



## Tansley review

# Plant responses to rising vapor pressure deficit

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Received: 31 May 2019  
Accepted: 4 February 2020

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## Contents

Summary	1550	VI. Modeling plant and ecosystem responses to VPD	1559
I. Introduction	1551	VII. Conclusion	1561
II. Rising VPD under global warming	1552	Acknowledgements	1561
III. Mechanisms of stomatal responses to VPD	1554	References	1562
IV. Variability in sensitivity to VPD across species and ecosystems	1555		
V. Impact of high VPD on carbon and water relations and drought-induced mortality	1557		

## Summary

*New Phytologist* (2020) **226**: 1550–1566  
doi: 10.1111/nph.16485

**Key words:** mortality, productivity, stomatal conductance, transpiration, warming.

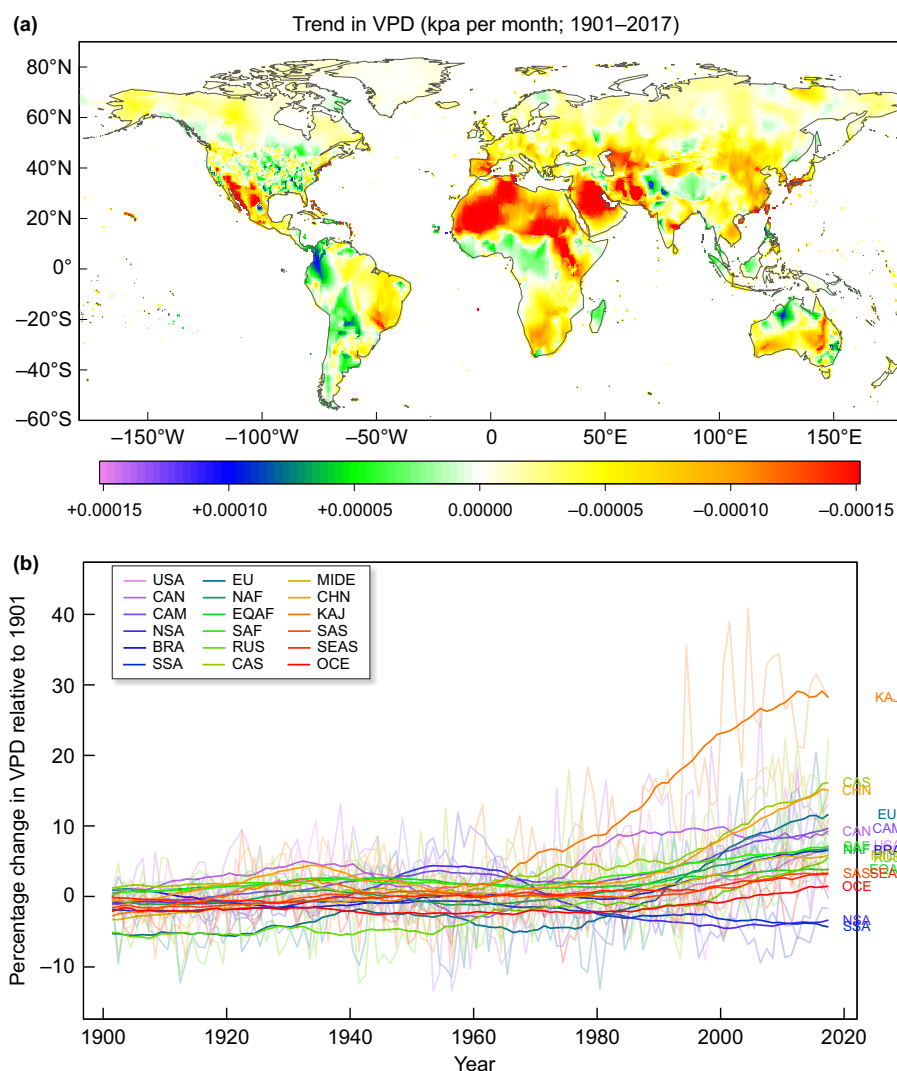
Recent decades have been characterized by increasing temperatures worldwide, resulting in an exponential climb in vapor pressure deficit (VPD). VPD has been identified as an increasingly important driver of plant functioning in terrestrial biomes and has been established as a major contributor in recent drought-induced plant mortality independent of other drivers associated with climate change. Despite this, few studies have isolated the physiological response of plant functioning to high VPD, thus limiting our understanding and ability to predict future impacts on terrestrial ecosystems. An abundance of evidence suggests that stomatal conductance declines under high VPD and transpiration increases in most species up until a given VPD threshold, leading to a cascade of subsequent impacts including reduced photosynthesis and growth, and higher risks of carbon starvation and hydraulic failure. Incorporation of photosynthetic and hydraulic traits in 'next-generation' land-surface models has the greatest potential for improved prediction of VPD responses at the plant- and global-scale, and will yield more mechanistic simulations of plant responses to a changing climate. By providing a fully integrated framework and evaluation of the impacts of high VPD on plant function, improvements in forecasting and long-term projections of climate impacts can be made.

## I. Introduction

The amount of water vapor that the air can hold – that is, the saturation vapor pressure – is a curvilinear function of air temperature (Lawrence, 2005). Thus, global land surface temperature rise is increasing the saturation vapor pressure of the atmosphere. However, the actual vapor pressure has not been increasing at the same rate, such that the difference between the saturation and actual vapor pressure, hereafter the vapor pressure deficit (or VPD), is rising (Hatfield & Prueger, 2015; Fig. 1; see Box 1 for summary of abbreviations used in the article). An increase in VPD, and more specifically in leaf-to-air vapor pressure deficit ( $VPD_L$ ), affects plant physiology independently of other drivers associated with climate change, for example elevated carbon dioxide concentrations ( $[CO_2]$ ). High VPD typically causes plants to close their stomata to minimize water loss and avoid critical water

tension within the xylem (Running, 1976), which occurs at the cost of reduced photosynthesis. Simultaneously, transpiration rate increases with high VPD up to a point, after which it either remains high or starts decreasing (Franks *et al.*, 1997), resulting in a further exacerbation of plant water stress. Along with its direct impact on plant physiology, high VPD results in increased rates of water loss from moist soils, in turn causing drying and heating of the terrestrial surfaces and contributing to more frequent and severe drought events and plant water stress (Dai, 2013). As such, VPD is a major determinant of global water resources and plant water relations, and could become increasingly important for vegetation dynamics over the coming decades due to its chronic, global, temperature-driven rise.

While much of our attention has been directed towards plant responses to high temperature (Hughes, 2000; Lindner *et al.*, 2010; Way & Oren, 2010), reduced precipitation (Bréda *et al.*, 2006;



**Fig. 1** Trend in annual vapor pressure deficit (VPD) for the period 1901–2017, estimated using VPD calculated from air temperature and vapor pressure from the Climate Research Unit (CRU) v. TS 3.26 (Harris *et al.*, 2014) (a), and percent change in VPD relative to 1901 averaged for the regions given here. Bold lines have a 10-yr smoothing function applied (United States (USA), Canada (CAN), Central America (CAM), Northern South America (NSA), Brazil (BRA), Southwest South America (SSA), Europe (EU), Northern Africa (NAF), Equatorial Africa (EQAF), Southern Africa (SAF), Russia (RUS), Central Asia (CAS), Mideast (MIDE), China (CHN), Korea and Japan (KAJ), South Asia (SAS), Southeast Asia (SEAS), Oceania (OCE)) (b). [Correction added after online publication 20 March 2020; the x-axis of panel (a) and key descriptors in panel (b) have been corrected.]

**Box 1** List of abbreviations. 11.1.

Abbreviation	Definition
VPD	Air vapor pressure deficit (commonly in kPa)
VPD <sub>L</sub>	leaf-to-air vapor pressure deficit (commonly in kPa)
$e_s$	Saturation vapor pressure (commonly in kPa)
$e_a$	Actual vapor pressure (commonly in kPa)
RH	Relative humidity in the atmosphere (commonly in %)
$g_s$	Stomatal conductance (commonly in mol of $H_2O\ m^{-2}\ s^{-1}$ )
$g_{sref}$	$g_s$ at 1 kPa VPD
$\Psi_L$	Leaf water potential (commonly in MPa)
$K_{leaf}$	Leaf hydraulic conductance (commonly in $mmol\ of\ H_2O\ m^{-2}\ s^{-1}\ MPa^{-1}$ )
$G_{surf}$	Stand-level surface canopy conductance (commonly in mol of $H_2O\ m^{-2}\ s^{-1}$ )
$A$	Photosynthetic $CO_2$ assimilation (commonly in $\mu mol\ of\ CO_2\ m^{-2}\ s^{-1}$ )
$T$	Transpiration (commonly in mm of $H_2O\ d^{-1}$ )
$\delta^{13}C$	Carbon isotopic composition (commonly in ‰)
$c_i/c_a$	The ratio of intercellular ( $c_i$ ) to ambient ( $c_a$ ) $CO_2$ concentrations
$[CO_2]$	Atmospheric carbon dioxide concentration (commonly in ppm)
$m$	Slope between $g_s$ and $\log_e(VPD)$ (commonly in mol of $H_2O\ m^{-2}\ s^{-1}\ log_e(kPa)$ )
ET	Evapotranspiration (commonly in mm of $H_2O\ d^{-1}$ )
NPP	Net primary productivity (commonly in $g\ C\ m^{-2}\ yr^{-1}$ )
GEP	Gross ecosystem-level productivity (commonly in $g\ C\ m^{-2}\ yr^{-1}$ )
iWUE	Intrinsic water use efficiency (commonly in $\mu mol\ of\ CO_2\ mol^{-1}\ of\ H_2O$ )
$\lambda$	Lagrange multiplier
$P$	Leaf xylem pressure (commonly in MPa)
$K$	Soil-to-canopy hydraulic conductance per leaf area (commonly in $mmol\ of\ H_2O\ m^{-2}\ s^{-1}\ MPa^{-1}$ )
$P_{soil}$	Soil water potential (commonly in MPa)
$V_{cmax}$	Maximum carboxylation velocity (commonly in $\mu mol\ of\ CO_2\ m^{-2}\ s^{-1}$ )
$J_{max}$	Maximum rate of electron transport (commonly in $\mu mol\ of\ CO_2\ m^{-2}\ s^{-1}$ )

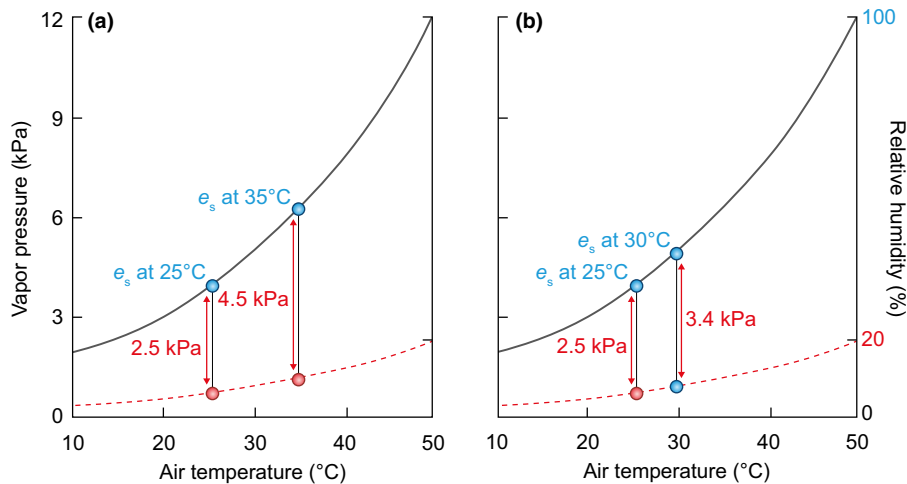
Allen *et al.*, 2010; Knapp *et al.*, 2017) and rising atmospheric carbon dioxide concentration (Ceulemans & Mousseau, 1994; Ainsworth & Long, 2005), the independent physiological effects of high VPD on vegetation dynamics remain less explored. Part of the uncertainty associated with VPD impacts on plants relates to the difficulty of disentangling VPD effects from temperature, radiation and other climate drivers of plant function (but see Novick *et al.*, 2016). For instance, on a diurnal or seasonal basis, high VPD conditions tend to co-occur with high radiation, making it difficult to untangle their relative effects. Similarly, high VPD conditions also usually occur in nature concurrently with stresses such as heat waves and droughts (i.e. periods of anomalously low precipitation) that are often thought to have the dominant impact on plant physiology. However, the relative role of VPD vs other climatic

drivers, particularly other stressors associated with recent climate change, may be much higher than previously thought. For instance, extended periods of high VPD have been acknowledged as a primary driver of large-scale tree mortality in forest ecosystems (Breshears *et al.*, 2013; Williams *et al.*, 2013), as being positively correlated with wildfires (Williams *et al.*, 2014; Seager *et al.*, 2015), and as being responsible for reductions in crop production (Challinor & Wheeler, 2008; Lobell *et al.*, 2011, 2013; Asseng *et al.*, 2015; Zhao *et al.*, 2017).

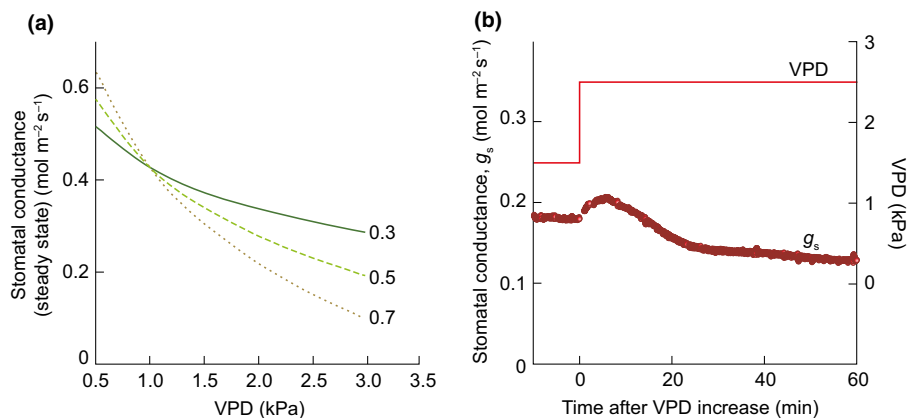
The primary objective of this review is to shed light on plant responses to high VPD. In the different sections we provide a review of fundamental knowledge on what VPD represents from a plant's perspective and how VPD is expected to shift under future climate conditions; describe the mechanisms by which stomata detect and respond to variation in VPD; highlight the variability in plant stomatal sensitivity to VPD across species and biomes, and its potential drivers; describe the recent trends in plant performance (i.e. photosynthesis, transpiration, growth and mortality) resulting from high VPD; and discuss how plant responses to VPD have been and may be incorporated in the next generation of small- and large-scale dynamic vegetation models. This review addresses VPD impacts in all climatic regions. Most empirical studies investigating VPD impacts include other co-varying factors; thus impacts of VPD on vegetation cannot always be discussed independently of other parameters, such as radiation, temperature and rising atmospheric  $CO_2$  concentrations. Although in this review we also included studies in which co-variation with other factors is present, we highlight and discuss which evidence includes other factors that could influence plant responses.

## II. Rising VPD under global warming

Over the past 30 yr, global surface temperature has risen by *c.* 0.2°C per decade (IPCC, 2019). Warming increases the amount of water vapor the air can hold at saturation – the saturation water vapor pressure ( $e_s$ ) (Bohren *et al.*, 2000). The actual vapor pressure of the air ( $e_a$ ) is constrained at the upper end by  $e_s$  so that as air temperature increases, so does the maximum amount of water vapor (i.e. there is equilibrium between evaporation and saturation).  $e_a$  is also dependent on the amount of moisture in the air. VPD, which is a direct measure of the atmospheric desiccation strength, represents the difference between  $e_s$  and  $e_a$  ( $VPD = e_s - e_a = e_s - (RH \times e_s/100)$ , where RH is the relative humidity in the air in percent; Monteith & Unsworth, 1990). Because  $e_s$  is driven only by temperature, it increases during periods of high air temperature (i.e. heat waves) and results in higher VPD following a nonlinear relationship (De Boeck *et al.*, 2010; Fig. 2). Long-term changes in VPD are still uncertain as they will depend both on  $e_s$  and on the extent of water movement limitation from the land surface to the atmosphere under future climate. While numerous studies have reported that RH will remain constant at the global scale under future scenarios (Dai, 2006; McCarthy *et al.*, 2009), others have suggested a negative (Byrne & O'Gorman, 2018) or positive (Shenbin *et al.*, 2006) trend at regional scales. Nevertheless, some studies have highlighted a sharp increase in global VPD in recent decades (Zhang *et al.*, 2015; Yuan *et al.*, 2019; Fig. 1), and others



**Fig. 2** Relationship between atmospheric vapor pressure (kPa), and relative humidity (%) as a function of air temperature. The bold line represents the saturation vapor pressure ( $e_s$ ) as a function of temperature (i.e. 100% humidity at any given temperature). Vapor pressure deficit (VPD, kPa) represents the difference between  $e_s$  (i.e. bold line) and the actual vapor pressure at a given temperature (dotted lines). Panel (a) shows shifts in VPD for one scenario representing typical temperature changes during extreme heat waves: relative humidity remains constant at 20% (red dotted line) but temperature increases from 25°C to 35°C, resulting in an increase in VPD of 2.0 kPa (i.e. from 2.5 to 4.5 kPa, red arrows). Panel (b) shows shifts in VPD corresponding to projected long-term changes in temperature and humidity under a business-as-usual scenario: relative humidity remains stable (20%; red dotted line) and air temperature rises by 5°C (from 25°C to 30°C), resulting in an increase in VPD of 0.9 kPa (i.e. from 2.5 to 3.4 kPa, red arrows). The figure highlights that with rising temperature we should expect a simultaneous increase in VPD both during extreme events (a) as well as over the long-term (b).



**Fig. 3** Sample steady-state (a) and dynamic (b) responses of stomatal conductance ( $g_s$ ) to vapor pressure deficit (VPD). Data are reproduced from (a) Mott & Parkhurst (1991), and (b) Buckley (2016). In (a), the symbols are experimental measurements and the lines are theoretical responses using the empirical model of Oren *et al.* (1999) ( $g_s = g_{s,ref} \cdot (1 - m \cdot \log_e(VPD/VPD_{ref}))$ ), where  $g_{s,ref}$  is the value of  $g_s$  at  $VPD = VPD_{ref} = 1$  kPa (taken from the experimental measurements in this example,  $g_{s,ref} = 0.43 \text{ mol m}^{-2} \text{ s}^{-1}$ ), and  $m$  represents the slope between  $g_s$  and  $\log_e(VPD)$ ; the numbers shown to the right of each line represent the corresponding value of  $m$ .

have predicted a continuous rise in VPD over the next century using general circulation models (Williams *et al.*, 2013; Ficklin & Novick, 2017).

Plant scientists interested in the physiological impacts of VPD variation (i.e. at the leaf- or plant-level) often use  $VPD_L$  to estimate VPD from a plant perspective because the leaf temperature can deviate from that of the ambient air (i.e. it can become higher or lower via transpirative cooling). The temperature of plant canopies is a function of energy exchange processes that are dependent on the amount of energy that enters via solar radiation and ambient heat, and energy that exits the canopy via heat loss, reflected light and transpired water (Monteith & Unsworth, 1990). Boundary layers surrounding each leaf, or the

entire canopy, allow transpired water to humidify the air surrounding the leaves, uncoupling VPD at the leaf surface from that in the bulk air (Jarvis & McNaughton, 1986). As canopy–atmosphere coupling decreases and boundary layer increases, the role of radiation on leaf temperature becomes more important, while the role of  $T$  is progressively reduced. Consequently,  $VPD_L$  is the more accurate value for the evaluation of the leaf water balance (and possibly for the whole plant- and even canopy-level).  $VPD_L$  is calculated as the difference in the water vapor pressure in the leaf (usually assuming saturation vapor pressure within the stomatal pore, i.e. 100% RH, but see later sections on this assumption) minus the water vapor pressure of the ambient air (Dai *et al.*, 1992; Day, 2000; Marchin *et al.*, 2016).



### III. Mechanisms of stomatal responses to VPD

A rapid increase in  $VPD_L$  typically induces a decrease in steady-state stomatal aperture and stomatal conductance,  $g_s$  (Fig. 3a). In seed plants (though not in seedless plants), this response is preceded by a transient change in  $g_s$  in the opposite direction; that is stomata 'pop open' before closing following exposure to increased  $VPD_L$  (Fig. 3b), within 2–25 min (Buckley *et al.*, 2011). The transient response arises from a decrease in the 'backpressure' imposed on stomata by epidermal cells, and the steady-state response arises from an even larger drop in guard cell turgor, driven by the actively mediated efflux of osmotic solutes (Buckley, 2005). Overall, no consensus exists on the exact sensing mechanisms and processes driving the stomatal closure response to increased  $VPD_L$ . In angiosperms this response is thought to involve active sensing of water status in cells somewhere within the leaf, possibly in the mesophyll, the vasculature, and/or in stomatal guard cells themselves, likely mediated by hormonal signals like abscisic acid (Saliendra *et al.*, 1995; Comstock & Mencuccini 1998; Buckley, 2005; McAdam & Brodribb, 2016). Leaf water potential ( $\Psi_L$ ) and hydraulic conductance ( $K_{leaf}$ ) determine how epidermal water potential and guard cell turgor respond to changes in  $VPD_L$  (Sharpe *et al.*, 1987) and thus are likely major controls of stomatal response to  $VPD_L$  (Franks & Farquhar 1999). Midday depression in  $g_s$  is common in many plant species (Schulze *et al.*, 1974; Grassi *et al.*, 2009) and has been associated with variation in midday stem water status (Zhang *et al.*, 2013), supporting the idea that stomatal response to  $VPD_L$  is strongly related to the hydraulic characteristics of the whole plant, as well as the leaf (Brodribb & Jordan, 2008).

Stomatal regulation is directly responsible for controlling leaf-level transpiration ( $T$ ) response to  $VPD_L$  so that when  $VPD_L$  is low and stomata are fully open,  $T$  increases linearly with  $VPD_L$ . However, the effects of  $VPD_L$  on water loss vary widely among species. By re-evaluating a large set of  $g_s$  and  $T$  responses to  $VPD_L$ , Monteith (1995) concluded that in most studies, stomatal closure was induced by guard cells sensing the increased rate of  $T$  through the stomatal pore. This 'feed-back' response results in  $T$  increasing nearly in proportion to  $VPD_L$  (regime A in Monteith, 1995). However, other studies reported declining rates of  $T$  under high  $VPD_L$  (Schulze *et al.*, 1972; Franks *et al.*, 1997; Cunningham, 2004; Whitley *et al.*, 2013). This phenomenon is known as the 'feed-forward' response (Farquhar, 1978). While various mechanisms have been proposed to explain this response, further experiments are required to improve our understanding of this topic.

Similarly, stomatal responses to diurnal variation in  $VPD_L$  can also strongly influence photosynthetic  $CO_2$  assimilation ( $A$ ) to a varying degree across species. For instance,  $A$  declined by 9.4%, 13.6%, 21.0%, 29.4% and 36.6%, respectively, in *Zea mays*, *Spartina townsendii*, *Castanospermum australe*, *Nicotiana tabacum*, and *Ricinus communis* (Long & Woolhouse, 1978; Dai *et al.*, 1992; Cunningham, 2005) (see Supporting Information Fig. S1). While, to our knowledge, no study has investigated the impacts of high  $VPD_L$  on photosynthetic capacity (i.e. maximum carboxylation velocity  $V_{cmax}$  and maximum rate of electron transport  $J_{max}$ ) independent of drought or temperature impacts, some findings

suggest that extended stomatal closure induced by high  $VPD_L$  could alter  $V_{cmax}$  and  $J_{max}$ . For instance, Flexas *et al.* (2006) found that stomatal closure triggers the down regulation of Rubisco activity (potentially because of the decreased activation state of the enzyme) in response to a certain threshold of  $g_s$  in  $C_3$  plants, resulting in lower  $V_{cmax}$  and  $J_{max}$ . However, the relative impact of  $VPD_L$  on  $V_{cmax}$  and  $J_{max}$  and the physiological meaning of these hypothetical changes, remains unknown and deserves further attention in future studies.

A critical assumption in calculations of gas exchange parameters such as  $g_s$  is that intercellular air spaces inside leaves remain saturated with water vapor, particularly when  $VPD_L$  increases to values above *c.* 2 kPa (Cernusak *et al.*, 2018). To calculate  $g_s$  and intercellular  $CO_2$  concentration ( $a_i$ ), it is typically assumed that intercellular water vapor ( $e_i$ ) is at saturation, so that the vapor pressure can be inferred from measurements of leaf temperature (Gaastra, 1959). Over the last 50 or so years, several attempts have been made to verify this assumption, with some results supporting it (Farquhar & Raschke, 1978; Jones & Higgs, 1980) and others suggesting that unsaturation takes place at moderate to high  $VPD_L$  (Jarvis & Slatyer, 1970; Ward & Bunce, 1986; Canny & Huang, 2006; Cernusak *et al.*, 2018). This diversity of potential unsaturation across species may reflect the dynamic nature of  $g_s$ . In species with a relatively sensitive stomatal response to  $VPD_L$ , adjustment of  $g_s$  will likely regulate  $T$  such that no appreciable unsaturation occurs (Buckley *et al.*, 2017; Cernusak *et al.*, 2019). In other species, a slower or less sensitive stomatal response may allow for unsaturation transiently or at intermediate  $VPD_L$  before stomata have closed and slowed  $T$  sufficiently (Holloway-Phillips *et al.*, 2019). Still other species may show appreciable unsaturation during steady-state gas exchange at high  $VPD_L$ , as was recently observed in two semi-arid conifer species, which showed unsaturation as low as  $0.8 \times e_s$  (Cernusak *et al.*, 2018). Such low values of intercellular relative humidity are a challenge to our current understanding of intra-leaf water relations (Buckley & Sack, 2019) but also present an opportunity for new explorations of internal hydraulic design.

In this review, we focus on physiological responses to  $VPD_L$  at a range of scales, with the response of  $g_s$  being critical among these. One typically infers a response of  $g_s$  by measuring  $T$  and assuming saturation of  $e_i$ , so that  $g_s$  can be calculated. If  $e_i$  becomes less than saturated as  $VPD_L$  increases, then  $g_s$  will have been underestimated in those instances. However, the response of  $T$  itself will still have been measured without bias, and the response of  $T$  to  $VPD_L$  could still be faithfully reconstructed from the inferred  $g_s$ . The difference if  $e_i$  became unsaturated would be that the increasing resistance to  $T$  with increasing  $VPD_L$  would have actually been shared between the stomata and the mesophyll. This situation is analogous to inferring a parameter such as  $V_{cmax}$  from the response of photosynthesis to variation in  $a_i$ , but assuming that  $a_i$  is equal to  $c_c$ , the chloroplastic  $CO_2$  concentration. This is common practice (Wullschlegel, 1993; Walker *et al.*, 2014), even though it is well known that  $c_c$  is less than  $a_i$  due to mesophyll resistance to  $CO_2$  diffusion. In the case of mesophyll resistance to transpiration, we know much less about when and to what extent it occurs. Therefore, we recommend that practitioners continue to interpret  $T$  responses to  $VPD_L$  as resulting

entirely from the action of  $g_s$ , while the challenging work of better understanding the nature of unsaturation of  $e_i$  continues in parallel.

In terms of modeling the response of  $g_s$  to  $VPD_L$ , it is important to realize that most empirical datasets used to fit parameters for different vegetation types (Lin *et al.*, 2015) will have been collected under the assumption that  $e_i$  was saturated. In such a case, the impact of unsaturation, if it occurred, on  $T$  will already have been incorporated into the fitted parameters that define the stomatal response function to  $VPD_L$ . If unsaturation occurred it would have made the  $g_s$  response appear to be more sensitive to increasing  $VPD_L$  than it actually was; that is, stomata would have appeared to close more in response to increasing  $VPD_L$  than would be estimated from the physical change in aperture. Where the aim of modeling is to estimate the transpiration flux from the land surface, and if fitted parameters for modeling  $g_s$  (Franks *et al.*, 2018) were defined with empirical  $g_s$  measurements that assumed  $e_i$  to be saturated, one should not further correct for unsaturation of  $e_i$  in modeling  $T$ . This would effectively be doubly accounting for unsaturation of  $e_i$ .

#### IV. Variability in sensitivity to VPD across species and ecosystems

##### 1. Variability in $g_s$ sensitivity across species

Stomatal sensitivity to  $VPD_L$ , often described in terms of the slope between  $g_s$  and  $\log_e(VPD_L)$  (Oren *et al.*, 1999; Fig. 3a), reflects the magnitude of stomatal closure with increasing  $VPD_L$ , and therefore represents the primary strategy by which plants regulate gas exchange in response to rising  $VPD_L$ . Decades of research on stomatal behavior have highlighted the fact that stomatal sensitivity to  $VPD_L$  is highly variable across and within species (Whitehead *et al.*, 1981; Körner *et al.*, 1989; McNaughton & Jarvis, 1991; Cunningham, 2004, 2005; Creese *et al.*, 2014; Gao *et al.*, 2015). Even within a plant, stomatal sensitivity to  $VPD_L$  can differ between leaves that have different functions, morphology, and anatomical traits such as stomatal pore depth and density (Warritt *et al.*, 1980; Appleby & Davies, 1983; Streck, 2003). Using empirical data, Oren *et al.* (1999) found a consistent relationship between  $g_s$  at low  $VPD_L$  ( $g_{sref}$  corresponding to  $g_s$  at 1 kPa  $VPD_L$ ) and sensitivity to  $VPD_L$ , whereby plants with higher  $g_{sref}$  tend to be more sensitive to increasing  $VPD_L$  (i.e. more rapid stomatal closure). Oren *et al.* (1999) generalize this result by observing that, when the dependence of conductance on VPD is expressed as  $g_s = g_{sref}[1 - m \log_e(VPD/VPD_{ref})]$ , the parameter  $m$  is approx.  $0.6 \times g_{sref}$  for a large range of mesic species, suggesting that stomatal regulation occurs systematically near a constant  $\Psi_L$  value. However, a reduced sensitivity was found for desert species ( $m = 0.4 \times g_{sref}$ ), highlighting a less strict regulation of  $\Psi_L$  as  $VPD_L$  increases in more drought-tolerant species (Oren *et al.*, 1999) and suggesting different sensitivities to  $VPD_L$  between plant functional groups.

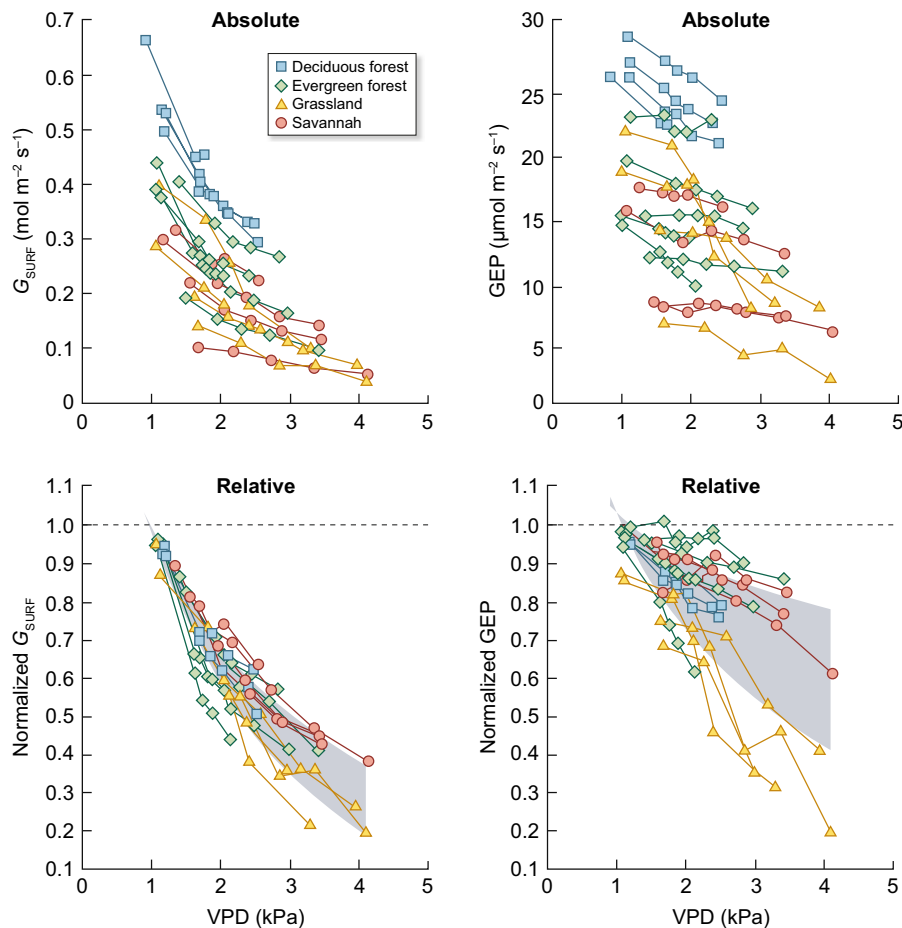
These findings are consistent with the observation that both leaf and stem hydraulic capacity are strongly related to stomatal sensitivity to  $VPD_L$  (Brodribb & Jordan 2008; Zhang *et al.*, 2013) and attest to the fundamental role of plant hydraulics in driving

stomatal aperture in response to  $VPD_L$  variation. A clear distinction in stomatal sensitivity to  $VPD_L$  could therefore be expected between isohydric and anisohydric plant species (e.g. those that hold  $\Psi_L$  more constant via stomatal closure vs those that allow  $\Psi_L$  to drop more significantly; Tardieu & Simmoneau, 1998), whereby the relatively isohydric species could have stronger stomatal sensitivity to  $VPD_L$  compared to anisohydric ones. For instance, Cunningham (2004) found higher stomatal sensitivity in tropical trees relative to temperate ones and suggested that these responses could be linked to their isohydricity (i.e. higher stomatal sensitivity in isohydric species relative to anisohydric ones). However, no measure of water potential was conducted in this study to confirm this hypothesis. Although identifying such behaviors could have strong implications for vegetation models, most studies investigating isohydric/anisohydric strategies have been strongly focused on soil moisture responses (Martinez-Vilalta *et al.*, 2014) and the evolution of leaf-level variables over timescales of weeks. Frameworks that mathematically link isohydricity and sensitivity to  $VPD_L$  have been recently developed (Sperry *et al.*, 2017; Novick *et al.*, 2019), but they await extensive empirical validation and must contend with the fact that  $VPD_L$  and soil moisture are coupled at long (weekly) but not short (i.e. diurnal) timescales. Improving our interpretation and predictive power will require future work to investigate how these processes vary between plant functional groups, and how trait coordination within plants relates to stomatal sensitivity to  $VPD_L$  and could vary in predictable ways along environmental gradients. Furthermore, a scaling-up of these leaf- or plant-level responses to  $VPD_L$  at ecosystem or landscape scales would be needed to assess the impacts of these different stomatal behaviors on the global water cycle and feedbacks to climate regulation.

##### 2. Variability in $G_{surf}$ sensitivity across ecosystems

For decades, sap flow measurements and eddy covariance flux towers have provided rich information about the relationship between canopy stomatal function and VPD (Pataki *et al.*, 1998a; Baldocchi, 2003), though caution is required when using this approach to estimate the stomatal sensitivity to VPD as differences between canopy and air temperature need to be accurately accounted for (Schymanski & Or, 2017). Furthermore, when using flux tower data to make inferences about transpiration and canopy conductance, care should be taken to exclude data collected when soil and canopy interception and evaporation represent a large fraction of measured evapotranspiration (ET; for example, by filtering for conditions when the canopy and soil are wet, Fig. 4).

Tower-derived observations of ET, and also sensible heat and momentum fluxes, are sufficient to invert the Penman–Monteith (P–M) equation for ET to produce stand-level surface canopy conductance ( $G_{surf}$ ; Kim & Verma, 1991). The P–M equation (Penman, 1948; Monteith, 1965) is a widely used model for transpiration and ET that is most commonly applied at the ecosystem scale, which matches the scale at which flux tower data are collected. It blends approaches for modeling transpiration and ET emerging from both conservation of mass and energy. It is forced by net radiation, VPD, wind speed and temperature. The



**Fig. 4** Eddy covariance flux data are useful for understanding how the response of surface conductance (left column) and gross ecosystem productivity (right column) respond to vapor pressure deficit (VPD). When shown as absolute values, both conductance and gross ecosystem productivity (GEP) are negatively related to VPD, but the variability from one site to the next is quite large (see absolute values). However, if the site-level data are normalized by their rates at a reference VPD of 1 kPa, the cross-site variability at a given VPD is considerably reduced, particularly for conductance (see relative values). As predicted from theory, the sensitivity of conductance to VPD ( $m$ ) is greater than the sensitivity of GEP to changes in VPD, reflecting the fact that intrinsic water use efficiency (iWUE) often increases with rising VPD. The gray shaded area shows the range of the model  $y = 1 - m \log_e(\text{VPD})$ , for the range of  $m$  representing  $\pm 3$  SE for the slope parameter derived from linear regression. The data represent a subset of the FLUXNET Tier1 tower sites, where GEP is provided by FLUXNET and  $G_s$  is estimated following the approach of Novick *et al.* (2016). To reduce confounding effects from radiation and soil moisture, which co-vary with VPD, this analysis was limited to periods of high radiation ( $> 400 \text{ W m}^{-2}$ ) and the site-specific curves represent the average of responses determined within unique soil moisture bins ( $n = 5$  at each site).

model requires an estimate of both surface and aerodynamic conductance to water vapor, but the latter can be estimated with reasonable confidence from wind observations and *a priori* assumptions about key meteorological length scales (including the momentum roughness length and the zero-plane displacement; see Novick *et al.*, 2016 for example). Thus, all of the input variables to the P–M equation are ‘known’ from flux tower data except  $G_{\text{surf}}$ , so that the equation can be solved for  $G_{\text{surf}}$  to create a half-hourly time series. While  $G_{\text{surf}}$  is not a perfect proxy for  $g_s$ , as it contains information reflecting both stomatal and soil resistance to evaporation, these interactions can be minimized through careful data screening or ET partitioning (Sulman *et al.*, 2016; Li *et al.*, 2019).

Across sites and biomes,  $G_{\text{surf}}$  measurements consistently confirm the typical inverse and non-linear relationship between conductance and VPD (Novick *et al.*, 2016; Li *et al.*, 2019; Fig. 4).

From one site to the next, the parameters of the relationship between tower-derived  $G_{\text{surf}}$  and VPD vary, reflecting cross-site differences in canopy structure, soil properties and species. For instance, using ET measurements, and derived  $G_{\text{surf}}$  estimations from 38 Ameriflux sites spanning a wide range of biomes, Novick *et al.* (2016) demonstrated that the relationship between  $G_{\text{surf}}$  and VPD is dependent on moisture regimes. Moreover, the sensitivity of  $G_{\text{surf}}$  to VPD was strongly reduced when moving from mesic to xeric sites (Fig. 4), suggesting stronger VPD control on gas exchange in wetter regions relative to drier ones. Furthermore, these findings suggest that the relative importance of VPD in driving  $G_{\text{surf}}$  may be especially increased in mesic ecosystems in the future with global warming (Novick *et al.*, 2016), as  $dG_{\text{surf}}/d\text{VPD}$  is especially steep when VPD is relatively low, consistent with hydraulic theory (McDowell & Allen, 2015). At the same time, stomatal sensitivity to VPD can also shift within a given ecosystem



in response to climatic variability. For example, atmospheric warming and increased VPD were found to reduce stomatal sensitivity to VPD, resulting in deterioration of water dynamics and reduced gas exchange, independently of precipitation regimes (Grossiord *et al.*, 2018). Interestingly, this response varied between isohydric and anisohydric species, suggesting some link between isohydricity and sensitivity to VPD (Grossiord *et al.*, 2017b).

However, when structural, functional and climatic characteristics of the biome are controlled for by dividing the  $G_{\text{surf}}$  by a reference conductance at VPD = 1 kPa, the relationship between  $G_{\text{surf}}$  and VPD becomes much more generic across sites (Novick *et al.*, 2016; Li *et al.*, 2018, Fig. 4). Specifically, the ecosystem-scale  $m$  is  $0.5 \pm 0.07$  when ensemble-averaged across sites. This result agrees well with theory, and species leaf-level results, as described in the previous section (Oren *et al.*, 1999), and this confirms the usefulness of  $G_{\text{surf}}$  as a proxy for stomatal conductance. Encouragingly, analysis of  $G_{\text{surf}}$  estimated from weather station data using the so-called ETRHEQ approach (for Evapotranspiration from Relative Humidity at Equilibrium) also produced reasonable convergence in the normalized VPD response across sites (Rigden *et al.*, 2018). While not a direct observation of ET, the ETRHEQ is highly data-driven and shows great potential for increasing our understanding of ET and  $G_{\text{surf}}$  dynamics in biomes where meteorological stations are more abundant than flux towers. Ultimately, these ecosystem-scale relationships have many practical uses and applications. Most land-surface models have a stand-scale resolution, and new approaches representing stomatal sensitivity to VPD benefit from testing with ecosystem-scale data (Bonan *et al.*, 2014; Franks *et al.*, 2018). They could also inject dynamic plant feedbacks into drought monitoring indices like the Palmer Drought Severity Index, particularly if those indices use a P–M type formulation to represent ET (Ficklin *et al.*, 2015). Finally, estimates of conductance from flux towers already have a rich and continuing history of being blended with remotely-sensed vegetation indices and models like P–M to develop coarse-scale conductance and ET data products (Hulley *et al.*, 2017).

## V. Impact of high VPD on carbon and water relations and drought-induced mortality

### 1. Transpiration, photosynthesis and gross ecosystem productivity responses to high VPD

Plant- and ecosystem-level transpiration responses to increasing VPD are complex, and encompass increasing and decreasing water use and sap flux velocity depending on the range of VPD and on other environmental variables like soil moisture (Whitehead & Jarvis, 1981; Benyon *et al.*, 2001). Earlier work has shown that although leaf water potentials and  $g_s$  strongly decrease with rising VPD, transpiration rates tend to increase and remain high for a wide range of species originating from distinct habitats, consistent with the ‘feed-back’ response discussed in section III (Granier *et al.*, 1992; Pataki *et al.*, 1998b; O’Grady *et al.*, 1999; Meinzer, 2003; Bovard *et al.*, 2005; Hölscher *et al.*, 2005; Kupper *et al.*, 2011, but see Whitley *et al.*, 2013 among others for evidence of a ‘feed-forward’ response leading to reduced  $T$  with high VPD). This

response leads to a more rapid depletion of soil moisture, thereby increasing the risk of experiencing drought stress faster, particularly if high VPD conditions are combined with reduced precipitation (Will *et al.*, 2013; Duan *et al.*, 2014).

Photosynthetic carbon assimilation ( $A$ ) is directly related to stomatal conductance, but this relationship is mediated by the intrinsic water use efficiency ( $iWUE = A/g_s$ ), so that the response of photosynthesis to VPD depends on the stomatal sensitivity to VPD but also on the extent to which  $iWUE$  itself changes as VPD rises. Some clues about the nature of the  $iWUE = f(VPD)$  relationship emerge from gas exchange theory, which implies a saturating (or hyperbolic) relationship between  $A$  and  $g_s$  (Farquhar & Sharkey, 1982). When VPD is relatively low, initial increases in VPD will reduce  $g_s$  but not  $A$ , such that  $iWUE$  increases with increasing VPD. However, eventually, severe restrictions to  $g_s$  imposed by high VPD will limit  $A$ , which may be independently decreased by declining soil moisture and non-stomatal limitations to biochemical capacity, including reduced mesophyll conductance (Flexas *et al.*, 2012). As a result,  $iWUE$  will saturate or even decline as VPD continues to rise. Thus, the overall relationship between  $iWUE$  and VPD is likely hyperbolic (Zhang *et al.*, 2019), and the sensitivity of photosynthesis to VPD will likely be weaker than the sensitivity of conductance to VPD.

Both tree-rings and eddy covariance flux towers are useful tools for testing this prediction across sites and over long periods of time. The isotopic composition of tree rings can be analyzed for information about historic change in  $iWUE$  (Francey & Farquhar, 1982). Flux towers provide information about stand-level photosynthesis (i.e. gross ecosystem productivity, or GEP) as well as surface conductance, such that stand-level  $iWUE$  can be calculated as  $GEP/G_{\text{surf}}$ . Several recent studies have focused explicitly on the sensitivity of  $iWUE$  and GEP to historic changes in VPD. Although these studies commonly do not separate temperature from VPD impacts, the effects of rising  $CO_2$  were accounted for by using various statistical approaches such as removing low-frequency trends (Andreu-Hayles *et al.*, 2011) or partial least squares regressions (e.g. Wang *et al.*, 2018). In general, these studies find that the relationship between  $iWUE$  and VPD is positive (Andreu-Hayles *et al.*, 2011; Frank *et al.*, 2015; Wang *et al.*, 2018), with the predicted unimodal relationship between  $iWUE$  and VPD being observed in some sites that experience exceptionally high VPD. Practically, and as illustrated in Fig. 4, this means that the sensitivity of photosynthesis to VPD is lower than the sensitivity of conductance to VPD, but it is nonetheless substantial. Moreover, several recent tree-ring studies identify rising VPD (considered concurrently with increasing temperature) as an important limitation to tree growth (Williams *et al.*, 2013; Babst *et al.*, 2019), suggesting that among other processes (e.g. reduction in phloem transport), reductions to photosynthesis at high VPD could be sufficient to limit the supply of carbon to growth sinks, at least for current climate conditions.

Moreover, to persist in response to high temperature and VPD rise, plants will need to regulate their temperature, particularly that of photosynthetically-active tissues. During periods of optimum soil water supply and non-limiting VPD<sub>L</sub>, plants can passively thermoregulate their foliar temperature with their transpiration



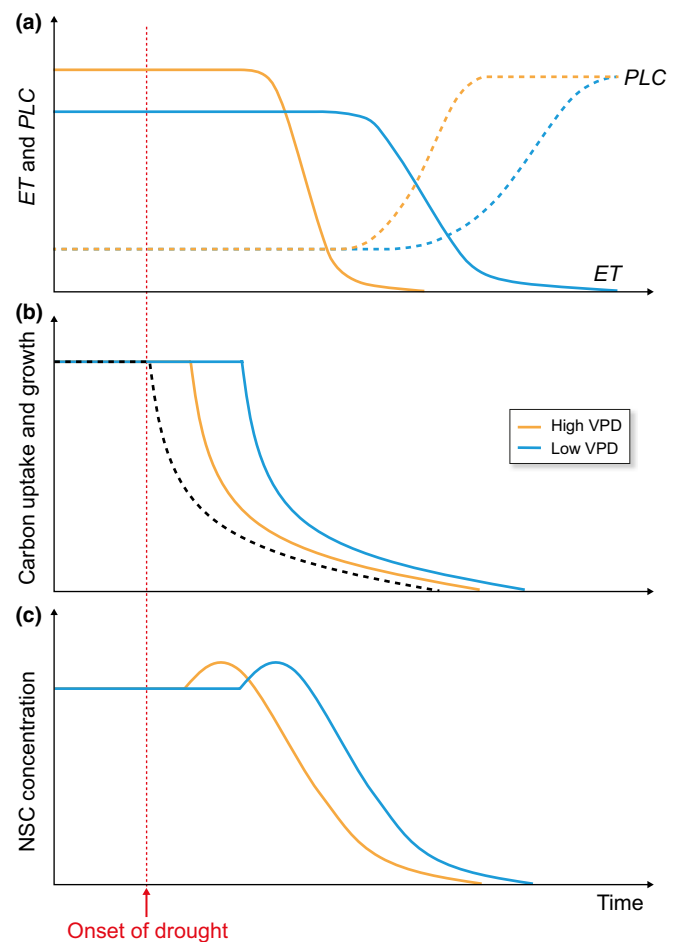
flux (Mahan & Upchurch, 1988). The ‘cooling effect’ of  $T$  arises because a substantial amount of energy that would otherwise heat the leaf is used to convert each mole of liquid water to water vapor. Extended periods of high  $T$  (resulting from high VPD) could result in an impaired cooling of leaves and heating of plant canopies (Gates, 1968), particularly if combined with drought stress. In general, plants can adjust efficiently to higher temperatures by shifting their temperature optimum, in temperate regions within a few hours. However, when canopy temperatures are chronically beyond an optimal temperature threshold, photosynthetic rates will decrease and reduce the capacity of plants to perform vital functions, including taking up carbon from the atmosphere through photosynthesis (Berry & Bjorkman, 1980). At high foliar temperatures, mostly occurring during heat waves and depending on the duration of exposure ( $T_{\text{leaf}} > 40^{\circ}\text{C}$ ), cellular injury – including protein denaturation, inactivation of enzymes in chloroplasts, loss of membrane integrity or even cell death – can occur, leading to a lethal collapse of the cellular organization (Wahid *et al.*, 2007; Teskey *et al.*, 2015). These injuries eventually lead to inhibition of growth and diminish photosynthetic uptake of carbon. As heat waves are often, but not always, accompanied by drought, the susceptibility to heat induced damages is exacerbated significantly. However, although foliar thermoregulation is a crucial process for the long-term maintenance of terrestrial ecosystems, few studies have investigated the mechanisms driving this process, the interaction between thermoregulation, plant water relations, and high VPD, and their feedbacks to ecosystem resilience.

## 2. Role of high VPD in drought-induced plant mortality

Elevated VPD has been identified as having a significant role in recent and future drought-associated mortality events (Breshears *et al.*, 2013; Stovall *et al.*, 2019). Observations of recent vegetation die-offs (widespread and fast mortality events) of conifers in southwestern USA have been more strongly correlated with VPD than with either temperature or precipitation anomalies (Williams *et al.*, 2013). For conifers throughout the Northern Hemisphere, the implication of rising VPD is widespread range reductions due to elevated mortality (McDowell *et al.*, 2016). Rising VPD may also be involved in driving increased Amazonian tree mortality (Brienen *et al.*, 2015; McDowell *et al.*, 2018). Consistent with this, multiple studies have droughted trees to death more rapidly via elevated temperature treatments in glasshouse settings (Adams *et al.*, 2009; Will *et al.*, 2013; Zhao *et al.*, 2013), but no manipulative mortality studies have yet attempted to disentangle the impacts of elevated VPD and high temperature.

In addition to the observations of growth and mortality that are consistent with a growing VPD limitation, theory suggests that rising VPD must impact plant hydraulics such that vegetation shifts, including rapid mortality, are likely. Fundamentally, the mechanisms by which rising VPD may accelerate the risk of mortality are consistent with the transpiration and stomatal responses to VPD. Specifically, if elevated VPD causes elevated ET it should increase the risk of hydraulic failure, or catastrophic dehydration, by exacerbating the water potential drop within

foliage and wood (Will *et al.*, 2013; Cochard, 2019). This effect is amplified by an enhanced VPD-driven evaporation resulting in soil water loss and desiccation, increasing drought stress via lack of soil water (Fig. 5a). Ultimately, higher ET should result in less time required to reach a threshold beyond which ET must decline and hydraulic failure (defined as the percentage loss of conductance in Fig. 5a) must increase. Stomatal closure during periods of elevated VPD may also lead to reduced growth and allocation to carbohydrates via a decrease in photosynthesis (Fig. 5b), which if the stomatal closure is sufficiently strong and prolonged, could lead to carbon starvation (Martínez-Vilalta *et al.*, 2012) including

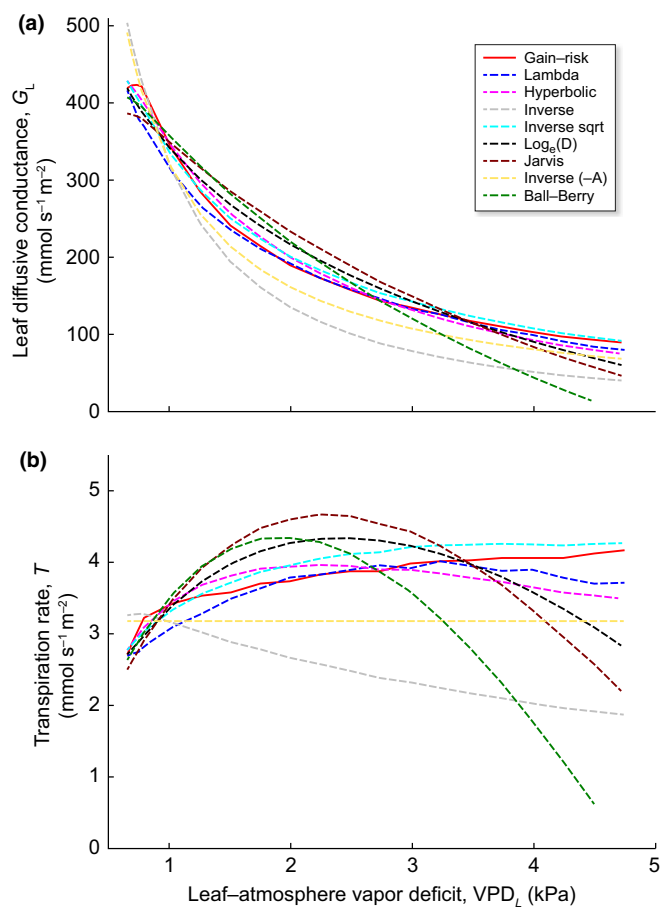


**Fig. 5** Conceptual figure highlighting the potential mechanisms of hydraulic failure and carbon starvation during drought under low and high vapor pressure deficit (VPD). After drought inception (red dashed vertical line) and under constant low (blue) or high (orange) VPD, evapotranspiration (ET) will decrease as soil moisture declines, but the drop in ET will occur earlier and be faster under high VPD. Thus, hydraulic failure (defined here as the percentage loss of conductance, PLC, the orange dashed and dotted blue lines) will occur faster under high VPD due to increasing embolism (a); growth (dotted black line) and carbon uptake through photosynthesis will decline more rapidly under higher VPD due to lower PLC and increasing tissue temperature (b); non-structural carbohydrate (NSC) content and defensive capacity increases for a short time due to the imbalance of growth, and photosynthesis declines, with a more rapid NSC and defensive capacity loss in higher VPD environments (c). Ultimately, the risk of drought-induced mortality through hydraulic failure (a) and carbon starvation (c) is higher – and both occur more rapidly – under increasing VPD.

failure to defend against biotic attack (Fig. 5c; McDowell *et al.*, 2011).

Long-term field experiments where atmospheric temperature and VPD are manipulated and combined are particularly useful for anticipating the impacts of rising VPD on plant mortality risks, particularly as the effects may occur in cascades (i.e. short vs long-term impacts, Fig. 5). Several systems have been established in which the independent and combined effects of drought, heat stress or high atmospheric  $[\text{CO}_2]$  on tree functioning are tested (Hanson *et al.*, 2011; Grossiord *et al.*, 2017a), but to our knowledge only one field experiment manipulates VPD independently of other drivers (Kupper *et al.*, 2011). Using mist

fumigation in experimental forest plots in south-eastern Estonia, the free air humidity manipulation (FAHM) increases air humidity over ambient levels, thereby reducing VPD. The experiment revealed that high humidity (i.e. low VPD) resulted in reduced  $T$ , aboveground growth and photosynthesis (reviewed in Oksanen *et al.*, 2018). However, while some effects may be attributed to reduced VPD, others may be partially explained by the condensation of water onto the leaf surface induced by the misting system employed at the site. Water retention on the leaf surface could directly impair stomatal functioning, gas exchange and photosynthesis (Ishibashi & Terashima, 1995). New experiments combining multiple stresses (e.g. VPD  $\times$  temperature or VPD  $\times$  drought) are urgently needed to help shed light on longer-term plant survival under rising VPD.



**Fig. 6** Nine model scenarios of the stomatal response to leaf-to-atmosphere vapor pressure deficit,  $\text{VPD}_L$ . (a) Response of leaf diffusive conductance to water vapor ( $G_L$ ). (b) Response of leaf transpiration rate ( $T$ ). Red curve is the gain-risk model and the dashed blue is the  $\lambda = dT/dA$  model, where  $\lambda$  is constant at the initial (low  $\text{VPD}_L$ ) value from the gain-risk simulation (curves from Sperry *et al.*, 2017). The seven remaining curves were fit to maximize the  $r^2$  with the red gain-risk  $G_L$  to facilitate comparison. Five of these curves have  $G_L$  proportional to  $f(\text{VPD}_L) \cdot A$ , where  $A$  is the photosynthetic rate taken from the red gain-risk curve. Their five  $f(\text{VPD})$  functions were as follows: pink,  $1/(1 + \text{VPD}_L/\text{VPD}_0)$  (Lohammer *et al.*, 1980); grey,  $1/\text{VPD}_L$  (Lloyd, 1991); cyan,  $1/\text{VPD}_L^{0.5}$  (Lloyd, 1991); brown,  $1 - \text{VPD}_L/\text{VPD}_0$  (Jarvis, 1976); green, RH, where  $\text{VPD}_L$  was converted to relative humidity (RH) (Ball *et al.*, 1987). The last two curves have  $G_L$  proportional to  $f(\text{VPD}_L)$ . The  $f(\text{VPD}_L)$  functions were: black,  $g_{\text{sref}} - m \log_e(\text{VPD}_L)$  ( $g_{\text{sref}} = G_L$  at  $\text{VPD}_L = 1$  kPa); yellow:  $1/\text{VPD}_L$  (Oren *et al.*, 1999).  $\text{VPD}_0$ ,  $g_{\text{sref}}$ , and  $m$  are curve-fitting parameters.

## VI. Modeling plant and ecosystem responses to VPD

### 1. At the plant level

The approaches to modeling stomatal response to vapor pressure deficit can be grouped into three categories: mechanistic, empirical and goal-oriented. Mechanistic models predict the stomatal response from known or hypothetical stimulus-response pathways (Pieruschka *et al.*, 2010; Buckley & Mott, 2013). They are useful for studying these pathways and directing their further study, but the physiological parameters in some versions of such models are difficult to estimate experimentally, making them impractical for general predictive purposes (Buckley & Mott, 2013). However, mechanistic models have been successfully adapted and applied in woody crops (Diaz-Espejo *et al.*, 2012; Rodriguez-Dominguez *et al.*, 2016) and forest trees (Buckley *et al.*, 2012; Wang *et al.*, 2016).

The empirical approach to modeling the  $G_L$  response to  $\text{VPD}_L$  (as actively controlled by the stomatal  $g_s$  component) does not require mechanistic closure and is perhaps most widely used for prediction (Rowland *et al.*, 2015; Kennedy *et al.*, 2019). The stereotypical stomatal closure response to increasing  $\text{VPD}_L$  lends itself to curve fitting, and a host of similar equations have been used to express  $G_L$  as monotonically declining with  $\text{VPD}_L$  (Fig. 6a). Multiplying the  $f(\text{VPD}_L)$  function by the photosynthetic rate ( $A$ ) can account for independent interactions with photosynthesis (as in Fig. 6a: hyperbolic, inverse, inverse square root, Jarvis, Ball-Berry curves) (Leuning, 1995). The curve fitting parameters determine a maximum  $G_L$  at low  $\text{VPD}_L$  and determine the rate of  $G_L$  decline as  $\text{VPD}_L$  increases (the stomatal sensitivity to  $\text{VPD}_L$ ). Once fitted to past data, the parameters are used to extrapolate the future. One challenge is knowing which model is best for every situation – though they are qualitatively similar in representing stomatal closure with  $\text{VPD}_L$  (Fig. 6a), there are fundamental differences in the transpiration response (Fig. 6b). Some functions predict a peak in  $T$ , others a plateau or gradual rise; one gives a flat  $T$  response (inverse without  $A$ ), and one a decline (inverse with  $A$ ). Another challenge is that the fitted parameters for the chosen model will vary within species as factors such as soil moisture or  $\text{CO}_2$  concentration change, and they will vary across species. Progress can be made by recognizing that greater maximum  $G_L$  correlates with greater

sensitivity (Kaufmann, 1982; Yong *et al.*, 1997; Oren *et al.*, 1999) and that maximum  $G_L$  is also a function of soil moisture, ambient  $CO_2$ , and other environmental cues (Leuning, 1995). More curve fitting can be used to handle these interactions for particular situations (Jarvis, 1976), but in the absence of any guiding principle the empirical approach is difficult to generalize with confidence.

Goal-oriented modeling based on an optimization criterion has the greatest potential for prediction. If we assume a physiological objective of stomatal regulation, and if we can model that objective, we automatically know how the stomata must behave in any situation to realize the assumed goal. Such a model will be equally consistent in its predictions regardless of the combination of environmental stimuli or underlying mechanism. An early goal-oriented model proposed that stomata regulate so as to maximize the cumulative photosynthesis for a fixed amount of cumulative transpiration over a given period of time (Cowan & Farquhar, 1977). This predicts that stomata act to maintain  $dT/dA = \lambda$ , where  $\lambda$  is the Lagrangian multiplier for this constrained-optimization problem. The challenge is *a priori* knowledge of what  $\lambda$  should be as a function of plant and environment. Without knowing what  $\lambda$  should be ahead of time, the modeler is effectively using an empirical approach where  $\lambda$  is derived by fitting data (e.g. Fig. 6, blue dashed; Medlyn *et al.*, 2011).

A more tractable stomatal goal is to prevent leaf xylem pressure ( $P$ ) from ever dropping below some threshold ( $P_t$ ) which represents the onset of stress-induced damage such as loss of turgor or hydraulic conductance (Oren *et al.*, 1999; Pieruschka *et al.* 2010; Tyree & Sperry, 1988). The stomatal response at  $P = P_t$  and steady-state is calculated as  $G_L = K/VPD_L \cdot (P_{soil} - P_t)$ , where  $K$  is the soil-to-canopy hydraulic conductance per leaf area and  $P_{soil}$  is the soil water potential (Fig. 6, yellow dashed 'inverse-A' curve). This equation incorporates plant hydraulic traits into the  $G_L$  response and correctly predicts several observations (Oren *et al.*, 1999): As  $P$  falls to  $P_t$ ,  $G_L$  approaches an inverse function of increasing  $VPD_L$ , which is broadly consistent with empirical equations for the  $VPD$  response (Fig. 6a, compare yellow-dashed line);  $G_L$  at a given limiting  $VPD_L$  decreases with more negative  $P_{soil}$ ;  $G_L$  sensitivity to  $VPD_L$  increases with a greater maximum  $G_L$ ;  $G_L$  scales proportionately with  $K$ ; the initial rise in  $T$  with  $VPD_L$  saturates as  $P$  approaches  $P_t$ ; and a decline in  $T$  that is occasionally seen at high  $VPD_L$  (Franks *et al.*, 1997) is consistent with a drop in  $K$  under such conditions. Easy to implement, and consistent with at least some mechanistic hypotheses (Pieruschka *et al.* 2010), such a scheme can improve large-scale models (Williams *et al.*, 1996). But this approach is too simple. It predicts a strictly isohydric response to rising  $VPD_L$  (Fig. 6b;  $T$  is constant with  $VPD_L$ ; yellow dashed line) and falling  $P_{soil}$ , when most species are anisohydric in allowing  $P$  to become more negative (Martinez-Vilalta *et al.*, 2014). Moreover, by itself the approach cannot account for the independent feedbacks between photosynthesis and  $G_L$ .

More recent goal-oriented approaches also incorporate plant hydraulics but propose that stomata balance the stress-related risk of opening with the opportunity for photosynthetic gain (Mencuccini *et al.*, 2019; Wolf *et al.*, 2016). The risk can be calculated from a cavitation vulnerability curve, and it eventually rises non-linearly with continued stomatal opening, reaching a maximum

when  $T$  induces complete hydraulic failure. The gain rises immediately on stomatal opening and continues to a maximum as modeled photosynthesis saturates. Setting the maximum risk and gain to 1 gives them equal weight in the trade-off, and the actual stomatal opening that maximizes the gain minus the risk at that instant can be calculated (Sperry *et al.*, 2017). This algorithm produces a  $VPD_L$  response very similar to many empirical models (Fig. 6, red lines) and integrates interactions with light, temperature, ambient  $CO_2$ , and soil moisture. The degree of anisohydry (i.e. the degree to which  $T$  increases with  $VPD_L$ ; Fig. 6b, red line) is dictated by photosynthetic capacity and vulnerability to cavitation. Importantly, the responses can be predicted *a priori* from traits of photosynthetic and hydraulic capacity. Quantitatively the gain-risk approach fits experimental observations as well or better than empirical models (Venturas *et al.*, 2018; Wang *et al.*, 2019). Different formulations of the optimal gain vs stress trade-off are possible (Eller *et al.*, 2019; Mencuccini *et al.*, 2019), including additional considerations such as phloem export (Hölttä *et al.*, 2017; Huang *et al.*, 2018). But the temptation to complicate comes at the risk of adding unknown parameters which have to be retroactively fit, reducing predicting power. Nevertheless, modeling the stomatal response from a gain vs stress trade-off appears to be a promising way to improve over the purely empirical approach.

## 2. At the global level

Land-surface models represent processes that regulate the exchange of carbon, water and energy fluxes between the atmosphere and biosphere by coupling plant physiology with vegetation dynamics (Sellers *et al.*, 1996). Despite a large variety of land-surface modeling approaches, the models are similar in that they aim to scale processes that occur at leaf level and individual organism level to investigate global-scale questions and can be applied in either offline or fully coupled 'online' simulations, with general circulation models providing meteorology. A range of land-surface modeling approaches exist where, at the highest level, models can be split between whether they use diagnostic or prognostic approaches, with diagnostic approaches combining simple light-use efficiency models with remote-sensing observations for variables like the normalized difference vegetation index, leaf area index or soil moisture, for example (see Yuan *et al.*, 2019). By contrast, prognostic models aim to represent ecosystem dynamics with numerical representations of processes using semi-empirical to fully mechanistic approaches (Bonan *et al.*, 2003). These include the category of 'dynamic global vegetation models' that represent demography via establishment, growth and mortality (Sitch *et al.*, 2013).

Plant physiological responses to VPD are linked to vegetation mortality in land-surface models in one or more of several interacting ways, including carbon deficits via negative net primary production (NPP) or declines in growth efficiency, and water stress via hydraulic failure, in addition to mortality via non-VPD related processes such as heat stress or light competition (Prentice *et al.*, 2007; McDowell *et al.*, 2011). Land-surface models operate on the principle of balancing water demand with water supply. The models generally compute atmospheric water demand, that is,



$E_{\text{demand}}$  or VPD, using gridded fields of observed or simulated vapor pressure (Harris *et al.*, 2014) via the Penman–Monteith approach and estimate the assumed saturated vapor pressure within the leaf, from air temperature or with simple biophysical models to estimate leaf temperature. Alternatively,  $E_{\text{demand}}$  can be estimated from empirical relationships relating evaporation efficiency and surface conductance to air temperature and longwave radiation (Monteith, 1995). Land-surface models diverge in terms of how  $E_{\text{demand}}$  is related to  $g_s$ . Models with sub-daily timesteps, such as CLM (Bonan *et al.*, 2003), ORCHIDEE (Krinner *et al.*, 2005), ED (Moorcroft *et al.*, 2001) or JULES (Best *et al.*, 2011), use modifications of the Ball–Berry model (Ball *et al.*, 1987) to relate VPD to  $g_s$ . The LPJ model, whose timesteps are daily or longer (Sitch *et al.*, 2003), modifies non-water stressed conductance by the ratio of  $E_{\text{demand}}$  and  $E_{\text{supply}}$ , where  $E_{\text{supply}}$  is related to plant available water in the soil column. In both approaches, stomatal closure induced by increasing VPD leads to less GEP and thus lower growth efficiency or negative NPP related mortality.

Alternative schemes for linking VPD with plant mortality use a hydraulic architecture approach to estimate the water potential along a soil–plant–atmosphere continuum. This modeling approach, also known as SPA or the soil–plant–atmosphere canopy model (Williams *et al.*, 1996), calculates the transport of water, that is, the supply, as proportional to hydraulic gradients and resistances along the continuum. Water potentials for the soil, stem and leaves emerge as prognostic variables related to water availability, tree height and tissue properties. The implementation of SPA-based modeling theory into land-surface models is an active area of research (Hickler *et al.*, 2006; Bonan *et al.*, 2014; Christofferson *et al.*, 2014; Mencuccini *et al.*, 2019) as it provides a more mechanistic approach for linking  $g_s$  with atmospheric water demand and soil water availability. In addition, hydraulic architecture modeling approaches provide a more direct link to simulating mortality because of how they control hydraulic failure and xylem cavitation (McDowell *et al.*, 2011). Modeling approaches simulate the loss of conductance due to cavitation as an s-shaped vulnerability curve, where cavitation is related to water potential that causes a 50% loss of conductivity (Tyree and Sperry, 1989; Hickler *et al.*, 2006). Some land-surface models incorporate acclimation processes by altering carbon allocation to above (stem) and belowground (root) pools, which can then feedback into modifying the whole-pathway resistances that contribute to the leaf water potentials and, ultimately, the leaf conductance (Hickler *et al.*, 2006).

Simulated leaf and canopy conductance, their environmental responses, and interannual and decadal dynamics are evaluated using a range of techniques (Yuan *et al.*, 2019). These include comparisons with flux towers (Blyth *et al.*, 2010; Raczka *et al.*, 2013), tree rings (Frank *et al.*, 2015) and cuvette measurements (Cernusak *et al.*, 2013). Key questions on the relationship between the global carbon and water cycles have been advanced by understanding the role of VPD and canopy conductance processes that bridge spatial scales (Jung *et al.*, 2017), soil moisture (Humphrey *et al.*, 2018) and vegetation dynamics (Stocker *et al.*, 2019). These studies include broader insights into hydrologic

responses to VPD via changes in runoff, coupling with the atmosphere due to adjustments in surface roughness, and partitioning of radiation vs VPD effects on photosynthesis (Roderick *et al.*, 2014; Greve *et al.*, 2017).






## VII. Conclusion

Global VPD has increased over recent decades (Fig. 1) and is expected to continue to rise in the future. High VPD conditions reduce stomatal conductance and photosynthesis while simultaneously increasing plant water losses through transpiration. Although these impacts vary across biomes and plant functional types, and may be mitigated in part over the long-term by increasing CO<sub>2</sub> concentrations, they will likely result in reduced primary productivity and amplified drought-induced plant mortality worldwide. To enable mechanistic predictions of future VPD impacts at local and global scales, key processes driving plant responses to VPD need to be addressed in future work. Many advances have been made in recent years in our modeling approaches of VPD impacts at plant and global scales, but future developments will require further progress in our empirical knowledge of plant responses to rising VPD. For instance, no consensus exists regarding the exact sensing mechanisms driving stomatal closure in response to rising VPD (and whether they respond differently to temperature- vs humidity-driven changes in VPD) and how these mechanisms may vary between plant functional groups or along environmental gradients. Future work should focus on separating temperature- vs humidity-driven impacts of VPD by using controlled experiments (e.g. growth chambers; humidity manipulation in the field), possibly across a broad range of species. Furthermore, modeling and empirical efforts should be directed towards examination of the antagonistic impacts of VPD rise and other projected changes, such as increasing atmospheric CO<sub>2</sub> concentrations, reduced precipitation and global warming.

## Acknowledgements

CG was supported by the Swiss National Science Foundation SNF (5231.00639.001.01). TNB was supported by the National Science Foundation (Award 1557906) and the USDA National Institute of Food and Agriculture (NIFA) (Hatch project 1016439). BP was supported by the NASA Terrestrial Ecology Program. KN was supported by the USDA NIFA Agriculture and Food Research Initiative (Grant 2017-67013-26191) and NSF (Award 1552747). We would like to thank the reviewers and the editor for their thoughtful comments and efforts towards improving the manuscript.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Response of net  $CO_2$  assimilation rate to leaf-to-air vapor pressure deficit in four species.

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