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Review

Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress

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Plant responses to drought and heat stress have been extensively studied, whereas post-stress recovery, which is fundamental to understanding stress resilience, has received much less attention. Here, we present a conceptual stress-recovery framework with respect to hydraulic and metabolic functioning in woody plants. We further synthesize results from controlled experimental studies following heat or drought events and highlight underlying mechanisms that drive post-stress recovery. We find that the pace of recovery differs among physiological processes. Leaf water potential and abscisic acid concentration typically recover within few days upon rewetting, while leaf gas exchange-related variables lag behind. Under increased drought severity as indicated by a loss in xylem hydraulic conductance, the time for stomatal conductance recovery increases markedly. Following heat stress release, a similar delay in leaf gas exchange recovery has been observed, but the reasons are most likely a slow reversal of photosynthetic impairment and other temperature-related leaf damages, which typically manifest at temperatures above 40 °C. Based thereon, we suggest that recovery of gas exchange is fast following mild stress, while recovery is slow and reliant on the efficiency of repair and regrowth when stress results in functional impairment and damage to critical plant processes. We further propose that increasing stress severity, particular after critical stress levels have been reached, increases the carbon cost involved in reestablishing functionality. This concept can guide future experimental research and provides a base for modeling post-stress recovery of carbon and water relations in trees.

Keywords: carbon allocation, hydraulic conductance, non-structural carbohydrates, post-drought, post-heat, recovery, stress legacy, trees, xylem embolism.

Introduction

Recent climate extremes have increased our awareness of stress-induced forest decline (Choat et al. 2018). Droughts combined with high temperatures and large evaporative demand—so-called hot or global-change-type droughts—are thought to be the main causes responsible for observed increases in tree mortality globally (Allen et al. 2015). Such drought-induced mortality is often facilitated by pest and pathogen attacks or compounding drought events (Anderegg et al. 2015a). Further, if drought frequency increases and

the time between stressful periods decreases, recovery rate might determine survival (Schwalm et al. 2017). For example, Anderegg et al. (2015b) analyzed radial growth data from several forest sites across the globe and detected a clear trend of incomplete stem-growth recovery persisting for years after an extreme drought. Because most of our experimental research to date has focused on the stress event per se, we know little about stress-recovery dynamics and underlying mechanisms. This is an oversight since recovery trajectories can provide relevant information on stress impacts and stress resilience (Ingrisch and Bahn 2018).

Our physiological understanding of forest and woody plant recovery following extreme hot and dry weather events is limited, because (i) we are missing detailed and long-term observations, (ii) studies of extremes in natural systems are often opportunistic (e.g., [Ciais et al. 2005](#)) and (iii) post-event weather conditions may influence the recovery progress ([Li et al. 2016](#), [He et al. 2018](#)). For example, growth in Douglas-fir trees was shown to be suppressed years after an extreme heatwave, but it was not possible with field data to differentiate the additional impacts of the drier than usual conditions in the following year ([Sergent et al. 2014](#)). Hence, in field observations, we cannot easily tease apart the impact of an extreme heatwave from the effect of subsequent conditions. To discern the impacts of current (recovery) from antecedent (stress) conditions, and to evaluate recovery from various possible stress responses, we need a better understanding of the underlying mechanisms. A promising route to take is studying post-stress recovery of plant physiology under controlled conditions. This can provide the necessary mechanistic understanding to interpret field observations and ultimately to incorporate recovery processes into vegetation models.

Fundamental plant physiological processes are reflected in carbon (C) and water relations, which are sensitive to heat and drought stress. Plant C and water dynamics are tightly coupled at the leaf level via stomata, which are closely regulated to maintain hydraulic integrity, while optimizing C uptake ([Tyree and Zimmermann 2002](#)). Photosynthesis, C allocation and growth interact with other metabolic processes and are in turn sensitive to changes in environmental conditions and the hydraulic state of plants. Hence, stress severity and other extrinsic and intrinsic factors will determine whether hydraulic and metabolic changes persist or whether they can be reversed upon stress release (see [Gessler et al. 2017](#)).

In this review we devise a stress-recovery framework linking physiological stress impacts to recovery rate and success. To guide the framework, we review and synthesize controlled experimental studies that address post-heat (high temperature and large evaporative demand) and post-drought recovery dynamics in juvenile woody plants, and we discuss the underlying mechanisms of hydraulic and metabolic recovery at the plant and leaf level. In order to address the limitation of experiments being mainly conducted on non-mature plants, experimental findings are compared to studies on mature stands and modeling concepts are introduced. Finally, we propose future research topics along the lines of the suggested conceptual approach.

Stress-recovery framework

Recovery success of different physiological processes over time is typically measured relative to a control treatment or to pre-stress conditions and generally falls into three broad categories: partial, complete and compensatory recovery

([Xu et al. 2010](#)). Complete recovery can occur with and without repair mechanisms involved. Physiological processes that were down-regulated during stress, but without damage of the underlying tissue or supply pathways, may be simply reactivated. An example of this scenario is instantaneous recovery of stomatal conductance (g_s) or enzyme activity after minor water limitation. In contrast, if stress resulted in tissue damage, energy and C need to be diverted from other biological pathways, which may reduce growth or other functionalities. Under this scenario, partial recovery is most likely and damaged tissues may often not be fully restored. Compensatory recovery is when stress-induced reductions are recompensed by investments into alternative processes and tissues. Recompensing processes can be found at different levels, including shifts between stomatal and mesophyll conductance ([Cano et al. 2014](#)), a prolonged leaf longevity ([Arend et al. 2016](#)) or allocation to roots at the cost of shoot growth ([Poorter et al. 2012](#)). In some cases, overcompensation even occurs, as has been shown in previously drought-stressed trees growing taller than control trees ([O'Brien et al. 2017](#)).

Stress severity and the underlying physiological processes determine if stress-impacts are quickly reversible or if permanent damage occurs ([Miyashita et al. 2005](#)). If stress is too severe or the recovery strategy of the plant is not appropriate, feedback loops (or vicious circles) may occur. For example, substantial leaf shedding decreases the ability for C assimilation for prolonged periods after stress release ([Ruehr et al. 2016](#)), which often occurs in combination with non-reversible losses in hydraulic conductance (LC) and hence manifest internal water limitation ([Blackman et al. 2009](#)). The longer periods of decreased photosynthesis are, the more important the availability of non-structural carbohydrate (NSC) reserves becomes. Our proposed stress-recovery framework links plant hydraulic and metabolic stress responses to recovery pace and success ([Figure 1](#)). We postulate that specific changes in plant physiology during drought or heat stress can indicate recovery trajectories and propose a set of stress-recovery indicators: g_s , down-regulation of photosystem II (PSII), loss of conductance in xylem (LC_x) and outside-xylem (LC_{ox}) tissues, decrease in NSC levels and visible tissue damage/senescence. Using these, three phases of stress occurrence that relate to different recovery trajectories can be distinguished, as follows:

Mild stress—fast recovery

Drought stress, including both soil and atmospheric drought, increases hydraulic tension, which affects g_s first, but as long as g_s does not decline for an extended time below critical levels (i.e., near stomatal closure) and LC does not occur, responses should be fast and completely reversible ([Figure 1a](#)). Under heat stress conditions, reductions in g_s are typically less pronounced ([Ameje et al. 2012](#)) than under drought and initial decreases in PSII due to high temperatures (T) should be quickly

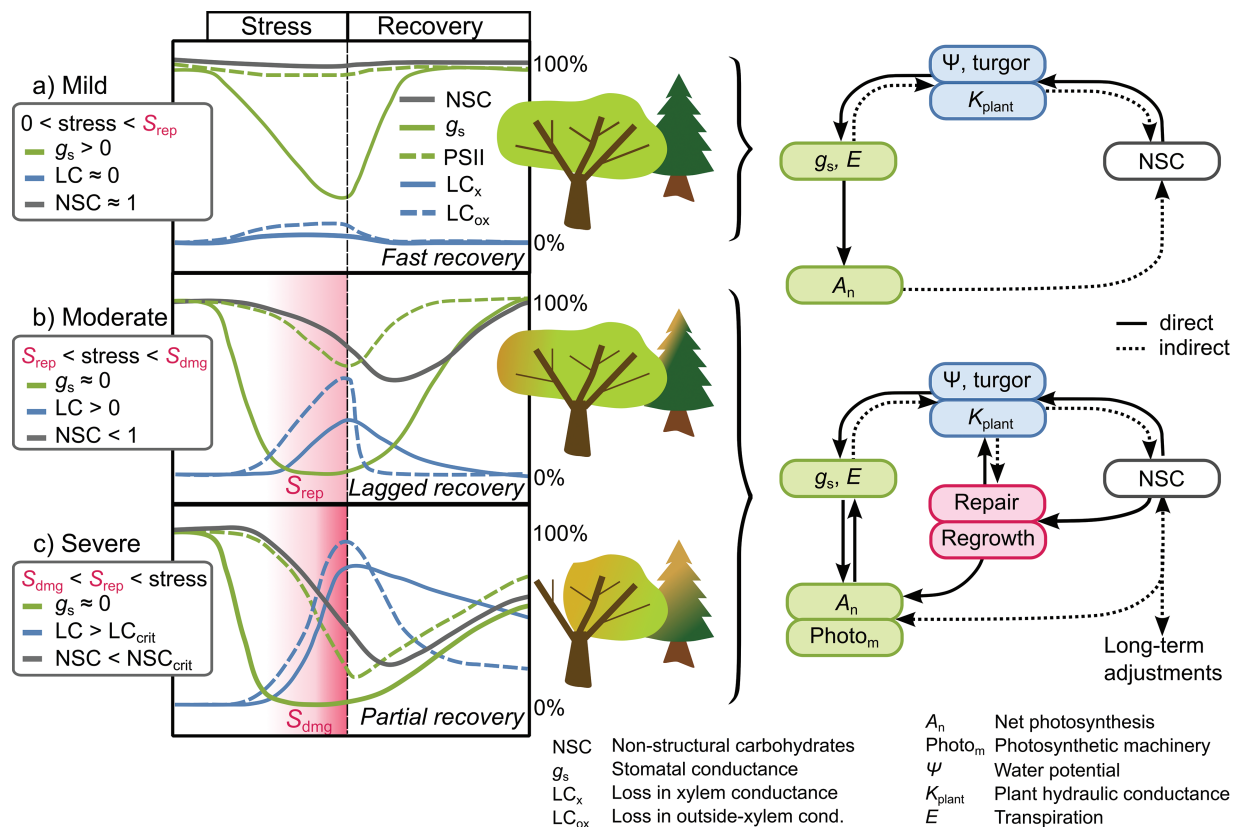


Figure 1. Conceptual framework of post-stress recovery in woody plants during one vegetation period. The pace and success of hydraulic and metabolic recovery is determined by stress impacts on physiological indicators including tissue vitality/senescence, stomatal conductance (g_s), loss of hydraulic conductance in xylem (LC_x , particular under drought) and outside-xylem (LC_{ox}), functioning of PSII and NSC. (a) Mild stress is fully reversible and increases in ψ and turgor (influenced through osmotic potential and NSC) allow stomata to reopen and photosynthesis to increase instantaneously. (b) Moderate stress causes functional impairment (S_{rep}) and reversal involves active repair mechanisms. (c) Severe stress results in structural damage (S_{dmg}) and recovery will be slow and dependent on regrowth of lost and damaged tissues, which may restore functionality in the long-term. Repair and regrowth are supported by available NSC.

reversible, as long as critical T have not been reached (Hüve et al. 2011). Stress-related reductions of C income can result from reduced g_s , temperature-limited photosynthesis and/or increased respiration rates, but should be restricted to the stress period. In summary, mild stress characterized by low intensity and duration should result in fast recovery rates.

Moderate stress—delayed recovery

Exposure to higher T ($>40^\circ\text{C}$) can cause PSII inhibition and results in tissue necrosis (Hüve et al. 2011; Curtis et al. 2014), which typically delays recovery. Under progressing drought, photosynthetic impairment evolves near stomata closure, typically characterized by a sudden increase in sub-stomatal CO_2 concentrations (C_i ; Flexas and Medrano 2002). In addition, despite closed stomata, if plants continue to desiccate hydraulic impairment develops (Meinzer et al. 2009; Li et al. 2016). The LC typically begins in roots and leaves, and initial LC in leaves is dominated by outside-xylem limitations (LC_{ox} , i.e., down-regulation of aquaporins and cell shrinkage; see Charra-Vaskou et al. 2012; Scoffoni et al. 2017). We characterize the degree of stress that is needed to reach such impairment by a threshold,

S_{rep} , that is species- or plant-type specific (see Figure 1b). We can assume that LC_{ox} and/or photosynthetic impairment are reversible, and hence complete recovery occurs with delay. Recovery from such conditions involves repair mechanisms that should be associated with increased C costs, which we express as a decrease of NSC, following recent observations (Yang et al. 2016; Trifilò et al. 2017).

Severe stress—impaired recovery

If the stress dosage is further increasing, non-reversible tissue damage develops. Continued high temperature stress will result in persisting leaf damages, while desiccation will ultimately result in massive LC in both outside-xylem and xylem tissues. This stress level is characterized by a second threshold, S_{dmg} (Figure 1c). As outlined above, complete recovery is unlikely under these circumstances or occurs only slowly via regrowth, provided that the apical and cambial meristematic tissues are still functioning (Brodribb et al. 2010; Li et al. 2016). This rebuilding of damaged tissue places demands on internal C resources. During these situations, NSC levels maintained during stress might be critical to provide sufficient energy and C for

repair and regrowth in the long term. However, plants may die if C resources are not adequate, or if subsequent droughts and/or additional stressors appear.

Stress-recovery mechanisms

Different mechanisms have to be considered to explain the recovery of metabolic and hydraulic functions. Following drought release, rehydration first increases water potential (ψ) and restores cell turgor, which is essential to most metabolic processes. Thus, pre-dawn (ψ_{pd}) and midday leaf water potential (ψ_{md}) recover typically within several hours up to a few days following re-watering (Blackman et al. 2009; Posch and Bennett 2009; Brodribb et al. 2010) alongside fast changes in gene expressions (Meyer et al. 2014) and down-regulation of abscisic acid (ABA; Liang and Zhang 1999; Loewenstein and Pallardy 2002; Brodribb and McAdam 2013; Torres-Ruiz et al. 2015a; Skelton et al. 2017). This evidenced fast increase in ψ post-drought is based on water transport via remaining intact xylem conduits. It is typically not related to the recovery of hydraulic conductance or leaf gas exchange, which usually lags behind. Although high T stress has different damaging effects than drought, a similar delay in leaf gas exchange recovery has been observed (Ameje et al. 2012; Duarte et al. 2016). In the following, we discuss these short- and medium-term physiological responses in more detail. In addition, we report recovery times of different physiological variables from controlled experimental studies. It should be noted that we are not explicitly investigating feedback loops that may occur via leaf senescence or reduced growth at the plant or community level, but mainly focus on physiological responses to either drought or heat stress at the tissue level.

Post-drought recovery

Following drought release, the often-observed initial fast rehydration is accompanied by a much slower recovery of leaf gas exchange and associated variables (Figure 2a). Considering the effect of drought severity on recovery times, indicates that with increasing drought stress (here drought-induced minimum ψ) recovery of g_s becomes delayed. To put this in context of our framework, we should highlight the underlying processes of this delay. Separating the studies along our criterion of mild versus moderate/severe stress was possible for LC_x as stress indicator (not enough data for the other indicators, see Table S1 available as Supplementary Data at *Tree Physiology* Online). We found that g_s recovered quickly following mild drought (no LC_x , 4 days), but at more critical stress levels (LC_x of 42% on average, $n = 19$), g_s recovery took more than five times longer (Welch's t-test, $t = -5.3$, $P < 0.01$, Figure 3b). Note that this recovery length presents an underestimation because the post-stress observation period was in 60% of the studies too short to observe complete recovery. Next, we will address

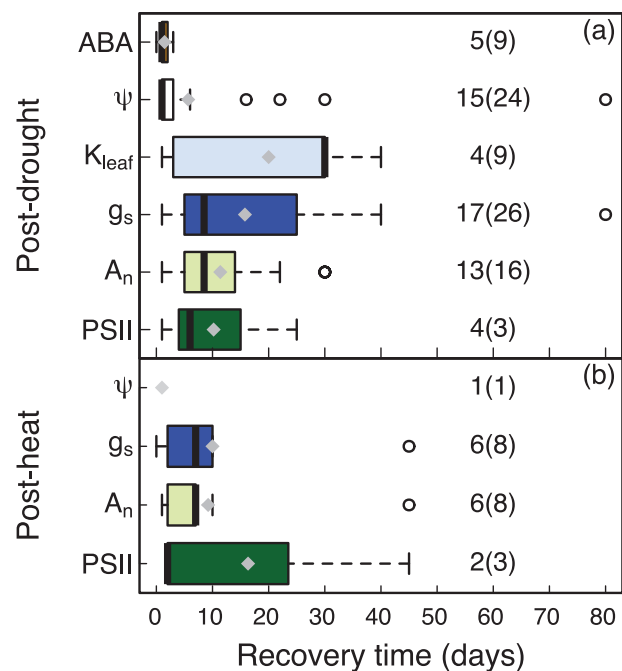


Figure 2. Post-drought and post-heat recovery duration of ABA, leaf water potential (preferentially ψ_{pd}), leaf hydraulic conductance (K_{leaf}), stomatal conductance (g_s), net photosynthesis (A_n) and PSII performance in woody plants. Data have been synthesized from controlled experimental studies (see Table 1) and for ABA additional studies were included (Liang and Zhang 1999; Loewenstein and Pallardy 2002; Brodribb and McAdam 2013; Torres-Ruiz et al. 2015a; Skelton et al. 2017). In case complete recovery has not been observed, the maximum post-stress observation period is assigned as recovery duration. Numbers beside indicate the number of experimental studies and the number of woody plant species (in parentheses). Gray diamonds are averages. In four studies in which ψ_{pd} has not been reported, ψ_{md} or ψ_x was used in the analysis, and missing g_s was substituted by transpiration data and missing PSII measurements were substituted by J_{max} . Note that a thorough analysis based on stress severity is challenged by the small number of species/studies, but see Figure 3.

reasons for a hydraulic limitation of leaf level gas exchange during recovery and further discuss the influence of metabolic feedback mechanisms.

Hydraulic limitations Stomatal pores of woody plants progressively close during drought when turgor in stomatal guard cells declines, caused by a combination of falling leaf ψ and a rising concentration of ABA. Due to continued evaporative water loss after stomatal closure, ψ continues to decline and LC develops (Tyree and Sperry 1989; Meinzer et al. 2009; Choat et al. 2018). Because hydraulic sensitivities differ among plant functional types (PFTs), species and plant organs, LC occurs at different ψ thresholds (Tyree and Zimmermann 2002; Meinzer and McCulloh 2013). Distal organs such as roots and leaves tend to be more vulnerable than stems (Bartlett et al. 2016), and LC in roots and leaves can develop earlier during drought. Such limitations to water transport typically manifest within the xylem, LC_x , mainly via air embolisms and cell wall

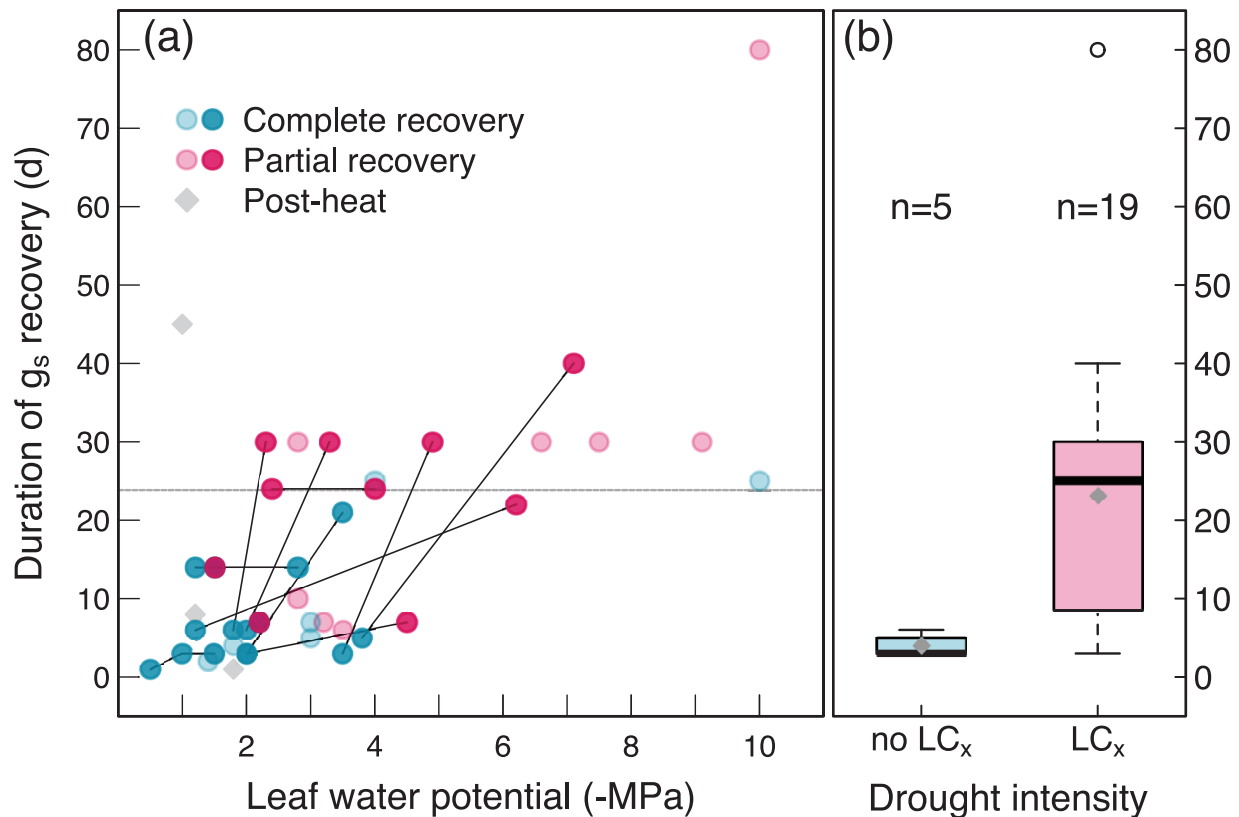


Figure 3. Duration of stomatal conductance (g_s) recovery (complete and partial recovery) related to stress intensities in woody plants. (a) The relationship of stress-induced minimum leaf water potential and g_s recovery duration following drought (26 species) and heat stress (3 species); solid colors and connecting lines indicate different drought intensities experienced by the same plant species within the same study. The intermittent gray horizontal line indicates the average time during which drought recovery has been observed. (b) g_s recovery duration separated into mild drought (no loss of xylem conductance) and moderate to severe drought (LC_x of 10–80%; $42\% \pm 6$ on average). Data on drought-induced xylem LC are reported in Table S1 available as Supplementary Data at *Tree Physiology Online*. Note that missing g_s was substituted by transpiration data.

collapse (Brodribb and Cochard 2009; Zhang et al. 2016), but also outside the xylem, LC_{ox} , in extra-xylary tissues via down-regulation of aquaporins and cell shrinkage (Sack et al. 2016).

Here we focus on LC_{ox} in leaves, which have been more intensively investigated than roots (Cuneo et al. 2016). Leaf xylary cell wall collapse and outside-xylem limitations have been found to dominate the initial decline in leaf hydraulic conductance (K_{leaf} ; Charra-Vaskou et al. 2012; Zhang et al. 2016) up to the turgor loss point (Scoffoni et al. 2017). During recovery, these losses in LC_{ox} typically quickly reverse via cell rehydration and active metabolic processes, including upregulation of aquaporins (Laur and Hacke 2014). Several studies have found a relatively fast (within 1–5 days) reversal of K_{leaf} from mild to moderate drought (Blackman et al. 2009; Brodribb and Cochard 2009; Chen et al. 2010; Torres-Ruiz et al. 2015a). This shows that initial losses in K_{leaf} , which can be attributed largely to LC_{ox} , are, in accordance with our framework, fully reversible (Figure 1a). However, if the turgor loss point has been exceeded and xylem embolisms develop, K_{leaf} recovery should be delayed (Scoffoni et al. 2012) and the time for

hydraulic recovery increases (Lo Gullo et al. 2003; Blackman et al. 2009; Brodribb and Cochard 2009).

With increasing hydraulic tension, the accumulation of xylem embolisms in leaves, branches, stems and roots is inevitable. Whether or not these damages to the water transport system of plants can be reversed after re-wetting has not yet been completely solved. Refilling of embolized xylem conduits is known to be physically possible when transpiration ceases and xylem tensions are close to zero (Clearwater and Goldstein 2005). However, refilling may also occur when the xylem is under tension, but the practical evidence is still heavily debated (for detailed reviews see Clearwater and Goldstein 2005; Brodersen and McElrone 2013). A possible mechanism of refilling under tension could involve osmotic pressure, generated by sugar release from living parenchyma cells (Nardini et al. 2011), which are more abundant in the wood of angiosperms than conifers. Despite such differences, a recent meta-analysis could not detect altered recovery performance between angiosperms and conifers (Yin and Bauerle 2017) post-drought. Together with increasing experimental evidence, this suggests that embolism

refilling might be less common than previously assumed (Choat et al. 2015, 2018; Creek et al. 2018).

A much slower mechanism for regaining hydraulic conductance is by growing new sapwood. This strategy indicates that a critical stress level has been exceeded and development of new xylem will depend on available C resources (Figure 1b and c). Regaining hydraulic conductance via regrowth has for instance been observed in gymnosperms (*Callitris* sp.) after extreme drought conditions, when stem LC_x reached $>80\%$ and trees slowly recovered transpiration and K_{plant} (whole-plant hydraulic conductance) alongside basal stem growth (Brodribb et al. 2010). The rate of basal area increment correlated well to K_{plant} , which slowly recovered by 0.5% per day. Regrowth has also been shown to be important in deciduous trees when drought caused $>90\%$ LC_x in aboveground woody tissue and 100% leaf mortality (Yanyuan et al. 2010; Li et al. 2016). Because regrowth is a comparatively slow process, the emerging LC and g_s recovery trajectories are relatively flat (Blackman et al. 2009; Brodribb et al. 2010), as indicated by our framework following moderate to severe stress (Figure 1b and c).

Metabolic processes Stomatal closure is a main cause of reduced photosynthesis (A_n) during drought stress, and A_n rates recover quickly after mild drought (Arend et al. 2016; Birami et al. 2018). However, with progressing drought when g_s declines below $0.05 \text{ mol m}^{-2} \text{ s}^{-1}$ (Flexas and Medrano 2002), photochemical and biochemical impairment can develop (Limousin et al. 2010) additionally to hydraulic and metabolic constraints. Because C uptake is minimal, the regeneration of Rubisco and synthesis of adenosine triphosphate becomes strongly limited, and NSC reserves may decline (Adams et al. 2017). This critical stress level, S_{rep} , concurs with an increase in C_i because CO_2 is no longer used as a substrate for photosynthesis. Hence, following the release from moderate to severe drought stress, both metabolic repair and regaining hydraulic functioning are prerequisites for photosynthetic recovery (Figure 1b and c).

A possible divergence between hydraulic and metabolic recovery becomes apparent when analyzing the results of experimental studies that observed g_s and A_n recovery patterns post-drought. While the average recovery duration of leaf level g_s and A_n does apparently not differ much (Figure 2a), comparing the ratio of full versus partial recovery, we find that complete recovery of A_n has been more frequently observed (85%) than complete recovery of g_s (55%). The preferential recovery of A_n over g_s increases intrinsic water-use-efficiency ($WUE = A_n/g_s$) and has been observed in a few tree species from temperate and semi-arid biomes, including temperate *Fagus sylvatica* (Galle and Feller 2007), Mediterranean Aleppo pine (Birami et al. 2018) and drought-adapted Eucalypt species (Cano et al. 2014; Martorell et al. 2014; Creek et al. 2018). The underlying mechanisms of increased WUE are most likely preferred recovery of mesophyll conductance (g_m ; Flexas et al.

2008; Cano et al. 2014), enhanced biochemical capacity (Cano et al. 2014) and a faster repair of photosynthetic than hydraulic damage (e.g., Galle and Feller 2007; Posch and Bennett 2009; Creek et al. 2018). We can hypothesize that a faster recovery of A_n has the advantage of supporting increased metabolic demands, which in turn may facilitate hydraulic recovery.

Post-heat recovery

Following heat release, most of the analyzed experimental studies (Table 1) show a delayed recovery of g_s , A_n and PSII (Figure 2b)—similar to observations under post-drought. However, since the number of published studies is relatively low ($n = 7$), we refrain from a detailed differentiation of recovery pace based on heat stress impacts, but discuss critical T thresholds, heat exposure and related metabolic responses. We will further focus on the following question: is delayed leaf gas exchange caused by heat-induced hydraulic impairment, similar to post-drought, or by a feedback mechanism from down-regulated photosynthesis and other metabolic processes?

Hydraulic limitations The few studies on high T responses of plant hydraulics indicate that hydraulic conductance might not be critically affected during conditions of sufficient water supply (Way et al. 2013; McCulloh et al. 2016). An increase in hydraulic conductance with increasing T , as observed (Way et al. 2013), can mitigate leaf T stress by evaporative cooling. However, under combined heat stress and increased vapor pressure deficit (VPD), ψ_{pd} and ψ_{md} have been found to decline to a modest degree (Duarte et al. 2016; Drake et al. 2018), but apparently without implications for hydraulic integrity (e.g., no change in K_{leaf} , Drake et al. 2018). However, at much higher T ($>45^\circ\text{C}$) membranes and living tissues can become severely damaged (Teskey et al. 2015; Birami et al. 2018) and LC_{ox} in leaves and roots should develop. In addition, if heat stress is accompanied by drought, drying accelerates and LC becomes likely. Under these extreme conditions, hydraulic impairment may contribute to a delayed recovery of leaf gas exchange.

Metabolic processes The impact of high T on the C metabolism of plants can be more obvious because photosynthetic and respiratory enzymes and biological membranes respond directly to T changes. There is evidence that the heat-induced down-regulation of A_n caused by increases in photorespiration and reduced activity of Rubisco and PSII is quickly reversible below 40°C (mild stress). However, if T rises above 40°C , longer lasting or permanent impairment of the photosynthetic apparatus via degradation of Rubisco, damage to PSII and thylakoid membranes may develop (Hüve et al. 2011; Teskey et al. 2015). In addition, the degradation of photosynthetic and respiratory capacity may manifest at high T due to increased fluidity and leakiness of cell and organelle membranes (Hazel 1995), and a continued exposure can

Table 1. Overview of experimental studies ($n=20$) reporting post-drought or post-heat recovery dynamics in woody plant gas exchange and hydraulic properties over several days to weeks. Given are plant species, plant functional type (PFT) separated into angiosperm (A) or gymnosperm (G), stress treatment with minimum ψ and PLC (if available), the length of post-stress observation and type of experiment. Recovery is separated in complete and partial recovery; in case of complete recovery (recovery to $> 80\%$ of control/pre-stress values), the length of recovery is given in days (in parentheses). Reported variables are: predawn leaf water potential (ψ_{pd}), midday leaf water potential (ψ_{md}), xylem water potential (ψ_x), stomatal conductance (g_s), leaf-level transpiration (E) plant-level transpiration (E_p), percentage loss in xylem conductivity (LC_x, see Table S1), stem hydraulic conductance (K_{stem}), leaf hydraulic conductance (K_{leaf}), light-saturated leaf-level net photosynthesis (A_n), effective quantum yield of photosystem II ($\Phi PSII$), maximum quantum yield of light-saturated PSII (F_v/F_m), maximum quantum yield of PSII (F_v/F_m), electron transport (J_{max}), basal area growth and leaf area, as well as concentrations of abscisic acid (ABA), non-structural carbohydrates (NSC) and proline.

Species	PFT	Plant age (yr)	Treatment	Complete recovery	Partial recovery	Post-stress length	Type	Reference
<i>Acacia confusa</i>	A	0.2	Drought (ψ_{pd} -0.5 MPa) Drought	ψ_{pd} (1 d), A_n (1 d) ABA (1 d), g_s (1 d) ψ_{pd} (1 d), A_n (3 d)		12 d	Controlled pot experiment	(Liang and Zhang 1999)
<i>Leucaena leucocephala</i>	A	0.2	Drought (ψ_{pd} -1.5 MPa) Drought (ψ_{pd} -1.2 MPa) Drought (ψ_{pd} -1.5 MPa)	ABA (1 d), g_s (3 d) ψ_{pd} (1 d), A_n (10 d) ABA (3 d), g_s (15 d) ψ_{pd} (2 d), A_n (14 d) ABA (3 d), g_s (15 d)		14 d		
<i>Juglans nigra</i> ² , <i>Quercus alba</i> , <i>Q. velutina</i> ² , <i>Salix nigra</i> ² , <i>Populus deltoides</i>	A	0.5	Drought (ψ_{pd} -1 to -2 MPa)	ψ_{pd} (1 d), ψ_{md} (1 d) ABA (2 d), g_s (2-4 d)		11 d	Controlled pot experiment	(Loewenstein and Pallardy 2002)
<i>Fagus sylvatica</i>	A	4	Drought (36 d; ψ_{pd} -2.8 MPa)	ψ_{pd} (1 d), A_n (30 d) F_v/F_m (15 d), $\Phi PSII$ (15 d)	g_s	30 d	Semi-controlled pot experiment	(Galle and Feller 2007)
<i>Quercus pubescens</i>	A	4	Drought (50 d; ψ_{pd} -4 MPa)	ψ_{pd} (1 d), A_n (20 d) g_s (25 d), F_v/F_m (15 d), $\Phi PSII$ (15 d)		30 d	Semi-controlled pot experiment	(Gallé et al. 2007)
<i>Prosopis velutina</i>	A	1 & 4	Drought (ψ_{pd} -1.2 to -2.8 MPa) Drought (ψ_{pd} -3.8 to -5.2 MPa)	A_n , g_s (3-7 d)	A_n , g_s	7 d	Semi-controlled rain-out shelter	(Resco et al. 2009)
<i>Tasmania lanceolata</i> ¹ , <i>Hakea lissosperma</i> ¹ , <i>Lomatia tinctoria</i> ¹ , <i>Atherosperm moschatum</i>	A	3-4	Drought (ψ_{md} -1.8 to -3.8 MPa) Drought (ψ_{md} -2.3 to -7.1 MPa)	ψ_{md} (2 d), E_p (8-12 d), K_{leaf} (6-12 d) ψ_{md} (2-10 d)	E_p , K_{leaf}	25-40 d	Controlled pot experiment	(Blackman et al. 2009)

Continued

Table 1. Continued.

Species	PFT	Plant age (years)	Treatment	Complete recovery	Partial recovery	Post-stress length	Type	Reference
<i>Allocauarina luehmannii</i>	A	1	Drought (36 d; ψ_{pd} -1.2 MPa) Drought (61 d; ψ_{pd} -6.2 MPa)	ψ_{pd} (1 d), ψ_{md} (1 d), g_s (10 d), A_n (10 d) ψ_{pd} (20 d), ψ_{md} (20 d), A_n (20 d), $\Phi PSII$ (10 d), F_v/F_m (20 d) ψ_{md} (1 d), E_p (3 d) K_{leaf} (5 d) ψ_{md} (16 d), E_p (21 d) K_{leaf} (21 d)	g_s , F_v/F_m	22 d	Controlled pot experiment	(Posch and Bennett 2009)
<i>Lagarostrobos franklinii</i>	G	3–5	Drought (ψ_{md} -2 MPa) Drought (ψ_{md} -3.5 MPa)	ψ_{md} (1 d), E_p (3 d) K_{leaf} (5 d) ψ_{md} (16 d), E_p (21 d) K_{leaf} (21 d)		25 d	Controlled pot experiment	(Brodribb and Cochard 2009)
<i>Callitris columellaris</i> , most resistant	G	3–5	Drought ψ_{md} -10 MPa, LC_x <10%	ψ_{md} (3 d), E_p (25 d) basal area (20 d)		80 d	Controlled pot experiment	(Brodribb et al. 2010)
<i>Callitris rhomboidea</i> , least resistant	G	3–5	Drought ψ_{md} -10 MPa, LC_x >80%		ψ_{md} , E_p basal area growth			
<i>Hevea brasiliensis</i>	A	2	Drought ψ_x -3 MPa	ψ_x (3 d), g_s (5 d), K_{leaf} (3 d), NSC^3	A_n	5 d	Controlled pot experiment	(Chen et al. 2010)
<i>Eucalyptus pauciflora</i>	A	2	Drought ψ_x -2.7 MPa, LC_x ~80%	ψ_x (6 h), K_{stem} (6 h), A_n (10 d)	E , g_s	10 d	Controlled pot experiment	(Martorell et al. 2014)
<i>Eucalyptus pauciflora</i> / <i>E. dumosa</i>	A	0.5	Drought 53 d; ψ_{pd} -1.5 / -2.4 MPa Drought 53 d; ψ_{pd} -2.8 / -4 MPa	ψ_{pd} (1 d), g_s (14 d) g_m (14 d), A_n (14 d) ψ_{pd} (1 d), g_s (24 d) g_m , A_n (14 d)	g_s (<i>E. dumosa</i>) g_s (<i>E. dumosa</i>)	24 d	Controlled pot experiment	(Cano et al. 2014)
<i>Olea europea</i>	A	1	Drought ψ_{pd} -3.5 MPa, LC_x ~30%	ψ_{pd} , ψ_{md} (1 d), K_{leaf} , (1 d), ABA (1 d) A_n (10-20 d), $PSII$ (20-30 d)	g_s	6 d	Controlled pot experiment	(Torres-Ruiz et al. 2015a)
<i>Fagus sylvatica</i> (different provenances)	A	3	Drought ψ_{pd} -1.8 MPa	ψ_{pd} & ψ_{md} (1 d) K_{stem} (7 d), NSC^4		90 d	Semi-controlled mesocosms	(Arend et al. 2016)
<i>Laurus nobilis</i>	A	2	Drought (90 d) ψ_{pd} -1.0, ψ_{md} -2.7 MPa Drought (20 d)	ψ_{pd} & ψ_{md} (1 d) K_{stem} (7 d), NSC^4 ψ_{pd} , ψ_{md} & K_{stem} (1 d) g_s & A_n (7 d), NSC^5	g_s , A_n	7 d	Controlled pot experiment	(Trifilò et al. 2017)
<i>Robinia pseudoacacia</i>	A	2	Drought ψ_{pd} -3 MPa	ψ_{pd} (3 d), g_s (7 d) E (5 d), A_n (5 d)		7 d	Semi-controlled pot experiment	(Yan et al. 2017)
<i>Amorpha fruticosa</i> ¹	A	2	Drought ψ_{pd} -3.2 MPa	ψ_{pd} (3 d), A_n (5 d)	E , g_s			

Continued

Table 1. Continued.

Species	PFT	Plant age (years)	Treatment	Complete recovery	Partial recovery	Post-stress length	Type	Reference
<i>Acacia aneura</i>			Drought	Ψ_{md} (1 d)	$g_s, K_{leaf}, K_{root}, K_{stem}$	30 d	Controlled pot experiment	(Creek et al. 2018)
<i>Eucalyptus coolabah</i>			Ψ_{md} -9.1 MPa, LC_x 67%	E (14 d), A_n (14 d)				
			Drought	Ψ_{md} (3 d)	$g_s, K_{leaf}, K_{root}, K_{stem}$			
<i>Eucalyptus populnea</i>			Ψ_{md} -6.6 MPa, LC_x 35%	E (30 d), A_n (30 d)				
			Drought	Ψ_{md} (30 d)	$g_s, K_{leaf}, K_{root}, K_{stem}$			
<i>Quercus macrocarpa</i> , <i>Q. muehlenbergii</i>	A	mature	Ψ_{md} -7.5 MPa, LC_x 63%	E (30 d), A_n (30 d)	A_n, g_s	7 d	Field, controlled leaf temperature	(Hamerlynck and Knapp 1996)
<i>Pinus taeda</i>	G	0.5	Heatwaves (45–50°C) 3 x 7 d	A_n (4 d), F_v'/F_m' (4 d), $\Phi PSII$ (4 d)			Controlled pot experiment	(Ameye et al. 2012)
<i>Quercus rubra</i>	A	4	Heatwaves (45–50°C)	E (1 d), F_v'/F_m' (-)	$A_n, PSII$			
<i>Pseudotsuga menziesii</i>	G	4	Heatwaves (32–45°C) 2 x 14 d	g_s (10 d), E (2 d), A_n (2d) basal area ⁶ (7 d)		10/90 d	Controlled pot experiment	(Ruehr et al. 2016)
			Heatw. & drought	A_n (2d), basal area ⁶ (7 d)	g_s, E			
<i>Robinia pseudoacacia</i>	A	4	Heatwaves 2 x 14 d		g_s, E, A_n , leaf area, basal a. growth ⁶			
			Heatw. & drought		g_s, E, A_n , leaf area, basal a. growth ⁶			
<i>Pseudotsuga menziesii</i>	G	5	Heatwaves (34–43°C) 3 x 14 d (2 nd year)	ψ_{pd} (1 d)	$g_s, A_n, g_{min}, I_{max}$	45 d	Controlled pot experiment	(Duarte et al. 2016)
			(ψ_{md} -2 MPa)					
<i>Eucalyptus parramattensis</i>	A	c. 1	Heatwave (40–44°C) 1 x 4 d	E (1 d), A_n (1 d)		1 d	Field, controlled chambers	(Drake et al. 2018)
			(ψ_{md} -1.8 MPa)	K_{leaf} (-), basal area (-)				
<i>Pinus halepensis</i>	G	0.8	Heatwaves (38–42°C) 2 x 4 d	g_s (8 d), A_n (7 d) NSC (< 20 d)		20 d	Controlled pot experiment	(Birami et al. 2018)
			(ψ_{md} -1.2 MPa) heatw. & drought		g_s, A_n, NSC			
			(ψ_{md} -1.8 MPa)					

¹Shrubs.²only ABA values reported.³leaf NSC and proline concentrations remain elevated.⁴stem NSC soluble sugars decrease, starch remains elevated.⁵stem NSC no change in concentration between drought and recovery.⁶post-stress observation for 90 d.

cause permanent damage to leaf tissues including leaf necrosis (Colombo and Timmer 1992; Hüve et al. 2011).

The thermotolerance of leaf metabolism can provide a marker to identify when critical stress thresholds are passed. Recently it has been shown that the critical leaf T at which PSII becomes disrupted (T_{crit}) occurs between 41.5 and 50.8 °C globally, with higher T tolerance in warmer climates (O'Sullivan et al. 2017). The onset of T_{crit} (or T_{50} as used by others, Curtis et al. 2014; Drake et al. 2018) refers to the critical stress value, S_{rep} , which indicates that photosynthetic recovery will be delayed and dependent on repair mechanisms (Curtis et al. 2014). At ~ 10 °C above T_{crit} , respiration rates start to decline, reflecting loss of mitochondrial function and beginning tissue death (O'Sullivan et al. 2017). However, several factors may influence the thermotolerance of tissues during heatwaves including preconditioning through a priori synthesis of heat shock proteins (Teskey et al. 2015), emissions of volatile organic compounds (Brunetti et al. 2014; Sharkey and Monson 2017), leaf cooling (Birami et al. 2018; Drake et al. 2018) and heat exposure time (Colombo and Timmer 1992).

Leaf cooling and heat exposure are critical factors that need further consideration. Under conditions of well-water supply, leaf cooling is sufficient to prevent leaves from heating above air T (Drake et al. 2018). However, when water supply becomes limiting stomata close and leaves can heat up. A 2–3 °C increase in leaf T between well-watered and water-limited trees during a heatwave can trigger substantial damage and delays gas exchange recovery (Birami et al. 2018). Heat exposure or heat dosage is another important aspect determining heat impacts. There is clear evidence that the same damage to leaf tissues can manifest at lower T but longer exposure (e.g., 50% needle damage from 50 min at 46 °C or from 10 min at 50 °C; Colombo and Timmer 1992). In the stress-recovery studies synthesized here, the length and the frequency of the heatwaves differed strongly (Table 1). After a single heatwave of 4 days (T_{max} c. 43–44 °C), A_n recovered immediately in *Eucalyptus* trees (Drake et al. 2018), while following three heatwaves of 7 days each (T_{max} c. 47–52 °C), A_n recovery took ~ 4 days in loblolly pine and much longer in northern red oak (Ameje et al. 2012). Delayed recovery was even more pronounced following three heatwaves of 14 days each (T_{max} c. 38–43 °C), when A_n did not recover in Douglas-fir seedlings within 2 months (Duarte et al. 2016). In both studies in which delayed A_n recovery has been reported, heat stress resulted in an impairment of the photosynthetic apparatus (Ameje et al. 2012; Duarte et al. 2016). This shows that post-heat recovery depends on stress impacts, which are mainly triggered by heat dosage, leaf T thresholds and T preconditioning.

After critical T levels have been passed, leaf gas exchange recovery is closely linked to the repair of photosynthetic and metabolic processes (Ameje et al. 2012; Duarte et al. 2016; Birami et al. 2018). This observation, together with an absence

of hydraulic impairment (Duarte et al. 2016; Drake et al. 2018), indicates that A_n and g_s recovery is largely metabolically limited. The most probable scenario is that the repair of the photosynthetic machinery and other cell and organelle membranes is constrained by reduced energy, carbohydrate (Birami et al. 2018) and/or nutrient availability (Gessler et al. 2017). Moreover, other metabolic processes, such as leaf sugar accumulation, caused by impaired phloem loading or low sink activities can pose additional limitations (Fatichi et al. 2014).

Repair and growth post-stress

Recovery from moderate and severe stress involves energy demanding repair processes. However, C assimilation is initially low following stress release, therefore remobilization of plant C resources, particular NSCs, and its allocation via phloem transport is a critical process during recovery. The few studies that have investigated post-drought carbohydrate concentrations report NSC fractions to decline in leaves (Chen et al. 2010; Hagedorn et al. 2016; Yang et al. 2016), roots (Yang et al. 2016) and woody stems (Tomasella et al. 2017). These observations are in accordance to NSCs being consumed post-drought to support repair and regrowth. Such a clear pattern, does not always emerge, and different responses among tissues and NSC compounds have been found (Galiano et al. 2017; Yan et al. 2017; Pflug et al. 2018). These differences could be species-specific, a result of the different stress intensities applied and their implications for phloem transport or the timing when NSCs are measured post-stress. Next we will discuss experimental evidence and possible underlying mechanisms that determine C availability for repair and regrowth post-stress. We will mainly focus on drought recovery, as very little information exists on growth and NSC levels post-heat.

Energy and C supply from NSCs and other C storage compounds should be particularly critical in plants that have been severely damaged (Figure 1) and is for example required to produce new leaves after drought-induced senescence (Newell et al. 2002; Sala et al. 2012). In addition, readily available NSCs might contribute to recover hydraulic function and could be involved in the refilling of embolized conduits (Clearwater and Goldstein 2005; Brodersen and McElrone 2013; Tomasella et al. 2017) or support the rebuilding of new functional xylem tissue. However, direct evidence for the role of NSCs during recovery is still scarce. More evidence has been collected for NSC dynamics during drought and persisting long-term droughts are frequently associated with lower NSC levels (in particular non-osmotic starch) and larger declines in roots than shoots (Adams et al. 2017; Yan et al. 2017), because phloem transport might be impaired (Ruehr et al. 2009). Similar observations of NSC dynamics have been made during heat stress when C uptake was reduced (Birami et al. 2018). Such stress-induced reductions in NSCs and other C reserve compounds (e.g., lipids)

may limit post-stress repair processes (Trifilò et al. 2017; Birami et al. 2018).

To identify patterns of NSC dynamics post-stress, we need to consider that NSCs fulfill roles other than purely metabolic C supply. Soluble sugars, typically the largest fraction of NSCs (Hartmann and Trumbore 2016), are important compounds for plant signaling and osmoregulation especially during drought conditions. Following rewetting and subsequent recovery of ψ_{md} , the leaf osmotic potential should increase, while sugar concentrations may decrease (Salmon et al. 2015). Such a transition can be gradual, as found in rubber trees recovering from drought, where leaf proline—an osmoprotectant—decreased alongside leaf sugar concentrations over several days (Chen et al. 2010). Hence, sugars not needed to maintain a low osmotic potential could either be transformed to storage pools (Galiano et al. 2017) to prepare for future stress events, or could be allocated to leaves (Zang et al. 2014) and roots (Hagedorn et al. 2016) for repair and regrowth. Interestingly, these studies further show that—after photosynthesis had sufficiently recovered—recent assimilates contributed mostly to respiration, an indication of the important role of recent C for restoring plant function following mild to moderate drought (Zang et al. 2014; Hagedorn et al. 2016). In contrast, following severe stress events and slow A_n recovery, we may expect NSC and other storage compounds to be heavily consumed to support repair and regrowth (Figure 1c).

Under the proposed framework, regrowth of dysfunctional or lost tissue is a prerequisite to regain full function once persisting damage has occurred. Fast upregulation of growth could be particularly critical after functional tissues have been lost. For instance, stem growth can contribute significantly to hydraulic recovery via xylem formation (Brodribb et al. 2010). In contrast, delayed leaf formation can improve the ratio of supporting xylem to leaf area and thus result in a better sapwood-to-leaf ratio and higher leaf-specific conductance (Chen et al. 2010). Despite its overall importance in understanding plant recovery following severe stress, studies reporting growth dynamics post-stress are relatively scarce, and responses have been reported from fast, overcompensating to slow growth recovery (Olesinski et al. 2011; Ruehr et al. 2016; O'Brien et al. 2017). Delayed growth recovery has been found to be more distinct following extreme drought episodes. Reductions in root growth (Olesinski et al. 2011), tree height (Montwé et al. 2014) and tree diameter (Sergent et al. 2014; Anderegg et al. 2015b) have been observed in mature trees until growth rates may recover years later. Such persisting reductions in secondary growth have also been linked to lagged mortality in mature trees post-drought (Berdanier and Clark 2016). An underlying mechanism of declining growth and eventually death could involve the depletion of NSC resources until C demand exceeds C reserves and supply, and hence maintenance respiration can no longer be sustained.

Ways forward: modeling and future research directions

Post-stress modeling and C cost of recovery

Current regional- and global-scale vegetation models have a relatively coarse view on C and water dynamics in plants and are only beginning to describe plant hydraulic processes (Xu et al. 2016; Kennedy et al. 2019). In addition, these models do not address stress-related functional impairment and/or irreversible damage and the recovery of plant metabolic and hydraulic systems. A recently developed recovery model at the tree scale links hydraulic damage and leaf loss to tree C gain and illustrates that both, hydraulic damage and available NSCs impact recovery rate (Trugman et al. 2018). Under this recovery framework the dynamics of post-stress NSCs are directly linked to the degree of hydraulic damage (Figure 4), because damaged trees must divert C stores to grow new functional xylem, which in turn restores whole-plant photosynthetic capacity. However, if NSC levels fall below a certain threshold, trees are unable to support xylem growth any longer and subsequently cannot meet respiratory demands and die. Because respiratory demands of cambium and phloem are lower in smaller trees, they are able to recover from greater LC_x than larger trees. Apart from such tree size-specific differences, there is a fixed C cost involved

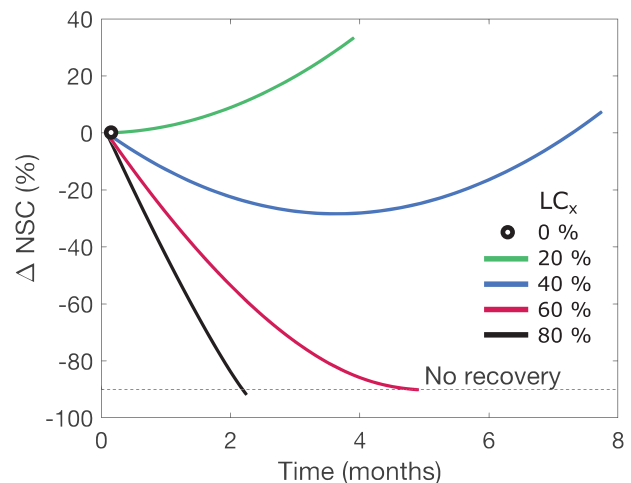


Figure 4. Relative changes in tree NSC content and duration of recovery following release from different drought intensities. The NSC dynamics under increasing loss of xylem conductance (LC_x) were derived from a post-drought recovery model (Trugman et al. 2018) for trees with a diameter at breast height of 10 cm. The model assumes that NSCs (here starch) are allocated to support regrowth of drought-damaged xylem. Note that recovery is instant after mild drought with no loss of hydraulic conductance ($LC_x = 0\%$; open circle). Following moderate drought ($LC_x = 20\%$; light green line), NSC levels can increase after drought release, because photosynthesis is sufficient to support regrowth of functional xylem. However, recovery following severe drought ($LC_x \geq 40\%$) results in heavy depletion of NSCs, as reduced photosynthesis is not efficient to support regrowth of large xylem areas. If NSC levels are depleted below 10% (intermittant gray line), recovery is assumed to fail and the tree dies.

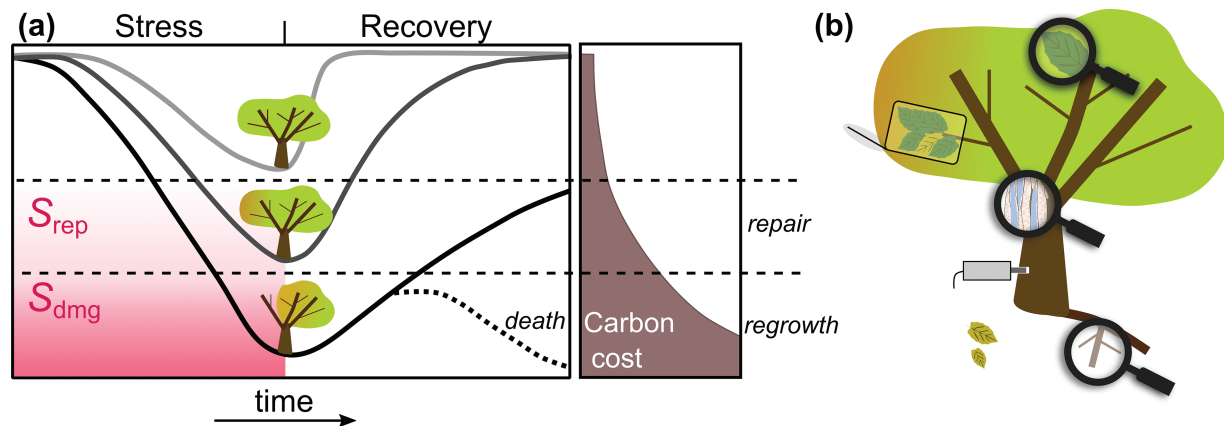


Figure 5. Exemplary stress and recovery trajectories related to C costs and measurements of sensitive tissues and processes. (a) Possible scenarios of plant performance related to the overall plant C cost during intensifying stress and post-stress recovery. (b) Experimental measurements to link post-stress recovery performance to the C cost of repair and regrowth; magnifying glasses highlight sensitive tissues and processes that should be assessed for changes in NSC, hydraulic conductance and other damages.

with tissue damage in the model proposed by Trugman et al. (2018). However, as discussed throughout this review, there is a wide spectrum of functional impairment and damage severity that may be less costly than tissue replacement. These are typically reversible damages (e.g., LC_{ox} , photosynthetic impairment, protein degradation) and the time needed for recovery should scale with the degree of impairment and repair efficiency. Thus, future model development should consider the overall C cost related to a variety of stress-induced changes in functionality and increasing costs involved when certain stress levels are passed (Figure 5a). To put such a concept in mechanistic terms, the C costs of stress impacts at the tissue level need to be quantified in relation to recovery strategies and rates.

Future research agenda

In order to achieve a more mechanistic understanding of post-stress recovery as a platform for model development, we would like to highlight three promising research directions: (i) the relationship of individual stress impacts and recovery rates, (ii) the C cost of stress and recovery and (iii) the impact of post-event conditions on recovery dynamics. We will discuss these research suggestions mainly focusing on controlled experiments, but also highlight the need for manipulative field studies. Combining studies under controlled conditions with field experiments and observations provides a well-founded base for interpreting complex post-stress recovery dynamics at a mature tree or forest level.

Based on our suggested framework, three important stress-recovery indicators are photosynthetic impairment, LC and leaf vitality (i.e., necrosis or senescence). These stress markers are not all-inclusive, but will facilitate comparison of stress impacts and recovery among studies if routinely measured. Considering heat stress impacts, the degree of photosynthetic impairment (e.g., inferred from fluorescence parameters or $A-C_i$ curves)

and/or leaf damage should be related to leaf T and heat dosage. Dealing with drought or combined heat–drought stress, knowledge on LC_{ox} (e.g., estimated from changes in K_{leaf} before turgor loss) and/or LC_x are key. Drought-induced LC_x can be inferred from literature values (e.g., Martin-StPaul et al. 2017) or directly measured from cut branches (Sperry et al. 1988). The cutting artifact (i.e., artificial increase in embolism when xylem is cut under tension) remains a lingering problem (Wheeler et al. 2013) and methods need to be adapted accordingly, in particular when dealing with long-vesselled species (Torres-Ruiz et al. 2015b). Here, novel optical techniques can provide helpful cross-validation (Choat et al. 2015; Brodribb et al. 2016). Following stress release, the derived stress indicators need to be linked to recovery rates. Here E , g_s or A_n provide diagnostic recovery metrics and half-life times ($t_{1/2}$) inform on recovery rates (Brodribb and Cochard 2009; Li et al. 2016).

Another research focus is the C cost of stress and recovery (Figure 5a), which particularly involves understanding C allocation towards repair and regrowth. To tackle this, experiments considering tissue respiration alongside changes in C input (A_n , Figure 5b), C storage (e.g., NSC, lipids) and biomass are needed. Cross-comparisons among studies are facilitated if similar set-ups and methods are used. For instance, tissue NSC concentrations ought to be measured in accordance to standardized procedures (Landhäusser et al. 2018). Another strategy is to quantify changes in basal area increment via high-resolution dendrometers (accounting for water dynamics), which informs on structural C investments towards regaining hydraulic functioning. Root growth dynamics are often neglected and are challenging to measure, but are definitely needed to complete the picture on C allocation and hydraulic recovery.

With regard to interpreting field observations, we need to understand the influence of environmental conditions on recovery performance. For instance, while soil rehydration occurs

immediately in controlled pot experiments and other abiotic conditions are favorable, this is rarely the case in natural environments. In fact, we know next to nothing about the influence of environmental conditions on recovery success. Besides water availability, other potential abiotic drivers of recovery rates are temperature, VPD (Trugman et al. 2018), soil nutrients (Gessler et al. 2017) and atmospheric [CO₂] (Hamerlynck et al. 2000). The influence of these factors on recovery performance has to be considered via multi-factorial experiments. In the long term, the mechanistic insights gained from studying stress resilience in potted seedlings need to be tailored towards an understanding of mature tree and forest responses. Therefore, addressing both seedling and mature tree recovery under field conditions are necessary follow-up steps. Overall, such experiments are complex and demand collaborative efforts between research labs.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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References

- Adams HD, Zeppel MJB, Anderegg WRL et al. (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nat Ecol Evol* 1:1285–1291.
- Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:1–55.
- Ameye M, Wertin TM, Bauweraerts I, McGuire MA, Teskey RO, Steppe K (2012) The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO₂ atmospheres. *New Phytol* 196:448–461.
- Anderegg WRL, Hicke JA, Fisher RA et al. (2015a) Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol* 208:674–683.
- Anderegg WRL, Schwalm C, Biondi F et al. (2015b) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349:528–532.
- Arend M, Sever K, Pflug E, Gessler A, Schaub M (2016) Seasonal photosynthetic response of European beech to severe summer drought: limitation, recovery and post-drought stimulation. *Agric For Meteorol* 220:83–89.
- Bartlett MK, Klein T, Jansen S, Choat B, Sack L (2016) The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. *Proc Natl Acad Sci USA* 113:13098–13103.
- Berdanier AB, Clark JS (2016) Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests. *Ecol Appl* 26:17–23.
- Birami B, Gattmann M, Heyer AG, Grote R, Arneith A, Ruehr NK (2018) Heat waves alter carbon allocation and increase mortality of Aleppo pine under dry conditions. *Front For Glob Change* 1:1–17.
- Blackman CJ, Brodribb TJ, Jordan GJ (2009) Leaf hydraulics and drought stress: response, recovery and survivorship in four woody temperate plant species. *Plant Cell Environ* 32:1584–1595.
- Brodersen CR, McElrone AJ (2013) Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Front Plant Sci* 4:108.
- Brodribb TJ, Cochard H (2009) Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiol* 149:575–584.
- Brodribb TJ, McAdam SAM (2013) Abscissic acid mediates a divergence in the drought response of two conifers. *Plant Physiol* 162:1370–1377.
- Brodribb TJ, Bowman DJMS, Nichols S, Delzon S, Burlett R (2010) Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytol* 188:533–542.
- Brodribb TJ, Skelton RP, McAdam SAM, Bienaimé D, Lucani CJ, Marmottant P (2016) Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. *New Phytol* 209:1403–1409.
- Brunetti C, Ferrini F, Fini A, Tattini M (2014) New evidence for the functional roles of volatile and non-volatile isoprenoids in stressed plants. *Agrochimica* 58:61–76.
- Cano FJ, López R, Warren CR (2014) Implications of the mesophyll conductance to CO₂ for photosynthesis and water-use efficiency during long-term water stress and recovery in two contrasting eucalyptus species. *Plant Cell Environ* 37:2470–2490.
- Charra-Vaskou K, Badel E, Burlett R, Cochard H, Delzon S, Mayr S (2012) Hydraulic efficiency and safety of vascular and non-vascular components in *Pinus pinaster* leaves. *Tree Physiol* 32:1161–1170.
- Chen J-W, Zhang Q, Li X-S, Cao K-F (2010) Gas exchange and hydraulics in seedlings of *Hevea brasiliensis* during water stress and recovery. *Tree Physiol* 30:876–885.
- Choat B, Brodersen CR, McElrone AJ (2015) Synchrotron X-ray microtomography of xylem embolism in *Sequoia sempervirens* saplings during cycles of drought and recovery. *New Phytol* 205:1095–1105.
- Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE (2018) Triggers of tree mortality under drought. *Nature* 558:531–539.
- Ciais P, Reichstein M, Viovy N et al. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–533.
- Clearwater MJ, Goldstein G (2005) Embolism repair and long distance water transport. In: Holbrook MN, Zwieniecki MA (eds) *Vascular transport in plants*. Elsevier Academic Press Burlington, MA, USA, pp 375–399.
- Colombo SJ, Timmer VR (1992) Limits of tolerance to high temperatures causing direct and indirect damage to black spruce. *Tree Physiol* 11:95–104.

- Creek D, Blackman Chris J, Brodribb TJ, Choat B, Tissue DT (2018) Coordination between leaf, stem, and root hydraulics and gas exchange in three arid-zone angiosperms during severe drought and recovery. *Plant Cell Environ* 41:2869–2881.
- Cuneo IF, Knipfer T, Brodersen CR, McElrone AJ (2016) Mechanical failure of fine root cortical cells initiates plant hydraulic decline during drought. *Plant Physiol* 172:1669–1678.
- Curtis EM, Knight CA, Petrou K, Leigh A (2014) A comparative analysis of photosynthetic recovery from thermal stress: a desert plant case study. *Oecologia* 175:1051–1061.
- Drake JE, Tjoelker MG, Vårhammar A et al. (2018) Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. *Glob Chang Biol* 24:2390–2402.
- Duarte AG, Katata G, Hoshika Y, Hossain M, Kreuzwieser J, Arneth A, Ruehr NK (2016) Immediate and potential long-term effects of consecutive heat waves on the photosynthetic performance and water balance in Douglas-fir. *J Plant Physiol* 205:57–66.
- Fatichi S, Leuzinger S, Körner C (2014) Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *New Phytol* 201:1086–1095.
- Flexas J, Medrano HH (2002) Drought-inhibition of photosynthesis in C3 plants: Stomatal and non-stomatal limitations revisited. *Ann Bot* 89:183–189.
- Flexas J, Ribas-Carbó M, Diaz-Espejo A, Galmés J, Medrano H (2008) Mesophyll conductance to CO₂: current knowledge and future prospects. *Plant Cell Environ* 31:602–621.
- Galiano L, Timofeeva G, Saurer M, Siegwolf R, Martínez-Vilalta J, Hommel R, Gessler A (2017) The fate of recently fixed carbon after drought release: towards unravelling C storage regulation in *Tilia platyphyllos* and *Pinus sylvestris*. *Plant Cell Environ* 40:1711–1724.
- Gallé A, Haldemann P, Feller U (2007) Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. *New Phytologist* 174:799–810.
- Galle A, Feller U (2007) Changes of photosynthetic traits in beech saplings (*Fagus sylvatica*) under severe drought stress and during recovery. *Physiol Plant* 131:412–421.
- Gessler A, Schaub M, McDowell NG (2017) The role of nutrients in drought-induced tree mortality and recovery. *New Phytol* 214:513–520.
- Hagedorn F, Joseph J, Peter M et al. (2016) Recovery of trees from drought depends on belowground sink control. *Nat Plants* 2:16111.
- Hamerlynck EP, Huxman TE, Loik ME, Smith SD (2000) Effects of extreme high temperature, drought and elevated CO₂ on photosynthesis of the Mojave Desert evergreen shrub, *Larrea tridentata*. *Plant Ecol* 148:183–193.
- Hamerlynck EP, Knapp AK (1996) Photosynthetic and stomatal responses to high temperature and light in two oaks at the western limit of their range. *Tree Physiology* 16:557–565.
- Hartmann H, Trumbore S (2016) Understanding the roles of nonstructural carbohydrates in forest trees - from what we can measure to what we want to know. *New Phytol* 211:386–403.
- Hazel JR (1995) Thermal adaptation in biological membranes: is homeoviscous adaptation the explanation? *Annu Rev Physiol* 57:19–42.
- He B, Liu J, Guo L, Wu X, Xie X, Zhang Y, Chen C, Zhong Z, Chen Z (2018) Recovery of ecosystem carbon and energy fluxes from the 2003 drought in Europe and the 2012 drought in the United States. *Geophys Res Lett* 45:4879–4888.
- Hüve K, Bichele I, Rasulov B, Niinemets Ü (2011) When it is too hot for photosynthesis: heat-induced instability of photosynthesis in relation to respiratory burst, cell permeability changes and H₂O₂ formation. *Plant Cell Environ* 34:113–126.
- Ingrisch J, Bahn M (2018) Towards a comparable quantification of resilience. *Trends Ecol Evol* 33:251–259.
- Kennedy D, Swenson S, Oleson KW, Lawrence DM, Fisher R, Lola da Costa AC, Gentile P (2019) Implementing plant hydraulics in the community land model, version 5. *J Adv Model Earth Syst*.
- Landhäusser SM, Chow PS, Dickman LT et al. (2018) Standardized protocols and procedures can precisely and accurately quantify non-structural carbohydrates. *Tree Physiol* 38:1764–1778.
- Laur J, Hacke UG (2014) Exploring *Picea glauca* aquaporins in the context of needle water uptake and xylem refilling. *New Phytol* 203:388–400.
- Li S, Feifel M, Karimi Z, Schuldt B, Choat B, Jansen S (2016) Leaf gas exchange performance and the lethal water potential of five European species during drought. *Tree Physiol* 36:179–192.
- Liang J, Zhang J (1999) The relations of stomatal closure and reopening to xylem ABA concentration and leaf water potential during soil drying and rewatering. *Plant Growth Regul* 29:77–86.
- Limousin JM, Misson L, Lavoie A-V, Martin NK, Rambal S (2010) Do photosynthetic limitations of evergreen *Quercus ilex* leaves change with long-term increased drought severity? *Plant Cell Environ* 33:863–875.
- Lo Gullo MA, Nardini A, Trifilò P, Salleo S (2003) Changes in leaf hydraulics and stomatal conductance following drought stress and irrigation in *Ceratonia siliqua* (carob tree). *Physiol Plant* 117:186–194.
- Loewenstein NJ, Pallardy SG (2002) Influence of a drying cycle on post-drought xylem sap abscisic acid and stomatal responses in young temperate deciduous angiosperms. *New Phytol* 156:351–361.
- Martin-StPaul N, Delzon S, Cochard H (2017) Plant resistance to drought depends on timely stomatal closure. *Ecol Lett* 20:1437–1447.
- Martorell S, Diaz-Espejo A, Medrano H, Ball MC, Choat B (2014) Rapid hydraulic recovery in *Eucalyptus pauciflora* after drought: linkages between stem hydraulics and leaf gas exchange. *Plant Cell Environ* 37:617–626.
- McCulloh KA, Petitmermet J, Stefanski A, Rice KE, Rich RL, Montgomery RA, Reich PB (2016) Is it getting hot in here? Adjustment of hydraulic parameters in six boreal and temperate tree species after 5 years of warming. *Glob Chang Biol* 22:4124–4133.
- Meinzer FC, McCulloh KA (2013) Xylem recovery from drought-induced embolism: where is the hydraulic point of no return? *Tree Physiol* 33:331–334.
- Meinzer FC, Johnson DM, Lachenbruch B, McCulloh KA, Woodruff DR (2009) Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Funct Ecol* 23:922–930.
- Meyer E, Aspinwall MJ, Lowry DB, Palacio-Mejia JD, Logan TL, Fay PA, Juenger TE (2014) Integrating transcriptional, metabolomic, and physiological responses to drought stress and recovery in switchgrass (*Panicum virgatum* L.). *BMC Genomics* 15:527.
- Miyashita K, Tanakamaru S, Maitani T, Kimura K (2005) Recovery responses of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. *Environ Exp Bot* 53:205–214.
- Montwé D, Spiecker H, Hamann A (2014) An experimentally controlled extreme drought in a Norway spruce forest reveals fast hydraulic response and subsequent recovery of growth rates. *Trees* 28:891–900.
- Nardini A, Gullo MAL, Salleo S (2011) Refilling embolized xylem conduits: is it a matter of phloem unloading? *Plant Sci* 180:604–611.
- Newell EA, Mulkey SS, Wright JS (2002) Seasonal patterns of carbohydrate storage in four tropical tree species. *Oecologia* 131:333–342.

- O'Brien MJ, Ong R, Reynolds G (2017) Intra-annual plasticity of growth mediates drought resilience over multiple years in tropical seedling communities. *Glob Chang Biol* 4235–4244.
- Olesinski J, Lavigne MB, Krasowski MJ (2011) Effects of soil moisture manipulations on fine root dynamics in a mature balsam fir (*Abies balsamea* L. Mill.) forest. *Tree Physiol* 31:339–348.
- O'Sullivan OS, Heskell MA, Reich PB et al. (2017) Thermal limits of leaf metabolism across biomes. *Glob Chang Biol* 23:209–223.
- Pflug EE, Buchmann N, Siegwolf RTW, Schaub M, Rigling A, Arend M (2018) Resilient leaf physiological response of European beech (*Fagus sylvatica* L.) to summer drought and drought release. *Front Plant Sci* 9:1–11.
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30–50.
- Posch S, Bennett LT (2009) Photosynthesis, photochemistry and antioxidative defence in response to two drought severities and with re-watering in *Allocasuarina luehmannii*. *Plant Biol* 11:83–93.
- Resco V, Ewers BE, Sun W, Huxman TE, Weltzin JF, Williams DG (2009) Drought-induced hydraulic limitations constrain leaf gas exchange recovery after precipitation pulses in the C3 woody legume, *Prosopis velutina*. *New Phytologist* 181:672–682.
- Ruehr NK, Offermann CA, Gessler A, Winkler JB, Ferrio JP, Buchmann N, Barnard RL (2009) Drought effects on allocation of recent carbon: from beech leaves to soil CO₂ efflux. *New Phytol* 184:950–961.
- Ruehr NK, Gast A, Weber C, Daub B, Arneith A (2016) Water availability as dominant control of heat stress responses in two contrasting tree species. *Tree Physiol* 36:164–178.
- Sack L, Buckley TN, Scoffoni C (2016) Why are leaves hydraulically vulnerable? *J Exp Bot* 67:4917–4919.
- Sala A, Woodruff DR, Meinzer FC (2012) Carbon dynamics in trees: feast or famine? *Tree Physiol* 32:764–775.
- Salmon Y, Torres-Ruiz J, Poyatos R, Martinez-Vilalta J, Meir P, Cochard H, Mencuccini M (2015) Balancing the risks of hydraulic failure and carbon starvation: a twig scale analysis in declining scots pine. *Plant Cell Environ* 38:2575–2588.
- Schwalm CR, Anderegg WRL, Michalak AM et al. (2017) Global patterns of drought recovery. *Nature* 548:202–205.
- Scoffoni C, McKown AD, Rawls M, Sack L (2012) Dynamics of leaf hydraulic conductance with water status: quantification and analysis of species differences under steady state. *J Exp Bot* 63:643–658.
- Scoffoni C, Albuquerque C, Brodersen C, Townes SV, John GP, Bartlett MK, Buckley TN, McElrone AJ, Sack L (2017) Outside-xylem vulnerability, not xylem embolism, controls leaf hydraulic decline during dehydration. *Plant Physiol* 173:1197–1210.
- Sergent A-S, Rozenberg P, Bréda N (2014) Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. *Ann For Sci* 71:697–708.
- Sharkey TD, Monson RK (2017) Isoprene research - 60 years later, the biology is still enigmatic. *Plant Cell Environ* 40:1671–1678.
- Skelton RP, Brodribb TJ, McAdam SAM, Mitchell PJ (2017) Gas exchange recovery following natural drought is rapid unless limited by loss of leaf hydraulic conductance: evidence from an evergreen woodland. *New Phytol* 215:1399–1412.
- Sperry J, Donnelly J, Tyree M (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ* 11:35–40.
- Teskey R, Wertin T, Bauweraerts I, Ameye M, McGuire MA, Steppe K (2015) Responses of tree species to heat waves and extreme heat events. *Plant Cell Environ* 38:1699–1712.
- Tomasella M, Häberle K-H, Nardini A, Hesse B, Machlet A, Matyssek R (2017) Post-drought hydraulic recovery is accompanied by non-structural carbohydrate depletion in the stem wood of Norway spruce saplings. *Sci Rep* 7:1–13.
- Torres-Ruiz JM, Diaz-Espejo A, Perez-Martin A, Hernandez-Santana V (2015a) Role of hydraulic and chemical signals in leaves, stems and roots in the stomatal behaviour of olive trees under water stress and recovery conditions. *Tree Physiol* 35:415–424.
- Torres-Ruiz JM, Jansen S, Choat B et al. (2015b) Direct x-ray microtomography observation confirms the induction of embolism upon xylem cutting under tension. *Plant Physiol* 167:40–43.
- Trifilò P, Casolo V, Raimondo F, Petrusa E, Boscutti F, Gullo MAL, Nardini A (2017) Effects of prolonged drought on stem non-structural carbohydrates content and post-drought hydraulic recovery in *Laurus nobilis* L.: the possible link between carbon starvation and hydraulic failure. *Plant Physiol Biochem* 120:232–241.
- Trugman AT, Detto M, Bartlett MK, Medvigy D, Anderegg WRL, Schwalm C, Schaffer B, Pacala SW (2018) Tree carbon allocation explains forest drought-kill and recovery patterns. *Ecol Lett* 21:1552–1560.
- Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annu Rev Plant Physiol Plant Mol Biol* 40:19–36.
- Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. (2 edn.). Springer, Berlin, Germany, pp 175–214.
- Way DA, Domec J-C, Jackson RB (2013) Elevated growth temperatures alter hydraulic characteristics in trembling aspen (*Populus tremuloides*) seedlings: implications for tree drought tolerance. *Plant Cell Environ* 36:103–115.
- Wheeler JK, Huggett BA, Tofte AN, Rockwell FE, Holbrook NM (2013) Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. *Plant Cell Environ* 36:1938–1949.
- Xu X, Medvigy D, Powers JS, Becknell JM, Guan K (2016) Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytol* 212:80–95.
- Xu Z, Zhou G, Shimizu H (2010) Plant responses to drought and rewatering. *Plant Signal Behav* 5:649–654.
- Yan W, Zhong Y, Shangguan Z (2017) Rapid response of the carbon balance strategy in *Robinia pseudoacacia* and *Amorpha fruticosa* to recurrent drought. *Environ Exp Bot* 138:46–56.
- Yang Q, Zhang W, Li R, Xu M, Wang S (2016) Different responses of non-structural carbohydrates in above-ground tissues/organs and root to extreme drought and re-watering in Chinese fir (*Cunninghamia lanceolata*) saplings. *Trees* 30:1863–1871.
- Yanyuan L, Maria AE, Xiping D, TM T (2010) Recovery of *Populus tremuloides* seedlings following severe drought causing total leaf mortality and extreme stem embolism. *Physiol Plant* 140:246–257.
- Yin J, Bauerle TL (2017) A global analysis of plant recovery performance from water stress. *Oikos* 126:1377–1388.
- Zang U, Goisser M, Grams TEE, Häberle K-H, Matyssek R, Matzner E, Borken W (2014) Fate of recently fixed carbon in European beech (*Fagus sylvatica*) saplings during drought and subsequent recovery. *Tree Physiol* 34:29–38.
- Zhang Y-J, Rockwell FE, Graham AC, Alexander T, Holbrook NM (2016) Reversible leaf xylem collapse: a potential 'circuit breaker' against cavitation. *Plant Physiol* 172:2261–2274.