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Underappreciated plant vulnerabilities to heat waves

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Summary

With climate change, heat waves are becoming increasingly frequent, intense, and broader in spatial extent. However, while lethal effects of heat waves on humans are well documented, the impacts on flora are less well understood, perhaps except for crops. We summarize recent findings related to heat wave impacts including: sub-lethal and lethal effects at leaf and plant scales, secondary ecosystem effects, and more complex impacts such as increased heat wave frequency across all seasons, and interactions with other disturbances. We propose generalizable practical trials to quantify the critical bounding conditions of vulnerability to heat waves. Collectively, plant

vulnerabilities to heat waves appear to be underappreciated and understudied, particularly with respect to understanding heat-wave driven plant die-off and ecosystem tipping points.

Key words: climate change, die-off, drought, extreme events, heat waves, mortality, warming

I. Introduction

Substantial upticks in extreme climatic events in the last decade have exposed an alarming gap in the scientific literature with regard to their ecological impacts: we have focused disproportionately on mean change, over extremes, when it is the extremes that induce widespread impacts such as mortality and ecosystem state change (Smith, 2011; IPCC, 2012; Ruthrof *et al.*, 2018). Similarly, plant scientists have prioritized research on drought and its impact on physiological dynamics at the expense of studying heat stress *per se.* For example, only ~1% of >400 references relating to plant mortality reviewed for 2010-2015 had results of experiments that proceeded through mortality and included a warming treatment with drought (Allen *et al.*, 2015).

Changes in the rate and extent of plant mortality associated with climate change and the underlying mechanisms have rapidly become one of the most pressing issues in plant science over the past decades. Related research (Fig. 1) initially focused on drought alone (ambient drought) and then progressed to focus on “hotter drought” or “global-change-type drought” where drought occurs under warmer conditions as global temperatures increase (Breshears *et al.*, 2005; Allen *et al.*, 2015). Such hotter drought, observed globally (Allen et al., 2010; 2015) ,has been shown experimentally to hasten tree mortality during drought (Adams *et al.,* 2009; 2017) as warming exponentially increases vapor pressure deficit (Breshears *et al.*, 2013; Grossiord et al. 2020).

Legacy effects of prior drought have also been shown to be influential (Liu *et al.*, 2018; Matusick *et al.*, 2018). However, an important but little studied aspect of plant response to climate change is the effect of heat waves on plant mortality (Fig. 1)—a topic also largely absent from recent climate assessments (IPCC, 2014; IPCC, 2018). Heat wave effects on plants were previously reviewed primarily in terms of sub-lethal effects at tissue and leaf scales, with some information on seedling mortality (Teskey *et al.*, 2015). Recently, however, forest die-off in southwestern Australia was directly linked to a heat wave that occurred during an ongoing “hotter drought” (Matusick *et al.*, 2013). This same heat wave event extended across >5 degrees of latitude of Western Australia, causing substantial mortality in >10 species of trees and shrubs (Ruthrof *et al.*, 2018). In addition, other demographic events such as recruitment (Adams *et al.*, 2017) and cone production (Enright *et al.*, 2015; Parmenter *et al.*, 2018) are also temperature sensitive and are likely affected by heat waves. Collectively, these recent findings suggest the importance of heat waves on plant responses may be highly underappreciated in a warming world.

The definition of a heat wave varies among research sectors (Perkins & Alexander, 2013). The most commonly used meteorological definition (i.e. regardless of ecological consequences) for a terrestrial heat wave is three or more consecutive days where the maximum temperature is over the 90th percentile for a particular location at a particular time (Perkins & Alexander, 2013). With only a small increase in mean temperature at a site, there is a large increase in the number of days over a given temperature threshold, as well as in number of heat wave events (Fig. 2). The frequency of very hot days (those exceeding the 99^{th} percentile of daily maximum temperature) has more than tripled during the past century (Founda *et al.*, 2004; Founda, 2011; Scherrer *et al.*, 2016). On top of projections of increasing mean global temperatures (IPCC, 2018), global climate models project an increase in frequency, intensity and duration of heat waves in the future (Meehl & Tebaldi, 2004; Seneviratne *et al.*, 2012; Coumou *et al.*, 2013; IPCC, 2013; Perkins-Kirkpatrick & Gibson, 2017; Guerreiro *et al.*, 2018), as well as increases in absolute record temperatures (Abatzoglou & Barbero, 2014). Land area affected by heat waves is expected to quadruple by 2040 (Coumou & Robinson, 2013). Furthermore, in combination with drought, the increase in intensity of heat waves has been linked to land–atmosphere coupling, with dry soils due to drought further amplifying temperature extremes, especially in Europe (Miralles *et al.*, 2019), and parts of Northern Australia (Hirsch *et al.*, 2019).

In this Tansley Insight, we summarize key recent findings related to heat wave impacts in context of four levels of impacts—sub-lethal, lethal at the plant scale, secondary ecosystem effects, and more complex compound events—such as increased heat wave frequency and occurrence at novel times of the year, as well as interactions with other disturbances. We emphasize woody plants and crops, although our discussion has relevance for non-crop herbaceous plants. We conclude by identifying urgent and practical trials required to understand the bounding conditions of vulnerabilities of plants and ecosystems to heat waves that must be addressed if we are to predict the full magnitude of anticipated consequences associated with rapid climate change. Space limitations and the focus of

Tansley Insights on recent literature preclude detailed discussion of prior related plant ecophysiology studies, although heat wave effects are reviewed in Teskey *et al*. (2015) and earlier work on thermal effects (e.g., Hahdy, 1936; Nelson, 1952).

II. Heat wave effects: sub-lethal, lethal, secondary, and compound

Sub-lethal impacts. Heat waves induce a range of sub-lethal impacts on plants spanning physiological function, growth, and reproduction, including trait types (annual, perennial; C3,C4) and settings (natural, agricultural) (Niu *et al.*, 2014; Felton & Smith, 2017). Physiologically, minimum leaf conductance influences plant water loss to the atmosphere, which can affect the intensity of heat waves (Kala *et al.*, 2016; Duursma *et al.* 2019). In plants that have undergone but survived observational and experimental heat waves, a decoupling has been documented in which photosynthesis decreases while transpiration increases (De Kauwe *et al.*, 2019). Additionally, heat wave experiments on a range of *Eucalyptus* tree species revealed warming and heatwave induced reductions in photosynthesis and nocturnal stomatal conductance (Aspinwall *et al*., 2019, Resco de Dios *et al*., 2018). There is strong concurrence that such physiological relationships need to be further resolved and subsequently implemented appropriately into models (Urban *et al.* 2017; de Dios *et al.* 2018; Duursma et al. 2019). In particular, the relative roles of temperature, atmospheric drought, and soil drought need to be understood in the context of different trait groups.

In terms of growth and reproduction, heat wave impacts on annual crops include lower biomass and yield in maize (simulated heat waves: *Zea mays*, Siebers *et al*., 2017) and predicted yield reductions in Africa and Asia of 15-35% via reduced pollen viability and seed mass (Ortiz *et al*., 2008). Within natural ecosystems, heat waves significantly affect seed set and canopy cover (Groom *et al*., 2004; Enright *et al*., 2015). In southwestern Australia, an iconic tree, *Banksia hookeriana,* experienced a >50% reduction in seed set in response to increased temperature coincident with chronic drought (Enright *et al.*, 2015). Such studies highlight profound demographic impacts, as well as the difficulty most field-based studies have in attributing impact to drought, to heat waves, or to both. Thus, heat waves are likely an underestimated factor in assessing sub-lethal plant impacts of climate change, including those relevant to global food security (Battisti & Naylor, 2009; Feng *et al*., 2019; Mehrabi, 2020).

Lethal effects at the plant and organ level. Plant mortality related to heat and drought has become a topic of major interest (McDowell *et al.*, 2008), with rapid expansion in the literature (Choat *et al.*, 2018; Brodribb *et al.*, 2020). The few studies that have experimented with heat waves, however, primarily test agricultural species' crop loss and yield reductions (Zampieri *et al.*, 2017). For annual crops, crop failure is closely related to plant lethality whereas for perennials, crop failure may be sub-lethal or lethal, although there are few published studies on this. Heat over drought impacts on crops are emphasized by modelling of simultaneous crop failure for which risk increases disproportionately as global temperature increases from 1.5 to 2°C (Gaupp *et al.*, 2020). Experimental heat waves with drought resulted in increased mortality in *Pinus halepensis* seedlings, explained by high needle temperatures resulting from low transpiration rates, rather than from hydraulic failure in the shoot (Birami *et al.*, 2018). Heat wave impacts on native plant species and their associated ecosystems are increasingly reported and are best documented in terms of mortality for tree and shrub species in southwestern Australia (Matusick *et al.*, 2013; Ruthrof *et al.*, 2018; but see Drake *et al.,* 2018 for survival through an experimental heat wave). Heat wave impacts on native species and ecosystems are unlikely to be mitigated by management interventions used for crops such as irrigation, fertilization, shading, and thinning, thereby increasing mortality risks.

Plants that survive longer during a heat wave or other heat-drought events can regulate their heat exchange with the surrounding air via convection or latent heat loss (Parkhurst & Loucks, 1972). Heat exchange from leaf to air is greatly affected by leaf size and shape (Leigh *et al.*, 2017). For example, a two-day heat wave of >45 ^{o}C extensively damaged shrub leaves, but less so for thicker leaves (Groom *et al.*, 2004). Roots, particularly in shallow soils, can be sensitive to heat stress, although most past studies on intact plants have imposed chronic rather than abrupt heat stress (e.g., heat waves; Heckthornet al. 2013).

Secondary effects on ecosystems. Heat waves can also have secondary or indirect effects on ecosystems (Matusick *et al.,* 2018; Nowicki *et al.*, 2019). For example, a heat wave and drought-induced forest die-off in southwestern Australia triggered significant loss of live standing biomass (49.3 t carbon ha$^{-1;}$ Walden *et al.*, 2019). That forest die-off event resulted in adult mortality and altered regeneration of a key midstorey species, *Banksia grandis,* indirectly affecting an important food source of an endangered cockatoo (Steel *et al.*, 2019). There have also been shifts in rhizosphere microbial communities following heat-wave triggered forest die-off (Hopkins *et al.*, 2018). Collectively, these examples paint a picture of cross-scale, secondary impacts of heat waves. Attempts to predict ecological impacts of heat waves should recognize that direct and indirect biotic and abiotic effects can operate through different and often interacting pathways (Nowicki *et al.*, 2019).

Compound events and sequences. Heat waves, like any environmental disturbance, are draped across heterogeneous landscapes experiencing many other disturbance events such as fire, flood, fragmentation, and drought. Therefore, heat wave impacts are not isolated but interact with other events which may have already occurred, co-occur (especially drought or fire), or will occur in the near future. A useful conceptual framework is 'linked and compound' disturbances (Buma, 2015), where linked disturbances relate to an altered probability of occurrence, extent, or severity of a second event, and compound disturbances relate to the biotic response such as survival or regeneration following a second event being altered due to the initial event (see Gower *et al.*, 2015 for examples of both types). These interactions may be additive but just as likely multiplicative, thereby increasing or decreasing heat wave impacts depending on disturbance type, timing, order, and ecosystem. For example, increased fuel loads from a heat wave/drought event elevated fire potentials in eucalypt forest (Ruthrof *et al.*, 2016). Hotter drought including a heat wave can also be a precursor to insect attack (Seaton *et al.*, 2015; Wills & Farr, 2017; Seaton *et al.*, 2020).

III. Insights and research needs

Heat wave events present a profound disruption to plants and ecosystems globally via the pathways and mechanisms we briefly highlighted here. In a review of drought impacts on forests, the following factors were designated as 'high confidence factors' related to plant mortality driven by hotter drought that we argue also apply similarly to heat wave impacts: (1) droughts eventually occur everywhere; (2) warming produces hotter droughts; (3) atmospheric moisture demand increases nonlinearly with temperature during drought; (4) mortality can occur faster in hotter drought, consistent with fundamental physiology; (5) shorter droughts occur more frequently than longer droughts and can become lethal under warming, increasing the frequency of lethal drought nonlinearly; and (6) mortality happens rapidly relative to growth intervals needed for forest recovery (Allen et al., 2015). Beyond these six factors, we identify two new high confidence factors that indicate heat waves are likely to become a significant problem: (7) heat waves will become more frequent and extensive as a result of warming, and (8) the shift towards increased frequency of heat waves will result in more lethal events, analogous to (5), because temperatures will increasingly surpass mortality thresholds with extreme heat wave conditions. Together, heat wave events pose a major global threat which will become increasingly evident. Because of the past focus on drought, scientific knowledge has lagged and the science community now finds itself playing catchup with urgent knowledge deficits in key aspects of heat wave impacts.

Rapid global change underscores the urgency of generating applicable knowledge that is global in scope portraying vulnerability of organisms and ecosystems to heat wave events; time is not on our side to conduct lengthy mechanistic-oriented studies, at least initially. We know that annual crop failure can occur in hours to days. Based on temperature response surfaces for chronic warming with drought (Adams *et al.* 2017), we have evidence that responses to mortality may increase linearly with warming (Fig. 3). We hypothesize heat wave atop drought to accelerate these responses (Fig. 3). To gain an integrative understanding of the magnitude, scope, and vulnerability of key plants globally to heat waves, we suggest a battery of trials should be conducted using controlled (e.g. growth chamber), standardized single heat wave events (Fig. 4). While recognizing that probabilities of heat wave duration and magnitude will vary through space and time as warming progresses, we nonetheless suggest that a common heat wave event would enable direct controlled comparisons that could be adjusted subsequently with site- and time-specific probabilities of occurrence. We suggest a 10^{o}C magnitude and a 7-day duration as a heat event over ambient conditions during the hottest weeks of the year, which should be of sufficient severity to trigger responses, but with a reasonable probability of occurrence so as not to be too unusual (>~99th percentile). We suggest first testing the effect of this type of heat wave event for representative species in the different ecosystem types in Earth systems models, as well as for key crop species. We then propose systematic testing of heat wave magnitude, duration and base/ambient temperature effects to rapidly expand our understanding of their impacts. Species chosen for study should span a broad range of traits and ecosystem types including critical agricultural and native foundational species. We propose the most urgent work should focus on four essential and practical trials that scientists progressively implement to assay lethal and sub-lethal (e.g. biomass and reproduction) responses. Each of the four trials proposed assess overall heat wave vulnerability, heat wave attributes of timing, duration, and magnitude, and impacts from sub-lethal to lethal. Together, the battery of trials proposed would delineate the bounding thresholds for single heat wave events. Whether via this plan or some other, we urgently need to focus on developing globally relevant datasets to enable rapid estimation of vulnerability of spatiotemporal risks of heat waves on plants and the ecosystem services they provide.

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Figure Legends

Fig. 1. A matrix of representative studies, including experimental, reviews and observations examining non-lethal, lethal impacts under ambient, warming and heat wave conditions on trees. E, Experiments; R, Reviews; O, Observations.

Fig. 2. Daily maximum temperature (a), number of days over 40°C (b) and number of heat wave events (c) for Perth, Western Australia for historic (1911-1936; grey) and current (1989-2018; red) periods. A small change in the overall distribution has led to a 2x increase in days >40°C and a 1.5x increase in heat wave events. The Perth Airport station is part of the Australian Bureau of Meteorology (BOM) quality controlled station database: ACORN-SAT http://www.bom.gov.au/climate/data/acorn-sat/. Site number 9021, latitude: 31.93°S, longitude: 115.98°E, elevation: 15 m, data available from 1910. Heat wave indices were calculated using CLIMPACT2 (https://github.com/ARCCSS-extremes/climpact2) using a 1971-2000 reference period.

Fig. 3. Hypothesized relationships between duration of stress (drought / mean warming / compounded by heat wave) and temperature (T) (including a threshold for heat waves) and their effect on plants (not stressed, sublethal, dying, initiation of first dead, through population die-off).

Fig. 4. A proposed general and flexible set of four essential and practical trials to quantify the bounding conditions of heat wave vulnerability. Growth chamber studies on seedlings and saplings, while limited in some respects, provide an opportunity for controlled comparisons across key species in quantifying relative sensitivities. Initial growth chamber experiments would generate a common baseline where ambient temperature (e.g. mean diurnal temperature cycles from the hottest 4 weeks of the year based on local climate history), preceded with a period of plant acclimation (e.g. minimum ~4 weeks) and started under well watered soil conditions that initiate a single dry down. When soil moisture begins to become highly limiting (e.g., when a soil moisture retention curve of volumetric water content vs. water potential reaches the inflection point (van Genuchten 1980)). Priority measurements would be growth, biomass, reproductive output, browning, and death, but could include more mechanistic physiological measures when feasible. We deliberately prioritize a ‘whole plant’ approach to achieve globally synthetic data but acknowledge ample opportunities to measure plant organs such as leaves and roots.

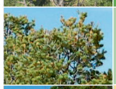
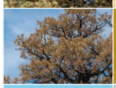
		Ambient base temperature	Warmer base temperature	Heat wave – alone or compounded
	No stress under well-watered conditions	Birami *et al.* (2018) *Pinus halepensis* (E)	McDowell *et al.* (2019) *Pinus edulis* (E)	Birami *et al.* (2018) *Pinus halepensis* (E) Aspinwall *et al.* (2019) Multiple spp. (E)
	Stress from seasonal drought	Teskey *et al.* (2015) Multiple spp. (R)	Blackman *et al.* (2019) *Corymbia calophylla* (E)	
	Initial responses to extreme drought, including crown die-back	Teskey *et al.* (2015) (R)		
	Initiation of tree mortality	Birami *et al.* (2018) *Pinus halepensis* (E)	Allen *et al.* (2010) FEM Multiple spp. (R–O)	Birami *et al.* (2018) FFGC *Pinus halepensis* (E)
	Population scale die-off	Allen & Breshears (1998) *Pinus ponderosa* (O)	Breshears *et al.* (2005) *Pinus edulis* (O)	Ruthrof *et al.* (2018) Multiple spp. (O)

Figure 1

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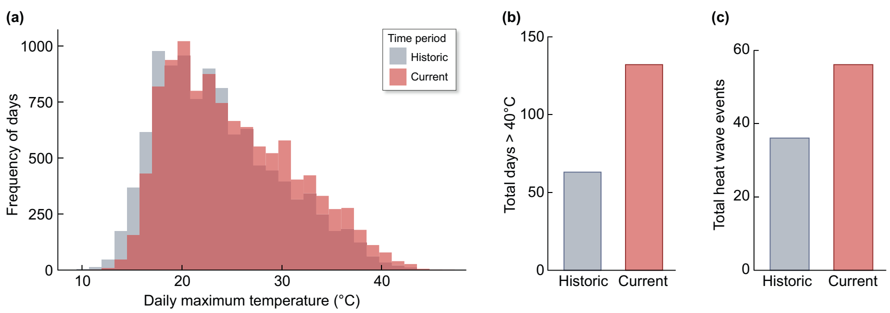

Figure 2

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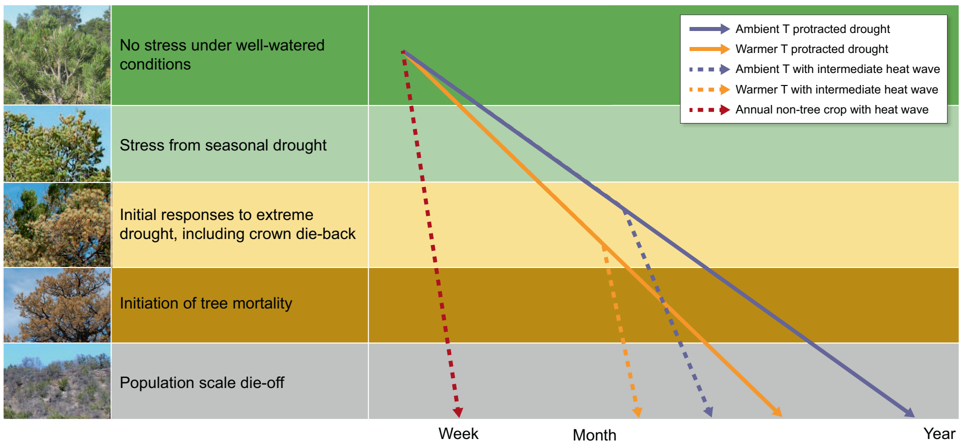

Figure 4

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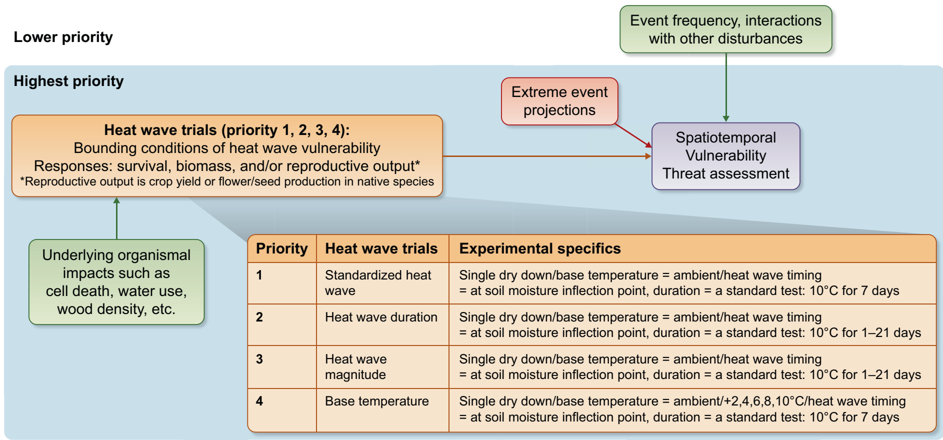

Figure 4

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