

# Impacts of rising atmospheric dryness on terrestrial ecosystem carbon cycle

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# Abstract

Rising atmospheric dryness is affecting the terrestrial ecosystem carbon cycle through its influence on plant physiology. In this Review, we synthesize historical and projected trends in atmospheric vapour pressure deficit (VPD), a proxy for atmospheric dryness, and the mechanisms by which it affects the terrestrial carbon cycle. Since the late 1990s, global mean VPD has increased at a mean rate of  $0.0155 \pm 0.0041$  hPa yr<sup>-1</sup>. VPD-driven reductions in leaf area index  $(0.11 \pm 0.07 \text{ m}^2 \text{ m}^{-2} \text{ hPa}^{-1}, 1982-2015)$ , gross primary production (13.82  $\pm$  3.12 PgC hPa<sup>-1</sup>, 1982–2015), light use efficiency  $(0.04 \pm 0.02 \text{ gC MJ}^{-1} \text{ hPa}^{-1}, 2001-2020)$  and net ecosystem production  $(5.59 \pm 1.15 \,\mathrm{PgC} \,\mathrm{hPa^{-1}}, 1982 - 2013)$  have been observed globally. However, attributing changes in the terrestrial carbon cycle to VPD is still challenging, owing to the confounding influence of other environmental factors, such as soil moisture, temperature and radiation. The mechanisms underlying plant responses to VPD – which include stomatal closure, hydraulic failure, abscisic acid biosynthesis, and cascading effects on fires and soil moisture deficits – are also poorly constrained, limiting the predictive capabilities of terrestrial carbon cycle models. Future research should prioritize establishing global VPD-manipulation experiments to enhance understanding of feedbacks between VPD, plants and the carbon cycle, and these mechanisms should then be integrated into terrestrial carbon cycle models.

# **Sections**

Introduction

Past changes in atmospheric dryness

Impact on terrestrial carbon cycling

Mechanisms

Future changes in atmospheric dryness

Summary and future perspectives

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### Introduction

Warming over land is intensifying, leading to a global increase in atmospheric dryness¹. Vapour pressure deficit (VPD) — defined as the difference between the actual water vapour pressure (AVP) and the saturation water vapour pressure (SVP, the maximum potential atmospheric water vapour pressure) — is considered a reliable proxy for atmospheric dryness². Since the late 1990s, rising VPD has emerged as an important indicator of ongoing global climate change⁴, with SVP substantially increasing with air temperature (7–8% per °C)² as AVP has remained relatively stable⁵. The result of these asymmetric changes is a widespread increase in VPD⁴.6 that is projected to continue and potentially accelerate under future climate warming¹. As VPD affects the water potential gradient between plants and the atmosphere, these changes bring uncertain consequences for the biosphere⁵.

Rising VPD negatively affects the terrestrial carbon cycle in a number of ways<sup>8</sup>. Higher VPD increases atmospheric water demand, which in turn increases the water potential gradient from plants to atmosphere. In turn, stomatal closure, a passive response driven by declining turgor pressure<sup>9</sup>, is induced in plants to limit water loss<sup>10</sup> through preventing excessive transpiration<sup>11</sup>. However, stomatal closure also limits gas exchange and reduces the concentration of internal cellular carbon dioxide, leading to reduced photosynthesis and gross primary production (GPP)<sup>12</sup>. Increased VPD can also negatively affect plants through triggering abscisic acid synthesis, accelerating leaf senescence and modulating leaf phenology<sup>13</sup>. Extremely high VPD could even result in tree mortality<sup>14</sup>, reduce regeneration<sup>15</sup>, alter species composition<sup>16</sup> and increase the risk of vegetation fires<sup>17</sup>. Thus, VPD has a potentially strong influence on the global terrestrial carbon sink<sup>18</sup>.

The effects of VPD on terrestrial carbon cycling, although recognized, have probably been underestimated owing to coincident variations in other environmental factors<sup>8,19,20</sup>. Consequently, the relative impact of VPD on the terrestrial carbon cycle – when compared with other factors such as air temperature, soil moisture and solar radiation – remains highly debated<sup>21,22</sup>. Although VPD was thought to exert a limited influence on global terrestrial carbon cycle<sup>21</sup>, emerging evidence indicates that the impact of VPD could surpass the effect of CO<sub>2</sub> fertilization<sup>4</sup>, soil moisture stress<sup>22</sup> and thermal stress<sup>19</sup>. VPD effects have also been simulated in Earth system models (ESMs) coupling global vegetation with the atmosphere, through representing leaf stomata<sup>23</sup> and plant physiological processes. However, existing ESMs overlook VPD impacts on plant phenology, tree mortality and vegetation fires<sup>24</sup>. Thus, a comprehensive synthesis of the underlying relationships and mechanisms is needed to accurately predict future changes in the global carbon cycle in response to rising VPD.

In this Review, we synthesize observational and model-based evidence of global temporal trends and spatial variations in VPD across biomes and climate zones. We then explore the consequences for the terrestrial carbon cycle by summarizing the direction and magnitude of VPD influence on GPP, phenology, plant growth, leaf area index (LAI), non-structural carbohydrates (NSCs), tree mortality and net ecosystem

production (NEP). Next, we consider the plant physiological mechanisms underlying these responses, and the cascading impacts on natural fires and soil water deficit. We then discuss predicted future changes in VPD and the implications for carbon cycling. Finally, we recommend strategies for field experiments and model algorithm development that will further advance understanding of VPD impacts on carbon cycling.

# Past changes in atmospheric dryness

Atmospheric dryness has intensified since about the early 1900s<sup>4,25,26</sup> across the majority (78.6%) of the global land area<sup>4</sup> (Fig. 1a). Globally averaged VPD during the growing season (defined as mean monthly temperatures above 0 °C; ref. 4) increased slowly before the late 1990s, at a rate of  $0.0016 \pm 0.0003$  hPa yr<sup>-1</sup>, followed by a tenfold acceleration to  $0.0155 \pm 0.004 \text{ hPa yr}^{-1}(\text{ref. 4})$  (Fig. 1b). This widespread increase in VPD was primarily driven by anthropogenic warming, which caused an exponential increase in SVP with rising temperature whereas AVP increased more gradually<sup>4,24</sup>. VPD trends of the same direction have also been observed during other time periods, although with varying magnitude  $(0.012 \pm 0.001 \,\text{hPa yr}^{-1}\,\text{between }1984 \,\text{and }2016^{27}\,\text{and}$  $0.032 \pm 0.004 \text{ hPa yr}^{-1}$  between 2000 and 2019<sup>28</sup>). However, the spatial density of meteorological stations used in the Climate Research Unit dataset was highly limited before 1930, especially in tropical and boreal areas, potentially introducing uncertainties in the trend in the early 1900s<sup>29</sup>.

The rate of increase in VPD varies between different climate zones. Between 1999 and 2015, VPD in arid climates increased 2.3 times faster than in humid regions (Fig. 1c) owing to warming being 20–40% higher in arid regions, leading to a more rapid increase in SVP<sup>30</sup>. In addition, limited water availability in arid regions reduces plant transpiration and lowers AVP<sup>31</sup>. Growth rate in VPD also varies across different biomes owing to vegetation type (Fig. 1d), with the increase slowest in forest ecosystems, followed by shrublands, croplands and grasslands (Fig. 1d).

The rate of VPD increase also varied between seasons. In general, VPD is higher in spring than autumn, owing to the springtime air temperature increase elevating SVP before surface and atmospheric moisture has recovered from winter dormancy  $^{32,33}$ . Conversely, higher evapotranspiration and vegetation activity in autumn lead to increased AVP and lower VPD  $^{32,33}$ . As a result, the increasing trend in VPD differs between spring and autumn at a rate of  $0.0042 \pm 0.0053 \, hPa \, yr^{-1}$  (1999–2015) (Fig. 1b).

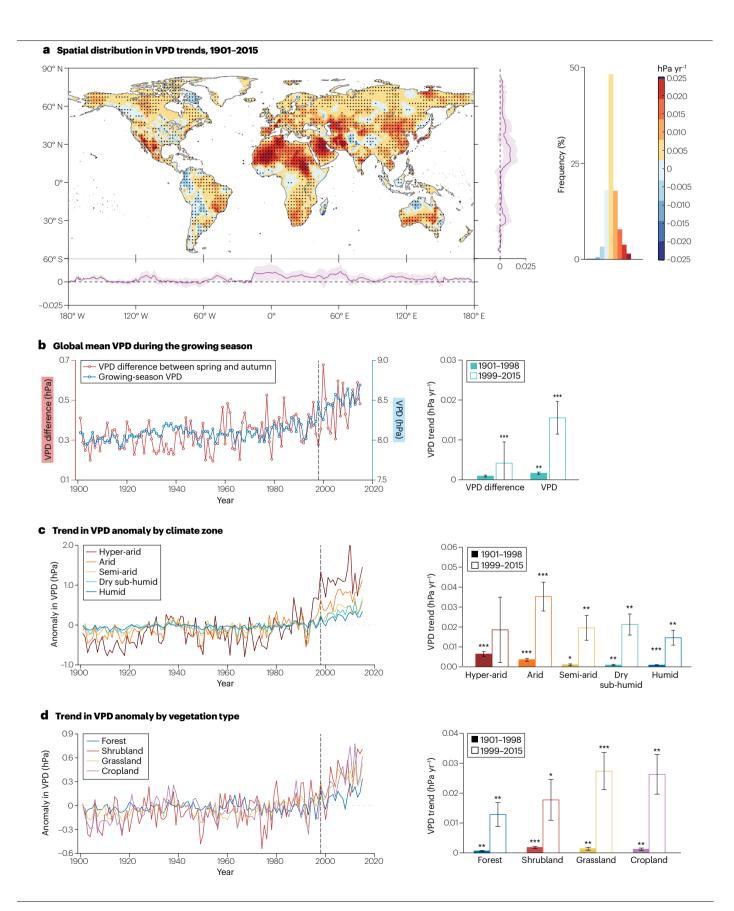
Overall, these heterogeneous spatial and seasonal trends in VPD highlight the unequal exposure and vulnerability of global ecosystems to increasing atmospheric dryness. These differences emphasize the need for region-specific assessments of carbon cycle responses<sup>8</sup>.

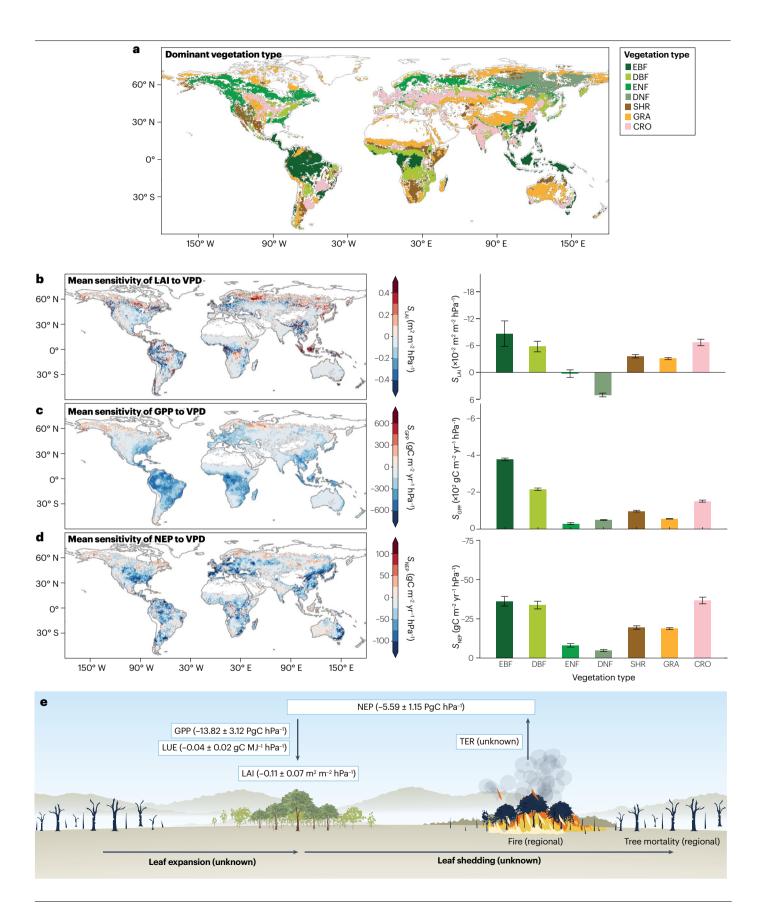
### Impact on terrestrial carbon cycling

Atmospheric dryness can substantially affect many processes in the terrestrial carbon cycle. VPD impacts on GPP, phenology, plant growth, leaf area, NSCs, tree mortality and NEP are now discussed.

**Fig. 1**| **Historical changes in vapour pressure deficit across terrestrial ecosystems. a**, Spatial distribution of trends in growing-season vapour pressure deficit (VPD) (1901–2015)<sup>29</sup>. Plus signs (+) denote trends significant at the 0.05 level. **b**, Left panel, long-term trends in global mean VPD during the growing season (blue), and difference between spring (March to May) and autumn (September to November) (red). Right panel, global mean VPD and differences in VPD for 1901–1998, and 1999–2015. **c**, Long-term trends (left) and differences (right) in global VPD anomalies from 1901 to 2015 by climate zone (based on

aridity index for 1961–1990; see Supplementary Fig. 1). **d**, Long-term trends (left) and differences (right) in VPD anomalies from 1901 to 2015 by vegetation type (classification based on ref. 235). Data aggregated to a spatial resolution of  $0.5^{\circ} \times 0.5^{\circ}$ . Error bars represent one standard deviation; \*, \*\*\* and \*\*\*\* represent statistically significant differences at the 0.05, 0.01 and 0.001 levels. Since the 1900s, the rise in VPD has intensified, with its magnitude differing substantially across biomes, vegetation types and time periods.





### $Fig.\,2\,|\,Sensitivity\,of\,ter restrial\,carbon\,cycling\,to\,rising\,atmosphere\,dryness.$

**a**, Dominant vegetation type (classification based on ref. 235 and over 50% areal abundance  $^{236,237}$ , aggregated to  $0.5^{\circ} \times 0.5^{\circ}$  spatial resolution). **b**, Mean sensitivity of leaf area index (LAI) ( $S_{\text{LAI}}$ , 1982–2015, ref. 4), defined as the slope of partial linear correlation between ecosystem carbon cycle variables and vapour pressure deficit (VPD) using a multiple regression approach (left), and mean values by vegetation type (right). **c**, As in **b**, for gross primary production (GPP) ( $S_{\text{GPP}}$ , 1982–2015, ref. 4). **d**, As in **b**, for net ecosystem production (NEP) ( $S_{\text{NEP}}$ , 1982–2013, ref. 18). **e**, Summary

of the known and unknown global sensitivity of terrestrial ecosystem carbon cycle variables to VPD. Error bars represent one standard error. Global estimates of VPD impacts on LAI, GPP, light use efficiency (LUE) and NEP are available across terrestrial ecosystems, but quantitative characterizations of the impacts on phenology, plant growth, non-structural carbohydrates and tree mortality are lacking. CRO, cropland; DBF, deciduous broadleaf forest; DNF, deciduous needleleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRA, grassland; SHR, shrubland; TER, terrestrial ecosystem respiration.

### **Gross primary production**

VPD has emerged as a critical driver of terrestrial GPP, corresponding to the rates of photosynthesis in terrestrial ecosystems. GPP has a fundamental role in determining the carbon budget of terrestrial ecosystems  $^{34}$ . Evidence from eddy covariance—light use efficiency (LUE) models  $^4$  consistently indicates a decreasing trend in GPP as VPD increases across a range of ecosystem types  $^{35-39}$ . Overall, satellite-based estimates indicate that the annual average global GPP decreased by  $13.82 \pm 3.12 \, \text{PgC} \, \text{yr}^{-1}$  in response to an increase of 1 hPa in VPD  $^4$  (Fig. 2e).

Specifically, the response of GPP to VPD varied across vegetation types (Fig. 2c). GPP in evergreen broadleaf forests (–378  $\pm$  7 gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ) and deciduous broadleaf forests (–216  $\pm$  7 gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ) is most sensitive to VPD (Fig. 2c). Conversely, evergreen needleleaf forests (–29  $\pm$  5 gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ), deciduous needleleaf forests (–49  $\pm$  2 gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ) and grasslands (–55  $\pm$  1 gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ) exhibit the lowest sensitivity (Fig. 2c). GPP responses to VPD were comparable in shrublands (–97  $\pm$  4 gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ) and croplands (–151  $\pm$  6 gC m $^{-2}$  yr $^{-1}$ hPa $^{-1}$ ) (Fig. 2c).

Negative responses of GPP to increasing VPD emerge beyond a certain threshold (Fig. 3a). When VPD is low, any increase might reduce stomatal conductance without notably affecting photosynthetic  $CO_2$  assimilation  $^{24}$ . As rising VPD is often accompanied by elevated temperatures, warming might conversely enhance photochemistry when the VPD constraint is minimal  $^{40}$ . When VPD exceeds a certain threshold, however, limitations on stomatal conductance surpass those associated with elevated temperatures, resulting in substantial limitation photosynthetic carbon assimilation  $^{41}$  and reduction in GPP (Fig. 3a). Similarly, plants might also raise their LUE under rising VPD when VPD remains below a certain threshold, and decline LUE beyond this threshold  $^{42}$  (Fig. 3b). Plant water use efficiency also increases initially with rising VPD, saturates at a certain VPD threshold and decreases beyond the threshold  $^{43,44}$ . The combined effect of these factors on GPP is challenging to disentangle.

This threshold of VPD influence on GPP varies with vegetation type (Fig. 3a). Grasslands, being more sensitive to atmospheric dryness<sup>45</sup>, often display a high capacity for rapid stomatal regulation and have a small VPD threshold (5.83 hPa) (Fig. 3a). In contrast, deciduous broadleaf forests are equipped with smaller and more numerous stomata enabling them to finely adjust their stomatal conductance<sup>46</sup>. Thus, deciduous broadleaf forests can maintain higher stomatal conductance and transpiration under elevated VPD, giving them a higher threshold of 9.18 hPa (ref. 46) (Fig. 3a). Mixed forests have a relatively low VPD threshold (6.59 hPa) (Fig. 3a), possibly owing to species diversity promoting belowground water partitioning<sup>47</sup>, whereas shrublands have a moderate VPD threshold (8.41 hPa) (Fig. 3a).

The role of VPD in regulating vegetation production remains unclear owing to strong covariation of VPD with air temperature, soil moisture and physiological changes in plants<sup>48,49</sup>. Satellite-based solar-induced fluorescence<sup>21</sup> suggests that soil moisture has a dominant

positive influence on global ecosystem production, particularly in arid and semi-arid ecosystems. Conversely, VPD impacts were greater in humid ecosystems<sup>8,48</sup> where increased atmospheric dryness can substantially constrict vegetation production<sup>22</sup>, especially during times of drought<sup>50,51</sup>. Eddy covariance observations also show that VPD had a stronger influence on GPP than low soil moisture over the growing season in humid and mesic ecosystems<sup>52</sup>. Further evidence from satellite estimates indicated that GPP and VPD have a stronger negative correlation in humid regions than in arid regions<sup>53</sup>. Thus, as humid areas contribute more to global vegetation production than arid regions, increased atmosphere dryness could substantially affect global vegetation production.

# Phenology

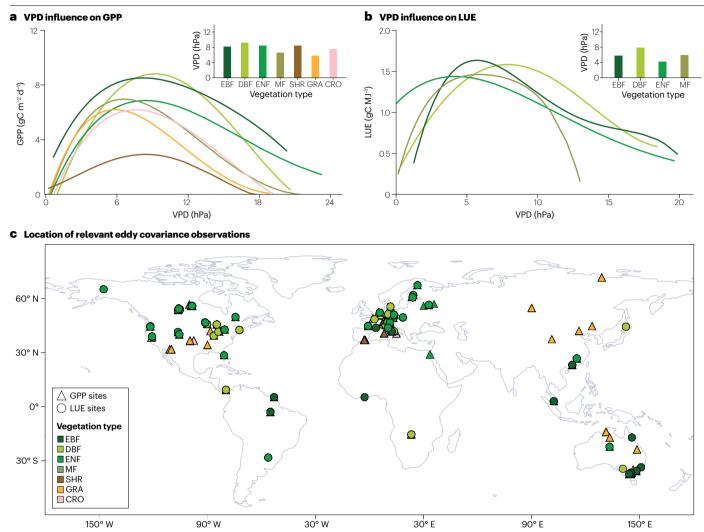
Increasing VPD can influence plant phenology, affecting both the timing of autumn leaf senescence and the rate of new leaf expansion<sup>54</sup>. In turn, these changes regulate the overall length of the growing season, ultimately affecting vegetation productivity and the terrestrial carbon sink<sup>32,55</sup>.

Prolonged exposure to high VPD can trigger the production of abscisic acid in plants, which accelerates autumn leaf senescence  $^{56}$ , resulting in a shorter growing season  $^{57}$ . This effect is particularly evident in tropical regions, where VPD is the strongest climatic cue for shedding of old leaves in humid Amazonian rainforests. Indeed, the influence of VPD surpasses precipitation, temperature, radiation and soil moisture in regulating plant leaf phenology  $^{41,58}$ . Litterfall seasonality across 100 tropical sites is 11% and 36% in phase with soil moisture and precipitation, respectively, but 94% in phase with VPD  $^{59,60}$ . In addition, rising VPD can hasten the autumn leaf senescence in some arid ecosystems  $^{61,62}$ .

High VPD can also diminish leaf expansion rate  $^{63}$  and, thus, is considered an important environmental factor affecting leaf expansion in crops  $^{64}$ , grasses  $^{65}$  and woody plants  $^{66}$ . For example, field experiments indicate that the rate of maize leaf expansion had a strong negative correlation with the atmospheric VPD  $^{67}$ , with an average sensitivity of  $0.2 \, \text{mm day}^{-1} \, \text{hPa}^{-1}$ . The primary pathway by which VPD influences leaf expansion is by reducing the number of epidermal cells  $^{66}$ , which correlate with leaf size. Notably, impacts of VPD on leaf expansion rate and the number of epidermal cells operate on a longer temporal scale than VPD impacts on GPP, with leaf expansion rate decreasing sharply 2 days after high VPD treatment  $^{64}$ .

# Plant growth and leaf area index

Rising VPD also strongly inhibits radial (stem diameter) and vertical plant growth (tree height). VPD is an important factor in influencing radial growth across temperate and tropical forests<sup>68–70</sup>. For example, in a temperate deciduous forest, stem growth decreased linearly by 1.7 mm<sup>2</sup> per day for every 0.1 kPa increase in VPD<sup>71</sup>. Similar limitations to stem diameter growth in response to VPD have been observed in



**Fig. 3** | **Thresholds of VPD influence on terrestrial ecosystem carbon cycling. a**, Gross primary production (GPP) versus rising vapour pressure deficit (VPD)<sup>42</sup>. Inset: VPD thresholds where rising VPD begins to limit GPP per vegetation type. **b**, As in **a**, for light use efficiency (LUE) with rising VPD<sup>238</sup>. **c**, Eddy covariance tower sites for observing the influence of VPD on GPP and LUE. There are

notable but different thresholds where rising VPD begins to limit GPP across various vegetation types. CRO, cropland; DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRA, grassland; MF, mixed forest; SHR, shrubland.

boreal forests $^{72}$ . Indeed, VPD has a greater influence on tree radial stem growth than rainfall and soil moisture, especially for trees growing in humid or semi-humid forests $^{73}$ , and some semi-arid ecosystems $^{74,75}$ . Radial growth in trees determined primarily by growing-season cambial activity is greater in months with low VPD than high VPD conditions, supporting the substantial impact of VPD on tree radial growth via constrained cambial activity $^{76}$ .

Rising VPD also induces reduced vertical growth in plants<sup>77</sup>. Elevated VPD should favour species of shorter stature<sup>77,78</sup> as taller plants are more vulnerable to hydraulic failure via embolism resulting from atmospheric dryness<sup>79</sup>. Numerous experiments demonstrate that plant height is notably affected by long-term exposure to high VPD, with plant height and VPD being negatively correlated<sup>77,80</sup>. Indeed, evidence for 112 species shows that the greater the increase in VPD, the stronger the decrease in plant height<sup>77</sup>. In addition, the height of

annual or biennial plants is more strongly affected by VPD than other plant types  $^{77}$ .

Rising VPD could affect the terrestrial carbon cycle by limiting LAI growth  $^{81,82}$ . The global greening trend observed in satellite-derived LAI and Normalized Difference Vegetation Index (NDVI) prior to the late 1990s has since stagnated and potentially reversed in response to the marked increase in VPD $^4$ . Globally, as VPD increased, annual mean LAI decreased at a rate of  $0.11\pm0.07~m^2~m^{-2}~hPa^{-1}$  (Fig. 2e). Satellite-derived near-infrared reflectance of vegetation (NIRv) suggests that approximately 69.3% of vegetated areas show negative correlations between the interannual variability of NIRv and VPD during 1982–2015 (ref. 18).

The magnitude of the LAI response to rising VPD varies across biomes, ranging from -0.086 to +0.051 m<sup>2</sup> m<sup>-2</sup> hPa<sup>-1</sup> (Fig. 2b). Specifically, negative LAI responses to VPD were found in evergreen broadleaf forests  $(-0.086 \pm 0.029$  m<sup>2</sup> m<sup>-2</sup> hPa<sup>-1</sup>), croplands  $(-0.067 \pm 0.007$  m<sup>2</sup> m<sup>-2</sup> hPa<sup>-1</sup>),

deciduous broadleaf forests  $(-0.058\pm0.012~\text{m}^2\,\text{m}^{-2}~\text{hPa}^{-1})$ , shrublands  $(-0.036\pm0.004~\text{m}^2~\text{m}^{-2}~\text{hPa}^{-1})$  and grasslands  $(-0.031\pm0.002~\text{m}^2~\text{m}^{-2}~\text{hPa}^{-1})$ . Conversely, positive responses were observed in deciduous needleleaf forests  $(0.051\pm0.004~\text{m}^2~\text{m}^{-2}~\text{hPa}^{-1})$  and evergreen needleleaf forests  $(0.003\pm0.009~\text{m}^2~\text{m}^{-2}~\text{hPa}^{-1})$ . These positive responses are probably attributable to needleleaf forests using an anisohydric strategy to maintain stomatal openings and extract water from deep soil layers under high VPD conditions  $^{47,83,84}$ .

Atmospheric dryness could also affect the growth of plant organs through changes in carbon allocations<sup>85</sup>. Plants commonly use adaptive strategies optimizing carbon allocations between leaves and roots to ensure survival and growth under chronic water stress<sup>86,87</sup>. However, rising VPD can restrict plant growth by reducing the allocation of carbon from photosynthesis to sapwood88, slowing down radial enlargement<sup>89,90</sup>. In addition, plants under drought conditions preferentially allocate carbon to root systems at the cost of stem radial expansion<sup>91</sup>. For example, tropical moist forests tend to constrain allocations to stems and roots92, allocating more carbon to growing new leaves at the beginning of the dry season (July–September) when incoming shortwave downwelling radiation increases<sup>55,93-96</sup>. Conversely, dry-season old leaf abscission in plants experiencing severe dry-season water stress can avoid hydraulic failure and carbon starvation<sup>97-99</sup>. Thus, VPD influences seasonality in leaf shedding and leaf flush processes via coordinating carbon allocation<sup>55,100</sup>.

### Non-structural carbohydrates

Rising VPD also affects NSCs, which are carbohydrates not involved in the formation of cell walls or other structural components in plants. NSCs primarily exist in the form of soluble sugars (such as glucose, fructose, sucrose) and starch, serving as mobile and rapidly degradable carbon sources and energy reserves within plant tissues<sup>101</sup>. Short-term high VPD could temporarily promote NSC accumulation as a stress response<sup>102</sup>. However, long-term exposure to elevated VPD tends to suppress photosynthesis, thereby reducing the synthesis of soluble sugars and starch, and NSC accumulation<sup>103</sup>.

As VPD increases, plants often simultaneously break down starch to generate soluble sugars to sustain osmotic regulation and energy supply. Under prolonged high-VPD stress, plants might also prioritize allocation of limited carbon resources to roots or storage organs (such as starch accumulation) rather than leaves<sup>104</sup>. In turn, canopy photosynthesis is limited with negative feedbacks on NSCs accumulation. Thus, together, high-VPD-induced declines in photosynthesis and increases in the consumption of soluble sugars limit NSC accumulation<sup>105</sup>.

### Tree mortality

Rising VPD also accelerates tree mortality<sup>78</sup>, reducing ecosystem carbon storage capacity and promoting carbon emissions<sup>24,106</sup>. Rising VPD is recognized as a major driver of tree mortality across boreal forests<sup>39</sup>, temperate forests<sup>107</sup> and moist tropical forests<sup>78,108</sup>. Estimates quantifying the sensitivity of tree mortality rates to rising VPD range from 0.36% hPa<sup>-1</sup> to 1.58% hPa<sup>-1</sup> (Supplementary Fig. 2). However, no global-scale quantitative evaluation of tree mortality in response to rising VPD exists.

The influence of VPD on tree mortality differs between tree species  $^{109-114}$ . At the regional scale, slow-growing species and small trees exhibit a lower mortality response, whereas fast-growing species and large trees are less resistant to atmosphere dryness  $^{16,115}$ . In addition, the risk of mortality in deciduous species (11%) is greater than that of

evergreen species (0.55%)<sup>116</sup>. These differences among tree species might shift ecosystems towards slow-growing species under increased VPD, reducing terrestrial carbon sequestration rates<sup>117</sup>.

Mortality events can also eliminate specific plant species, decreasing plant diversity and increasing ecosystem susceptibility to water stress<sup>118</sup>. For example, species richness has declined rapidly in response to rising VPD in the humid Amazon evergreen forests<sup>119</sup> (Supplementary Fig. 3). Similarly, in some arid ecosystems, high VPD during the warm season exerts upregulated effects on the mortality, with deciduous broadleaf trees exhibiting higher mortality rate than conifer species<sup>120</sup>.

# Net ecosystem production

Rising VPD greatly affects terrestrial NEP. Negative impacts of rising VPD on NEP have been observed across a range of ecosystem types, including forests, grasslands, croplands, tundra and coastal wetlands<sup>121–123</sup>. For example, eddy covariance observations at 12 managed grasslands in New Zealand demonstrated a deficit in NEP in response to rising VPD that was independent of soil moisture conditions<sup>124</sup>. However, global-scale observations are lacking.

Twelve terrestrial ecosystem models indicate a global mean sensitivity of NEP to rising VPD of  $-5.59\pm1.15$  PgC hPa $^{-1}$  (ref. 18) (Fig. 2e). The response across ecosystem types was highly variable (Fig. 2d), with the highest sensitivity in croplands  $(36.71\pm2.13$  gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ), evergreen broadleaf forest  $(36.21\pm3.02$  gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ), and deciduous broadleaf forest  $(33.78\pm2.44$  gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ), whereas evergreen needleleaf forests  $(8.09\pm1.10$  gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ) and deciduous needleleaf forests  $(4.76\pm0.66$  gC m $^{-2}$  yr $^{-1}$  hPa $^{-1}$ ) exhibited lower sensitivities (Fig. 2d). The low sensitivities in shrublands and grasslands are probably due to their low stomatal conductance and deep rooting systems, which enhance their ability to access water from deep soil layers  $^{125,126}$ .

The negative impacts of VPD on ecosystem NEP were primarily observed under high-VPD conditions, as with GPP owing to its strong influence on NEP. Atmospheric dryness does not limit carbon uptake when VPD is low<sup>125,127</sup>. As VPD rises, ecosystem NEP initially increases until it reaches a peak, after which it begins to decline. For example, NEP peaked when VPD increased to 15.4–19.8 hPa at one grassland and two cropland sites in the US Corn Belt<sup>127</sup>. However, the optimum VPD for NEP has been reported to be 25–30 hPa for several other croplands in North America<sup>128,129</sup>. Similar VPD thresholds have been observed in coastal mangrove ecosystems (approximately 25.0 to 29.5 hPa)<sup>123</sup>, with NEP rising as VPD increased to around 20 hPa before steeply decreasing under higher VPD<sup>130</sup>.

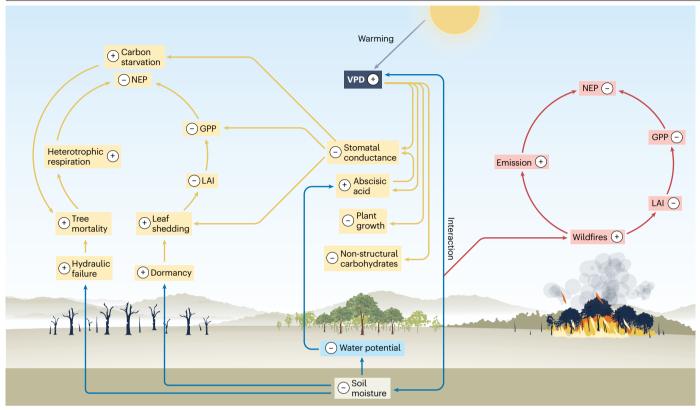
Overall, global in situ and satellite observations have quantified the negative impacts of rising VPD on LAI, GPP, LUE and NEP across terrestrial ecosystems. Conversely, quantitative information on impacts on other terrestrial carbon cycles, such as phenology, plant growth, NSCs and tree mortality, is still scarce.

# **Mechanisms**

Rising VPD primarily affects terrestrial carbon cycle via two pathways  $^{88}$ , one involving several carbon sequestration processes and another influencing processes related to plant mortality. The role of the mechanisms underlying these processes and acclimation effects in determining the impact of changing VPD on the carbon cycle are now discussed.

### Stomatal closure and hydraulic failure

Stomatal conductance response to VPD strongly influences changes in carbon cycle processes under increasing atmosphere dryness. When water loss from transpiration exceeds uptake by roots, plants reduce



**Fig. 4** | **The impacts of atmosphere dryness on terrestrial carbon cycle.** Plus symbols indicate a positive response to increasing vapour pressure deficit (VPD), whereas minus symbols indicate a negative response. Yellow arrows represent the influence of VPD on terrestrial carbon cycling. Blue arrows represent the

influence of VPD on hydrological cycling in ecosystems. Red arrows represent the influence of wildfires on carbon cycles. Rising VPD could affect plant physiology, growth and terrestrial carbon cycling via a number of pathways.

the stomatal aperture or even close stomata entirely to minimize water loss  $^{13l-134}$ . This action reduces  $\mathrm{CO}_2$  passage into leaf cells from the atmosphere, decreasing photosynthesis  $^{13l-134}$  (Fig. 4) and directly affecting carbon uptake, sinks, tree growth and survival  $^{108,135}$ . Decreased stomatal conductance also alters physiological processes in plants, further limiting photosynthesis  $^{136}$ . For instance, leaf stomatal closure induced by rising VPD increases mesophyll resistance  $^{137}$ , thereby reducing the rate of  $\mathrm{CO}_2$  fixation by rubisco and leading to increased water and nitrogen costs associated with carbon acquisition. In addition, decreased photosynthesis leads to insufficient carbon substrate for metabolism and a limited supply of NSCs, ultimately causing carbon starvation  $^{109,138}$ , a major factor contributing to global tree mortality.

Stomatal conductance responses to VPD also vary between plants with different water regulation strategies <sup>139,140</sup>. For instance, isohydric plants typically adjust their stomatal openings to limit water loss, whereas anisohydric plants regulate xylem embolisms to limit water loss while still maintaining stomatal opening <sup>140,141</sup>. These divergent stomatal responses to VPD differentially affect vegetation growth and the terrestrial carbon cycle. For example, productivity in anisohydric ecosystems (such as grasslands) across the United States is three times more sensitive to VPD than that in isohydric ecosystems <sup>36</sup>. Yields of other anisohydric crops, including rice and maize, also strongly depend on seasonal VPD<sup>136</sup>. However, responses to VPD might be confounded by temperature stress <sup>77,142</sup>. As high temperatures often accompany high

VPD, plants might increase or sustain stomatal conductance to maintain optimal leaf temperatures for photosynthesis, particularly under heat shock scenarios that can irreversibly damage photosynthetic machinery<sup>142–144</sup>.

Regulating xylem water transport is another adaptive strategy that plants use in response to atmospheric dryness. High VPD increases the water potential gradient across the atmosphere, plant and soil, decreasing plant water potential <sup>21</sup> (Fig. 4). Hydraulic failure might occur when VPD-induced water losses surpass water uptake, causing high tension of xylem-bound water <sup>145</sup> and xylem cavitation <sup>146</sup>. Hydraulic failure, together with carbon starvation, are the two primary theoretical explanations to tree mortality induced by drought <sup>147–151</sup>. Hydraulic failure induced by high VPD might further impair the nutrient uptake <sup>152</sup> and indirectly limit plant growth, as transpiration helps to drive nutrient migration to the root <sup>153</sup> and solute transport to shoots <sup>154</sup>. The rate of nutrient transport in the xylem notably decreases as hydraulic failure occurs, leading to reduced absorption of mineral nutrients <sup>155</sup>, including nitrogen, phosphorus, potassium, magnesium and iron <sup>152,155–158</sup>.

# Abscisic acid biosynthesis

The biosynthesis of abscisic acid, a phytohormone associated with drought-induced plant stress, is highly sensitive to the water potential of leaves<sup>159</sup>. As leaf turgor pressure declines<sup>160–162</sup>, plants upregulate various stress-induced solutes and proteins and promote abscisic acid

biosynthesis  $^{162-165}$ . Elevated abscisic acid levels can be observed just 20 minutes following VPD increasing from 7 to 15 hPa (ref. 166). Plants under high-VPD conditions exhibit increased leaf abscisic acid content compared with those in low-VPD environments  $^{167}$ .

Accumulated abscisic acid is recognized by intracellular receptor proteins  $^{168,169}$ , initiating signal transduction pathways that activate anion channels in guard cells. This activation leads to an efflux of anions, depolarizing the plasma membrane and subsequently activating potassium (K<sup>+</sup>) efflux channels, resulting in the loss of various ions and water in the guard cells  $^{13,170,171}$ . The outcome is a reduction of vacuolar turgor pressure and volume within the guard cells, which leads to stomatal closure. Abscisic-acid-deficient mutants do not exhibit an increase in foliar abscisic acid levels or stomatal closure response when VPD rises  $^{162,172,173}$  (Fig. 4), indicating that abscisic acid has a central role in VPD-induced stomatal closure. However, despite a slower response in abscisic-acid-insensitive mutants, they can still close their stomata under high-VPD conditions  $^{9,174}$  which suggests that stomatal response to VPD involves both abscisic-acid-dependent and non-abscisic-acid-dependent components.

Apart from regulating stomatal conductance and influencing plant growth, abscisic acid accumulation in leaves can affect other critical physiological processes within plants 13,175,176. Abscisic acid content in aerial tissues can limit the rate of new leaf expansion 63, influence leaf morphology 177,178, and regulate flower development and sexual differentiation 161,179,180. Additionally, abscisic acid accumulation accelerates the senescence of older leaves through transcriptional regulation 13, which alters leaf phenology and canopy structure 181. However, it remains unclear whether abscisic acid produced in response to soil drying or high VPD can directly trigger leaf senescence, or whether it accelerates senescence indirectly by reducing stomatal conductance and photosynthesis 182.

### Vegetation fires and soil moisture deficits

VPD also affects the carbon cycle through cascading effects on fires, which can induce large-scale carbon emission and plant mortality large in mortality, reflecting the increased flammability of fuels under atmospheric dryness large increased flammability of fuels under atmospheric dryness large and fire probability) vary by region. For instance, fire area sensitivities vary between the western US ( $S_{\rm fire\,area} = 422\,{\rm km^2\,hPa^{-1}}$ ), Europe (246 km² hPa<sup>-1</sup>), China (130 km² hPa<sup>-1</sup>) and boreal Siberia (1,154 km² hPa<sup>-1</sup> below 3.6 hPa) (Supplementary Fig. 2). VPD also contributes to interannual variability in fire activity across continents las, advances fire-season onset las and impedes post-fire recovery by creating unsuitable conditions for seedling survival and regeneration lass.

Atmospheric aridity enhances the probability of fire across various vegetation types globally<sup>189</sup>, but the pathways of VPD influence on fire activities are multifaceted. High VPD reduces moisture content in organic matter<sup>190,191</sup>, desiccates plant tissues, increases flammability, and promotes ignition, spread and combustion<sup>17,192</sup>. For example, satellite-based observations indicate a 45% decrease in live fuel moisture and a 2% decrease in dead fuel moisture for every 10-hPa increase in VPD<sup>193</sup>. Plant physiological trait responses to VPD can notably affect fire behaviour. For example, the increase in burned area per unit rise in VPD is greater in forests dominated by species with open stomata or shallow root systems than in forests dominated by species with tighter stomatal control<sup>185</sup>. Plant control over transpiration rates through stomatal closure influences water regulation and ignition risk: for instance, isohydric plants might help to reduce fire spread more than anisohydric

plants  $^{185}$ . Consequently, the ongoing rise in VPD might exacerbate fire regimes globally  $^{17,194}$ .

Pronounced high VPD also exhibits cascading effects on soil moisture <sup>10,195</sup>. High VPD often enhances atmospheric evaporative demand, promoting evapotranspiration and accelerating soil drying <sup>10,195</sup> (Fig. 4). This effect is particularly pronounced in humid ecosystems <sup>24</sup>, where soil moisture is initially sufficient to sustain evapotranspiration <sup>196</sup>. In addition to the impact of high VPD, reduced soil moisture further curtails evapotranspiration by restricting water availability and triggering additional stomatal closure <sup>197</sup>, limiting vegetation production and causing large-scale plant mortality. As evapotranspiration declines, a greater proportion of net radiation is allocated to sensible heat flux, ultimately elevating air temperatures <sup>198</sup>. Thus, VPD effects are compounded by effects with mutual causes, such as soil water deficit, that further complicate the quantification of VPD impacts on carbon cycles <sup>20,88</sup>.

# Plant and ecosystem acclimation to rising VPD

Over time, plant acclimation, whereby plants adjust to high atmospheric dryness, could to some extent mitigate the negative impacts of rising VPD on the carbon cycles<sup>77</sup>. Plants under high VPD often exhibit elevated chlorophyll content in their canopy leaves<sup>199</sup>. Plants can also increase leaf nitrogen and phosphorus concentrations as part of their acclimation to rising VPD<sup>77</sup>. Additionally, plants often decrease their number of leaves and reduce tree height to acclimate to high-VPD conditions<sup>77</sup>, as vulnerability to embolism increases with plant height<sup>79</sup>.

At the ecosystem level, species composition might change substantially in acclimation to increasing VPD. In humid ecosystems, recruitment and growth rates of species with high hydraulic safety are substantially higher than those with low hydraulic safety<sup>15</sup>. Species with high hydraulic safety invest in enhanced mechanical stability and defence, leading to narrower xylem conduits, denser wood and lower xylem conductivity. Consequently, these species exhibit slower growth rates and reduced mortality risk<sup>16,200</sup>. By comparison, plants in arid regions typically reduce evapotranspiration as VPD increases to effectively conserve soil moisture<sup>10</sup>. This adaptive acclimation strategy to cope with aridity preserves water for periods of low atmospheric demand, thereby enabling ecosystems to fix carbon with relatively lower water loss<sup>201</sup>.

The mechanisms by which atmospheric dryness affects carbon cycling in terrestrial ecosystems manifest in reduced plant stomatal conductance, increased risk of plant hydraulic failure, and promotion of the abscisic acid biosynthesis, which all substantially restrict plant growth. Atmospheric dryness intensifies the frequency and severity of wildfires and leads to soil drought, which indirectly decrease terrestrial carbon sinks. However, plants and ecosystems also exhibit acclimation, which can to some extent mitigate the negative impacts of atmospheric dryness.

# Future changes in atmospheric dryness

Projections from ESMs consistently show that VPD will increase under anthropogenic warming, with the rate and magnitude of increase being enhanced under scenarios of high greenhouse gas emissions. These changes are not uniform across regions and could profoundly affect plant physiology, ecosystem productivity and the stability of the carbon cycle.

# Projected changes in VPD

Global atmospheric dryness will continue to increase owing to anthropogenic warming <sup>202</sup>. ESMs consistently indicate a global increase in VPD

# a Projected distribution in VPD **b** Annual global mean VPD SSP5-8.5 (mean ± 1 s.d.) SSP2-4.5 (mean ± 1 s.d.) SSP1-2.6 (mean ± 1 s.d.) VPD (hPa) 2015 SSP1-2.6 2060 2100 Year C Rate of change in VPD by climate zone SSP5-8.5 SSP2-4 5 SSP1-2.6 0.15 SSP2-4.5 VPD trend (hPa yr¹) 0.10 0.05 SSP5-8.5 0.00 24 Hyper-arid Semi-arid Dry sub-humid VPD (hPa)

**Fig. 5** | **Projected changes in global VPD between 2015–2100. a**, Spatial distribution of vapour pressure deficit (VPD) based on ensemble output from the 14 Coupled Model Intercomparison Project (phase 6, CMIP6) Earth system models for scenario SSP1-2.6 (top), SSP2-4.5 (middle) and SSP5-8.5 (bottom) for the period 2015–2100 (ref. 202). **b**, Change in annual VPD across the three scenarios,

2015–2100. Shading represents one standard deviation.  $\mathbf{c}$ , Trend in global mean VPD from 2015 to 2100 by climate zone (classified based on the average aridity index during 1961–1990; see Supplementary Fig. 1). \*\*\* and \*\* denote trends significant at the 0.01 and 0.05 levels. Projections consistently predict intensified VPD under different scenarios and across different climate zones.

from intermediate (Shared Socio-economic Pathway 2-4.5, SSP2-4.5) to high (SSP5-8.5) emission scenarios, highlighting the impact of greenhouse gas emissions on atmospheric dryness  $^{27,203}$ . Under SSP1-2.6, a low-emission scenario, VPD is projected to stabilize around 2060, with a net increase of less than 1 hPa in the twenty-first century  $^{202}$ . The increase in VPD is more pronounced in high-emission scenarios, particularly under SSP5-8.5, which projects that the global mean increase in VPD will exceed 3 hPa between 2020 and 2100 (ref. 202). However, Coupled Model Intercomparison Project (phase 6) (CMIP6) ESMs probably underestimate future decreases in near-surface relative humidity  $^{204}$ , implying that the future VPD might also be underestimated.

Although all scenarios project increasing trends, the rate of increase in VPD will vary across different climate zones (Fig. 5). The most rapid increases in VPD are expected in arid regions, with the trend in hyper-arid areas projected to reach approximately  $0.13 \pm 0.03$  hPa yr<sup>-1</sup> under SSP5-8.5 (Fig. 5e). A slower rate of VPD increase in hyper-arid regions is projected under SSP2-4.5 and SSP1-2.6 ( $0.05 \pm 0.02$  hPa yr<sup>-1</sup> and  $0.02 \pm 0.01$  hPa yr<sup>-1</sup>, respectively). Such substantial increases in VPD could notably intensify the frequency and severity of droughts, further exacerbating water stress <sup>14,190</sup>.

Moderate trends in VPD are projected in arid regions, increasing at  $0.08\pm0.02$  hPa yr $^{-1}$  under SSP5-8.5 with slower rates of change under SSP2-4.5 and SSP1-2.6. In comparison, both dry sub-humid and humid regions will experience relatively small increases in VPD. Under SSP5-8.5, the VPD trend will reach  $0.04\pm0.01$  hPa yr $^{-1}$  in dry sub-humid regions and  $0.03\pm0.01$  hPa yr $^{-1}$  in humid regions. Smaller trends are projected under SSP2-4.5 and SSP1-2.6.

Thus, higher emissions will lead to notable increases in VPD across all regions, particularly in dry areas. Conversely, lower emissions will slow the rate of increase and help to maintain more stable conditions, especially in humid regions.

# Potential impacts on future carbon cycle

Most state-of-the-art ESMs focus on projecting future changes in GPP and often predict a continuous increase in global GPP owing to the  ${\rm CO_2}$  fertilization effect<sup>205</sup>. However, substantial uncertainties remain regarding the complex environmental impacts on GPP<sup>20,206</sup>. The effects of other meteorological variables could counteract the positive feedback between GPP and rising  ${\rm CO_2}$  concentration, especially concurrent increases in VPD<sup>205</sup>.

The Common Land Model  $^{207}$ , integrated with a prognostic vegetation phenology model, aims to account for these concurrent environmental factors. It projects uptrends in annual mean LAI and total GPP under SSP1-2.6, but downtrends under SSP2-4.5, SSP3-7.0 and SSP5-8.5 by 2100. These trends are largely attributed to the increasing atmospheric dryness  $^{208}$ . This response is in agreement with independent projections from ESMs that estimate a transition from positive  $(0.05\pm0.12\,\mathrm{gC}\,\mathrm{m}^{-2}\,\mathrm{ppm}^{-1}\,\mathrm{during}\,1982-1996)$  to negative indirect  $\mathrm{CO}_2$  effects  $(-0.05\pm0.03\,\mathrm{gC}\,\mathrm{m}^{-2}\,\mathrm{ppm}^{-1}\,\mathrm{during}\,2086-2100)$  on the vegetation carbon uptake  $^{209}$ . As the climate continues to warm, global VPD is likely to increase substantially, enhancing the impacts of VPD on the terrestrial ecosystem carbon cycle.

The limited number of existing projections of VPD impacts on forest mortality consistently highlight risks of increasing background mortality and die-off events<sup>106</sup>. Empirical models predict substantial losses of conifer trees across the southwestern region of North America around the year of 2050 owing to increased atmospheric dryness<sup>106</sup>. Additionally, beyond traditional metrics like soil moisture, VPD has been identified as the most important predictor of fire probability in some areas. For example, in Australia, fire risk in mesic forests would increase by 65% as VPD rose from 25 to 70 hPa (ref. 210). The probability of fire activity could even be doubled with each unit increase in VPD in subtropical China<sup>211</sup>.

However, there is still large uncertainty among ESMs simulating the impacts of atmospheric drought on the carbon cycle. For instance, ESMs tend to underestimate the important role of VPD in regulating diurnal photosynthesis<sup>212</sup>. Eddy covariance observations indicate that VPD is the dominant driver contributing to the widespread afternoon depression of photosynthesis in terrestrial vegetation globally. Conversely, the majority of ESMs simulate an increase in afternoon photosynthesis<sup>212</sup>. In addition, little attention has been given to assessing the performance of ESMs in terms of the impact of atmospheric dryness on the other variables of carbon cycle.

### Summary and future perspectives

Atmospheric dryness has substantially increased with climate warming \$^4. Since the late 1990s, global VPD has increased at a rate of  $0.0155 \pm 0.0041$  hPa yr  $^{-1}$ , approximately an eightfold acceleration in the rate of drying. These changes in VPD have affected the terrestrial carbon cycle. At the global scale, rising VPD can reduce GPP by  $13.82 \pm 3.12$  PgC hPa  $^{-1}$ , LUE by  $0.04 \pm 0.02$  gC MJ  $^{-1}$  hPa  $^{-1}$ , NEP by  $5.59 \pm 1.15$  PgC hPa  $^{-1}$  and LAI by 0.11 m  $^{2}$  m  $^{-2}$  hPa  $^{-1}$ . The mechanisms underlying these responses to rising VPD include stomatal closure to constrain vegetation photosynthesis, induced hydraulic failure to intensify plant mortality, enhanced abscisic acid biosynthesis to regulate leaf phenology, synthesis of plant NSCs and structural growth. The resultant cascading effects of VPD lead to increased occurrence and severity of fires and soil moisture deficits. VPD is projected to increase by between  $^{-1}$  hPa (SSP1-2.6) and 3 hPa (SSP5-8.5) by the end of the twenty-first century.

Advances in the implementation of VPD-manipulation experiments are needed to address knowledge gaps. To provide global-scale insights, future experiments should focus on reaching a consensus regarding the exact mechanisms by which plant stomata respond to VPD<sup>213</sup>. Comprehensive physiological variables should be measured to examine their individual impacts on stomatal conductance. Quantifying how stomatal conductance responds to interactions between variables is also important. The impacts of VPD on leaf phenology and structural growth in temperate and boreal climate zones should

be a particular focus, given the important control of temperature on leaf phenology and plant growth relative to other environmental variables at high latitudes<sup>61</sup>. It is also challenging to quantify global-scale VPD-induced tree mortality via cascading effects on wildfires and soil water deficits<sup>138</sup>. The contributions of rising VPD to wildfires and soil dryness should be quantified via in situ and satellite observations. In addition, the mechanisms by which wildfires and soil dryness affect tree mortality should be investigated.

VPD impacts on carbon cycles also need to be isolated from the influence of other climate variables. Attempts have been made to isolate VPD impacts using partial correlation analysis, data binning and machine learning approaches<sup>8,21</sup>. However, global manipulation experiments are needed to quantify the impacts of VPD on carbon cycles through controlling other environmental factors such as soil moisture, temperature and radiation.

VPD-manipulation experiments should also account for heterogeneity in species-dependent and biome-dependent responses to rising VPD at the global scale. Experiments should quantify the responses of different plant species and ecosystems to high VPD 77,142. VPD-manipulation experiments should also fully consider the unequal exposure of various ecosystems and climate zones to increasing atmospheric dryness, helping to establish region-specific and time-specific scenarios. Building more extensive and representative VPD-manipulation networks, operating over a range of spatial scales, is essential to evaluate the potential impacts of VPD on carbon cycle processes.

In addition, VPD-driven physiological processes need to be integrated into carbon cycle models. Despite substantial progress in modelling VPD impacts since the late 1990s, process-based model algorithms representing responses in photosynthesis, hydraulic transport, leaf phenology and mortality are still needed.

Plant stomata models that simulate stomatal conductance responses to elevated VPD can capture changes associated changes in photosynthesis. However, existing models typically assume a fixed proportional relationship between stomatal conductance and VPD, when actually this relationship varies across species<sup>214</sup>. Field and satellite-based observations of hydraulic traits<sup>215</sup> and turgor responses<sup>216</sup> in various vegetation types are needed to inform these algorithms to more accurately represent hydraulic responses to rising VPD.

Persistent knowledge gaps in the simulation of plant hydraulic transport in response to rising VPD also need to be addressed. Vulnerability curves, which describe conductivity changes in xylem or other conduits in response to water potential, are widely integrated into existing hydraulic models 146,217,218. However, these models typically assume time-invariant vulnerability curves and fail to account for dynamic embolism refilling or the formation of new xylem in response to hydro-climatic stresses 219. In addition, most hydraulic models focus on xylem vulnerability curves and omit root and leaf vulnerability curves 146. Therefore, dynamic vulnerability curves across the plant system should be integrated in plant carbon-cycle and growth models to reduce the uncertainties in simulating plant survival, vegetation productivity and associated carbon sink capacity 116.

To support these advances in simulating plant response to moisture stresses, comprehensive measurements of water potentials and vulnerability curves for roots, stems and leaves are needed. Additionally, instead of existing one-layer schemes, hydraulic models should use multiple-layer canopy models to capture within-canopy variability of VPD and leaf temperature, which can vary substantially across the canopy profile<sup>220</sup>.

Leaf phenology models typically rely on temperature as a key driver when simulating seasonal canopy leaf dynamics, represented as leaf flushing and shedding<sup>221</sup>. However, these models perform poorly intropical regions<sup>221</sup> owing to the lack of representation of VPD-related mechanisms and their critical role in this climate zone<sup>100</sup>. This limitation can be overcome by incorporating VPD-driven phenology models into ESMs to capture the seasonality of LAI and leaf age<sup>55,222</sup>. Future research should determine VPD influence on plant hormone signalling and physiological responses, thereby improving the predictive capability of phenology models.

Plant growth models that simulate wood formation typically omit the influence of VPD on this process, despite water stress effects being incorporated into wood formation models<sup>223,224</sup>. Models such as TreeRing 3<sup>225</sup> and CAMBIUM<sup>226</sup> use stomatal resistance and xylem water potential to quantify the influence of soil moisture stress on wood formation<sup>223</sup>, and other models include turgor pressure as a driver of growth in cambial and enlarging cells<sup>227,228</sup>. However, these models often overlook relationships between VPD and stomatal resistance<sup>11</sup>, xylem water potential<sup>229</sup> and turgor pressure<sup>85</sup>.

Empirical and process-based models should better represent the role of VPD as a driver of tree mortality<sup>230</sup>, which could be achieved through improved representation of plant hydraulic failure<sup>215</sup> and integration of plant traits<sup>231</sup>. For instance, key plant traits strongly determine the threshold of tree mortality under severe atmospheric and soil water stress, such as the water potential that corresponds to a 50% loss in hydraulic conductivity<sup>231</sup>. Models should also represent plant trait variability within species driven by chronic stress, biotic attack, competition, past damage and other factors<sup>15,231</sup>. Starvation-related mechanisms should also be incorporated into tree mortality models<sup>138</sup>. For instance, phloem transport failure can intensify localized carbon starvation and should be integrated<sup>232,233</sup>.

Existing tree mortality models also often overlook plant acclimation. Plants can modify root depths, leaf area and other critical traits in anticipation of severe droughts, thereby improving their chance of survival<sup>138</sup>. Finally, processes influencing mortality, such as infectious plant diseases, often concurrent with changes in VPD, are not yet adequately incorporated into ecosystem process models<sup>234</sup>. Advancing understanding of the impacts of rising VPD on plants will therefore require coordinated efforts to extend experimental and empirical observations to develop robust algorithms that can be integrated into complex modelling frameworks.

# Data availability

All the data that support the findings are openly available. The air temperature and AVP from the Climate Research Unit are available at https://crudata.uea.ac.uk/cru/data/hrg/. The annual precipitation and potential evapotranspiration from the TerraClimate data are obtained from https://climate.northwestknowledge.net/TERRACLIMATE/index\_directDownloads.php. The leaf area index and gross primary production from the Global Land Surface Satellite (GLASS) are available at https://www.glass.hku.hk/. The NEP from the Trendy data is obtained from https://globalcarbonbudgetdata.org/. The global land cover change dataset is available at https://gee-community-catalog.org/projects/glc\_fcs/. The eddy covariance observations from FLUXNET2015 are available at https://fluxnet.org/data/fluxnet2015-dataset/. The CMIP6 dataset is available at https://esgf-node.llnl.gov/search/cmip6/.

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### **Author contributions**

W.Y. and X.C. designed the manuscript. J.T., M.W., S.W. and W.X. researched data for the article. All authors reviewed and edited the manuscript before submission.

### **Competing interests**

The authors declare no competing interests.

### Additional information

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