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SPECIAL ISSUE REVIEW

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The impacts of rising vapour pressure deficit in natural and managed ecosystems

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Abstract

An exponential rise in the atmospheric vapour pressure deficit (VPD) is among the most consequential impacts of climate change in terrestrial ecosystems. Rising VPD

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has negative and cascading effects on nearly all aspects of plant function including photosynthesis, water status, growth and survival. These responses are exacerbated by land–atmosphere interactions that couple VPD to soil water and govern the evolution of drought, affecting a range of ecosystem services including carbon uptake, biodiversity, the provisioning of water resources and crop yields. However, despite the global nature of this phenomenon, research on how to incorporate these impacts into resilient management regimes is largely in its infancy, due in part to the entanglement of VPD trends with those of other co-evolving climate drivers. Here, we review the mechanistic bases of VPD impacts at a range of spatial scales, paying particular attention to the independent and interactive influence of VPD in the context of other environmental changes. We then evaluate the consequences of these impacts within key management contexts, including water resources, croplands, wildfire risk mitigation and management of natural grasslands and forests. We conclude with recommendations describing how management regimes could be altered to mitigate the otherwise highly deleterious consequences of rising VPD.

KEYWORDS
carbon cycling, climate change, drought, management, plant physiology

1 | INTRODUCTION

Rising atmospheric vapour pressure deficit (VPD) is a well-documented and global consequence of climate change (Figure 1, Ficklin & Novick, 2017; Grossiord et al., 2020; Yuan et al., 2019). VPD represents the difference between the vapour pressure of the air at saturation and the actual vapour pressure of the air. The former depends exponentially on temperature through the Clausius–Clapeyron relationship (Campbell & Norman 2000; Dingman et al. 2002), such that global temperature rise has promoted global increases in saturation vapour pressure. Actual vapour pressure, which is the product of relative humidity and saturation vapour pressure, has increased more slowly over land areas (Ficklin & Novick, 2017) due to oceanic influences that may suppress relative humidity (Byrne & O'Gorman, 2018) and land-atmosphere feedbacks that limit the supply of water for evapotranspiration (ET) (Seneviratne et al., 2006; Vicente-Serrano et al., 2018). As a result, VPD is rising globally at a pace that is likely to accelerate in the future (Yuan et al., 2019).

Because VPD represents the desiccating strength of the atmosphere, rising VPD promotes a cascade of responses within plants and ecosystems (Figure 2). Elevated VPD drives reductions in stomatal conductance that limit excessive transpirational water losses (Farquhar, 1978; Leuning, 1995; Running, 1976) but frequently reduce photosynthesis (Grossiord et al., 2020; Long & Woolhouse, 1978). Rising VPD also reduces the turgor pressure necessary for plant growth (Peters et al., 2021; Zweifel et al., 2021) and increases the occurrence of low plant water potentials that kill trees and reduce crop yields (Hammond et al., 2022; Lobell et al., 2014; McDowell & Allen, 2015. At the ecosystem scale, higher VPD increases evaporative demand for ecosystem ET, which accelerates soil drying (Zhou, Williams, et al., 2019) and drying of both live and dead plant biomass (Rao et al., 2023), leading to an overall intensification of the hydrologic cycle (Ficklin et al., 2022) and wildfire activity (Williams et al., 2019). Altogether, the consequences of rising VPD are profound and encompass a wide range of socially-relevant environmental systems and processes, including carbon uptake and storage, agricultural productivity, natural and water resources management and our ability to detect and forecast drought events (Figure 2).

However, while rising VPD is emerging as one of the most important impacts of climate change on plants and the services they provide, diagnosing these impacts and prescribing management solutions to mitigate them remains challenging. Much of the difficulty emerges from the fact that VPD trends are strongly coupled with changes in soil water, temperature and CO_2, making it difficult to fingerprint the impact of each on plant and ecosystem function (Grossiord et al., 2020; Lin et al., 2018; Novick et al., 2016). This paper offers a holistic perspective of the impacts of rising VPD on individual plants, entire ecosystems and managed socioenvironmental systems, paying particular attention to the independent and interactive influence of VPD in the context of a broader set of environmental changes. We begin by discussing mechanisms by which VPD affects the physiology, growth and mortality of individual plants, in isolation and combined with other nonstationary drivers (Section 2). These physiological mechanisms, which are foundational for the systems-level impacts discussed later, have been well-reviewed elsewhere (e.g., Grossiord et al., 2020). Thus, Section 2 offers a somewhat abbreviated summary that updates prior reviews and focuses attention on emerging topics (e.g., the role of nocturnal

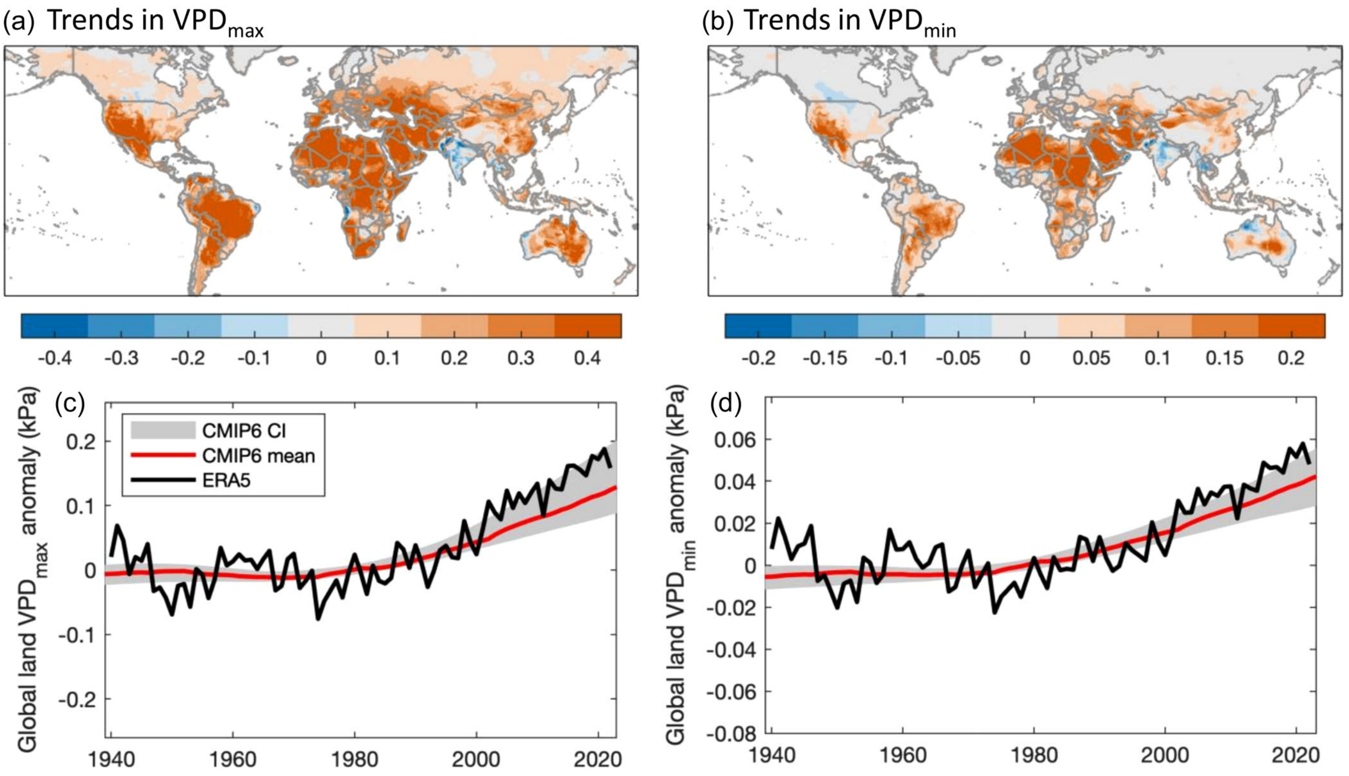

FIGURE 1 Global trends in historic vapour pressure deficit (VPD). The top panels show the total trend in daily maximum (a) and minimum (b) VPD from 1940 to 2022, determined from ERA5 reanalysis data (Hersbach et al., 2020). Shading indicates the linear magnitude of the VPD increase (in kPa) over the 43-year period. Bottom panels show anomalies in the area-weighted ERA5 global land surface time series for maximum VPD (c) and minimum VPD (d) relative to the 1951–2000 time periods (black line). Also shown in (c) and (d) are the ensemble average min and max VPD (presented as 31-year moving averages) from 20 models participating in the World Climate Research Programme Coupled Model Intercomparison Project Phase 6 (CMIP6 [Eyring et al., 2016]), using historical (1850–2014) and moderate emissions (SSP245, 2015–2099) scenarios. The grey shading brackets the 10th and 90th percentile averages. More details on methodology appear in the Supporting Information S1. [Color figure can be viewed at wileyonlinelibrary.com]

VPD trends). Next, we focus our attention on community and ecosystem scale responses to rising VPD (Section 3), including the potential for long-term shifts in community composition, carbon-cycle responses to the land-atmosphere feedbacks that couple soil water and VPD, and the underappreciated role by which thermodynamic processes determine vertical and horizontal VPD variability within and above vegetated canopies. Finally, Section 4 reviews the largely deleterious consequences of rising VPD for a range of managed systems and offers a set of recommendations to better prepare resource managers for a higher-VPD world. Key points from each of these sections are summarised in Boxes 1, 2 and 3.

2 | IMPACTS OF RISING VPD ON INDIVIDUAL PLANTS

2.1 | Leaf-scale impacts of rising VPD on gas exchange

When VPD is relatively high, the atmosphere is more desiccating, and stomata tend to close (at least at steady state, Buckley, 2016; Grossiord et al., 2020). The process happens within minutes (Buckley et al., 2011), and while the exact sensing mechanisms remain an active area of research, they seem to involve the differential impacts on leaf epidermal versus guard cells mediated by hormonal signals (Fu et al., 2022; McAdam & Brodribb, 2015). Notwithstanding some mechanistic uncertainty, the emergent pattern is well-established. Stomatal conductance (g_s) declines as VPD rises (Figure 2a), with abundant empirical evidence at leaf-to-global scales across a broad spectrum of plant functional types (Denham et al., 2021; Flo et al., 2022; Kimm et al., 2020; Meinzer, 1982; Novick et al., 2016; Oren et al., 1999; Roby et al., 2020; Urban et al., 2017). This dependence of g_s on VPD has also been incorporated into most empirical and phenomenological models of g_s (Ball et al., 1987; Cowan & Farquhar, 1977; Katul et al., 2009; Leuning, 1995; Medlyn et al., 2011, 2012, Sperry et al., 2017).

Reductions in g_s reduce transpiration (T) relative to a constant g_s scenario (Oren et al., 1999; Sperry et al., 2016). As a result, in natural settings, the relationship between T and VPD is typically parabolic (Figure 2b) with increasing T at low VPD, a progressive saturation as VPD rises and stomata close more fully, and an eventual decline in T as drying soils compound the VPD limitations to g_s (Poyatos et al., 2007).

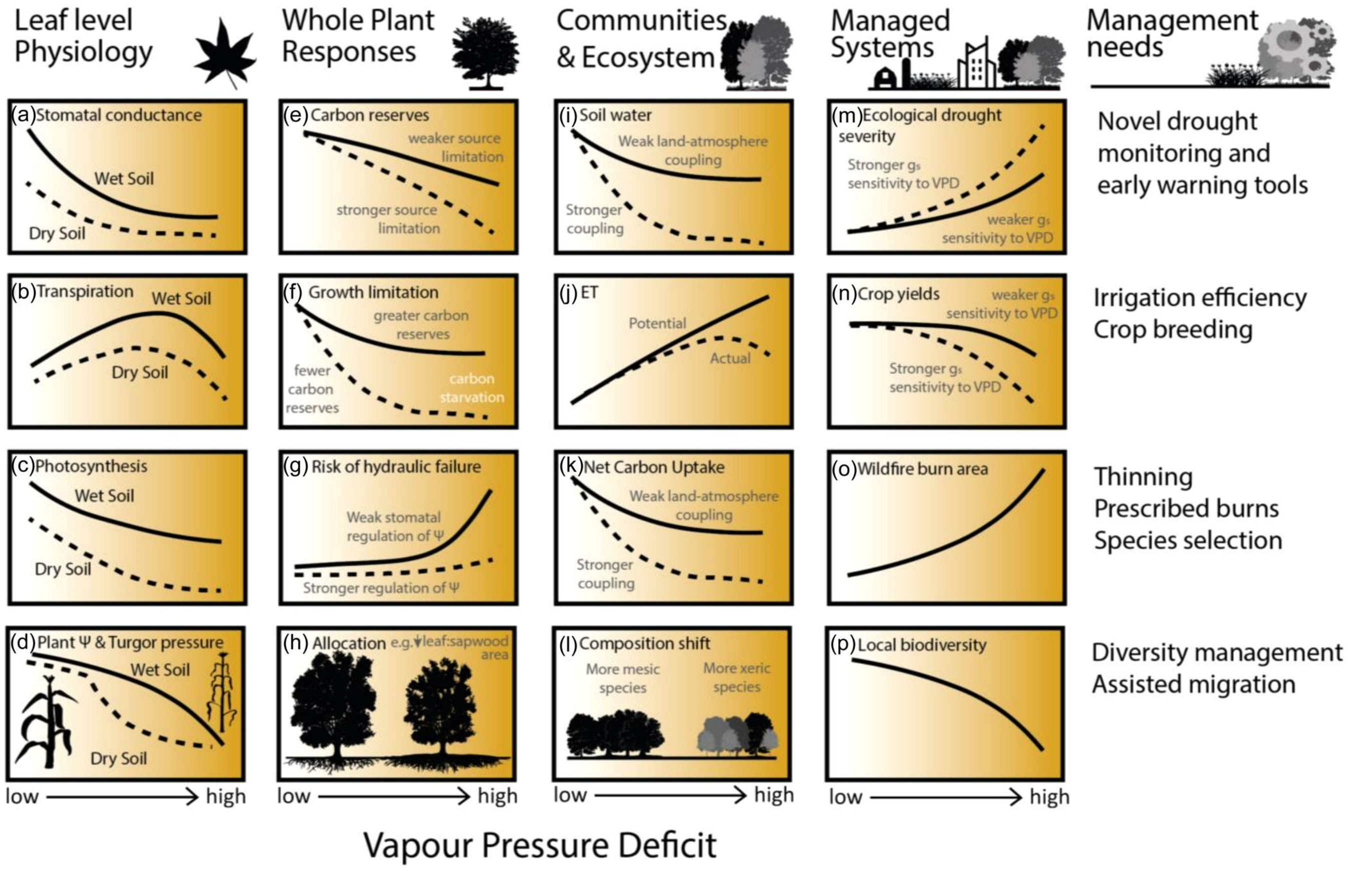

FIGURE 2 A conceptual illustration of the impacts of rising vapour pressure deficit for processes occurring at the scale of individual plant leaves (a–d), whole plants (e–h), entire ecosystems (i–l) and a range of managed systems (m–p). Key management opportunities are highlighted to the right. [Color figure can be viewed at wileyonlinelibrary.com]

While lower g_s is beneficial for plant water status, it comes with the consequence of reduced photosynthesis (*A*, Figure 2c). Because the relationship between A and g_s is saturating (Farquhar & Sharkey, 1982; Yi et al., 2019), reductions in *A* are initially less dramatic than reductions in g_s. However, this may not be true at higher VPD, when the relationship between g_s and *A* is complicated by changes in mesophyll conductance and leaf biochemistry (Drake et al., 2017; Flexas & Medrano, 2002; Yang et al., 2019; Zhou et al., 2013).

The precise sensitivity of g_s to VPD varies across species (Flo et al., 2022; Meinzer et al., 2013). Plants that have evolved to thrive in high humidity conditions are often not well adapted to prolonged periods of high VPD and may experience greater reductions in gas exchange (Schönbeck, Grossiord, et al., 2022). Interspecific variability in stomatal sensitivity to VPD also likely depends on plant hydraulic traits, since one of the consequences of reduced g_s is a reduced risk of negative excursions in plant water potential (Ψ) that can promote xylem embolism and failure of the hydraulic transport system. Higher stomatal sensitivity to VPD occurs in species with lower resistance to xylem embolism, higher xylem hydraulic conductivity, less allocation to sapwood relative to leaves and greater rooting depth (Flo et al., 2022)—a cohort of traits that corresponds with the 'fast' plant resource use strategy (*sensu* Reich, 2014). Plant height also matters. Darcy's law predicts that rising VPD will reduce g_s to a greater extent in taller trees due to the more negative leaf Ψ of taller trees necessary to overcome larger gravitational head losses (McDowell & Allen, 2015). This prediction has been confirmed empirically (Flo et al., 2021; Koch et al., 2004), particularly for sun-exposed leaves (Fernández-De-Uña et al., 2023).

Generalisable frameworks describing the linkages between stomatal sensitivity and overall plant water use strategies (or vice versa) are an important research area (Kannenberg et al., 2022). Stomatal regulation of Ψ is the basis of the popular 'isohydricity' framework, which categorises plants based on the stationarity of plant Ψ as drought evolves. The link between Ψ regulation and g_s is critical but complex; it depends in part on whole-plant hydraulics (Martínez-Vilalta & Garcia-Forner, 2017; Meinzer et al., 2016) and the subtleties of this relationship need to be considered (Feng et al., 2019; Guo et al., 2020). For example, from the classic drought-response strategies characterised by Levitt (1980): drought tolerance (i.e., the ability to endure low water potentials in plant tissues), water spender (i.e., drought avoidance by securing access to soil water resources) and water saver (i.e., drought avoidance by maximising water conservation, including stomatal closure), only the latter strategy would be expected to involve high stomatal sensitivities to VPD, and even then the effects of soil water availability and atmospheric drought on stomatal sensitivity are typically mingled.

BOX 1: Summary of the impacts of rising VPD on individual plants

Leaf-level gas exchange: Rising VPD reduces stomatal conductance, which usually reduces photosynthesis and limits transpiration. While these responses depend strongly on species and traits, greater stomatal sensitivity to VPD is expected for moist-adapted plants, taller trees and plants with a 'fast' resource use strategy.

Plant growth: Rising VPD limits plant growth by reducing the supply of carbon from photosynthesis (source-limitation) and by lowering internal turgor pressure which inhibits cell division and expansion (sink-limitation). Especially over short-time scales, low plant turgor can decouple carbon assimilation and growth. Disentangling the influence of soil water and VPD on plant growth is a major research need.

Plant survival: There is clear evidence that rising VPD is increasing plant mortality via mechanisms that include irreversible dehydration through hydraulic failure and carbon starvation. VPD-driven mortality is likely greater for taller trees. Isolating the effects of VPD from those attributable to soil drought and high temperatures remains challenging.

Connections with rising CO_2 and temperature: While the effects of rising CO_2 can mitigate or exacerbate VPD impacts, evidence suggests that the negative impacts of VPD frequently overwhelm the positive impacts of CO_2. Disentangling the impact of rising temperature from rising VPD is challenging, and more experiments that independently modify one or the other are necessary.

Plant-level adaptation and acclimation under rising VPD: Over long time scales, elevated VPD triggers an acclimation response characterised by increased rooting depth to increase water supply and/or a decrease in leaf area to reduce the water demand. It also exerts direct effects on plant reproductive development. We have much to learn about the timescales and variability in these responses across taxa and their interactions with plant traits.

BOX 2: Summary of the community and ecosystem-scale impacts of rising VPD

Shifts in community composition and plant interactions: Elevated VPD impacts both mortality patterns and post-mortality recruitment in ways that will likely change community composition, including shifts toward shorter broadleaf species in forests and toward C_4 species in grasslands. There is an urgent need to understand how increased VPD will affect the underlying mechanisms of competition, facilitation and complementarity between neighbouring species.

Land–atmosphere interactions and carbon cycling: Soil water and VPD are strongly coupled by land-atmosphere feedbacks driven by evapotranspiration, and mediated by plant characteristics like rooting depth and stomatal traits. The interplay between soil water and VPD is a predominant control on terrestrial carbon cycling, with VPD exerting an outsized influence in mesic systems. Disentangling the impacts of soil water and VPD on carbon uptake is an ongoing research challenge that would benefit from novel observation and modelling tools.

Within-site variability in VPD: Vertical and horizontal gradients of VPD within ecosystems are ubiquitous and depend on vegetation structure and microtopography. The VPD of the air (VPD_{air}) is frequently much lower than the leaf-to-air vapour pressure difference ($VPDiff_{leaf\text{-}air}$), which is more relevant to plant function. Using VPD_{air} in place of $VPDiff_{leaf\text{-}air}$ biases estimates of stomatal sensitivity to VPD.

2.2 | Impacts of rising VPD on plant growth

Increasing VPD decreases plant growth across much of the land surface (Dannenberg et al., 2020; Ding et al., 2018; Restaino et al., 2016; Park Williams et al., 2013)—an effect that has intensified over the past century (Babst et al., 2019). Reduced g_s under elevated VPD is one responsible mechanism, as it limits the supply of carbon needed for the synthesis of new tissue ('source limitation', Figure 2e). Elevated VPD can also lower plant water potentials, inhibiting the production of new cells in meristematic tissues. Specifically, for cell division to occur, cambial cells must approximately double in size (Cabon et al., 2020). This condition requires turgor pressure to exceed a certain threshold (Lockhart, 1965; Pallardy, 2010) which can not be reached when Ψ is low. Consequently, most growth (at least in tree stems) occurs during nocturnal periods when VPD is <0.4 kPa and plant Ψ is at its highest (Tumajer et al., 2022; Zweifel et al., 2021). By elevating transpiration, high VPD lowers plant Ψ (Figure 2d), resulting in a 'sink limitation' to growth via reduced turgor (Cabon et al., 2022; Körner, 2015; Muller et al., 2011; Peters et al., 2021). This mechanism is particularly relevant for plants whose stomata do not fully close at night, as rising VPD can increase nocturnal transpiration and decrease nocturnal Ψ. However, elevated daytime VPD can also drive a sink limitation by increasing the time that it takes for plant Ψ to equilibrate with soil Ψ at night (Bucci et al., 2004) and by increasing the rate of soil drying (see Section 3.2). The clear global increases in nocturnal VPD (Figure 1) certainly motivate future work to uncover how mechanistic links between VPD and growth manifest over seasonal to decadal time scales.

BOX 3: Summary of the resource management implications of rising VPD

Drought monitoring and water resources. Elevated VPD exacerbates drought conditions and is a major factor driving the likelihood of flash droughts. The importance of VPD for drought evolution is not well captured by most popular drought monitoring tools which treat plants as null or static participants in the hydrological cycle. Rising VPD is also likely to increase evapotranspiration in ways that reduce runoff and downstream water availability, necessitating more flexible approaches to water resource management.

Implications for crop yields. Elevated VPD is driving yield penalties in major agricultural hotspots across the globe, affecting a variety of staple crops that feed billions of humans. Breeding VPD-resilient cultivars and optimising irrigation scheduling are promising avenues to mitigate the impacts of rising VPD in croplands. Breeding improvements that target traits related to rooting depth, reproduction and nitrogen fixation may also be necessary.

Implications for wildfire: By accelerating the drying of live and dead fuels, rising VPD is increasing wildfire burn area across the world, though local effects are mediated by vegetation properties, including rooting depth and hydraulic traits. The relationship between VPD and wildfire reflects the coupling between VPD, soil water and temperature and care should be taken not to attribute an increase in wildfire damage to a single variable. Management approaches to reduce VPD-driven wildfire impacts include thinning and prescribed fire (to reduce fuel loads) and continued development of early drought warning systems.

Adaptive management for resilient natural systems. VPD effects are not yet incorporated into most long-term ecosystem management plans. Management for more biodiverse plant communities and for individual species that are better adapted to warmer and drier climates are likely to confer resilience to rising VPD. Approaches like thinning and genetic improvements for trees may have benefits in some systems, but a cross-disciplinary and multisector approach is needed to develop robust management plans.

When rising VPD reduces photosynthesis, a source limitation to growth is likely to co-occur with the sink limitation. When stored carbohydrates are sufficient, growth can be relatively unaffected if photosynthesis is limited (Figure 2f), provided that there are periods (e.g., at night) during which plant turgor is sufficient for cell division and expansion (Dietze et al., 2014; Martínez-Vilalta et al., 2016). This is particularly true in the tropics and other mesic ecosystems, where elevated VPD may reduce photosynthesis but does not always cause growth reductions (Herguido et al., 2016; Rowland et al., 2015) because growth is maintained through carbohydrate reallocation (Doughty et al., 2015). However, if photosynthetic reductions from elevated VPD are prolonged, stored carbohydrates will be depleted, and their buffering capacity for growth will be diminished (Figure 2f). This helps to explain why land surface models can accurately simulate growth at large scales using only source-driven constraints with no representation of sink limitations (Bonan, 2008; Cabon et al., 2022; Fatichi et al., 2019; Field et al., 1998).

Finally, it is important to recognise that reductions in soil water, which frequently co-occur with periods of elevated VPD (see additional discussion in Section 3), have the potential to exacerbate both source and sink limitations. Measurements of tree stem growth at a high temporal resolution (e.g., from automated dendrometry, Salomón et al., 2022) over which soil water and VPD are less coupled are important for disentangling the growth consequences of these two drivers.

2.3 | Impacts of rising VPD on plant survival

There is clear evidence linking increased VPD with plant mortality (Adams et al., 2009; Breshears et al., 2013; Hammond et al., 2022; Park Williams et al., 2013), coupled with strong theoretical arguments to expect higher VPD to increase mortality due to both hydraulic failure and carbon starvation (Mcdowell et al., 2022). Hydraulic failure, ultimately leading to irreversible cellular dehydration due to severe loss of hydraulic conductance (Choat et al., 2018), occurs because of greater xylem tension (e.g., lower xylem Ψ) which can be promoted directly by VPD-driven increases in transpiration, and indirectly through evaporative drying of the soil surface. While stomatal closure can reduce the risk of hydraulic failure (Oren et al., 1999; Sperry et al., 2016, Figure 2g), it comes with the consequence of reduced crown-level photosynthesis. Reduced photosynthesis promotes carbon starvation—the process by which limited carbohydrate availability impacts hydraulic, defensive and metabolic mechanisms that prevent mortality (Figure 2f), and which may be further exacerbated by the loss of canopy leaves under drought (Poyatos et al., 2013).

The mechanisms that govern the interaction between hydraulic failure and carbon starvation are complex and depend on many traits and their covariation (Choat et al., 2018), which challenges our understanding of which plant species are most vulnerable to VPD-driven increases in mortality. For example, increasing vulnerability to xylem embolism may be associated with deeper roots, allowing a plant to avoid severe hydraulic failure despite having vulnerable xylem (Benson et al., 2022; Chitra-Tarak et al., 2021; Matheny et al., 2017). Moreover, because soil water and VPD are strongly coupled over the seasonal and annual timescales over which plants die, disentangling the relative influence of each on plant survival is difficult. Some emerging evidence suggests the possibility of substantial VPD-induced embolism occurring in both seedlings and mature trees under conditions of abundant soil moisture (Bauman et al., 2022; Schönbeck, Schuler, et al., 2022; Wagner et al., 2022). Likewise, across tropical sites characterised by nonlimiting soil water, natural gradients in VPD drive variation in a wide range of plant responses and traits, including those that govern mortality risk (Binks et al., 2023). Nonetheless, manipulative or 'natural' experiments that alter VPD but not soil water remain scarce (but see Figure 3). Hydraulic modelling frameworks are also useful tools for predicting the risk of mortality in response to both drying soil and rising VPD (Mencuccini et al., 2019; Trugman et al., 2021), and for characterising the theoretical underpinnings of an emergent tendency for large trees to die more readily during droughts (Fernández-De-Uña et al., 2023; McDowell & Allen, 2015). However, while hydraulic modelling schemes are abundant, evaluating them requires concerted efforts to aggregate accessible and representative data on plant Ψ and other hydraulic variables (Novick et al., 2022).

Interactions with forest pests and pathogens will likely play an important role in determining tree survival under higher VPD. Because larger trees could have lower defensive capacity during droughts due to size-related hydraulic constraints, they may also be more vulnerable to pests and pathogens (Fernández-De-Uña et al., 2023; McDowell, 2011) which are more likely to attack stressed trees (Ayres & Lombardero, 2000; Raffa et al., 2008). Consequently, VPD-driven reductions to water status and carbon supply increase the risk of pest- and pathogen-driven mortality. Finally, mortality also depends on plant traits that regulate leaf temperature. Some species may fail to close stomata at high temperatures, presumably to avoid lethal overheating (Marchin et al., 2022), which can increase survival of some species during extreme drought even at the expense of higher water loss (Garcia-Forner et al., 2016). Even if stomata are fully closed, water losses from leaves can still increase due to cuticular conductance (e.g., water loss through nonstomatal pores, Duursma et al., 2019). While this behaviour may also prevent overheating (Aparecido et al., 2020), it can exacerbate and extend desiccation, which should increase the risk of hydraulic failure and irreversible dehydration (Blackman et al., 2016). Therefore, high cuticular conductance under elevated temperature could be an important mechanism underlying hydraulic failure under high VPD (Cochard et al., 2021).

2.4 | Confounding effects from rising CO_2 and temperature

Through direct and indirect mechanisms, concurrent increases in both temperature and CO_2 have the potential to mitigate, exacerbate and/or obscure the impacts of increasing VPD. Alone, rising CO_2 is associated with a mild degree of stomatal closure (Ainsworth & Rogers, 2007; Medlyn et al., 2001) and/or decreases in stomatal density and aperture (Lammertsma et al., 2011). Stomatal closure under rising CO_2 is a widely accepted mechanism for observed increases in plant water use efficiency (Lavergne et al., 2019; Poorter et al., 2022), though emerging evidence suggests that VPD-driven reductions in g_s can complicate the interpretation of water use efficiency trends (Zhang et al., 2019; Grossiord et al., 2020; Li et al., 2023; Ruffault et al., 2022). Rising CO_2 also tends to increase the

FIGURE 3 The VPDrought experiment—located near Valais, Switzerland—is the world's first atmospheric humidity and soil moisture manipulative experiment in a mature natural forest. It combines air humidity (and thus vapour pressure deficit) manipulation using a humidification system in the canopy of adult trees with soil water manipulation using a below-canopy throughfall exclusion system. Photo Credits: M. Schaub. https://www.wsl.ch/vpdrought. [Color figure can be viewed at wileyonlinelibrary.com]

temperature optimum of photosynthesis (Long, 1991), potentially mitigating the influence of heat stress during high VPD. On the other hand, rising CO_2 may promote greater leaf area (Walker et al., 2021) which can predispose trees to hydraulic failure during drought (Jump et al., 2017) and increase transpiration and interception evaporation in ways that reduce soil moisture and exacerbate VPD effects. Finally, rising CO_2 also alters allocation to carbon belowground (Walker et al., 2021) that can mitigate rising VPD impacts and reduce hydraulic vulnerability to embolism (Domec et al., 2010). Regardless of these various positive and negative responses to CO_2, the rise in mortality witnessed globally over the last few decades (Bauman et al., 2022; Hartmann et al., 2022; Mcdowell et al., 2018; van Mantgem et al., 2009) occurred while both CO_2 and VPD were rising, suggesting that increased CO_2 has not been able to completely offset the impact of increased VPD and drought.

The close relation between VPD and temperature makes it challenging to separate the effects of high VPD and high temperature on plant function. However, doing so is critical, because temperature affects plants through a broad array of direct mechanisms that operate independently of VPD, including (a) enzyme kinetics relevant for photosynthesis (Farquhar et al., 1980) and respiration (Atkin & Tjoelker, 2003); (b) diffusion rates that determine mesophyll conductance (von Caemmerer & Evans, 2015); (c) phenological cues (Kramer et al., 2000); (d) physiological structure of membranes (Gounaris et al., 1984); (e) adjustments to g_s, to facilitate evaporative cooling (Day, 2000; Urban et al., 2017) and (f) temperature-driven changes in the viscosity of water flowing through plants (Roderick & Berry, 2001). More indirectly, higher temperatures also tend to increase the rates of insect reproduction and survival (Ayres & Lombardero, 2000), further increasing the risk of attacks and outbreaks on trees which may already be experiencing novel levels of environmental stress.

Despite different mechanisms, high VPD and high temperature often appear to have qualitatively similar downstream effects on plant function—they both exacerbate reductions in photosynthesis (Dannenberg et al., 2022) and growth (Park Williams et al., 2013) under drought. However, the correlation between temperature and VPD may confound these results. For example, a recent study suggested that the independent effects of VPD and temperature on Northern Hemisphere GPP counteract, with VPD having a positive or neutral effect on GPP in humid areas (Zhong et al., 2023), while having a negative effect in more arid zones (Zhong et al., 2023). The tendency for VPD effects to overwhelm temperature effects in arid landscapes is consistent with Eamus et al. (2013), which used models to show that the combination of drought and increased VPD in an open woodland can be more deleterious to productivity and transpiration than the combination of drought and high temperature. Overall, we still have much to learn about the independent and interactive effects of VPD and temperature, and only a few studies have manipulated temperature and VPD independently of each other, usually for short periods of time (Barron-Gafford et al., 2007; Day, 2000; Schönbeck, Schuler, et al., 2022). More experiments are needed that isolate the impacts of temperature and VPD (e.g.-, Figure 3), and for longer periods of time.

2.5 | The potential for plant-level acclimation and adaptation to rising VPD

Both atmospheric and soil water deficits can drive acclimation in plant functional traits, along with shifts in allocation to above versus belowground biomass and to growth versus nonstructural carbon pools (Escudero et al., 2017; Ramírez-Valiente et al., 2017; Rosas et al., 2019). A recent meta-analysis on 112 species and 56 traits revealed that the long-term effects of VPD are wide-ranging, impacting plant water use, mineral nutrition, development, metabolism, growth and reproductive success (López et al., 2021). These effects were systemic, impacting traits across scales ranging from the cell/tissue to the organismal level. In general, the responses coalesced toward an 'anticipatory' response strategy favoring processes leading to reduced leaf area and height coupled with increased water acquisition through deeper roots. These responses support Darcy's law, which predicts that warmer and drier climates would favour the survival of vegetation that is shorter and equipped with a smaller evaporative surface (McDowell & Allen, 2015). Indeed, adjustments to leaf area and in the ratio of leaf-to-sapwood area (A_L:A_S), have been an extensively documented consequence of shifting water availability (Anderegg et al., 2022; Baldocchi & Xu, 2007; Kerr et al., 2022; Martínez-Vilalta et al., 2009; Piñol & Sala, 2000; Rosas et al., 2019). While changes in traits like A_L:A_S are likely a combined effect of VPD and soil water availability, at least one modelling study demonstrated that decreases in A_L:A_S could be explained exclusively by differences in VPD (Trugman et al., 2019). Similarly, Watson et al. (2023) used a novel, in-situ VPD manipulation experiment to demonstrate that a grass species experienced reduced leaf area and an increased root:shoot ratio only when soil drought was combined with elevated VPD.

While the results from these studies are converging and seemingly generalisable, much more remains to be uncovered about how plants respond to rising VPD in the long term (Rowland et al., 2023). The timescale and speed of acclimation to elevated VPD are poorly understood, and the extent of plasticity within species and the potential for intergenerational adaptation through epigenetics (Tricker et al., 2013) or genetic changes (Tamang et al., 2022) require further investigation. Rising VPD during reproductive phenology may also negatively impact anther opening (Bianchini & Pacini, 1996), pollen viability (Fonseca & Westgate, 2005) and female reproductive development (e.g., silk elongation rate, Turc et al., 2016), with important but incompletely understood consequences for reproduction and agricultural crop yields. Finally, elevated VPD has been recently shown to lead to higher N fixation (Monnens et al., 2023), at least over short timescales. This result is consistent with the meta-analysis of López et al. (2021), which showed that higher VPD triggers increased N accumulation in leaves. Thus, rising VPD may have an important but underappreciated role in governing global nitrogen cycling.

3 | COMMUNITY- AND ECOSYSTEM-SCALE IMPACTS OF RISING VPD

3.1 | VPD-driven shifts in community composition and plant interactions

Community composition is a function of plant demography and species interactions. Because demographic parameters manifest over years to centuries, it is difficult to conduct experiments to tease apart the role of VPD versus soil water (among other drivers) on shifts in community composition. Most observational evidence for compositional changes driven specifically by VPD come from experimental studies in grasslands. In one case, functional group composition shifted toward C_4 grass species (Wang & Wen, 2022), similar to past studies on soil drying (e.g., Taylor et al., 2014). Other work suggests that some herbaceous species may respond strongly to atmospheric drying while others respond more strongly to soil drying (Huynh et al., 2024).

In forests, the role of VPD in driving composition shifts can be informed by observed responses to naturally occurring drought coupled with theoretical inference. In general, compositional shifts are influenced by the severity, spread and frequency of disturbance events and the presence of surviving vegetation to provide seed sources, both of which are driven in part by VPD extremes (Breshears et al., 2013; Mcdowell et al., 2023). Drought can cause changes in forest community composition when mortality of pre-existing species is followed by recruitment of different species (Batllori et al., 2020; Martínez-Vilalta et al., 2016; Mitchell et al., 2014), especially when aridity and/or heat are elevated postdisturbance (Enriquez-de-Salamanca, 2022; Miller et al., 2021; Serra-Diaz et al., 2018; Talucci et al., 2019). Indeed, theoretical work suggests that compositional shifts are required to avoid future VPD stress in many forested ecosystems (Quetin et al., 2023). However, shifts toward more drought-tolerant species compositions are occurring at a much slower rate than required by the rate of increasing VPD, despite a sufficient seed reservoir of drought-tolerant species in most places (Quetin et al., 2023; Trugman et al., 2020). Given the mismatch between the timescales at which VPD is rising (e.g., decadal, see Figure 1) and the timescale of tree range shifts (e.g., centuries), strong VPD increases have the potential to drive substantial forest loss in addition to composition changes.

VPD impacts on community changes are also likely in non-disturbed systems. If rising VPD preferentially kills plants with certain traits, such as taller species (Bennett et al., 2015; Giardina et al., 2018; McDowell & Allen, 2015), those with shallower roots (Feng et al., 2023), or those with greater vulnerability to hydraulic failure (Quetin et al., 2023), it could lead to a slow persistent shift in the community composition, such as a transition from taller needleleaf species to shorter broadleaf species (Batllori et al., 2020; McDowell & Allen, 2015). Long term observational studies in intact forests have indeed observed transitions to species more tolerant of dry conditions (Esquivel-Muelbert et al., 2019).

Finally, we have a very limited understanding of how rising VPD will affect species interactions, especially competition (e.g., altered competitive hierarchies), facilitation (e.g., microclimate effects) and complementarity (e.g., partitioning of soil water sources). Existing evidence suggests that reduced VPD in higher diversity and higher biomass communities improves establishment of woody seedlings into grasslands (Wright et al., 2014, 2015). Vegetation has the capacity to promote substantial small-scale (e.g., microclimate) modifications to VPD (see extended discussion in Section 3.3), which can influence sapling recruitment (Hoecker et al., 2020) and affect patterns of both facilitation and competition, sometimes differentially. For example, a focal species was facilitated by neighbours in high VPD microclimates but limited by competition from neighbours in low VPD microclimates (Aguirre et al., 2021). These considerations are especially relevant in drylands, where microclimate gradients are often strong (Butterfield et al., 2016) and where vegetation 'nurse' effects may alleviate high VPD conditions (Anthelme & Michalet, 2009; Wright et al., 2014). In these landscapes, VPD-induced shifts in rooting depth of one species could affect soil water resources for the entire community.

3.2 | Land–atmosphere interactions governing soil water and VPD coupling and ecosystem carbon cycling

The dynamics of soil water and VPD are connected through two-way land–atmosphere interactions mediated by surface energy partitioning to ET (Zhou, Williams, et al., 2019; Zhou, Zhang, et al., 2019). Initially, increasing VPD leads to soil drying by enhancing ET (Or et al., 2013), though stomatal closure under higher VPD mediates the pace at which ET rises (see Section 2.1, Massmann et al., 2019). Thereafter, low soil water content begins to reduce ET by limiting water supply and inducing additional stomatal closure beyond that already imposed by higher VPD. As ET declines, more available surface energy is partitioned to sensible heat flux, which increases air temperature, further elevating VPD (Gentine et al., 2016). Consequently, soil water content and VPD are strongly coupled, especially at weekly to annual timescales (Lin et al., 2018; Liu, Gudmundsson, et al., 2020; Novick et al., 2016) and in semi-arid regions where soil moisture strongly regulates ET (Koster et al., 2004; Seneviratne et al., 2010). However, within a given climate regime, vegetation cover and structure play an important role in determining the extent to which soil water and VPD dynamics are coordinated. Root access to deep soil moisture, groundwater and rock water (Giardina et al., 2018; Mccormick et al., 2021) can reduce the magnitude of the soil moisture-VPD coupling and buffer the influence of heatwaves (Mu et al., 2021). Differences in stomatal sensitivity between forests and grasslands also permit the former to more conservatively regulate ET during heatwaves in ways that delay soil drying (Teuling et al., 2010).

The plant-mediated coupling between soil water and VPD has important consequences for terrestrial carbon cycling. Decades ago, it was recognised that annual to decadal variability in terrestrial net primary productivity is negatively correlated with atmospheric temperature, though at the time, the underlying mechanisms were elusive (Keeling et al., 1989; Keeling et al., 1995). Since then, increasingly long satellite and observational records combined with advances in earth-system modelling have helped fill this mechanistic knowledge gap (Piao et al., 2020). Experiments like the Global Land-Atmosphere Coupling Experiment (Koster et al., 2004; Seneviratne et al., 2013) established that the coupling between soil water and VPD tends to increase the occurrence of concurrent hot and dry extremes (Dirmeyer et al., 2021) and promote far more extreme excursions in VPD than would occur otherwise (Zhou, Williams, et al., 2019). As a result, much of the correlation between terrestrial net productivity and temperature can be attributed to temperature's impact on VPD and associated soil moisture feedbacks. These interactions explain the strength of the observed relationships between the atmospheric CO_2 growth rate and both soil moisture and temperature (Green et al., 2019; Humphrey et al., 2021). We also now understand that the sensitivity of global net productivity to drought and VPD has increased over the past 50 years (Liu et al., 2023; Wang et al., 2014)—a trend likely to continue in the decades ahead (Hsu & Dirmeyer, 2023; Zhou, Zhang, et al., 2019).

Looking forward, the relative importance of soil water and VPD in driving ecosystem carbon uptake is likely to change. While rising VPD is a global phenomenon, future changes in soil moisture will likely be more heterogeneous (Novick et al., 2016). Thus, the nature of the coupling between soil water and VPD is nonstationary (Humphrey et al., 2021), and resolving the independent contributions of each to ecosystem function is paramount. Historically, this has been hard to do, especially in observational settings. While experimental manipulation of soil water is relatively straightforward, only recently have tools emerged for experimental manipulation of VPD in situ (Watson et al., 2023, and see Figure 3). Some progress has been made by leveraging high-frequency (e.g., hourly) measurements of ecosystem carbon and water fluxes from flux tower networks or sap flux (Flo et al., 2022; Fu et al., 2022; Novick et al., 2016), which are collected at timescales over which VPD and soil water are largely uncoupled, permitting the role of each to be empirically isolated. These methods have also been extended to remote-sensing data sets reporting on proxies for carbon and water fluxes at continental scales (Fu et al., 2022; Liu, Gudmundsson, et al., 2020). Taken together, these studies report contradictory conclusions regarding the relative amplitude and impact of soil moisture and VPD, leading to much debate about which is the dominant control on plant function during drought (Fu et al., 2022; Kimm et al., 2020; Liu, Gudmundsson, et al., 2020; Novick et al., 2016; Rigden et al., 2020; Sulman et al., 2016). In reality, both matter and their relative contributions will reflect background climate conditions and the unique combinations of plant traits at a given site (e.g., Lowman et al. 2023). Refining model schemes to capture these patterns with fidelity remains an evergreen research challenge.

Finally, much of our understanding of soil water-VPD coupling at global scales relies on soil moisture products that are largely model-derived (Liu, Gudmundsson, et al., 2020; Zhou, Williams, et al., 2019). These models have several sources of error, including (a) a lack of representation of plant access to groundwater and rock moisture, (b) a lack of accounting for plant hydraulics, which results in models underestimating the impact of VPD (Liu, Kumar, et al., 2020), (c) inadequate representation of water stress response traits within plant functional types (Kannenberg et al., 2022; Liu et al., 2021) and (d) uncertainty in the relationship between soil moisture and soil water potential, noting that the latter is the more relevant driver of plant function (Novick et al., 2022). Likewise, estimates of VPD across the globe contain many of the structural uncertainties associated with station observations that have been widely documented for temperature and, to a lesser degree, for humidity observations (Harris et al., 2020; Willett et al., 2014). Modern reanalyses, such as ERA5, provide an alternative and dynamically consistent approach for estimating VPD globally, though they have known problems associated with changes in data assimilation through time (Bell et al., 2021). Addressing these model and data limitations is necessary to fully understand the effect of VPD at large scales, where surface processes influencing VPD could also act nonlocally, through advection and by changing overlying atmospheric flows and cloudiness.

3.3 | Within-site variability in VPD and associated uncertainties

Above bare soil and in the vertical airspace above short plant canopies, temperature decreases logarithmically with vertical elevation (Monin & Obukhov, 1954). However, in the space between the soil surface and the uppermost canopy leaves, radiation attenuation suppresses temperature, which can lower VPD. As a result, VPD tends to increase with vertical position within vegetative canopies, and especially in dense forests (Barker & Booth, 1996; Gentine et al., 2019; Vinod et al., 2023, but see Johnston et al., 2022, for evidence of an opposite trend in open-canopy forests). Horizontal variability in VPD within a forest canopy can also be pronounced, especially in heterogeneous ecosystems. Midday VPD is usually higher in more open areas and in canopy gaps (Davies-Colley et al., 2000; Thom et al., 2020; Williamson et al., 2020), with VPD edge effects extending for tens of metres (Davies-Colley et al., 2000). Within grassland canopies, VPD can vary strongly over very small distances (<1 m) and depends on aboveground standing biomass, composition and species diversity (Wright et al., 2014, 2021). Lower elevation, terrain concavity and slope aspects facing away from the equator have also been associated with lower VPD (Bilir et al., 2021; Jucker et al., 2018). Thus, uniformity of VPD within an ecosystem should not be assumed (Figure 4a).

Another important consideration is the gradient between the leaf-to-air vapour pressure difference (hereafter $VPDiff_{leaf\text{-}air}$) and the VPD_{air}. $VPDiff_{leaf\text{-}air}$ represents the difference between the saturation

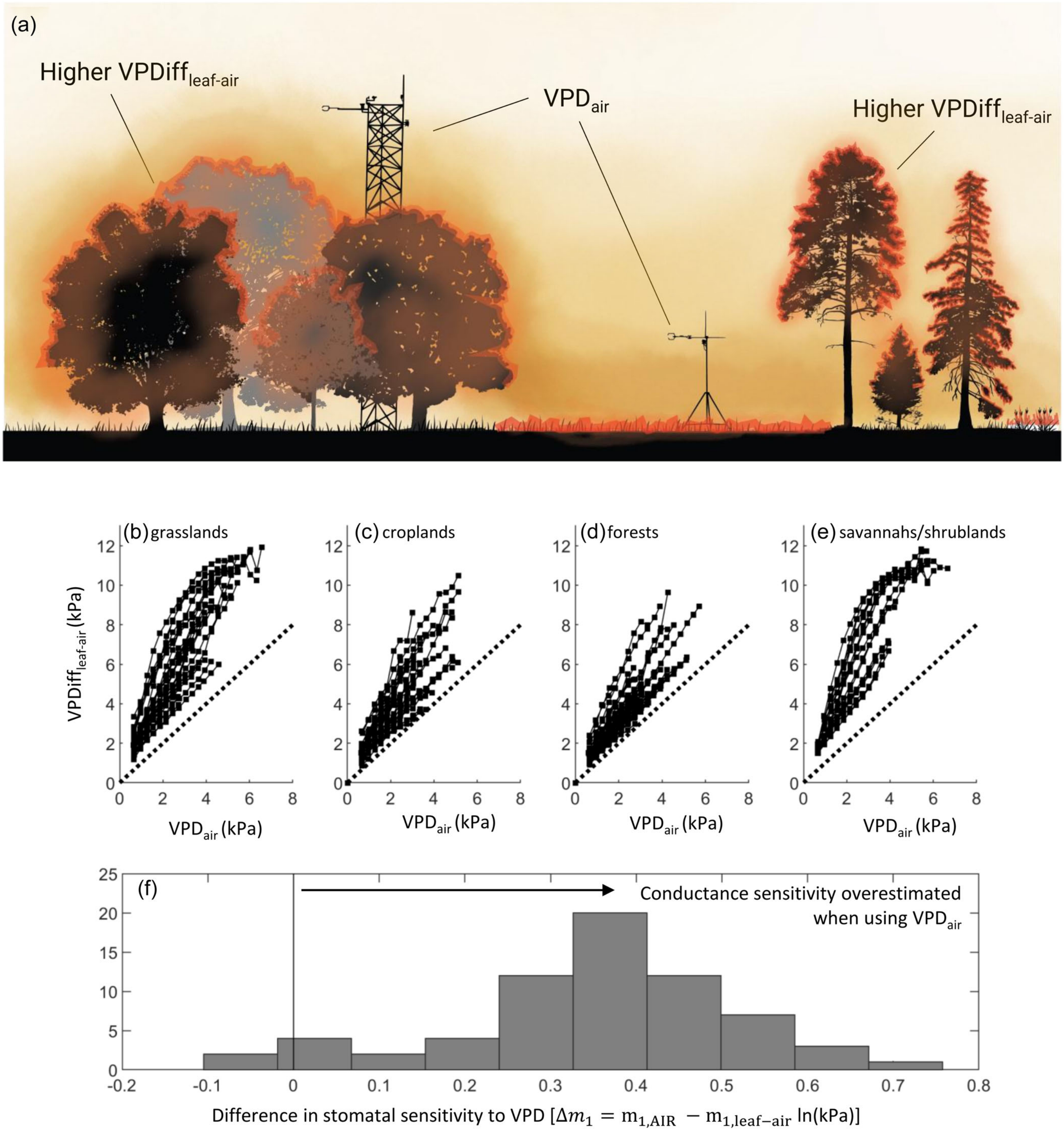

FIGURE 4 (a) Illustrates gradients in vapour pressure deficit (VPD) within and above canopies (note the very high VPD at the canopy surface). (b–e) Show the observed relationship between the VPD$_{air}$ and VPDiff$_{leaf\text{-}air}$ for more than 100 AmeriFlux towers (see Supporting Information for more details). In nearly all sites, the VPDiff$_{leaf\text{-}air}$ is greater than the VPD$_{air}$, sometimes by >5 kPa. (f) Shows that the sensitivity of conductance to VPD is overestimated when it is determined using VPD$_{air}$ versus VPDiff$_{leaf\text{-}air}$. Specifically, tower-derived time series of surface conductance (G$_{surf}$, a proxy for canopy stomatal conductance) were used to determine the sensitivity parameter m$_1$ of the model $G_{surf} = G_{surf,\ ref} \times [1 - m_1 \cdot \ln(VPD)]$ after Oren et al. (1999). Shown in (f) is the difference in m$_1$ when the model was forced by VPD$_{air}$ versus VPDiff$_{leaf\text{-}air}$. Additional methodological detail is provided in the Supporting Information. [Color figure can be viewed at wileyonlinelibrary.com]

vapour pressure inside the leaf and the actual vapour pressure in the surrounding air. VPDiff$_{leaf\text{-}air}$ is the vapour pressure gradient that drives diffusion of water vapour through stomata and is, therefore, the most relevant for explaining patterns in transpiration and stomatal conductance. VPD$_{air}$ represents the difference between the saturation and actual vapour pressure of the air itself. Based on surface energy balance considerations, during the daytime, the leaf surface will usually be warmer than the surrounding air (Still et al., 2022). In some ecosystems, the leaf-to-air temperature difference can be +10°C or more (Mildrexler et al., 2011; Novick and Barnes, 2023), though it varies considerably reflecting the local importance of evaporative cooling (including for leaf thermoregulation) and structural factors that determine canopy roughness and leaf boundary layer dynamics (De Kauwe et al., 2015; Lin et al., 2019; Novick & Barnes, 2023; Still et al., 2022). In contrast, relative humidity varies much more moderately within and above the canopy (Rockwell et al., 2022). As a result, the VPDiff$_{\text{leaf-air}}$ is usually substantially larger than VPD$_{\text{air}}$ (Figure 4a–e), especially when VPDair is high. Nonetheless, VPD$_{\text{air}}$ is frequently used as a proxy for VPDiff$_{\text{leaf-air}}$, especially in observational studies.

Failing to appreciate the difference between VPD$_{\text{air}}$ and VPDiff$_{\text{leaf-air}}$ has important implications. Empirically derived sensitivities of g_s and photosynthesis to VPD are likely overestimated when the VPD$_{\text{air}}$ is used instead of the VPDiff$_{\text{leaf-air}}$ (Figure 4f). These biases can obscure our species-level understanding of how gas exchange responds to VPD and become especially problematic when observed sensitivities are compared with theoretical expectations or implemented in models that do not account for VPD gradients. At the canopy scale, these biases can be reduced by using the Penman-Monteith equation to estimate leaf VPD (Lin et al., 2018) or by estimating the leaf saturation vapour pressure using canopy temperature data (Yi et al., 2020 and see Figure 4b–e). In leaf-level studies, leaf temperature is typically measured directly by portable photosynthesis systems, which reduces the problem somewhat, though challenges persist linked to differences between adaxial and abaxial temperatures as well as leaf thermocouple error (Mott & Peak, 2011). At all scales, the potential for undersaturation of vapour pressure inside the leaf, especially during periods of high VPD (Cernusak et al., 2018), can also affect the determination of VPDiff$_{\text{leaf-air}}$. All of these considerations most directly apply to sunlit leaves; in shaded areas of the understory, the difference between VPDiff$_{\text{leaf-air}}$ and VPD$_{\text{air}}$ may be less pronounced, but also more variable in space.

4 | IMPLICATIONS FOR MANAGED SYSTEMS

4.1 | Impacts of rising VPD on drought monitoring and water resources management

Because VPD determines the rate of evaporative water losses during drought, the global increase in VPD has important implications for downstream water resources. Rising VPD increases potential ET (PET) and, at least initially, actual ET, accelerating the rate of soil drying (see Section 3.2). The evolution of ET during drought depends on soil characteristics, including antecedent moisture conditions and the structural and textural properties that determine soil water retention (Novick et al., 2022; Zhao et al., 2022). ET dynamics also depend on vegetation characteristics; for example, drought may develop relatively slowly in forests (Christian et al., 2020) which can access deeper (and thus more slowly depleting) pools of water. Nonetheless, there is ample evidence that elevated VPD exacerbates drought conditions over a range of timescales (Dannenberg et al., 2022; Pendergrass et al., 2020; Williams, Cook, et al., 2022).

VPD plays a particularly important role in enhancing flash droughts, which are characterised by a period of unusually high VPD that rapidly increases ET and depletes soil moisture, especially if there is also below-average precipitation (Mahto & Mishra, 2023; Mo & Lettenmaier, 2015; Otkin et al., 2018; Wang et al., 2016). VPD is more strongly associated with flash drought onset than temperature or precipitation (Ford & Labosier, 2017) and soil moisture-VPD coupling can be three-to-five times higher during flash drought development than during other periods (Mahto & Mishra, 2023). The consequences of flash drought may be especially devastating for landscapes prone to wildfire (Rao et al., 2023 and see Section 4.3) and for agricultural systems (Otkin et al., 2018; Pendergrass et al., 2020 and see Section 4.2) where irrigation requirements may become more demanding in the future (Delucia et al., 2019), compounding water resource constraints and contributing to groundwater depletion (Condon, 2020).

Anticipating and preparing for drought events is a critical component of water resource management. However, most widely used metrics for drought monitoring and forecasting do not incorporate dynamic plant responses to rising VPD and declining soil water. Popular indices like the Palmer Drought Severity Index (PDSI, Palmer, 1965) and the Standardised Precipitation-Evapotranspiration Index (SPEI, Vicente-Serrano et al., 2010) are primarily based on the dynamics of precipitation and PET. While they agree reasonably well with soil moisture, streamflow and tree-ring records (Dai, 2011; Mishra & Singh, 2010; Vicente-Serrano et al., 2013), they tend to treat plants as static or over-simplified participants in the water cycle (Chang et al., 2023; Jiao et al., 2022; Swann et al., 2016) and assume that the actual and PET are equivalent. In reality, stomatal closure and other dynamic plant responses can cause actual ET to be substantially lower than PET, especially during periods of elevated VPD (see Figure 5a). This decoupling between actual and PET affects the dynamics of soil moisture (Figure 5b) but not necessarily PDSI and SPEI.

Some newer approaches for drought monitoring rely on remotely sensed proxies for actual ET, which should integrate stomatal dynamics. For example, the Evaporative Stress Index (or ESI, Anderson et al., 2011) is based on anomalies in the ratio of actual ET to PET, thereby incorporating the influence of dynamic stomatal regulation. Thus, ESI is viewed as a more reliable indicator of 'ecological drought' stress (e.g., moisture limitation that actually limits ecosystem function). The perspective on drought status provided by ESI can differ substantially from indicators like PDSI and SPEI (Figure 5c,d), which were conceived as tools for estimating meteorological and hydrological drought status. However, ESI can be confounded by changes in canopy structure which affect ET but do not necessarily reflect intrinsic drought stress (Chang et al., 2023).

Refining strategies to incorporate dynamic stomatal responses into drought monitoring and forecasting tools is a major need for

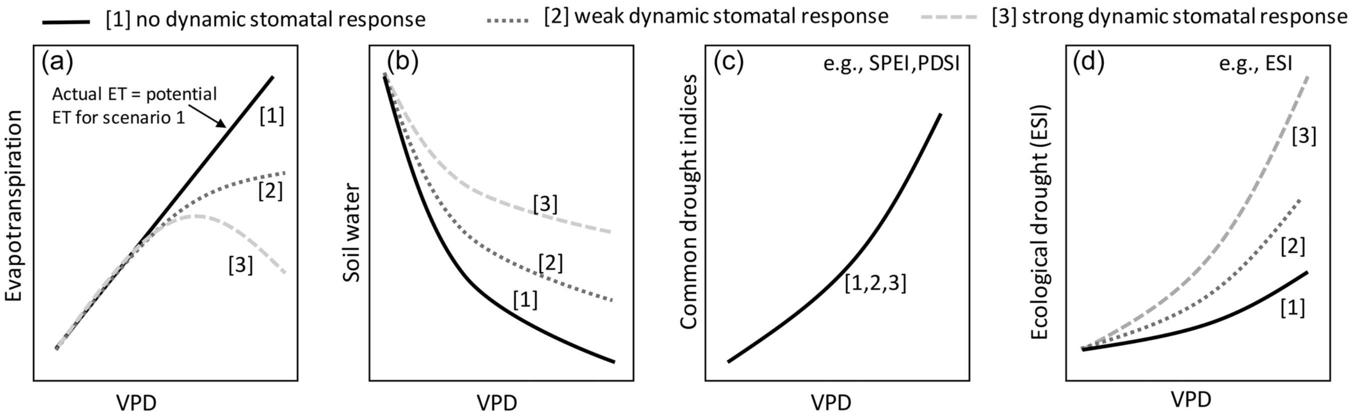

FIGURE 5 Dynamic stomatal responses to vapour pressure deficit (and/or soil drought) can decouple key drought indicators. Specifically, stomatal sensitivity to drought decouples the actual and potential evapotranspiration (a), promoting differences in actual soil water dynamics (b) that are not reflected by popular drought indices like SPEI and PDSI (c). Emerging ecological drought indices like Evaporative Stress Index accommodate these dynamic responses (d), prognosing more severe drought in ecosystems with strong stomatal sensitivity.

sustainable water resources management. Fortunately, satellite-based estimation of ET is rapidly evolving and has been used for various drought monitoring, water resources management and irrigation guidance. Some of these products estimate ET using empirical functions that predict dynamic stomatal responses to moisture and VPD stress (Fisher et al., 2020). Others rely on thermodynamic methods (e.g., ALEXI, Anderson et al., 2012) that leverage land surface temperature, integrating the influence of both soil moisture and VPD through the constraint of land surface energy balance. Other products like GLEAM (Martens et al., 2017) rely on a broad set of remotely sensed proxies for both environmental drivers and plant response to constrain ET rates, whereas systems like OpenET (Melton et al., 2022) provide an ensemble of ET estimates with the specific goal of maximising accessibility to a wide range of end-users.

VPD-driven changes in ET and soil moisture will also propagate into impacts on streamflow and runoff. If elevated VPD increases soil dryness, then infiltration during nonextreme precipitation events will be higher, enhancing groundwater recharge and subsequent baseflow (Ficklin et al., 2016). All else being equal, watersheds dominated by plants with a strong stomatal sensitivity to VPD (and thus lower ET during times of hydrologic stress) will have relatively high antecedent soil moisture, leading to overall larger amounts of runoff following precipitation events (Castillo et al., 2003). Elevated VPD will also result in greater evaporation from lakes and reservoirs (Friedrich et al., 2018; Zhao et al., 2022), and can indirectly alter streamflow through its tendency to increase wildfire (see Section 4.3), after which streamflow usually increases due to a decline in transpiration (Biederman et al., 2022; Williams, Livneh, et al., 2022; Wine et al., 2018).

Because the influence of VPD on runoff and streamflow may be watershed-dependent, it is challenging to prescribe generalisable strategies for adapting water resources infrastructure to a higher-VPD world. Moreover, while temperature-driven increases in saturation vapour pressure increase VPD and intensify droughts, they also increase the frequency and intensity of extreme precipitation (because the air can hold more water). This concurrent increase in both wet and dry precipitation extremes—known as hydrologic intensification—will almost certainly require managers to incorporate more flexibility into water resource infrastructure and design (Ficklin et al., 2022).

4.2 | Rising VPD impacts on crop yield and breeding and management opportunities for mitigation

Rising VPD is a major global driver of yield penalties for key staple crops such as maize, soybean and wheat. In the US Corn Belt, where soil moisture supply is usually adequate, VPD is a major factor impacting crop yield in any given year (Kimm et al., 2020; Li et al., 2019; Zhou et al., 2020). Multiple studies have found that a VPD increase 60–90 days after sowing is the single most important driver of agricultural yields in the United States (Lobell et al., 2014; Mourtzinis et al., 2019), and can lead to deceleration in yield gains from genetic engineering, and possibly even yield penalties (Lobell et al., 2014). Similar outcomes were reported for agricultural hotspots in China, including for rice (Zhang et al., 2017), and for nonstaple, specialty crops such as coffee (Kath et al., 2022). Looking forward, there is every reason to expect VPD impacts on agriculture to become more deleterious (Kimm et al., 2020; Sun et al., 2023), with VPD-driven losses on US maize predicted to be up to 30% in some areas (Lobell et al., 2014), and yield losses possible for lands providing up to ~75% of the global coffee supply (Kath et al., 2022).

Most of our understanding of VPD impacts in agriculture has emerged from empirical (e.g., regression) analyses that have been instrumental in identifying associations between in-season changes in VPD and yield outcomes. However, these approaches do not offer eco-physiological insights into the underlying mechanisms, which are still not fully understood. Alternative approaches, including those that leverage high-frequency flux tower data or process-based models, can better illuminate the relevant biophysical processes. For example, flux tower records reveal that stomatal response to VPD strongly regulates impacts on soybean and maize productivity in the United States (Kimm et al., 2020). Likewise, process-based crop models have shown that elevated VPD lowers photosynthetic rates and shortens the growing season of US maize (Hsiao et al., 2019) and drives systematic losses of US soybean yields (Sun et al., 2023).

Despite this progress, the physiological effects that are captured with these approaches remains limited, particularly in relation to the complex and systemic VPD effects on plant physiology reviewed in Section 2. Specifically, the effects of VPD on key processes such as mineral nutrition, nitrogen fixation, development, growth and reproductive success have yet to be considered in work aimed at understanding VPD effects on crop productivity. While integrating evidence from studies on noncrop species may address some of these unknowns, a particularly unique challenge in croplands is the need to differentiate VPD effects during growth and reproductive stages. While our understanding of VPD limitations to photosynthesis and turgor pressure are relevant for understanding plant growth, the impacts of VPD on reproductive success are potentially more complex. This is because they integrate a 'legacy effect' that arises from VPD-driven soil water deficits during flowering and seed-fill (Messina et al., 2015; Sinclair et al., 2010), with direct, organ-specific vulnerabilities to high VPD (e.g., faster anther opening, and delayed silk elongation rate in maize; López et al., 2021). Here, the 2012 US Midwest drought is an important case study. During this event, elevated VPD during the vegetation growth stage led to an over-depletion of soil moisture later in the summer that coincided with the reproductive stage. As a result, photoassimilate allocation to grain was limited (Guan et al., 2016) leading to devastatingly large impacts on crop yields (Rippey, 2015). A better understanding of VPD-driven impacts on grain filling will likely require ad hoc experimentation that emphasises the lagged effects of elevated VPD on reproductive success, and that considers a range of crop species, environmental contexts and nutrient regimes.

Notwithstanding these important knowledge gaps, we know enough to recommend strategies likely to confer increased cropland resilience in a higher-VPD world. Breeding, in concert with appropriate crop management practices, is a powerful avenue for mitigating the negative effects of rising VPD (Messina et al., 2015). A blueprint for developing VPD-resilient cropping systems has been the design and deployment of varieties that limit the pace at which transpiration increases as VPD rises (reviewed in Sinclair et al., 2017). These genotypes can out-yield standard genotypes under elevated VPD via a water-conservation strategy that reduces transpiration to enable higher levels of soil moisture during reproductive stages (Messina et al., 2015; Sadok et al., 2019; Sinclair et al., 2010; Ye et al., 2020). Deploying these genotypes within crop management practices that prioritise water conservation through mulching or no-till practices, and/or those that maximise soil storage capacity, are expected to further amplify these benefits. Other opportunities include the refinement of irrigation schemes. Conventional irrigation tools usually only consider soil moisture. A more efficient irrigation system that considers the status of both VPD and soil moisture could also be helpful to maintain crop productivity and conserve water (Zhang, Guan, Peng, Jiang, et al., 2021; Zhang, Guan, Peng, Pan, et al., 2021). Because periods of elevated VPD and reduced soil moisture usually co-occur, optimised irrigation can increase gas exchange by alleviating soil water stress and, to a lesser extent, reducing the local VPD (Figure 6). Due to the nonlinear relationships between gas exchange and both VPD and soil water, the greatest opportunities for irrigation to mitigate rising VPD will occur when neither soil water nor VPD are especially high (Figure 6, Zhang, Guan, Peng, Pan, et al., 2021).

4.3 | Wildfire risk and management

Just as elevated VPD accelerates soil drying, it can also accelerate the drying of both live and dead fuels, which increases ignitability and the potential for rapid wildfire spread (Rao et al., 2023; Rothermel, 1983). As a result, rising VPD is a major factor affecting wildfire dynamics in

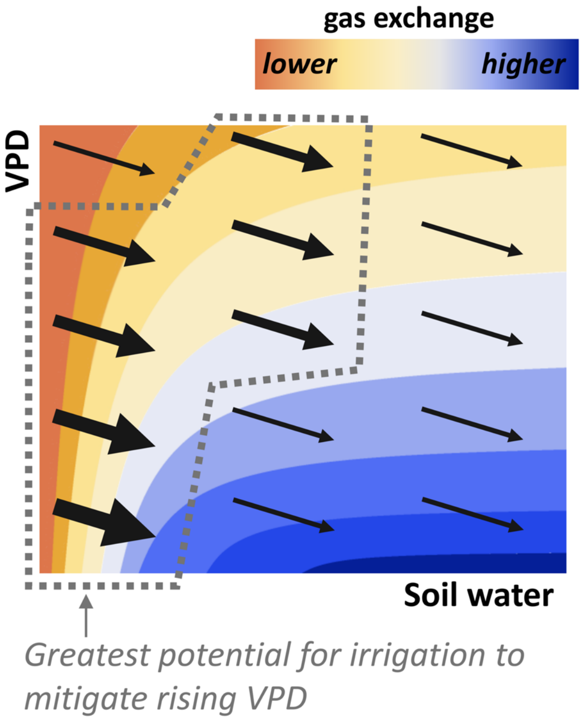

FIGURE 6 Irrigation to mitigate rising vapour pressure deficit (VPD). The figure illustrates the impact on plant gas exchange (e.g., g_s or A) of a generic irrigation application in the VPD-soil water space, where the magnitude of recovery in gas exchange is indicated by the size of the arrow. This representation assumes that irrigation primarily increases soil water but may also slightly decrease local VPD. Irrigation to mitigate rising VPD will be most effective when soil water is at least somewhat limited and VPD is not so high as to overwhelm the positive gains in soil water (and thus gas exchange). Based on results published by Zhang, Guan, Peng, Pan, et al. (2021). [Color figure can be viewed at wileyonlinelibrary.com]

many parts of the world (Abatzoglou et al., 2018; Clarke et al., 2022; Grillakis et al., 2022; Jain et al., 2021). In the western United States, where VPD impacts of wildfire are particularly well studied, fire occurrence, size, severity and burned area are all clearly and positively correlated with VPD (Abatzoglou & Williams, 2016; Abatzoglou et al., 2017; Juang et al., 2022, Parks & Abatzoglou, 2020).

At finer scales, the effect of VPD on wildfire characteristics is likely mediated by vegetation properties (Dickman et al., 2023). For example, remotely sensed estimates of live fuel moisture content show that VPD-driven increases in burn area were much greater in places where the sensitivity of moisture content to climatic drivers is high (because of soil hydraulics, root water uptake and stomatal properties, Rao et al., 2022). Fuel abundance and connectivity are also key regulators of the link between wildfire dynamics and aridification, in general (Abatzoglou et al., 2018; Pausas & Paula, 2012) and specifically in the western United States (McKenzie & Littell, 2017; Williams et al., 2019). The clear regulatory effect of fuel characteristics cautions against naively extrapolating from forested regions of the Western United States to regions with different fuel abundance and connectivity (see Figure 7). Moreover, because of the strong coupling between VPD, soil moisture and temperature (see Section 3.2), the importance of VPD in governing wildfire risk requires careful analysis and is probably over-estimated in studies that assume VPD is the sole relevant driver (Brey et al., 2021; Holden et al., 2018).

Looking forward, the relationship between key wildfire metrics and VPD may become more nonlinear, due to the geometric nature of wildfire growth: given abundant fuels, large fires have more potential for growth than small fires and thus any process, such as increasing VPD, that promotes larger fires will have an outsized and increasingly potent impact on the largest fires (Juang et al., 2022). Consequently, management efforts to reduce ignitions may not be especially effective in limiting the impacts of rising VPD on annual acreage burned. Our ability to predict VPD-driven impacts on wildfire into the future also requires careful consideration of trends in daytime versus nocturnal VPD. Because saturation vapour pressure responds nonlinearly to temperature via the Clausius–Clapeyron relation, VPD is generally more variable in the day than at night. As a result, assessments of wildfire response to seasonally averaged VPD (e.g., Figure 7) are thus biased toward daytime VPD conditions. Nonetheless, nighttime VPD appears to be crucially important to fire behaviour because the cool temperatures and low VPD experienced at night often provide a natural fire break. For example, warming-driven increases in nighttime VPD (see Figure 1) dramatically reduced the fraction of time when VPD is below flammability thresholds across much of the global land surface (Balch et al., 2022).

Management to mitigate VPD-driven intensification of wildfire hinges on early detection of drought conditions, as well as proactive fuel management at the landscape scale. Early flash-drought warning systems (Mohammadi et al., 2022) could enable management interventions (e.g., thinning, grazing) to partially mitigate negative impacts or at least allow fire management agencies time to optimise resource deployment. Similarly, early warning signs for tree mortality enabled by remote sensing (Liu et al., 2019; Rogers et al., 2018) could be helpful for strategies aimed at reducing dead fuels. Finally, there is ample evidence that fuel treatments including prescribed burns would reduce the fire risk associated with rising VPD (Kolden, 2019). However, the effectiveness of different fuel treatments

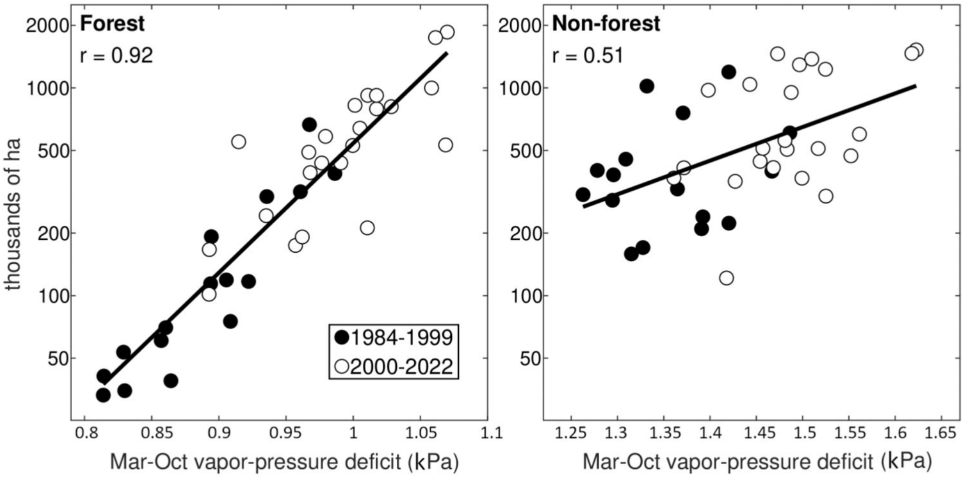

FIGURE 7 Scatter plots of annual western US forest and nonforest area burned by wildfires versus March–October (Mar–Oct) vapour pressure deficit (VPD) for the period from 1984 to 2022. Closed and open circles represent 1984–1999 and 2000–2022, respectively. Note the log-scale y-axis. Correlation coefficient indicates the Pearson's correlation between the x-axis variable and the logarithm of the y-axis variable. The 'Western US' is defined as the 11 western continuous states and forest area defined by Ruefenacht et al. (2008). Burned area data come from an updated version of the Western US MTBS-Interagency database developed by Juang et al. (2022). VPD data calculated from daily means of daily maximum temperature (Tmax), minimum temperature (Tmin) and relative humidity. Temperature data from TopoWx (Oyler et al., 2015) through 2016 and extended through 2022 with the daily NOAA nClimGrid data set (Durre et al., 2022). Relative humidity estimated from daily Tmax, Tmin and dew point from PRISM (Daly et al., 2008).

(e.g., thinning, prescribed burns) is likely to vary widely depending on landscape features and climate (Burke et al., 2021). Overall, more research is needed to improve our predictive ability of the effects of different wildfire risk reduction techniques in specific settings, and how to implement them in ways that minimise associated reductions in forest carbon storage (Krofcheck et al., 2018).

4.4 | Other opportunities for adaptive management for resilience in natural systems

Changes in VPD are among the most certain and widespread consequences of climate warming for plant function. However, relatively little attention has been devoted to incorporating VPD effects into natural resource management plants, which should have a long-term view, accounting for changes in climate and disturbance regimes with robust frameworks for risk assessment (Lecina-Diaz et al., 2021).

In forests, stand thinning increases tree water availability (Giuggiola et al., 2016; Mcdowell et al., 2006) and can be a useful method to reduce plant water stress and promote survival under elevated VPD. However, the effects of thinning on VPD responses are complex, as thinning tends to modify canopy microclimate, increasing VPD and temperature extremes (Rambo & North, 2009), which can lead to counterintuitive effects. In grasslands, vegetation composition can influence microclimate VPD by up to 2–3 kPa (English & Wright, 2021), and more biodiverse plant communities promote large local reductions in VPD in some areas (Wright et al., 2014). These changes in VPD are enough to modify water relations in plants (Wright et al., 2015) and potentially increase overall growth and productivity, though the effects may become diminished if rising VPD reduces transpiration and its associated cooling benefits. As such, grassland resource management programmes may benefit from a focus on microclimate cooling traits particularly under well-watered conditions.

In all ecosystems, selection for species adapted to warmer climates (e.g., assisted migration) may be another useful tool, especially when these decisions incorporate region-specific climate data and projections from process-based models to understand where and when risks might be most elevated (Hill et al., 2023; McAdam & Brodribb, 2015; Quetin et al., 2023). However, because the connection between VPD responses and vulnerability to drought-induced mortality is complex (see Section 2.3), it will still be difficult to make specific recommendations. The promotion and maintenance of functionally diverse communities seems a safer bet in this context, as there is ample evidence that more diverse communities tend to be more resilient to climatic extremes, including high VPD (Anderegg et al., 2018; Grossiord et al., 2020; Isbell et al., 2015).

Finally, higher VPD will have different impacts on different ecosystem services, and the corresponding tradeoffs need to be assessed. For instance, higher VPD could reduce carbon assimilation and, eventually, growth, but it would likely increase transpiration (at least to a point, see Section 2.1) which could adversely affect the provisioning of water resources downstream (Roces-Díaz et al., 2021). Finally, because specific recommendations may vary depending on the region, ecosystem type and the species present, experts from relevant fields such as ecology, climatology and hydrology, should collaborate to tailor the recommendations to specific contexts to promote more effective management approaches.

5 | SUMMARY AND RECOMMENDATIONS

Rising atmospheric VPD is a global phenomenon that has clear and usually deleterious impacts on a cascade of plant processes, including carbon sequestration, transpirational water loss, growth, productivity and survival. These impacts are exacerbated by land–atmosphere interactions that link the dynamics of VPD and soil drought, and over the long term, they will likely alter community composition and interspecific interactions. In the absence of new management approaches, the implications of rising VPD for managed systems are also stark, and include difficulties in monitoring and forecasting drought, more variable streamflow patterns, increased wildfire risk and losses in biodiversity and crop productivity. As a result, rising VPD is likely one of the most widespread and significant consequences of climate warming for terrestrial ecosystems.

Plant responses to rising VPD have been relatively well-studied over the past 10–20 years. We know that elevated VPD limits the gas exchange, growth and chances of survival generally, and especially for plants adapted to moist habitats and for taller trees. The underlying mechanisms are becoming better understood, but important gaps remain concerning the mechanisms by which stomata sense rising VPD and the potential for long-term adaptation. Evaluating mechanisms underpinning plant acclimation to rising VPD and its direct effect on reproductive success represent another major research need. At scales of individual plants and entire ecosystems, disentangling the influence of VPD from co-evolving and coupled drivers (including soil water, temperature and atmospheric CO_2) remains challenging. The most promising approaches for understanding the independent and interactive impacts of the drivers include novel strategies for in situ manipulation of VPD, greater availability of high-frequency ecophysiological time series (collected over subdaily timescales at which soil water and VPD dynamics are largely decoupled), and continued investment in the representation of plant hydraulic processes in land surface models. Both empirical and model-driven work should consider the potential for large microclimatic gradients in VPD, linked to vertical and horizontal heterogeneity in stand structure. It is also critical to recognise that the leaf-to-air vapour pressure difference (which is most relevant for many aspects of plant function) can differ substantially from the VPD of the air, and the former should be used in empirical and modelling work to every extent possible.

Our understanding of the management implications of rising VPD is still largely in its infancy. Nonetheless, it's clear that the consequences of rising VPD for water resources, crop yields, wildfire risk and natural resources could be profoundly negative if management approaches do not acknowledge that the atmosphere will become increasingly desiccating in the decades ahead. The most promising avenues for mitigation include refined drought forecasting approaches that incorporate dynamic plant responses to rising VPD, more flexible water resources infrastructure, crop breeding for VPD-resilient cultivars coupled with VPD-adapted irrigation strategies, proactive thinning and prescribed fire to minimise wildfire severity and natural resource management for more biodiverse ecosystems. These management shifts will be most successful when they are integrated across spatial and temporal scales and engage scientists representing a diversity of disciplinary perspectives.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are derived from resources available in the public domain. Specifically, ERA5 reanalysis data shown in Figure 1 are described in Hersbach et al. (2020) and available from https://cds.climate.copernicus.eu/ with the DOI: 10.24381/cds.143582cf. The CMIP6 model predictions shown in Figure 1 are described in Eyring et al. (2016) and accessible from https://wcrp-cmip.org/cmip-data-access/. The AmeriFlux data presented in Figure 4 are available from https://ameriflux.lbl.gov/data/download-data/, with DOIs for the individual site data sets given in the references. The data on wildfire burn area presented in Figure 7 are available from the Western US MTBS Interagency Database developed by Juang et al. (2022), accessible from https://www.mtbs.gov/. The VPD data presented in Figure 7 were determined from temperature data available from TopoWx (Oyler et al., 2015, https://www.scrim.psu.edu/resources/topowx/) and t \he NOAA nClimGrid data set (Durre et al., 2022, https://www.ncei.noaa.gov/products/land-based-station/nclimgrid-daily) and humidity data estimated from the PRISM data set (Daly et al., 2008) available from https://prism.oregonstate.edu/.

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NEON (National Ecological Observatory Network) (2022b) AmeriFlux BASE US-xBL NEON Blandy Experimental Farm (BLAN), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671893

NEON (National Ecological Observatory Network) (2022c) AmeriFlux BASE US-xBN NEON Caribou Creek - Poker Flats Watershed (BONA), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1617727

NEON (National Ecological Observatory Network) (2022d) AmeriFlux BASE US-xBR NEON Bartlett Experimental Forest (BART), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1579542

NEON (National Ecological Observatory Network) (2022e) AmeriFlux BASE US-xCL NEON LBJ National Grassland (CLBJ), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671894

NEON (National Ecological Observatory Network) (2022f) AmeriFlux BASE US-xCP NEON Central Plains Experimental Range (CPER), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1579720

NEON (National Ecological Observatory Network) (2022g) AmeriFlux BASE US-xDJ NEON Delta Junction (DEJU), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1634884

NEON (National Ecological Observatory Network) (2022h) AmeriFlux BASE US-xDL NEON Dead Lake (DELA), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1579721

NEON (National Ecological Observatory Network) (2022i) AmeriFlux BASE US-xDS NEON Disney Wilderness Preserve (DSNY), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671895

NEON (National Ecological Observatory Network) (2022j) AmeriFlux BASE US-xGR NEON Great Smoky Mountains National Park, Twin Creeks (GRSM), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1634885

NEON (National Ecological Observatory Network) (2022k) AmeriFlux BASE US-xHA NEON Harvard Forest (HARV), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1562391

NEON (National Ecological Observatory Network) (2022l) AmeriFlux BASE US-xHE NEON Healy (HEAL), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1617729

NEON (National Ecological Observatory Network) (2022m) AmeriFlux BASE US-xJE NEON Jones Ecological Research Center (JERC), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1617730

NEON (National Ecological Observatory Network) (2022n) AmeriFlux BASE US-xKA NEON Konza Prairie Biological Station—Relocatable (KONA), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1579722

NEON (National Ecological Observatory Network) (2022o) AmeriFlux BASE US-xKZ NEON Konza Prairie Biological Station (KONZ), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1562392

NEON (National Ecological Observatory Network) (2022p) AmeriFlux BASE US-xLE NEON Lenoir Landing (LENO), Ver. 3-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1773398

NEON (National Ecological Observatory Network) (2022q) AmeriFlux BASE US-xMB NEON Moab MOAB), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671896

NEON (National Ecological Observatory Network) (2022r) AmeriFlux BASE US-xML NEON Mountain Lake Biological Station (MLBS), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671897

NEON (National Ecological Observatory Network) (2022s) AmeriFlux BASE US-xNG NEON Northern Great Plains Research Laboratory (NOGP), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1617732

NEON (National Ecological Observatory Network) (2022t) AmeriFlux BASE US-xNQ NEON Onaqui-Ault (ONAQ), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1617733

NEON (National Ecological Observatory Network) (2022u) AmeriFlux BASE US-xNW NEON Niwot Ridge Mountain Research Station (NIWO), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671898

NEON (National Ecological Observatory Network) (2022v) AmeriFlux BASE US-xPU NEON Pu'u Maka'ala Natural Area Reserve (PUUM), Ver. 3-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1773399

NEON (National Ecological Observatory Network) (2022w) AmeriFlux BASE US-xRM NEON Rocky Mountain National Park, CASTNET (RMNP), Ver. 6-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1579723

NEON (National Ecological Observatory Network) (2022x) AmeriFlux BASE US-xRN NEON Oak Ridge National Lab (ORNL), Ver. 4-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1773400

NEON (National Ecological Observatory Network) (2022y) AmeriFlux BASE US-xSB NEON Ordway-Swisher Biological Station (OSBS), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671899

NEON (National Ecological Observatory Network) (2022z) AmeriFlux BASE US-xSC NEON Smithsonian Conservation Biology Institute (SCBI), Ver. 4-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671900

NEON (National Ecological Observatory Network) (2022aa) AmeriFlux BASE US-xSE NEON Smithsonian Environmental Research Center (SERC), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1617734

NEON (National Ecological Observatory Network) (2022bb) AmeriFlux BASE US-xSJ NEON San Joaquin Experimental Range (SJER), Ver. 4-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1671901

NEON (National Ecological Observatory Network) (2022cc) AmeriFlux BASE US-xSL NEON North Sterling, CO (STER), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1617735

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NEON (National Ecological Observatory Network) (2022ff) AmeriFlux BASE US-xST NEON Steigerwaldt Land Services (STEI), Ver. 5-5, AmeriFlux AMP, (Dataset). Available from: https://doi.org/10.17190/AMF/1617737

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NEON (National Ecological Observatory Network) (2022hh) AmeriFlux BASE US-xTE NEON Lower Teakettle (TEAK), Ver. 5-5, AmeriFlux AMP, (Dataset). : Available from https://doi.org/10.17190/AMF/1617738

NEON (National Ecological Observatory Network) (2022ii) AmeriFlux BASE US-xTR NEON Treehaven (TREE), Ver. 5-5, AmeriFlux AMP, (Dataset). : Available from https://doi.org/10.17190/AMF/1634886

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NEON (National Ecological Observatory Network) (2022kk) AmeriFlux BASE US-xUN NEON University of Notre Dame Environmental Research Center (UNDE), Ver. 5-5, AmeriFlux AMP, (Dataset). : Available from https://doi.org/10.17190/AMF/1617741

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NEON (National Ecological Observatory Network) (2022mm) AmeriFlux BASE US-xWR NEON Wind River Experimental Forest (WREF), Ver. 5-5, AmeriFlux AMP, (Dataset). : Available from https://doi.org/10.17190/AMF/1617742

NEON (National Ecological Observatory Network) (2022nn) AmeriFlux BASE US-xYE NEON Yellowstone Northern Range (Frog Rock) (YELL), Ver. 5-5, AmeriFlux AMP, (Dataset). : Available from https://doi.org/10.17190/AMF/1617743

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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