounted for only 8–17% of the measurement dates and were never longer than 3–4 consecutive months. In contrast, beginning in October 2001, all five measured piñon trees had plant water potentials below the zero assimilation point for 57–100% of the remaining measurement dates up through mortality [mortality of the five individual trees occurred at 10, 14, 21, 22, and 22 months (respectively) after October 2001]. Water potentials for all five trees were below the zero assimilation point for at least a 10-month consecutive period prior to mortality. Piñon trees exhibited signs of infestation by bark beetle (*Ips confusus*) only late in the 10 continuous months of water stress preceding mortality (8 months or later into that period), with infestation by bark beetles observed for all piñon individuals prior to mortality.

### Discussion

Piñon mortality appears to result from protracted water stress that is of sufficient severity to constrain these trees below their zero carbon assimilation point. This prolonged period without carbon uptake may exhaust stored carbon reserves and predispose the trees to the effects of other stressors, such as bark beetles. The limitation of leaf-level gas exchange implicit in this phenomenon is consistent with stomatal regulation of gas exchange to avoid water transport failure (Sperry et al. 2002; McDowell et al. 2008). Piñon is regarded as isohydric (West et al. 2007), regulating transpiration to maintain a constant mid-day leaf water potential as soil water potential varies. With declining soil water potential, isohydric 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-
measurements spanning a range of environmental conditions showed a similar relationship between photosynthesis and plant water potential, including the zero assimilation point (Lajtha and Barnes 1991). Second, the plant water potential associated with zero assimilation in piñon is the same as that observed at sites across the region and for other periods of time (Williams and Ehleringer 2000). Third, other studies have observed minimum values of plant water potential for *P. edulis* close to its zero assimilation threshold (West et al. 2007). With respect to the role of infestation by bark beetles, previous research has shown that susceptibility to infestation is interrelated with plant water stress (Allen and Breshears 1998; Breshears et al. 2005; Shaw et al. 2005). Our results are consistent with that perspective, and add to it in documenting the magnitude of water stress that occurred prior to observable infestation and subsequent tree mortality.

Our observations directly document plant water stress leading to widespread mortality; in contrast, only precipitation data have been available in many previous studies (eg Allen and Breshears 1998). Furthermore, because the conditions leading up to the piñon mortality that we document are associated with global change-type drought, our results may be particularly relevant for projecting future changes in vegetation under a changing climate. A concurrently developed synthesis on the mechanisms of tree mortality, which highlights drought responses by piñon and juniper as a case study, proposes a broad framework for the roles of cavitation, protracted water stress, associated carbon starvation, and biotic agents (eg bark beetles) in contributing to species-specific responses associated with tree mortality (McDowell et al. 2008). Our results support a key prediction of that framework: that piñon mortality is driven by protracted water stress and carbon starvation caused by stomatal closure to avoid cavitation, rather than by uncontrolled and extensive cavitation alone. In highlighting the contrasting trajectories of water stress between co-occurring species that diverge in patterns of mortality and survival following global change-type drought, our results provide a key insight on how climate change drives vegetation responses.

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### References


