



## Tansley review

# What plant hydraulics can tell us about responses to climate-change droughts

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## Summary

Climate change exposes vegetation to unusual drought, causing declines in productivity and increased mortality. Drought responses are hard to anticipate because canopy transpiration and diffusive conductance ( $G$ ) respond to drying soil and vapor pressure deficit ( $D$ ) in complex ways. A growing database of hydraulic traits, combined with a parsimonious theory of tree water transport and its regulation, may improve predictions of at-risk vegetation. The theory uses the physics of flow through soil and xylem to quantify how canopy water supply declines with drought and ceases by hydraulic failure. This transpiration ‘supply function’ is used to predict a water ‘loss function’ by assuming that stomatal regulation exploits transport capacity while avoiding failure. Supply–loss theory incorporates root distribution, hydraulic redistribution, cavitation vulnerability, and cavitation reversal. The theory efficiently defines stomatal responses to  $D$ , drying soil, and hydraulic vulnerability. Driving the theory with climate predicts drought-induced loss of plant hydraulic conductance ( $k$ ), canopy  $G$ , carbon assimilation, and productivity. Data lead to the ‘chronic stress hypothesis’ wherein  $>60\%$  loss of  $k$  increases mortality by multiple mechanisms. Supply–loss theory predicts the climatic conditions that push vegetation over this risk threshold. The theory’s simplicity and predictive power encourage testing and application in large-scale modeling.

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## I. Introduction

Climate change challenges our grasp of plant and ecosystem functioning. We need informed projections for how plants and their ecosystems will respond to new conditions. Plants are often water-limited, so regions experiencing novel ‘climate-change’

droughts are of particular concern (Allen *et al.*, 2010). How much drought stress can the standing vegetation experience before productivity declines and mortality rises? This is a practical question that has ramifications beyond impairing natural resources, including major feedbacks to climate and hydrology through altered water and carbon cycles (Bonan, 2008; Zhao & Running,

2010). In this review, we outline what plant hydraulics can tell us about how plants will respond to drought. Rather than give a retrospective summation of what has already been done, we offer a prospectus for how we can move forward and make better predictions of plant drought responses on large scales. Such predictions require models. Our objective is to identify critical hydraulic properties of plants, not all of which have been integrated into large-scale climate and landscape modeling. To encourage their integration, we provide a parsimonious theoretical framework. We begin by distilling a basic hydraulic theory of water supply and loss, then consider complications, move on to illustrate application, and conclude with drought impacts on productivity and mortality.

A central modeling problem that plant hydraulics can solve is a mechanistically based prediction of transpiration rate as a function of soil moisture and atmospheric vapor pressure deficit ( $D$ ). Much follows from that prediction: transpiration yields diffusive conductance to carbon dioxide ( $\text{CO}_2$ ) uptake, which constrains the carbon assimilation rate, which fuels respiration and growth, which influences plant productivity and survival, and ultimately ecosystem productivity and sink strength. Hence, we focus on hydraulic theory for deriving canopy transpiration rate ( $E$ ) and canopy diffusive conductance ( $G = E/D$ ) from climate. In the process, the corollary variables of xylem pressure ( $P$ ) and hydraulic conductance ( $k$ ) are involved. The causally downstream phenomena of productivity and mortality are discussed more qualitatively in the context of a 'chronic stress hypothesis' for predicting the risk of drought-related plant decline.

Modeling transpiration and diffusive conductance is a problem because their responses to soil and atmospheric drought cannot be deduced from meteorological variables such as those in Penman–Monteith type equations (Campbell & Norman, 1998). Missing from these physically sound equations is the plant. Plants have roots and xylem that influence the potential water supply for transpiration, and they have stomata that actively regulate transpirational water loss. Empirical functions can be incorporated to mimic stomatal responses to soil moisture and  $D$  (Jarvis, 1976; Ball *et al.*, 1987), but they lack the predictive power of a physically constrained equation grounded in a universal concept. As a result, capturing the drought response has proven difficult for ecosystem models (Powell *et al.*, 2013; Zuidema *et al.*, 2013).

Plant hydraulics provides a physically constrained bridge between the physiological regulation of transpiration and the environmental drivers of climate and hydrology. Xylem transport in particular is inherently grounded in physics, having much in common with soil water transport (Sperry *et al.*, 2002). Hence xylem flow is easy to model, providing the link between the soil moisture profile tapped by the root system and the evaporative demand above the canopy. The concept of using plant hydraulics to improve predictions of gas exchange reduction from drought has been profitably adopted by at least one ecosystem flux model, SPA (Williams *et al.*, 1996, 2001; Bonan *et al.*, 2014). Although somewhat successful, SPA simply limits transpiration by setting a minimum canopy xylem pressure, and it can underpredict the drought response (Powell *et al.*, 2013). The stand-level TREES (Mackay *et al.*, 2003) model currently incorporates xylem

cavitation (McDowell *et al.*, 2013) using the detailed hydraulic model of Sperry *et al.* (1998). The success of these approaches (see also Parolari *et al.*, 2014) argues for implementing more flexible and realistic hydraulic theory as a foundation for predicting plant drought responses.

This review elaborates on the following logic for applying plant hydraulics to climate-change predictions. (1) The transpiration stream flows through porous media over most of its length, and the physics of this flow can be used to define a 'supply function' for potential transpiration rate as a function of the canopy xylem pressure and tapped soil moisture profile. (2) The assumption that stomatal regulation of transpirational water loss will exploit, but not exceed, a limited supply is used to derive a transpiration 'loss function' from the supply function. (3) The supply–loss concept can accommodate diversity in key hydraulic traits. (4) Examples demonstrate the conceptual ease of driving the supply–loss framework with climate and hydrology. (5) The resulting predictions of water status, gas exchange, and productivity from climate indicate the degree of 'chronic stress' to the vegetation and hence the hypothetical risk of drought-related mortality, embodied by the 'chronic stress hypothesis'.

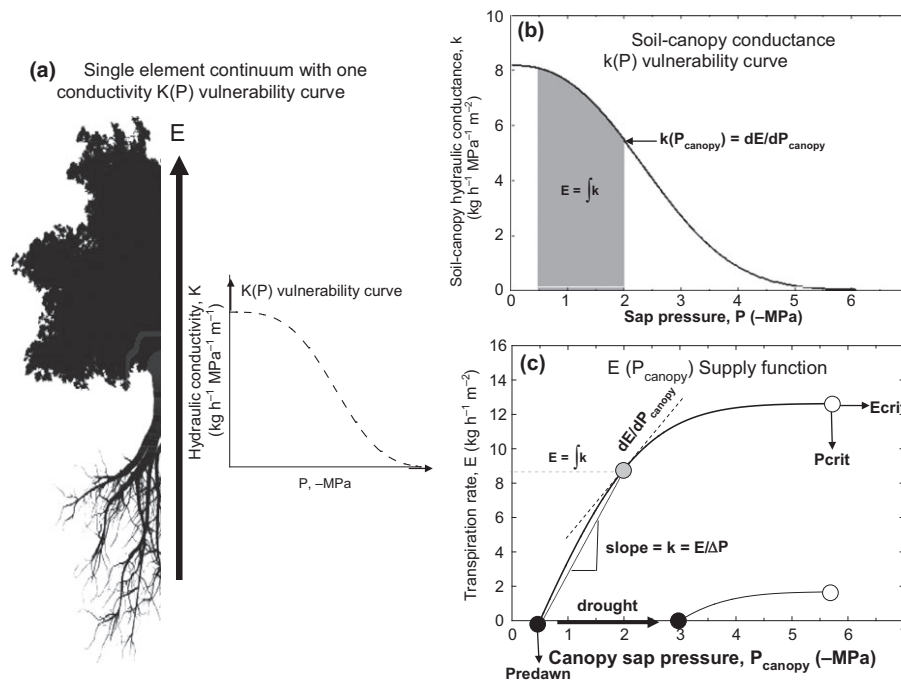
As a proof of concept, we illustrate key steps using a soil–plant–atmosphere model developed from Sperry *et al.* (1998). However, it is not the model particulars that are important at the moment, but rather the basic hydraulic principles and their predictive power. The intent is to increase the accessibility of the approach and encourage its wider evaluation by the community.

## II. The transpiration supply function

The supply function describes the potential rate of water supply for transpiration ( $E$ ) as a function of the canopy xylem pressure ( $P_{\text{canopy}}$ ) (Sperry *et al.*, 1998, 2002). The  $E(P_{\text{canopy}})$  supply function depends on how the hydraulic conductivity ( $K$ ) of soil and plant declines with more negative sap pressure ( $P$ ). Whether in the soil or in the dead xylem conduits of the plant, the transpiration stream is pulled through porous media by the wicking action of evaporating cell wall surfaces (Pickard, 1981). As the media are subjected to more negative sap pressure, water drains from more of the pore space, and the  $K$  of the media declines. The consequent  $K(P)$  function falls monotonically from a maximum  $K(K_{\text{max}})$  as  $P$  becomes more negative (Fig. 1a). The  $K(P)$  function is called a 'vulnerability curve' for xylem (Tyree & Sperry, 1989), and an 'unsaturated conductivity curve' for soil (Campbell, 1985).

To clarify how the  $K(P)$  behavior of porous media dictates the  $E(P_{\text{canopy}})$  supply function, we collapse the complexity of the soil–canopy transpiration stream into a single path that is composed of a medium with a single  $K(P)$  function (Fig. 1a). This simplification emphasizes the theoretical concepts at the expense of details added later.

The first step is to convert the  $K(P)$  conductivity vulnerability curve of the media (Fig. 1a) into the  $k(P)$  conductance vulnerability curve of the particular soil–canopy continuum (Fig. 1b). Conductivity ( $K$ , normalized by length and cross-sectional area) is an intrinsic property of a particular medium. Conductance ( $k$ ) depends in addition on how much media the water is flowing



**Fig. 1** Deriving the transpiration ‘supply function’ from a vulnerability curve. (a) A ‘single-element’ soil–canopy continuum has a transpiration stream ( $E$  arrow) flowing through a porous medium with one hydraulic conductivity vulnerability curve ( $K(P)$ ) along its length. (b) The  $k(P)$  hydraulic conductance curve ( $K$  converted to  $k$  per unit basal area) gives the soil–canopy hydraulic conductance at one soil = canopy pressure (no pressure drop:  $\Delta P = 0$ ). Integrating the  $k(P)$  curve over any  $\Delta P$  drop from soil to canopy yields the steady-state transpiration rate ( $E$ ) at that  $\Delta P$  (shaded  $E = \int k$  region under curve). (c) The  $E(P_{\text{canopy}})$  supply function at a given predawn sap pressure (black circles) as obtained by integrating the  $k(P)$  function for  $P =$  predawn to progressively greater canopy sap pressure ( $P_{\text{canopy}}$ ). The critical point (white circle with  $E_{\text{crit}}$  and  $P_{\text{crit}}$  extrema) corresponds to  $k(P) \approx 0$ . The  $dE/dP_{\text{canopy}}$  of the supply function (e.g. dashed  $dE/dP_{\text{canopy}}$  tangent at gray circle;  $P_{\text{canopy}} = -2$  MPa) equals the hydraulic conductance of the soil–canopy continuum exposed to that same  $P_{\text{canopy}}$  (e.g.  $k(P_{\text{canopy}})$  arrow in (b) at  $P = -2$  MPa). The  $E/(\text{predawn} - P_{\text{canopy}})$  slope (labeled gray diagonal) gives the hydraulic conductance of the soil–canopy path during transpiration when there is a soil-to-canopy  $\Delta P$  drop. Drought shifts the supply function to the right by lowering the predawn pressure (arrow), and flattens it by reducing  $E_{\text{crit}}$ .

through. The conversion from  $K$  to  $k$  is a matter of exchanging maximum hydraulic conductance ( $k_{\text{max}}$  for  $K_{\text{max}}$  in the  $K(P)$  function, keeping other curve shape parameters constant. Just as the  $K(P)$  conductivity vulnerability curve yields  $K$  of the medium exposed to a single value of  $P$ , the  $k(P)$  conductance vulnerability curve gives  $k$  of the entire continuum for a single value of  $P$  from soil to canopy (Fig. 1b). The  $k_{\text{max}}$  can be estimated from measurements under nonstressed conditions, or obtained from allometric relationships that are empirical (Meinzer *et al.*, 2005) or calculated from xylem anatomy and branching structure (Sperry *et al.*, 2012; Smith *et al.*, 2014; Smith & Sperry, 2014). Conductance can be expressed relative to a reference cross-sectional area at some point in the flow path. A seasonably stable reference, such as ground area or basal area (all figures express  $k$ ,  $E$  and  $G$  per basal area), ensures that changes in absolute conducting capacity are not obscured by changes in reference area (as might be the case if leaf area were used).

The second (and last) step is to convert the  $k(P)$  function to the  $E(P_{\text{canopy}})$  supply function. This is easily done with the integral transform method developed for similar problems in soil physics (Gardner, 1958; Campbell, 1985; Sperry *et al.*, 1998; Comstock & Sperry, 2000). To explain:  $E_i$  at  $P_{\text{canopy}} = P_i$  is the integral of the  $k(P)$  function from  $P_0$  at the soil end of the flow path to  $P_i$  at the canopy end:  $E_i = \int_{P_0}^{P_i} k(P) dP$ . To illustrate, in Fig. 1(b), the shaded ‘ $E = \int k$ ’ area between  $P_0 = -0.5$  and  $P_i = -2$  MPa equals

$E_i$ , which is plotted as the gray symbol on the  $E(P_{\text{canopy}})$  supply function in Fig. 1(c). The entire  $E(P_{\text{canopy}})$  function is obtained by holding  $P_0$  constant and performing the integration for the full range of  $P_i$ . Integrating over the monotonic decline in  $k$  with  $P_i$  yields a monotonic increase in  $E$  that effectively saturates at  $E_{\text{crit}}$  (Fig. 1c, white circle) as  $k$  approaches zero. The  $E_{\text{crit}}$  is the limiting steady-state  $E$ ; any greater  $E$  will drive  $k$  to zero and desiccate the canopy. Mathematically,  $k$  may not reach zero (depending on the equation chosen to represent  $k(P)$  decline; a two-parameter Weibull function is used here), but physiologically it effectively does, and a judgment of minimum relevant  $k$  ( $= 0.01 \text{ kg h}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$  in the figures) suffices to end the  $E(P_{\text{canopy}})$  supply function. This somewhat arbitrary endpoint is of little consequence for the essentially saturated value of  $E_{\text{crit}}$ , but will have a big effect on the corresponding  $P_{\text{crit}}$  ( $= P_{\text{canopy}}$  at  $E_{\text{crit}}$ ). Thus,  $E_{\text{crit}}$  is a more reliable point of reference for estimating safety margins from hydraulic failure than  $P_{\text{crit}}$ .

The  $E(P_{\text{canopy}})$  supply function contains much information. The  $P_0$  intercept, at  $E = 0$ , represents the predawn canopy sap pressure (no nocturnal transpiration) which integrates the rooted soil moisture profile (e.g. Fig. 1c, black ‘Predawn’ circle at  $-0.5$  MPa) and includes any gravitational gradient ( $-0.01 \text{ MPa m}^{-1}$ ). As  $E$  increments from 0, the disproportionately greater drop in  $P_{\text{canopy}}$  results from the loss of  $k$ . Graphically, the soil–canopy  $k$  ( $k = E/\Delta P$ )

is the slope of the line from the intercept at  $E=0$  to any particular  $E$  (e.g. Fig. 1c slope of  $E$  from  $P=-0.5$  to  $-2$  MPa). This slope becomes shallower as  $k$  drops with increasing  $E$ . The loss of  $k$  is greatest where pressures are most negative at the downstream  $P_{\text{canopy}}$  extreme. The downstream loss of  $k$  is graphically evident from the continuous decline in the  $dE/dP_{\text{canopy}}$  derivative along the  $E(P_{\text{canopy}})$  curve. By the fundamental theorem of calculus, the  $dE/dP_{\text{canopy}}$  derivative equals  $k(P_{\text{canopy}})$  from the conductance vulnerability curve. The  $k(P_{\text{canopy}})$  is the conductance if the *entire continuum* were exposed to  $P_{\text{canopy}}$ ; hence it corresponds to the local loss of hydraulic conductance at the canopy end of the flow path where  $P=P_{\text{canopy}}$ . To illustrate, in Fig. 1(c), the dashed  $dE/dP_{\text{canopy}}$  slope at  $-2$  MPa equals  $k(P_{\text{canopy}})$  at  $-2$  MPa on the conductance vulnerability curve (Fig. 1b,  $k(P_{\text{canopy}}) = dE/dP_{\text{canopy}}$  arrow). The corresponding  $k=E/\Delta P$  slope (Fig. 1c, gray slope) is greater because sap pressure is less negative than the  $-2$  extreme along most of the continuum. The  $dE/dP_{\text{canopy}}$  approaches zero at  $E_{\text{crit}}$ , indicating that the total loss of downstream hydraulic conductance limits the maximum steady-state rate of canopy water supply.

The supply function responds predictably to the depletion of soil moisture during drought (e.g. Fig. 1c, 'Drought' arrow). The predawn  $P_0$  intercept shifts to more negative values, and the  $E(P_{\text{canopy}})$  trajectory flattens as  $E_{\text{crit}}$  diminishes. The supply function gradually extinguishes as more negative predawn  $P$  drives  $E_{\text{crit}}$  to zero (Sperry *et al.*, 1998).

### III. The transpiration loss function

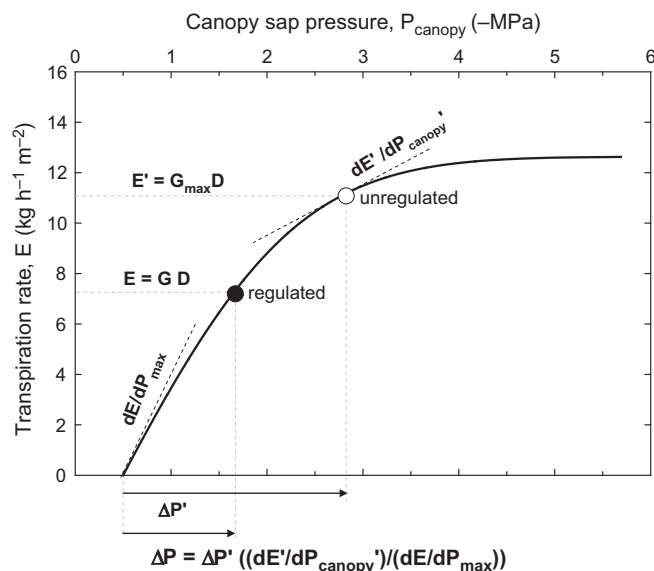
The loss function specifies where the plant regulates its actual transpiration rate along the  $E(P_{\text{canopy}})$  supply function. Regulation is achieved via control of canopy diffusive conductance ( $G$ ) mostly by stomatal movements. Much about the physiology of stomatal regulation in response to plant water status and drought is uncertain (Buckley & Mott, 2013), but a few points of clarity lay a foundation for approximating its phenomenology at the canopy scale.

Stomatal and canopy diffusive conductances generally decrease in response to soil and atmospheric water stress, with a sensitivity that can vary across species and circumstances (Schulze, 1986; Oren *et al.*, 1999). It is also evident that stomata rarely allow  $E_{\text{crit}}$  to be exceeded as long as soil moisture is still available (Hacke *et al.*, 2000; Sperry *et al.*, 2002; Holttta *et al.*, 2012). Such suicidal behavior would cause catastrophic desiccation, sometimes referred to as 'runaway cavitation' or 'hydraulic failure' (Tyree & Sperry, 1988). A point of clarity, true 'runaway' cavitation ( $E > E_{\text{crit}}$ ) is to be distinguished from 'stable' cavitation associated with  $E \leq E_{\text{crit}}$ . It is most likely that  $E_{\text{crit}}$  is only exceeded under extreme soil drought when stomata are maximally closed, and the tapped soil moisture profile (and plant) slowly dries until  $E_{\text{crit}} \approx 0$ , extinguishing the supply function (Davis *et al.*, 2002).

Given the stress-induced constraints on  $E$  supply rate, it makes sense to use the  $E(P_{\text{canopy}})$  supply function to predict an  $E(P_{\text{canopy}})$  transpiration loss function. Deriving the loss function is a significant step beyond the Sperry *et al.* (1998) framework which stopped at modeling the supply function. Three principles constrain the loss function. (1) It should mimic actual stomatal behavior. (2) The loss function should be mathematically

dependent on the supply function. This represents the critical simplifying assumption that traits influencing water supply and loss evolved in coordination. (3) The loss function should balance a trade-off between utilizing the full supply capacity (the investment in root and xylem), while controlling an inevitable loss of hydraulic conductance (costly to replace and consequential if not), and avoiding premature runaway cavitation (death by desiccation). The supply function derivative ( $dE/dP_{\text{canopy}}$ ) is the ideal variable to drive the loss function. As explained,  $dE/dP_{\text{canopy}}$  represents the limiting hydraulic conductance at the downstream end of the flow path, and it falls towards zero as  $E_{\text{crit}}$  is approached. Soil drought and high  $D$  both push the plant towards lower  $dE/dP_{\text{canopy}}$ . Progressive stomatal closure pushes back. A simple rule for a loss function is that stomata should close more as stress pushes  $dE/dP_{\text{canopy}}$  closer to zero. By following this rule, the plant will exploit its full supply capacity when stressed, but will do so in a conservative manner that controls the accumulation of stable cavitation and prevents runaway cavitation.

For demonstration, we derive a suitable supply-coupled loss function based on  $dE/dP_{\text{canopy}}$  (Fig. 2). It is not the only possibility, nor may it prove the best at quantitatively capturing stomatal regulation. The point is to show the promise of using the supply function to model stomatal responses to water stress. Our sample loss function requires one additional parameter, which is the maximum canopy diffusive conductance ( $G_{\text{max}}$ , representing

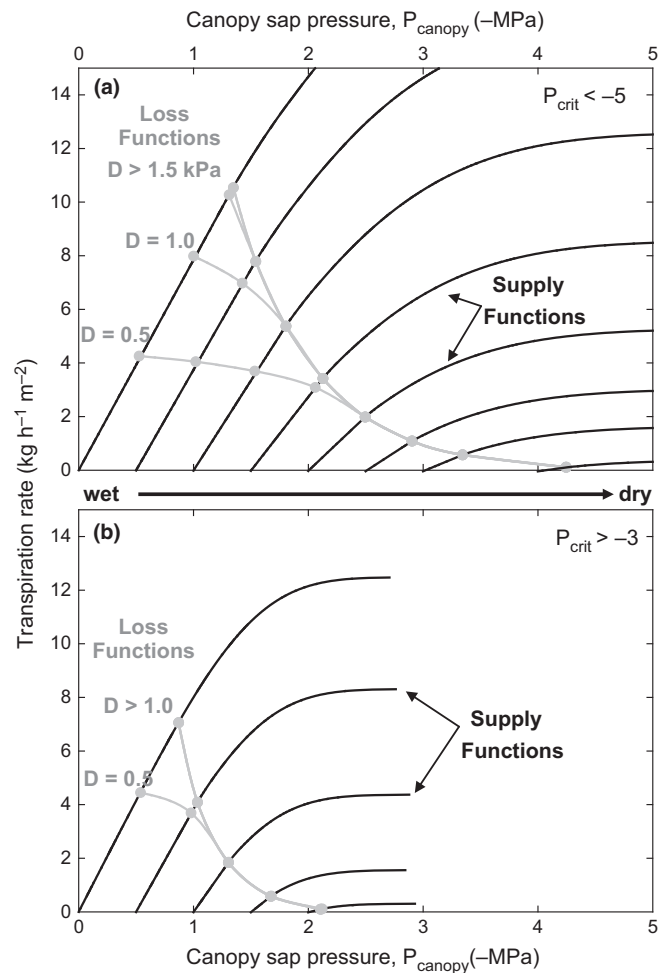


**Fig. 2** Derivation of a transpiration 'loss function' for the stomatically regulated transpiration rate ( $E$ ) (closed circle) from the transpiration supply function (solid black curve). The unregulated  $E'$  (open circle) is the product of maximum canopy diffusive conductance ( $G_{\text{max}}$ ) and vapor pressure deficit ( $D$ ). The corresponding unregulated pressure drop ( $\Delta P'$ ) is given by the supply function (outer set of gray dashed intercepts). Regulated  $\Delta P$  assumes that  $\Delta P'$  is reduced by the fractional drop in the unregulated  $dE'/dP_{\text{canopy}}$  (shallow dashed tangent) from its maximum (at predawn intercept; steeper dashed tangent; see equation under the  $x$ -axis). The  $\Delta P$  reaches a maximum before  $E'$  reaches  $E_{\text{crit}}$ , at which point  $\Delta P$  is assumed to saturate, indicating a maximal stomatal sensitivity to  $D$  that achieves constant  $E$  and  $\Delta P$ . The regulated  $E$  is given by the supply function at  $\Delta P$  (inner set of gray dashed intercepts). The required drop in  $G$  from  $G_{\text{max}}$  (resulting from partial stomatal closure) is given by  $E/D$ .

maximal stomatal opening). The  $E(P_{\text{canopy}})$  supply function is first calculated from the predawn  $P$  and the continuum  $k(P)$  function (as diagrammed in Fig. 1). The maximum  $dE/dP_{\text{canopy}}$  is at the predawn start of the curve (Fig. 2, dashed  $dE/dP_{\text{max}}$  tangent) and equals the maximum soil–canopy  $k$ . The  $E'$  in the absence of  $G$  regulation is given by  $E' = G_{\text{max}} \cdot D$ , and the corresponding  $dE'/dP_{\text{canopy}}$  derivative is read from the  $E(P_{\text{canopy}})$  supply curve (Fig. 2, 'Unregulated' open circle on supply function). The fraction  $(dE'/dP_{\text{canopy}})/(dE/dP_{\text{max}})$  drops from 1 to 0 as  $E'$  approaches  $E_{\text{crit}}$ , quantifying how close the plant is pushed to the critical point without stomatal closure. Stomatal regulation is assumed to reduce the unregulated pressure drop,  $\Delta P'$  (Fig. 2,  $\Delta P'$  arrow to Unregulated circle), by this fraction, such that the regulated drop  $\Delta P = \Delta P' \cdot ((dE'/dP_{\text{canopy}})/(dE/dP_{\text{max}}))$ . As  $E'$  increases, this  $\Delta P$  function reaches a maximum (obviously reached before  $dE'/dP_{\text{canopy}} \approx 0$  at  $E' = E_{\text{crit}}$ ). At this point, the biological  $\Delta P$  is assumed to saturate with  $D$  rather than to show an unrealistic decline. Thus, beyond this  $\Delta P$  saturation point the stomata are assumed to be maximally sensitive to  $D$  by closing sufficiently to keep  $E$  and  $P_{\text{canopy}}$  constant. The regulated  $\Delta P$  is used to find the regulated  $E$  from the  $E(P_{\text{canopy}})$  curve (Fig. 2, 'Regulated' closed circle). The regulated  $E$  divided by  $D$  yields the regulated  $G$ . The  $G_{\text{max}}$  can be obtained by tuning it to yield the observed  $E$  under well-watered 'reference' ( $k_{\text{max}}$ ) conditions. The loss function as described is not readily reducible to a single equation (nor is the supply function), but is a parsimonious numerical routine.

The loss function is intended to capture emergent stomatal behavior, not the physiological mechanism by which it is achieved. The math does not represent steps in a stimulus–response sequence. In general, however, it is physiologically feasible that stomatal regulation could involve the sensing of  $dE/dP_{\text{canopy}}$ . Active adjustments in stomatal aperture cause changes in  $E$ , and leaf cells could sense the consequent changes in  $P_{\text{canopy}}$  which will increase in amplitude with falling  $dE/dP_{\text{canopy}}$ . Short-term  $P_{\text{canopy}}$  dynamics could be coupled to the strength of a feedback signal influencing aperture adjustment as in components of various mechanistic stomatal models (Tardieu & Davies, 1993; Dewar, 2002).

Though simple and phenomenological, the supply-coupled loss function predicts the complex interactions between stomatal responses to  $D$ , soil drought, and soil–canopy hydraulic conductance (Fig. 3). Focusing first on the  $D$  response, as long as the soil is wet, higher  $D$  drives up  $E$  along the supply function (Fig. 3a, black 'Supply function' curves) until  $E$  and  $\Delta P$  saturate as dictated by the loss function (e.g. Fig. 3a, gray 'Loss function' points saturate at  $D > 1.5$  kPa for wet supply functions). Beyond the  $D$  saturation point, stomatal sensitivity is maximized and there is no further change in  $E$  and  $P_{\text{canopy}}$ . Drier soil enhances stomatal sensitivity by causing saturation at ever-lower  $D$ , resulting in the collapse to a single loss function as parent supply functions shift to more negative intercepts. Turning to the soil drought response, solving the loss function at a given  $D$  from progressively drier supply functions predicts a continuous drop in  $E$  during drought (Fig. 3a, gray 'Loss function' curves). The sensitivity of the stomata to soil drought (at a given  $D$ ) is indicated by the steepness of these loss functions: a steeper drop in  $E$  (and correspondingly less of a drop in  $P_{\text{canopy}}$ ) corresponds to a more sensitive stomatal response to soil



**Fig. 3** Transpiration loss functions isolate the combined effects of soil and atmospheric drought, and hydraulic vulnerability, on stomatal regulation. Loss functions (gray curves) are superimposed on their parent supply functions (black curves). (a) A hydraulically resistant plant with a pressure causing complete cavitation ( $P_{\text{crit}} < -5$  MPa). Atmospheric drought (greater vapor pressure deficit ( $D$ )) steepens the loss function by increasing the transpiration rate ( $E$ ) along a given supply function until sensitivity to  $D$  is maximized and  $E$  saturates (e.g. gray  $D > 1.5$  kPa point on wettest supply function). Sensitivity to  $D$  increases as soil drought truncates the supply function, ultimately yielding one loss function regardless of  $D$ . Sensitivity to soil drought is greatest at high  $D$  (upper loss function) where  $E$  decreases most steeply with regulated canopy pressure ( $P_{\text{canopy}}$ ). The stomatal response to both stresses is sufficient to avoid exceeding the critical points of supply functions. (b) A hydraulically vulnerable plant with a  $P_{\text{crit}} > -3$  MPa. Greater vulnerability increases the sensitivity of stomata to both  $D$  and soil drought, resulting in a more isohydric regulation pattern relative to the more resistant and anisohydric plant in the upper panel.

drying. Complete stomatal closure ( $E \approx 0$ ) is approached before  $E_{\text{crit}} \approx 0$  as required to avoid premature runaway cavitation.

The loss function is also sensitive to the  $K(P)$  vulnerability curve function of the transpiration pathway (Fig. 3a vs b). The more resistant is the  $K(P)$  function to cavitation, the more negative is  $P_{\text{crit}}$ , leaving the loss function more 'room' for carrying a transpiration stream despite drying soil (e.g. Fig. 3a,  $P_{\text{crit}} < -5$ ). Stomatal sensitivity to both  $D$  and soil drought is indicated by loss functions that converge less quickly and drop less steeply with soil

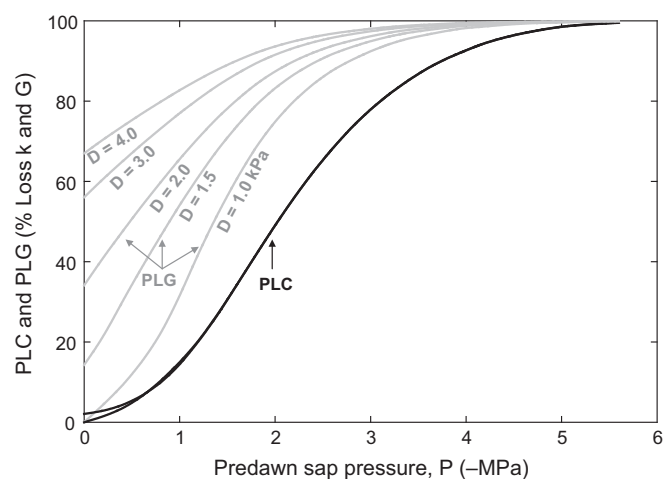
drying (Fig. 3a, gray curves). Conversely, the more vulnerable the  $K(P)$  function is to cavitation, the less negative is  $P_{\text{crit}}$  forcing the stomata to be maximally sensitive to  $D$  and soil drought (e.g. Fig. 3b,  $P_{\text{crit}} > -3$  MPa). This is indicated by loss functions converging more rapidly and dropping more steeply with drought (Fig. 3b, gray 'loss functions').

#### IV. General properties of the supply–loss theory

The supply–loss theory has general characteristics that persist regardless of particulars of the loss function, or whether the flow path consists of a single  $k(P)$  element (Fig. 1), or of several  $k(P)$  elements in series and parallel as discussed in 'variations on the theme.' (1) The theory defines the stomatal response to  $D$ , and to soil drought, and defines how these two responses interact (e.g. Fig. 3). In particular, the  $D$  response eventually saturates to prevent further water loss, it saturates faster in some species than others (Fig. 3b vs a), and it saturates faster in all species as soils dry and the drought response dominates. (2) The hydraulic vulnerability of the soil–plant continuum dictates a plant's position on the isohydric–aniso-hydric continuum. A plant with a 'resistant'  $k(P)$  allows midday  $P_{\text{canopy}}$  to fall considerably during soil or atmospheric stress, and stomatal control is minimally sensitive. This is anisohydric-type regulation exemplified by Fig. 3(a). Conversely, a plant with a 'vulnerable'  $k(P)$  function dictates a maximally sensitive stomatal response to stress and a minimal drop in  $P_{\text{canopy}}$  during soil or atmospheric drought. This is more isohydric-type behavior exemplified by Fig. 3(b). (3) Stress, whether from soil drought or high atmospheric  $D$ , results in a much greater reduction in gas exchange rate ( $E$  and  $G$ ) than in soil–canopy hydraulic conductance (Fig. 4; compare black PLC curve with gray PLG curves). Thus, a 'percentage loss of hydraulic conductivity' (PLC) metric of stress considerably underestimates consequent 'percentage loss of diffusive conductance' (PLG) which is at least (if not more) detrimental to plant health. The  $\text{PLG} > \text{PLC}$  property results from a stomatal control regime that must reduce  $E$  faster than the reduction in whole-plant  $k$  as required to avoid the critical point of the supply function.

All of these properties are qualitatively consistent with plant behavior. With respect to property (1), the increase in  $E$  with  $D$  typically saturates as stomatal closure becomes sufficient to prevent further water loss (Oren *et al.*, 1999). Species that saturate at higher  $D$  are often more resistant to cavitation (e.g. Fig. 3a) than those saturating at low  $D$  (Fig. 3b; Bush *et al.*, 2008; Litvak *et al.*, 2012). Saturation at low  $D$  has also been associated with soil drought, which also closes stomata independently of  $D$  (Schulze *et al.*, 1972; Thomas *et al.*, 2000).

Properties (2) and (3) are also generally supported by a recent meta-analysis of relationships between predawn and midday xylem pressure (Martinez-Vilalta *et al.*, 2014). Plants that maintained midday  $P_{\text{canopy}}$  near constant with soil drought (isohydric-type response) were also plants that were more vulnerable to cavitation; conversely, plants whose midday  $P$  dropped with drought (more anisohydric) tended to be more resistant to cavitation. This is consistent with property (2). The midday  $P$  was also usually observed to drop less rapidly than predawn  $P$  during drought,



**Fig. 4** Diffusive conductance ( $G$ ) declines faster during drought than soil–canopy hydraulic conductance ( $k$ ). Declines are represented as percentage loss of  $G$  (PLG; gray curves) and  $k$  (PLC; black curve) relative to no drought (predawn = 0) and vapor pressure deficit,  $D = 1$  kPa. The more rapid increase in PLG vs PLC with soil drought is exacerbated at high  $D$  (as labeled). Greater sensitivity of diffusive vs hydraulic conductance is required by a loss function that avoids the hydraulic critical point. Drought-induced loss of carbon dioxide assimilation and productivity should be more closely tied to PLG than PLC.

indicating a generally diminishing  $\Delta P$ . As  $\Delta P = E/k$ , the drop in  $\Delta P$  means that  $E$  is usually reduced more than the corresponding  $k$  during drought, consistent with property (3) (although exceptions exist; Franks *et al.*, 2007; Martinez-Vilalta *et al.*, 2014).

#### V. Variations on the theme

The single- $k(P)$ -element representation of supply–loss hydraulic theory (Fig. 1) is conceptually useful, but probably not very predictive in most applications. Adding additional  $k(P)$  elements as described in this section captures key hydraulic traits, and couples the plant to climate and hydrology. The easy integral transform conversions between  $k(P)$  and  $E(P)$  (Fig. 1) still apply at the element scale. However, linking the elements to generate the supply and loss functions for the whole continuum may require a numerical routine (e.g. multidimensional Newton–Raphson) depending on how the network is structured.

##### 1. Vulnerability segmentation

Multiple hydraulic conductance elements in series (e.g. soil, root, stem, leaf) are needed to represent 'vulnerability segmentation' where  $k(P)$  functions differ between plant and soil, and between plant organs (Tyree *et al.*, 1993). The transpiration stream also flows a short distance through living tissues of root and leaf, and as the  $k(P)$  behavior of this extra-xylary flow becomes better known (Scoffoni *et al.*, 2013) it could be incorporated as well. A general principle is that the element with the lowest hydraulic conductance in the series will have the dominant influence on the collective soil–canopy  $k(P)$  function, and hence the  $E(P_{\text{canopy}})$  supply and loss functions. Elements with low  $k$  at the start of the vulnerability curve, a steep drop in  $k$ , and a downstream location that develops

more negative  $P$ , will create bottlenecks and heavily bias the loss function.

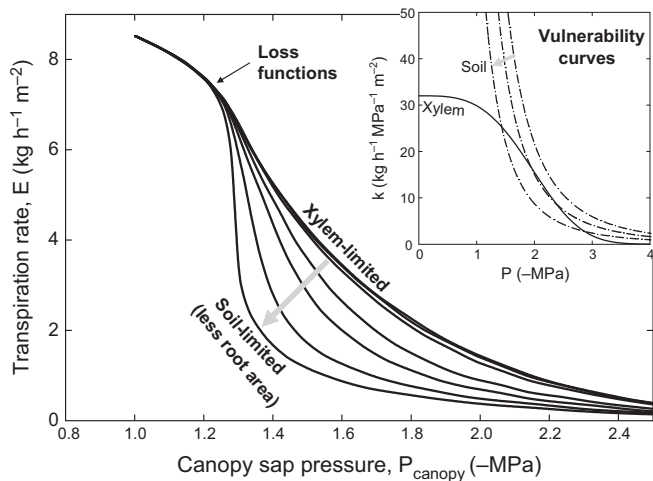
The ‘bottleneck’ principle is reflected in the question of whether soil or xylem is more limiting to plant water transport. Soil  $k(P)$  is radically different in form than xylem vulnerability curves (Fig. 5, Vulnerability curves inset). Soil curves are usually modeled from soil texture using ‘pedotransfer functions’ which take the form of an exponential drop in  $K$  from field capacity (van Genuchten, 1980; Campbell, 1985). The  $K(P)$  conductivity function can be converted to the  $k(P)$  conductance function by estimating the width of the rhizosphere (between bulk soil boundary and root surface), and the surface area of absorbing roots (Sperry *et al.*, 1998). Soil  $k(P)$  vulnerability curves start astronomically high compared with xylem  $k(P)$  curves (Fig. 5, dashed-dotted soil vulnerability curves), mainly because root surface area is hugely greater than xylem cross-sectional area. Hence, under wet conditions, the relatively low xylem  $k$  limits the loss function (Fig. 5, convergence to ‘xylem-limited’ loss function under less negative  $P_{\text{canopy}}$ ). As soils dry, however, the plunge in soil  $k$  can drop to the xylem range (Fig. 5, steep drop in soil vulnerability curves). The lower the root surface area, the greater the drop in soil  $k$  (Fig. 5, lower-most ‘Soil’ curves in inset), and the more of a bottleneck develops in the rhizosphere (Fig. 5, ‘soil-limited’ loss functions correspond to less root area). Given the uncertainty of soil  $K(P)$  models in dry soil (Assouline & Or, 2013), and the area of absorbing roots, a simplifying assumption is that root investment is just sufficient to approach the xylem limit across the  $P_{\text{canopy}}$  spectrum. Any more roots would be wasted for no water gain, and fewer roots would be a waste of investment in cavitation resistance (Sperry *et al.*, 1998, 2002). To the extent the assumption is false,

the theory will underpredict the magnitude of drought-induced reduction of  $k$ ,  $E$ , and  $G$ .

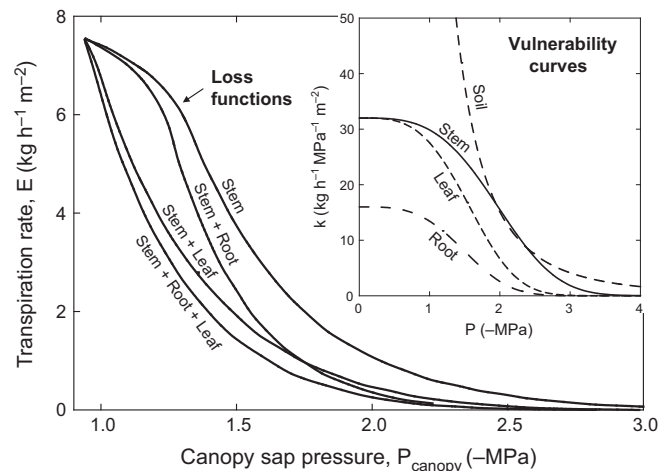
The bottleneck principle also explains the consequences of vulnerability segmentation within the xylem (assuming xylem-limited hydraulics). Xylem segmentation appears to be the rule rather than the exception, with stems often being more hydraulically resistant than leaves or roots (e.g. as in Fig. 6 inset; Sperry & Saliendra, 1994; Tsuda & Tyree, 1997; Pivovarov *et al.*, 2014). The least sensitive loss function is achieved by assigning all organs the most resistant vulnerability curve (Fig. 6; ‘Stem’ loss curve has the stem vulnerability curve in all organs). Incorporating the considerably more vulnerable root curve increases the sensitivity of the loss function (Fig. 6, ‘Stem + root’ curve), because roots become a bottleneck as soils dry out. The continuum is much more sensitive, however, to the incorporation of the leaf curve (Fig. 6, ‘Stem + leaf’ loss curve; ‘Leaf’ vs ‘Stem’ vulnerability curves). Leaves are the most downstream element, and although they are more resistant than roots in this example, they are exposed to more negative  $P$ , and so exert more of an influence. The most sensitive loss function incorporates complete vulnerability segmentation (Fig. 6, ‘Stem + root + leaf’). The effect of vulnerability segmentation will also be influenced by the relative initial  $k$  in each organ (e.g. Fig. 6;  $k(P)$  curves assume 50–25–25% of total minimum plant resistance in root–stem–leaf; Sperry *et al.*, 1998; Sack & Tyree, 2005).

## 2. Root distribution

Partitioning the belowground continuum into multiple root and rhizosphere elements represents the soil–root profile with discrete layers. The root depth profile determines: the predawn xylem pressure, and hence how the supply–loss functions shift as soils dry or wet up; the rate of soil drying with depth from transpirational



**Fig. 5** Soil hydraulic limitation can constrain the transpiration loss function. Loss functions were simulated for the same vapor pressure deficit, thus isolating the effect of soil drought. The ‘xylem-limited’ uppermost loss functions have sufficient root area to keep rhizosphere soil hydraulic conductance higher than xylem conductance despite soil drought (upper dash-dotted ‘Soil’ curve in Vulnerability curves inset); therefore the entire loss function is driven solely by xylem vulnerability curves. Reducing root area (gray arrows) causes soil hydraulic conductance to drop faster than the xylem during drought (lower ‘Soil’ curve in inset), resulting in soil-limited loss functions that are much more sensitive to soil drought. Soil ‘vulnerability curve’ functions in inset were modeled according to van Genuchten (1980).



**Fig. 6** Vulnerability segmentation alters loss functions. Loss functions shown are xylem-limited and for the same vapor pressure deficit. The least-sensitive loss function (‘Stem’) results from assigning the stem vulnerability curve (the most resistant xylem curve in the inset) to all organs. Adding the more vulnerable root curve increases sensitivity (‘Stem + root’). The same is true to a greater extent when just the leaf curve is added (‘Stem + leaf’), because the leaf is downstream from the root. Adding *both* root and leaf curves produces the most sensitive loss function (‘Stem + root + leaf’).

withdrawal; and the extent of nocturnal hydraulic redistribution (Horton & Hart, 1998). All three properties are essential for linking plant hydraulics to climate and hydrology.

### 3. Recovery of hydraulic conductance

Soil and xylem  $K(P)$  functions describe the loss of hydraulic conductivity in a porous medium as pressures drop during water stress. How much hysteresis is there in these curves when a stress episode is relaxed and pressures rise? In soil, refilling of pore space begins immediately on rewetting. Accounting for soil  $K(P)$  hysteresis (Mualem & Miller, 1979) is probably unnecessary because transpiration should be xylem-limited under wet soil conditions (Fig. 5).

In xylem, the degree of vulnerability curve hysteresis depends on the ability to refill embolized conduits in the short term or grow new xylem in the long. Bubble physics suggests that gas-filled conduits will not refill unless the surrounding sap pressure rises above near-atmospheric thresholds (Yang & Tyree, 1992). The transpiration stream can only reach such pressures when transpiration is minimal and soil is wet, conditions that also favor positive osmotic root pressures (Milburn & McLaughlin, 1974; Sperry, 1986, 1993; Yang & Tyree, 1992; Hacke & Sauter, 1996). Accordingly, vulnerability curves should exhibit prolonged hysteresis, with refilling limited to windows of high  $P$  opportunity. However, there is some evidence that sap pressures in embolized conduits can be actively elevated above the transpiration stream, driving frequent diurnal cycles of cavitation and reversal (Salleo *et al.*, 1996; Zwieniecki & Holbrook, 1998; Zwieniecki *et al.*, 2000; Bucci *et al.*, 2003; Brodersen *et al.*, 2010; Brodersen & McElrone, 2013). Although this mechanism is somewhat controversial because of measurement artifacts (Cochard *et al.*, 2000; Wheeler *et al.*, 2013), it would predict minimal vulnerability curve hysteresis.

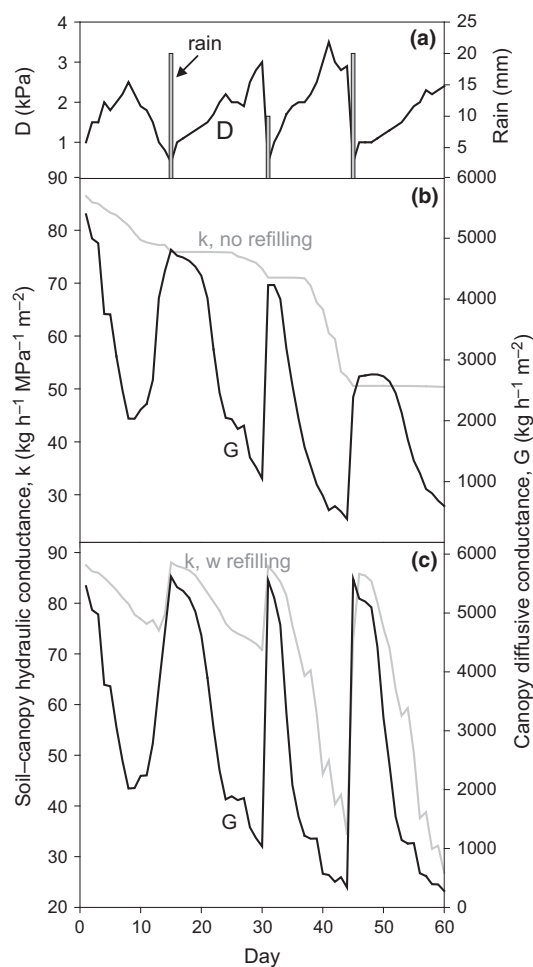
The evidence suggests that postdrought refilling can occur, but not in every species or circumstance (Salleo & Lo Gullo, 1993; Alder *et al.*, 1996; Hacke *et al.*, 2000; Hacke & Sperry, 2003; West *et al.*, 2008). The ability to refill after drought may depend on drought severity (Hacke & Sperry, 2003), and it may be inherently lower in more cavitation-resistant species (Ogasa *et al.*, 2013). While it is natural to assume that postdrought xylem refilling would always be advantageous (Klein *et al.*, 2013), examples in the next section suggest otherwise.

## VI. Predicting responses to climate

It is conceptually easy to drive the supply–loss theory (Figs 1, 2) as applied to a minimum set of conductance elements, with climate and hydrology at a landscape scale. The bulk soil moisture profile becomes an output that is driven by daytime transpiration withdrawal, nighttime hydraulic redistribution, and inputs from groundwater flow and precipitation. Spatial heterogeneity of vegetation, soil, climate, and hydrology could be handled as in current land surface models (Levis, 2010), but with plant functional types being defined by hydraulic traits (e.g. cavitation resistance, root distribution, and refilling ability). The spatial unit would be plots whose vegetation and substrate can be meaningfully

reduced to a single soil–plant–atmosphere continuum. The single catena would represent the parallel paths of the collective plot basal area. Vegetatively diverse stands could be handled by partitioning the catena into multiple hydraulic types. Arrays of plots constitute the landscape. The temporal scale would extend from the time step (*c.* half-hourly to daily) to a growing season for continuous simulation, with multiple growing seasons requiring parameter adjustment occasioned by the offseason (e.g. winter soil recharge and stand development). Simulation would be driven by time series of plot-specific precipitation and  $D$  obtained by downscaling regional climate models. The supply–loss theory would yield plot-specific time series of growing season soil–canopy  $k$ ,  $E$ ,  $P$  and  $G$ .

Example calculations visualize the input–output for the theory and also some effects of xylem refilling (Fig. 7). Daily time steps are used with a very simple treatment of transpiration withdrawal, infiltration, groundwater flow, and hydraulic redistribution. The midday  $D$  input (e.g. Fig. 7a, ‘ $D$ ’ line) represents the typical growing season range for central Utah, USA (Bush *et al.*, 2008).



**Fig. 7** Driving the supply–loss theory with climate: consequences of xylem refilling. An aspen (*Populus tremuloides*) stand with no groundwater input is simulated. (a) Climatic inputs: midday time course of vapor pressure deficit (line) and daily precipitation totals (Rain bars). (b) Output of midday soil–canopy hydraulic conductance (gray  $k$  line) in the absence of postdrought xylem refilling, and corresponding canopy diffusive conductance (black  $G$  line). (c) Same outputs, but with complete postdrought xylem refilling (W refilling).



The soil is initially at field capacity, sizeable rains occur every 15th day (Fig. 7a, ‘Rain’ bars), and there is no groundwater input. The vegetation is a stand of aspen (*Populus tremuloides*, *K(P)* from Hacke *et al.*, 2001).

Among the outputs is a time course of midday soil–canopy  $k$  and  $G$  (Fig. 7b). When there is no xylem refilling,  $k$  declines monotonically in a step-wise manner with each drought (Fig. 7b, gray  $k$  line). As a result, the postdrought rebound in  $G$  is damped, and a more conservative use of water develops. Conversely, if xylem refills (Fig. 7c), the postdrought rebound in  $k$  translates to full rebound in  $G$ . The consequently rapid water use creates more extreme reductions in  $k$  and  $G$  through the season. Thus, a potential advantage of *not* refilling is to prepare the plant for more conservative water use and less water stress during a progressively drier growing season. The outcome would probably be different where drought was followed by abundant rainfall because full recovery would maximize use of a nonlimiting water supply. This quick study illustrates how the theory can be used to infer the context-specific consequences of hydraulic traits.

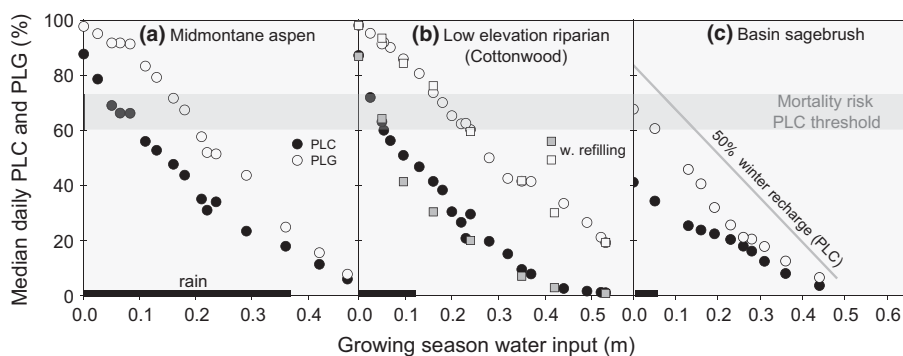
More generally, the theory can relate drought severity to the magnitude of the plant’s physiological response. To show how, growing seasons for three hydraulic types of woody vegetation in central Utah (USA) were simulated (Fig. 8): a low-elevation (1620 m) riparian cottonwood stand (*Populus fremontii*; Pockman & Sperry, 2000), midmontane aspen (2100–3000 m), and low-elevation (1300 m) sagebrush (*Artemisia tridentata*; Kolb & Sperry, 1999). Growing seasons start with soil at field capacity in keeping with the snow-driven hydrology of this temperate region (Dobrowolski *et al.*, 1990). Inputs from rain and groundwater were varied to simulate everything from a complete drought (no growing season water input) to no perceived drought (i.e. limited reduction in  $k$  or  $G$  of vegetation).

The simplest drought quantifier is the absolute amount of water added to the root zone during a growing season (Fig. 8, ‘Growing season water input’ axis), and simple physiological indices of the

drought response are growing season medians of midday PLC and PLG (relative to seasonal maxima; Fig. 8, black and white symbols, respectively). For all three vegetation types, at least 0.4 m of water input is needed to keep the median PLC below 10. As water input decreased below 0.4 m, median PLC and PLG increased in an approximately linear fashion, although the rate of increase was less in the cavitation-resistant and deeper rooted sagebrush (Fig. 8c). Whether or not the xylem refilled made little difference to the plant’s response (Fig. 8b, square ‘w. refilling’ symbols; circles represent no refilling). As predicted by the general behavior of the supply–loss framework (Fig. 4), median PLG increased faster with drought severity than PLC in all vegetation types. More complex drought indices (Heim, 2002) could be substituted for absolute water inputs, and various time course statistics could substitute for median PLC/PLG.

## VII. Implications for productivity and mortality: the chronic stress hypothesis

The scheme outlined provides a simple, yet mechanistically robust linkage between climate and the capacity of the plant to move water (soil–canopy  $k$ ) and access  $\text{CO}_2$  ( $G$ ). These are still esoteric variables if the goal is to predict drought effects on productivity and mortality. But it is easy to see how  $G$  could constrain productivity estimates. Briefly,  $G$  (expressed per unit leaf area) can be fed into photosynthesis models to obtain canopy and plot assimilation rate. Carbon allocation modeling can partition assimilation into its various sinks, including productivity (biomass growth). Many such models exist (Le Roux *et al.*, 2001), although they could benefit from a better understanding of phloem transport limitations (Sevanto, 2014). Being able to constrain estimates of drought-induced productivity decline by using hydraulically derived  $G$  would be an important advance for assessing impacts of climate-change droughts on ecosystem carbon cycling (Zhao & Running, 2010).



**Fig. 8** Projected drought impacts on plant health using a climate-coupled supply–loss framework. Median daily PLC (% loss hydraulic conductance of stand) and PLG (% loss diffusive conductance of canopy) over a central Utah (USA) growing season vs growing season water inputs (soil initially at field capacity). The gray band at *c.* 60–70 median PLC is associated with increased risk of mortality according to the ‘chronic stress’ hypothesis. (a) Midmontane aspen (*Populus tremuloides*) stand. Normal growing season rainfall (black ‘Rain’ bar) prevents PLC > 20, suggesting reliance on rain vs groundwater; 30% of normal rain would threaten stands. (b) Low-elevation, riparian cottonwood forest (*P. fremontii*). Normal rainfall barely keeps stands below the risk threshold, indicating reliance on riparian groundwater. Reductions in groundwater flow from long-term winter droughts or human usage would threaten stands. Adding xylem refilling makes little difference (square ‘w. refilling’ symbols). (c) Low-elevation basin sagebrush (*Artemisia tridentata*). Zero growing season water input fails to threaten stands when soil starts at field capacity, consistent with very low rainfall and remote water tables in sagebrush habitat. Stands would be threatened by dry winter–spring seasons that reduce soil recharge. Initial soil content of 50% field capacity would threaten stands even in a normal summer rain year (gray 50% recharge line for PLC).

It is more difficult to define a mechanistic link between hydraulic theory and mortality. Just as it can be difficult to pinpoint the actual cause of death in humans, it is proving difficult to do so in water-stressed trees (Sala *et al.*, 2010; Anderegg *et al.*, 2012a; McDowell *et al.*, 2013). Rather than attempt to specify each link in every chain of mortal causation, it is probably easier to identify 'risk factors' that can kill by innumerable proximal causes.

A growing body of work on drought mortality points to a hydraulic risk factor, embodied by what we call the 'chronic stress' hypothesis. According to this hypothesis, chronically high PLC (e.g. above *c.* 60) induced by cavitation tends to precede mortality. In a study of pinyon–juniper woodland (*Pinus edulis* and *Juniperus monosperma*), tree mortality was compared with tree hydraulics using the Sperry *et al.* (1998) model (Plaut *et al.*, 2012; McDowell *et al.*, 2013). Predicting soil–canopy PLC over multiple growing seasons suggested that none of the trees went 'critical' (PLC = 100), but trees of both species that ultimately died were unique in spending over 50% of their growing season days at a PLC > 68. The TREES model (Mackay *et al.*, 2003) came to a similar conclusion (McDowell *et al.*, 2013). Extensive study of natural aspen stands has associated mortality with PLC > 60 in root and stem segments, with the potential for a long lag time between PLC-inducing drought and ultimate death (Anderegg *et al.*, 2012b, 2013a). A link between branch PLC > 70 and dieback was found in several species growing naturally in Texas and Australia (Rice *et al.*, 2004; Kukowski *et al.*, 2013). A large number of pot or garden studies of controlled drought have come to similar conclusions (Tyree *et al.*, 2002, 2003; Brodrribb & Cochard, 2009; Kursar *et al.*, 2009; Brodrribb *et al.*, 2010; Galvez *et al.*, 2011, 2013; Mitchell *et al.*, 2012; Adams *et al.*, 2013; Barigah *et al.*, 2013; Urli *et al.*, 2013).

The chronic stress hypothesis does not specify the actual cause of death, which could be complex and variable. Cavitation itself may not kill the plant, because xylem pressures would have to drop to  $P_{crit}$  (soil–canopy PLC = 100) for desiccation to occur. Nevertheless, a large safety margin from  $P_{crit}$  can be associated with a very narrow margin of error from  $E_{crit}$  (e.g. Fig. 3b, drought-stressed supply–loss functions), and it is possible that brief excursions of  $E$  above the loss function 'ideal' (e.g. caused by rapid increases in  $D$ ) could trigger death by desiccation during severe drought (Davis *et al.*, 2002). But even if cavitation itself does not kill, chronically high PLC > 60 will certainly be associated with even higher PLG (> 80; Fig. 8), and hence chronically low photosynthetic rate and productivity (Lu *et al.*, 2010; Galvez *et al.*, 2011, 2013; Anderegg *et al.*, 2012b; Plaut *et al.*, 2012; Adams *et al.*, 2013; Limousin *et al.*, 2013; Poyatos *et al.*, 2013). Low  $k$  and  $P$  may also affect growth independently of photosynthetic rate by limiting cell expansion, reducing membrane permeability, and disrupting phloem transport (Woodruff *et al.*, 2004; Vilagrosa *et al.*, 2010; Sala *et al.*, 2012; Hartmann *et al.*, 2013; Mencuccini *et al.*, 2013; Sevanto *et al.*, 2013; Sevanto, 2014). Low photosynthetic rates increase susceptibility to heat and light stress (Chaves, 1991). All of these biotic stresses can increase susceptibility to pests (Mattson & Haack, 1987; Clifford *et al.*, 2013).

Short-term stresses associated with high PLC and low productivity may eventually trigger positive feedbacks that reinforce the persistence of high PLC after a drought is over. Such feedbacks could include reduced recovery of water uptake and transport by limited growth in root and shoot, loss of leaf area, impaired refilling, and even shifts towards a *more* vulnerable  $k(P)$  function (Resco *et al.*, 2009; Anderegg *et al.*, 2013b; Plaut *et al.*, 2013; Poyatos *et al.*, 2013; Sevanto *et al.*, 2013). Positive feedbacks would amplify shorter term reductions in  $k$ ,  $G$ ,  $P$  and productivity, creating a vicious cycle that ultimately dooms the plant long after the drought has passed. Such feedbacks have been implicated in the sometimes long lag time between drought and mortality (Anderegg *et al.*, 2013b).

The chronic stress hypothesis is more transparently inclusive than the hydraulic failure–carbon starvation framework (McDowell *et al.*, 2008), in that it avoids specifying why trees die from drought, hence acknowledging roles of multiple stresses that accompany reduced water transport. At the same time, it is explicit in identifying low plant hydraulic conductance as a risk factor. *Plants with chronically depressed hydraulic and diffusive conductances should die at higher rates.*

Although the chronic stress hypothesis is moot on the cause of death, it is a useful concept because PLC and PLG are readily predictable from climate (e.g. Fig. 8), and risk thresholds can be used to identify and forecast drought-related threats to plant health (Fig. 8, gray 'Mortality risk threshold' band). For example, the typical growing season rainfall in a midmontane aspen stand appears sufficient to keep median PLC at a relatively healthy 20 (Fig. 8a, horizontal 'Rain' bar on Water input axis), consistent with a strong reliance of these stands on summer rain (vs groundwater reliance; Anderegg *et al.*, 2013a). However, if growing season rain falls to  $\leq 30\%$  of typical values, these stands would reach or exceed the mortality risk threshold of PLC  $\geq 60$ . The conclusion from this mock simulation would be that midmontane aspen forests would be seriously threatened by a growing season drought of  $\leq 30\%$  normal rainfall.

The lower elevation cottonwood forest exhibits a different vulnerability (Fig. 8b). At valley elevations (*c.* 1650 m), typical growing season rain is barely sufficient to keep the cottonwood stand below the PLC threshold (Fig. 8b, 'Rain' bar). This is consistent with the absolute dependence of these riparian trees on groundwater for survival in a drier climate (Rood *et al.*, 2000). Groundwater flow is influenced mostly by long-term trends in winter precipitation (Castle *et al.*, 2014). Thus, these riparian species would be predicted to be more vulnerable to chronically low winter snowpacks (and human groundwater draw-down) than to summer droughts.

Different again is the low-elevation sagebrush example (Fig. 8c). Because of the deeper root system and greater cavitation resistance of sagebrush, these stands appear to survive even a completely dry summer with no groundwater input, because their maximum possible median PLC at zero water input is below the mortality threshold. This is consistent with the extremely low summer rainfall (Fig. 8c, Rain bar) and remote water table of the sagebrush habitat (Kolb & Sperry, 1999). Much of this shrub's water supply is from winter recharge of the rooting zone (Dobrowolski *et al.*,

1990). As a result, this species is most vulnerable to *winter* drought, even a short-term winter drought. Simulations indicate that a single dry winter that reduces soil recharge by 50% of field capacity would be more than enough to threaten sagebrush health by driving the stand above the mortality threshold (Fig. 8c, gray 50% winter recharge for median PLC).

These examples are hypothetical, but demonstrate the mechanistic rigor of using hydraulic theory to quantify plant responses to climate. The approach captures the likelihood that not all climatic variables are equally important across sites and plants. The theory's utility is not dependent on the validity or particulars of the chronic stress hypothesis. Regardless of whether subsequent observations support or undermine the existence or constancy of a particular PLC/PLG threshold for mortality, the ability to predict transpiration and productivity in response to drought is an important advance in and of itself. Nevertheless, it seems a robust assumption that plant health will decline over time if water and carbon are being exchanged at a fraction of normal rates.

### VIII. Conclusion

Plant hydraulics offers important tools for predicting how the planet's terrestrial vegetation will respond to climate change. We have emphasized basic hydraulic principles and their utility rather than details of implementation in hopes of encouraging the modeling community to experiment with the supply–loss concept and adapt it to their needs. The intentionally parsimonious theory we advance is no more complex than the representation of soil physics already present in most land surface models, and yet it provides a mechanistically based estimate of how plant water and CO<sub>2</sub> fluxes respond to soil and atmospheric water deficits. The rapidly growing database of vulnerability curves (Choat *et al.*, 2012) facilitates adding 'xylem physics' to close the gap between climatic water stress and the physiological regulation of gas exchange. Tying a water loss function to hydraulic supply is a powerfully simple way to represent complex stomatal regulation under water-limiting conditions. The concept of hydraulic types can augment the plant-functional-type approach already in use for representing species-specific drought responses, with care taken to incorporate intraspecific variation (Anderegg, 2014). Testing the hydraulic supply–loss theory is obviously a crucial step, but not a difficult one, given the number of suitably instrumented natural stands and plantations around the world.

### Acknowledgements

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