

# Capacitive effect of cavitation in xylem conduits: results from a dynamic model

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## ABSTRACT

**Embolisms decrease plant hydraulic conductance and therefore reduce the ability of the xylem to transport water to leaves provided that embolized conduits are not refilled. However, as a xylem conduit is filled with gas during cavitation, water is freed to the transpiration stream and this transiently increases xylem water potential. This capacitive effect of embolism formation on plant function has not been explicitly quantified in the past. A dynamic model is presented that models xylem water potential, xylem sap flow and cavitation, taking into account both the decreasing hydraulic conductance and the water release effect of xylem embolism. The significance of the capacitive effect increases in relation to the decreasing hydraulic conductance effect when transpiration rate is low in relation to the total amount of water in xylem conduits. This ratio is typically large in large trees and during drought.**

*Key-words:* capacitance; stomatal conductance; water storage; xylem transport.

## INTRODUCTION

Xylem embolism formation by cavitation causes a decrease in plant hydraulic conductance (Tyree & Sperry 1989), which could eventually lead to reduced photosynthetic rates and biomass production because of stomatal closure. Without stomatal control, excessive embolism formation would eventually lead to 'runaway cavitation' (Tyree & Sperry 1988), a situation where cavitation causes a decreased hydraulic conductance and xylem water potential, which in turn leads to more cavitation in a vicious cycle until all water conducting capacity is lost. Nevertheless, cavitation is a common occurrence in most plant species. Plants may not suffer permanently from the loss in hydraulic conductance caused by cavitation as embolized conduits are replaced by new conduits every year, and in many species embolized conduits have been documented to be refilled, even under considerable xylem water tensions (e.g. Salleo *et al.* 1996, 2001; Holbrook & Zwieniecki 1999; Melcher *et al.* 2001; Perks, Irvine & Grace 2004). Furthermore, as shown by a modelling study (Jones & Sutherland

1991), it may actually be better for a plant to allow some cavitation to occur in order to maintain higher gas exchange rates even if the loss in hydraulic conductance is permanent.

Another consequence of cavitation that has received little attention is that cavitation is always associated with a release of tension in the transpiration stream. As a xylem conduit cavitates, it becomes filled with water vapour or gas, and nearly all of the liquid water inside it is freed to the transpiration stream. As xylem conduits are quite inelastic and liquid water itself is practically incompressible, even a small amount of extra water released from an embolizing conduit will bring about a relatively large increase in the water pressure of the surrounding xylem tissue. Cavitation will therefore affect the water status of a plant positively in the short-term because of the capacitive effect described earlier. This was also demonstrated in an experiment by LoGullo & Salleo (1992) in which water from cavitated vessels rehydrated already dehydrated twigs of *Populus deltoides*.

Studies of whole-tree water use have suggested the possibility that cavitation plays a role in the water storage capacity of trees (e.g. Schulze *et al.* 1985; Cermák *et al.* 2007), and that the role of the water freed by cavitation needs further investigation. Meinzer, Clearwater & Goldstein (2001) suggested that water freed by cavitation might play a more important role in the water balance of a plant than was previously thought. The capacitive effect of cavitation was also measured by dehydration isotherms to be much larger than other water storage compartments for conifer species at physiologically important water potentials (Tyree & Yang 1990). Various measurements have also demonstrated that the stem water content of trees can vary seasonally by many tens of percents (e.g. Waring & Running 1978; Waring, Whitehead & Jarvis 1979; Nikinmaa *et al.* 1996, Scholz *et al.* 2007; Sperry, Meinzer & McCulloh 2008), and – at least in conifers – this change in stem water content can only come from changes in the number of embolized conduits. Waring *et al.* (1979) also calculated that these changes in stem water content play an important role in the water balance of trees by acting as water release and storage components, the magnitude of which is not marginal relative to transpirative water loss. But still, a theoretical framework is missing to quantify the effect. Although the relationships among cavitation, water

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potential and gas exchange have been studied extensively by manipulative experiments and modelling studies (e.g. Tyree & Sperry 1988; Bond & Kavanagh 1997; Salleo *et al.* 2000), the effect of the water released by cavitating conduits on plant water balance has not been explicitly taken into account. An exception to this is a study by Hölttä *et al.* (2002) where the water freed by cavitating conduits is taken explicitly into account when considering the effect of cavitation on xylem water potential.

In addition to cavitation, only the elastic shrinkage of xylem conduits (Irvine & Grace 1997; Perämäki *et al.* 2001) and living cells in the xylem and bark, and capillary storage in wood cell lumina can offer additional water retrieval and storage mechanisms (Tyree & Yang 1990; Tyree & Zimmermann 2002). Most of the capillary storage and retrieval of water occurs above water potentials of  $-0.5$  MPa so it is not an important capacitive mechanism encountered during typical midday transpiration rates (Tyree & Zimmermann 2002). Xylem conduits are quite inelastic, so their diurnal volumetric changes also contribute very little to capacitive water storage and retrieval (Perämäki *et al.* 2001). Conversely, more elastic living cells in the xylem and bark can potentially be a larger source of water during decreasing xylem water potential.

The aim of this study is to quantify the effects that cavitation has on plant water status, using a dynamic model based purely on physical principles and incorporating both effects of cavitation, namely, the loss of hydraulic conductance and the capacitive effect. It will be demonstrated that water freed by cavitation can buffer xylem water potentials against transient changes in transpiration and in fact protect a plant from runaway cavitation over short intervals. The effects of cavitation on stomatal gas exchange are considered for the case of isohydric stomatal control. It is also shown that relatively large amounts of cavitation could be beneficial for tree gas exchange, provided that embolized conduits are periodically refilled.

## A DYNAMIC FORMULATION OF CAVITATION

In a steady-state formulation of xylem water transport all capacitive effects are neglected and the effects of cavitation on plant water status are limited to the loss in conductance. A dynamic situation has to be considered in order to estimate the capacitive effect of cavitation on plant water status. In a numerical model, the model tree is divided into  $n$  homogeneous elements arranged in series without ramifications. Following a numerical model of dynamic xylem sap flow by Perämäki *et al.* (2001), transpiration occurs from the topmost element and water is drawn from the soil to the bottom-most element. Formulating the capacitive effect of cavitation follows Hölttä *et al.* (2002). The equations of xylem water flow ( $Q$ ), water mass in xylem conduits ( $m$ ), xylem conduit volume ( $V$ ; the volume that transports water), water pressure ( $P$ ) and xylem conductance ( $k$ ) are written for each element  $i$  (where  $i = 1$  at the bottom):

The change in the mass ( $\text{kg s}^{-1}$ ) of water in an element is

$$\frac{dm_i}{dt} = Q_{i,\text{in}} - Q_{i,\text{out}}, \quad (1)$$

where  $Q_{i,\text{in}}$  and  $Q_{i,\text{out}}$  are the water flow rates ( $\text{kg s}^{-1}$ ) in and out of the elements, respectively and they are written as

$$Q_{i,\text{in}} = \frac{k_i}{l_i}(P_{i-1} - P_i), \quad (2)$$

$$Q_{i,\text{out}} = Q_{i+1,\text{in}}, \quad (3)$$

where  $k_i$  is the hydraulic conductivity ( $\text{kg m Pa}^{-1} \text{s}^{-1}$ ),  $l_i$  is element length (m) and  $P_i$  is pressure (Pa). Water flow to the bottommost element is calculated from soil water potential, and water flow out of the topmost element is calculated from transpiration rate ( $T$ ;  $\text{kg s}^{-1}$ ).

$$Q_{1,\text{in}} = k_s(P_{\text{soil}} - P_1), \quad (4)$$

$$Q_{n,\text{out}} = T, \quad (5)$$

where  $k_s$  is the hydraulic conductance between the soil and the bottommost xylem element, and  $P_{\text{soil}}$  is the soil water potential. Hydraulic conductance is calculated from the Pammenter equation (Pammenter & Willigen 1998)

$$PLC_i = \{1 + \exp[a_i(P_i - b_i)]\}^{-1}, \quad (6)$$

$$k_i = k_{i,0}(1 - PLC_i), \quad (7)$$

where  $PLC_i$  is the relative loss of initial hydraulic conductance  $k_{i,0}$  caused by cavitation,  $b_i$  (Pa) is the  $PLC_{50}$  value, that is, the water potential for which half of the hydraulic conductivity is lost and  $a_i$  ( $\text{Pa}^{-1}$ ) is a parameter describing the steepness of the vulnerability curve in relation to water potential. The change in water pressure of an element is calculated from Hooke's law to be (Dainty 1963)

$$\frac{dP_i}{dt} = E \frac{1}{V_i} \frac{dV_i}{dt}, \quad (8)$$

where  $V_i$  is the volume ( $\text{m}^3$ ) of the water transporting elements (volume of the water filled conduit lumens in the element) and  $E$  is the elastic modulus (Pa) of the xylem conduits, approximated to be constant. The change in  $V_i$  is composed of two terms: one arising from water movement in or out of the element (the first term in Eqn 9) and another arising from the change in the gas volume caused by cavitation, the second term in Eqn 9

$$\frac{dV_i}{dt} = \frac{1}{\rho} \frac{dm_i}{dt} + \frac{dV_{g,i}}{dt}, \quad (9)$$

where  $\rho$  is water density ( $\text{kg m}^{-3}$ ), and  $dV_{g,i}$  is the change in the gas volume of the element caused by embolism formation ( $\text{m}^3$ ).

A linear relation is assumed between  $dV_{g,i}$  and the change in PLC, as was experimentally found by Tyree, Davis & Cochard (1994):

$$dV_{g,i} = V_i dPLC. \quad (10)$$

We recognize, however, that more complicated scenarios could occur depending on, for example, the redundancy of the conduit network (Tyree *et al.* 1994; Loepfe *et al.* 2007). Results for some more complicated scenarios for the relation are shown in the Supporting Information.

Equations 1 to 10 are solved numerically with the Runge–Kutta algorithm. Transpiration rate and soil water potential are given as boundary conditions to the model. The only addition to ‘traditional’ dynamic xylem water transport formulation is the second term on the right side of Eqn 9, which explicitly describes the change in the water-filled volume caused by cavitation. This increase in volume brings about a pressure rise, which is the capacitive effect of cavitation. In the simulations, it is assumed that the gas phase, water vapour or air, fills the embolizing conduits instantaneously. In reality, this might not always be the case (Hölttä, Vesala & Nikinmaa 2007), as it might take some time for the gas phase to fill an embolizing conduit. In this case, there is a time lag between the induction of cavitation and the full capacitive effect.

## THE CASE OF DECREASING SOIL WATER CONTENT (DROUGHT)

We use the dynamic cavitation model to study embolism formation during decreasing soil water content (drought). For that we need to model also the soil water potential and soil conductance as a function of soil water content using empirical soil water retention equations (Campbell 1974)

$$\Psi_s = \Psi_c \left( \frac{\theta}{\theta_{sat}} \right)^{-b_s}, \quad (11)$$

$$K_s(\Psi) = K_{sat} \left( \frac{\Psi_c}{\Psi_s} \right)^{2+3/b}, \quad (12)$$

where  $K_{sat}$  is saturated conductivity ( $\text{mol m}^{-1} \text{s}^{-1} \text{Pa}^{-1}$ ),  $\Psi_c$  is the air entry water potential (Pa),  $\Psi_s$  is the soil water potential (Pa),  $b_s$  an empirical coefficient (dimensionless) related to the clay content of the soil,  $\theta$  is volumetric water content ( $\text{m}^3 \text{m}^{-3}$ ) and  $\theta_{sat}$  is water content at saturation ( $\text{m}^3 \text{m}^{-3}$ ; assumed to be equal to the total pore fraction of the soil).

The effect of different soil layers and a varying water potential and soil conductivity as a function of distance away from the roots are not considered, instead soil water potential and soil conductivity will be given a spatially constant value for simplicity and also because soil water movement is not of main concern in this study. The water flux between the lowest compartment in tree and soil will be

$$Q_{in,1} = k_s(\Psi_s - P_1), \quad (13)$$

where  $k_s$  ( $\text{kg s}^{-1} \text{Pa}^{-1}$ ) is ‘the effective hydraulic conductance for water uptake by roots’.  $k_s$  is expressed in terms of  $K_s$  (adapted from Duursma *et al.* 2008) as

$$k_s = R_1 \frac{2\pi}{\log\left(\frac{r_{cyl}}{r_{root}}\right)} M_{H_2O} K_s, \quad (14)$$

where  $M_{H_2O}$  is the molar mass of water ( $0.018 \text{ kg mol}^{-1}$ ),  $R_1$  is root length index ( $\text{m root m}^{-2}$  soil surface area),  $r_{root}$  root radius (m) and  $r_{cyl}$  (m) the radius of a cylinder of soil to which the root has access to.

A subsequent decrease in the amount of soil water content is calculated from Eqn 13 assuming that water will be drawn from a certain soil volume ( $V_s$ ;  $\text{m}^3$ ).

$$\frac{d\theta}{dt} = \frac{Q_{in,1}}{V_s}. \quad (15)$$

The value for  $V_s$  can be estimated from soil rooting depth and the density of trees.

$$V_s = \frac{R_d}{D_t}, \quad (16)$$

where  $R_d$  is soil rooting depth [m] and  $D_t$  is density of trees [ $\text{m}^{-2}$  (soil area)].

## PARAMETRIZATION

The model tree is given a homogeneous structure, where xylem sapwood cross-sectional area and hydraulic conductivity are spatially constant. The model tree is exclusively composed of xylem sapwood, that is, no living tissue is included, therefore making the model more applicable to coniferous species (Sperry, Hacke & Pittermann 2006). However, some results for a structure with elastic tissue included are shown in the Supporting Information. The rate of cavitation, that is, the decline in hydraulic conductivity and the decrease in xylem water-filled conduit volume, is calculated from xylem potential using Eqn 6 at the topmost xylem element and, for simplicity, assumed to be the same throughout the entire tree. A more realistic option would be to iteratively assign a vulnerability function at each vertical height in the tree so that the embolism rate would be spatially constant. This, however, would be a tedious task and would not bring new insight into the phenomena under study. The number of elements  $n$  is given a value of 40 and the time step is given a value of 0.001 s. The time step had to be maintained at such a low value in order to prevent the xylem water potential from oscillating as cavitation occurs. This accuracy was deemed sufficient as increasing the spatial resolution or reducing the time step did not change the results noticeably although minor oscillations in xylem water potential still existed in some cases.

Values are assigned to the parameters in Eqns 1 to 9 describing tree structure and vulnerability to cavitation. The parameterization is presented in Table 1 and represents a typical Scots pine tree. The elastic modulus of xylem

**Table 1.** Parameters for the model tree structure

Parameter	Value
Tree height	10 m
Total amount of available water in sapwood	0.4 m <sup>3</sup>
Maximum transpiration rate ( $T$ )	$1.0 \times 10^{-6} \text{ m}^3 \text{ s}^{-1}$
Cumulative transpiration rate during one day	40 L
Elastic modulus of xylem conduits ( $E$ )	1 GPa
Xylem hydraulic conductivity ( $k$ )	$3 \times 10^{-12} \text{ m}^3 \text{ m}^2 \text{ Pa}^{-1} \text{ s}^{-1}$
Soil-xylem hydraulic conductance ( $k_s$ )	$1.2 \times 10^{-11} \text{ m}^3 \text{ Pa}^{-1} \text{ s}^{-1}$
Soil water potential ( $P_{\text{soil}}$ )	0 Pa (not in the drought case)

conduits was given a value of 1 GPa (Irvine & Grace 1997). Hydraulic conductivity ( $k$ ) is given a value of  $3.0 \times 10^{-12} \text{ m}^3 \text{ Pa}^{-1} \text{ s}^{-1}$ , and hydraulic conductance between the xylem and soil ( $k_s$ ) a value of  $1.2 \times 10^{-11} \text{ m}^3 \text{ Pa}^{-1} \text{ s}^{-1}$  (equivalent to hydraulic conductance over a 0.25-m distance of the xylem sapwood). Maximum transpiration rate is given a value of  $1.0 \times 10^{-6} \text{ m}^3 \text{ s}^{-1}$  and the volume of water in the xylem (sapwood cross-sectional area times tree height) is 0.4 m<sup>3</sup>. However, it turns out that the individual values for the transpiration rate and the volume of water in the xylem sapwood per se do not influence the model behaviour, but it is their ratio that is important. Therefore, we introduce a dimensionless scaling factor,  $G$ , and define it to be equal to the ratio of the total amount of water in the xylem conduits of the tree to the amount of water transpired in a day.  $G$  is a useful variable, among other factors, as it describes the magnitude of the capacitive effect of cavitation compared with the conductance effect.  $G$  can also be thought of as the ratio of water in storage to the demand of water for transpiration. A scaling factor of 1 for  $G$  may be typical of a young, small-diameter Scots pine sapling, whereas a scaling factor of around 10 is typical of a 30-year-old, 25-cm diameter Scots pine tree (Mencuccini & Grace 1996).

The relationship between the developing xylem water potential and vulnerability to cavitation determines how much cavitation occurs. When PLC<sub>50</sub>, that is, parameter  $b$  in Eqn 6, was varied, the value of the parameter  $a$  was also changed in inverse proportion to  $b$  to retain the proportionality between these two parameters (Cochard 2006). For a PLC<sub>50</sub> of  $-2 \text{ MPa}$ , parameter  $a$  was given a value of  $6.7 \times 10^{-6} \text{ Pa}^{-1}$ . The parameterization for the soil hydraulic properties during the decreasing soil water content case is presented in Table 2. The values chosen for soil rooting depth ( $R_d$ ) and density of trees ( $D_d$ ) lead to a volume of 5 m<sup>3</sup> from which the tree extracts its water. All parameters were chosen to represent accurately an example site, which is the Helsinki University SMEAR II forestry station in Hyytiälä, southern Finland. The site has a mean annual temperature of 2.9 °C, a mean annual precipitation of 710 mm and hosts a stand of 45-year-old Scots pine trees

with a mean tree height of approximately 16 m. Vesala, Haataja & Aalto (1998) provided a detailed description of the site.

## MODEL RUNS AND RESULTS

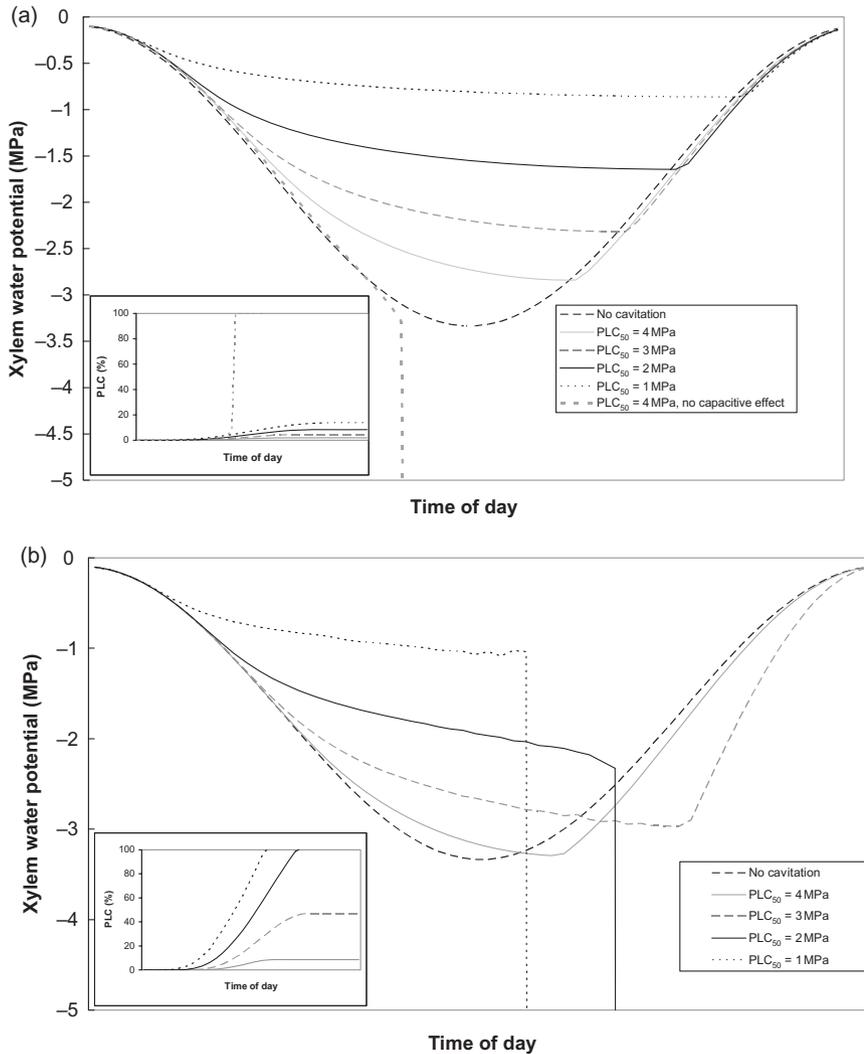
### The effect of cavitation on xylem water potential when transpiration is fixed

Diurnal transpiration rate was given a sinusoidal form (the positive half of the sine function with a period of 48 h multiplied by the maximum transpiration rate) and the dynamics of xylem water potential and cavitation during one day were modelled with the numerical model (Fig. 1). The value of the scaling factor  $G$  is 10 in Fig. 1a, and 1 in Fig. 1b. Various vulnerabilities to cavitation, that is, values of  $b$  (PLC<sub>50</sub>, i.e. the xylem water potential where half of the hydraulic conductance is lost because of cavitation) are shown for both cases. A case without cavitation and a case with cavitation but with the capacitive effect excluded (i.e. second term of Eqn 9 set to zero) are also shown for comparison to demonstrate explicitly the capacitive effect of cavitation. All conduits are assumed to be water-filled at the beginning of the simulation.

The water freed from cavitation buffers changes in transpiration effectively for the case where the value of the scaling factor  $G$  is 10 (Fig. 1a). With cavitation, xylem water potential remains much above the water potential of the case without cavitation. This demonstrates that the xylem can be extremely vulnerable to cavitation and still avoid 'run-away' cavitation during a single day without stomatal control because of the capacitive effect of water freed by cavitation. In case in Fig. 1b, the transpiration rate is so high compared with the amount of water in the xylem conduits (i.e.  $G$  is low) that the capacitance effect caused by cavitation is not an effective buffer against the declining effect of hydraulic conductance caused by cavitation. In both cases shown in Fig. 1, 'run-away' cavitation is achieved with all of the PLC<sub>50</sub> values in the graph if the capacitive effect of cavitation is taken away from the formulation. In addition to the increase in the level of xylem water potential, cavitation also causes a time lag between transpiration (transpiration is nearly in the same phase as water potential in the case with no cavitation) and water potential as water for the

**Table 2.** Parameters for the decreasing soil water case (based on Duursma *et al.* 2008)

Parameter	Value
$\psi_s$	$-0.68 \text{ kPa}$
$b_s$	4.14
$\theta_{\text{sat}}$	0.62
$K_{\text{sat}}$	$24.5 \text{ mol m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$
$r_{\text{cyl}}$	$4.25 \times 10^{-3} \text{ m}$
$r_{\text{root}}$	$3.0 \times 10^{-3} \text{ m}$
$R_t$	5300
$R_d$	0.5 m
$D_t$	$0.1 \text{ m}^{-2}$



**Figure 1.** Xylem water potential at the top of the model tree during 1 d for various vulnerabilities to cavitation with the ratio of total water in xylem conduits to daily transpiration equal to (a) 10 and (b) 1. Complete loss of conductivity (runaway cavitation) is reached when leaf water potential collapses. Inset: percent loss of conductivity (PLC) during 1 d for various vulnerabilities to cavitation with the ratio of total water in xylem conduits to daily transpiration equal to (a) 10 and (b) 1.

transpiration stream is also withdrawn from the cavitating conduits during increasing transpiration in addition to being pulled from the soil. Time lags of up to several hours have also been measured between transpiration and water potential/sap flow in various experimental studies (Schulze *et al.* 1985; Goldstein *et al.* 1998; Wullschlegel, Meinzer & Vertessy 1998).

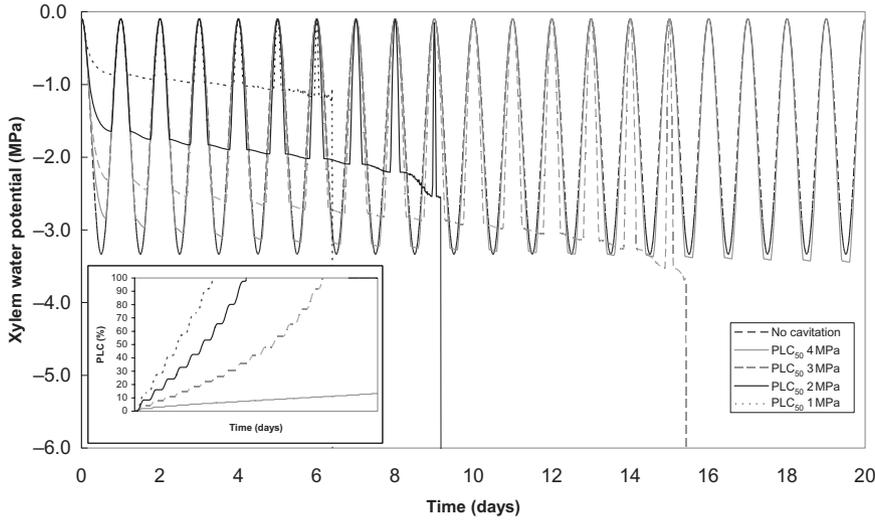
If the same transpiration rate as in Fig. 1a,b is maintained for many consecutive days without embolism refilling, the hydraulic effect of cavitation becomes more and more important compared with the capacitive effect. Figure 2 shows the case in Fig. 1a but now for 20 consecutive days without embolism refilling. With a higher vulnerability to cavitation, that is, lower PLC<sub>50</sub>, the capacitive effect of cavitation on the water balance is more clearly visible early during the modelled time period, but 'run-away' cavitation is reached sooner.

In all of these mentioned simulations, a proportional change in both transpiration rate and xylem volume did not change the results in any way as long as the hydraulic conductance was changed by the same factor as the transpiration rate, so that the xylem water potential remained the

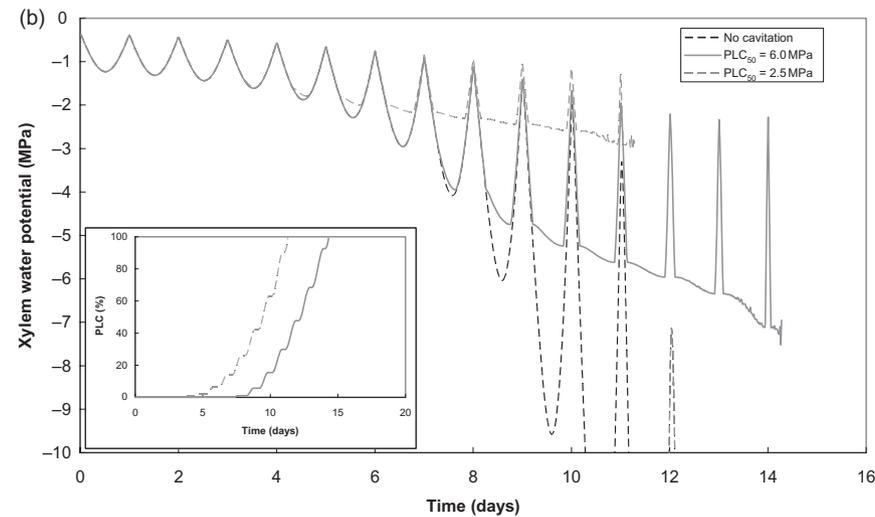
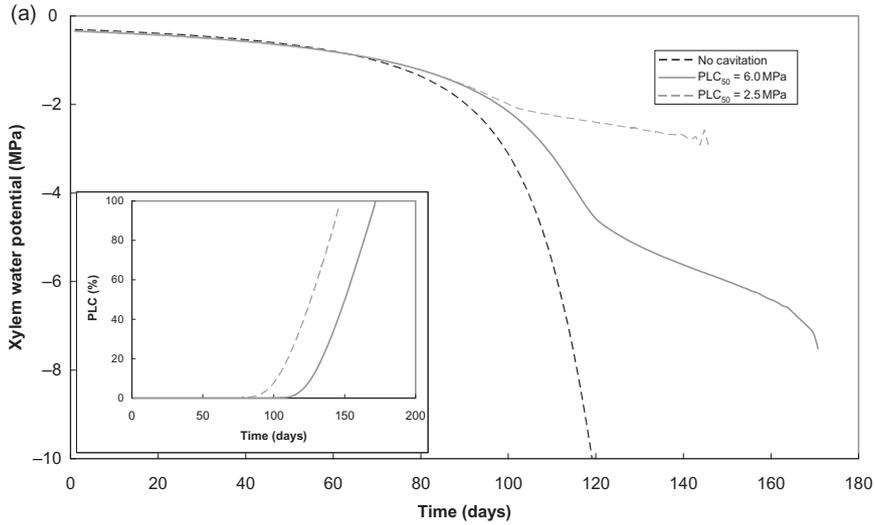
same (not shown). This allows the use of the scaling factor between xylem water volume and transpiration rate instead of considering the effects of many individual parameters on the results. Furthermore, with a scaling factor  $G = 1$ , a similar amount (although not exactly the same) of embolism is produced in one-tenth of the time compared with the case of  $G = 10$ .

### The case with decreasing soil water content (drought)

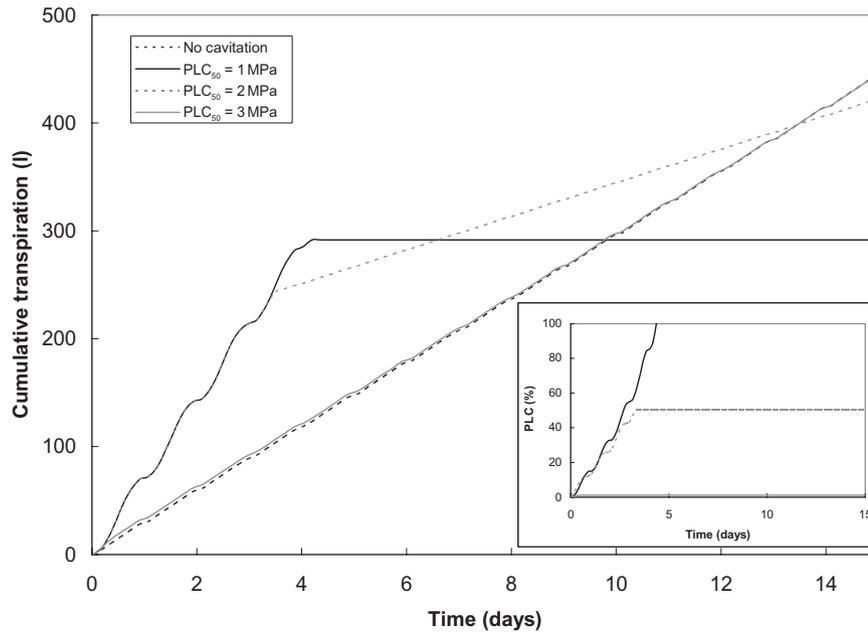
Next we simulated drought conditions with a decrease in transpiration to 2.5% (Fig. 3a) and to 25% (Fig. 3b) of its value compared with the case shown in Fig. 1b), that is, the scaling parameter  $G$  increases from 1 to 40 (Fig. 3a) or to 4 (Fig. 3b). This is mimicking complete (with only cuticular transpiration) or partial stomatal closure. Cases of various vulnerabilities (varying PLC<sub>50</sub>) to cavitation are shown. The leaf water potential remains higher during the drought when the xylem is more vulnerable to cavitation. Furthermore, the soil water potential (not shown) remains higher with higher vulnerability to cavitation as a larger part of the



**Figure 2.** Xylem water potential at the top of the model tree during 20 d for various vulnerabilities to cavitation with the ratio of total water in xylem conduits to daily transpiration equal to 10. Inset: percent loss of conductivity (PLC) during 20 d for various vulnerabilities to cavitation with the ratio of total water in xylem conduits to daily transpiration equal to 10.



**Figure 3.** Xylem water potential at the top of the model tree and percent loss of conductivity (PLC; inset) of a plant with and without cavitation during a decrease in soil water with transpiration decreased to (a) 2.5 and (b) 25 of its original value for  $G = 1$ . Complete loss of conductivity (runaway cavitation) is reached when leaf water potential line ends.



**Figure 4.** Cumulated transpiration for a case with isohydric stomatal control for cases with different vulnerabilities to cavitation. Inset: percent loss of conductivity (PLC) for cases with different vulnerabilities to cavitation.

water transpired is withdrawn from xylem instead of the soil. Even when over 99.9% of the xylem conduits are embolized (i.e. only 0.1% of conductance is left), the leaf water potential remains higher compared with the case with no cavitation. Only when practically all the xylem conduits have cavitated and there is no more water to be freed from cavitation, the xylem water potential collapses as runaway cavitation is reached. Naturally, the more vulnerable the plant is to cavitation, the sooner runaway cavitation is reached. When  $G$  is originally set to 10 like in the case of Fig. 1a (not shown) – that is, when the volume of the water in the tree xylem is 10 times larger than in Fig. 3a,b compared with the transpiration rate – the plant with a  $PLC_{50}$  of 2.5 or 6.0 MPa can survive without runaway cavitation up to many hundreds of days at the same time maintaining a higher water potential compared with the case without cavitation.

### Leaf gas exchange with isohydric stomatal control

Next, we let the transpiration rate vary diurnally as in the previous cases but in addition transpiration is sufficiently reduced when required in order to maintain water potential at all times above a threshold value (in this case  $-2.0$  MPa) to mimic isohydric stomatal control of transpiration. Figure 4 shows the cumulative transpiration from the beginning of the simulation, as a function of time, with  $G$  set to 10 (now total transpiration per day varies but the case without cavitation is used for the scaling). During the first several days, cumulative transpiration is much larger for the cases with cavitation compared with the case with no cavitation. In the cases with cavitation, the tree is able to maintain fully open stomata by withdrawing water by cavitation to replace the water lost to transpiration as long as the xylem water

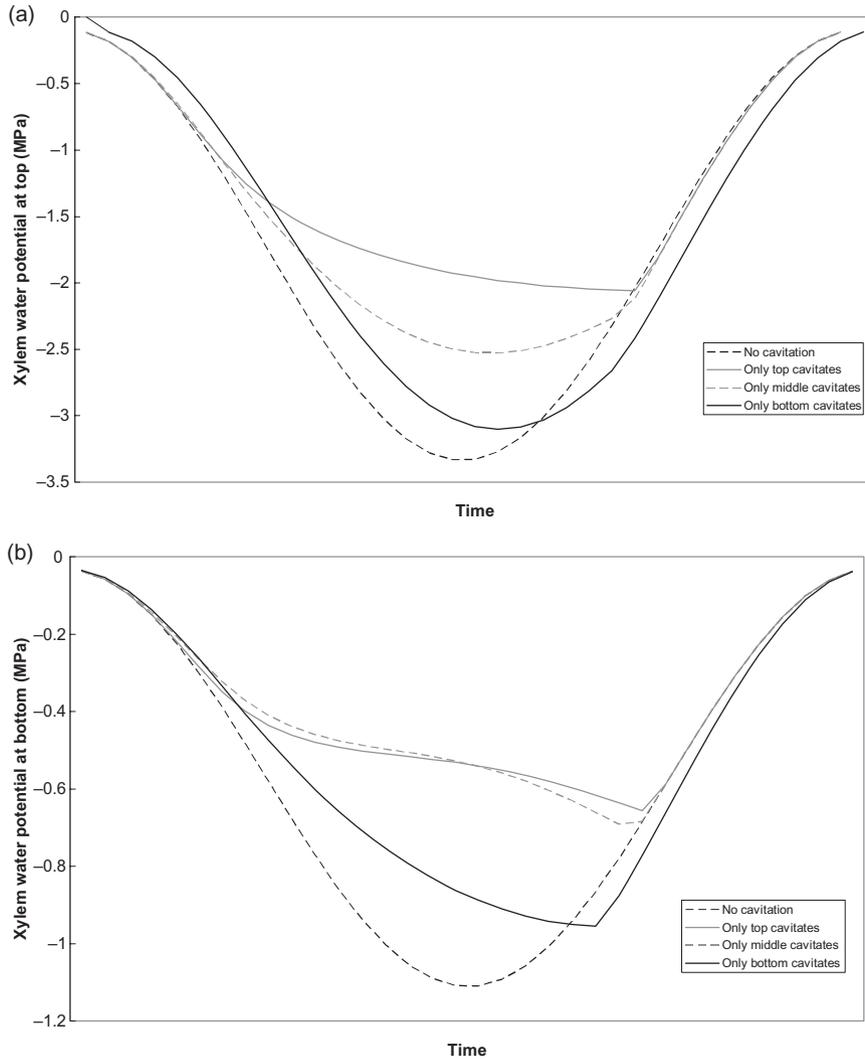
potential is maintained above the threshold. However, after the minimum water potential is reached, no more water can be released by cavitation and a steady state is reached. This steady-state stomatal conductance is now lower compared with case without cavitation because the hydraulic conductance has decreased because of cavitation.

Cavitation allows more gas exchange in the short-term with isohydric stomatal control because it frees water to the transpiration stream. Only in the long run, provided that no refilling of embolized conduits occurs, cavitation is unfavourable to cumulative leaf gas exchange. Theoretically, if embolism refilling occurs before this point, then cavitation will have allowed the plant to gain more carbon.

### Location of cavitation within the xylem pathway

Next, the simulations described in Fig. 1a were repeated but now the occurrence of cavitation was restricted to one-fourth of the xylem either at the top, middle or bottom. In each case, the cavitation rate was calculated based on the water potential of the topmost element of that part of the tree and cavitation rate of the other elements in that part were set to be equal to it. The vulnerability of the conduits was iteratively chosen for each case (i.e. for the top, middle and bottom fourths) to be such that the total amount of cavitation would be equal among the cases, 11% in the part in question. The other parameters were as before, with  $G = 10$ . A case with no cavitation is shown for comparison.

The capacitive effect of cavitation is larger, that is, the change in water potential because of the water released by cavitation is higher, the closer the position where cavitation occurs is to the leaves (Fig. 5). This is because when water is freed by cavitation nearer to the leaves, the transport distance to the evaporative surfaces is shorter and therefore



**Figure 5.** Xylem water potential at the (a) top and (b) bottom of the model tree during 1 d when cavitation is compartmentalized to one-fourth of the xylem with the ratio of total water in xylem conduits to daily transpiration equal to 10.

the viscous pressure losses caused by its transport are also lower.

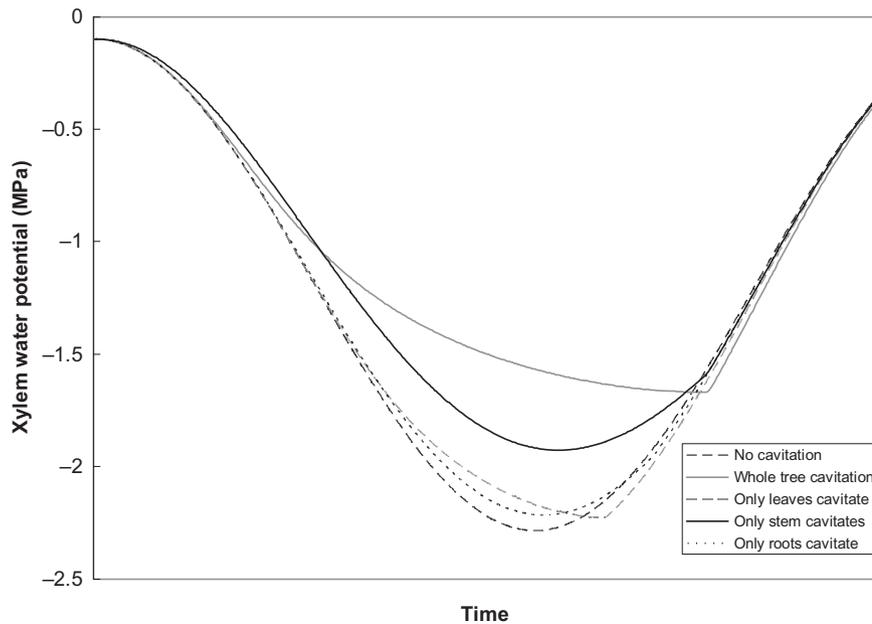
### Cavitation in a tree with various functional components

Finally, a simulation was made where the xylem pathway was divided into real functional components: leaves, stem + branches and roots, each of which was given realistic separate values of conductance and volume of water in the xylem conduits. The effect of cavitation of each on the plant water status was investigated. Table 3 shows the parameterization. Transpiration was fixed and xylem water potential

and embolism ratios were calculated (Fig. 6). In each case the cavitation rate was calculated in the topmost element of the compartment (i.e. in the topmost element of the leaf, stem + branch and root compartments) in question and cavitation rate of the other elements in that compartment were set to be equal to it. The vulnerability of the conduits was iteratively chosen for each compartment to be such that the total amount of cavitation would be equal (at 8%) among the different cases. *G* was set at 10. The other parameters were as before. A case with no cavitation is shown for comparison. Cavitation of the stem affects the water potential the most because it holds the largest amount of water. Cavitation in the leaves and roots contribute approximately

Compartment	Water in xylem conduits (percentage of the whole tree)	Hydraulic resistance (percentage of the whole tree)
Leaves	6%	44%
Stem + branches	67%	33%
Roots	28%	22%

**Table 3.** Parametrization of the volume and hydraulic resistance of the different compartments of a tree



**Figure 6.** Xylem water potential at the top of the model tree during 1 d for a model tree divided into functional components of leaves, stem + branches and roots.

equally to the water balance of the tree: roots have significantly more water in them compared to the leaves, so for a given loss in whole plant hydraulic conductance more water is freed, but on the other hand the capacitive effect per water freed is less significant as they are further away from the site of evaporation.

## DISCUSSION

A dynamic model reveals that cavitation may have a significant capacitive role in the xylem water relations of a plant. Provided that embolized conductive elements are refilled (Holbrook & Zwieniecki 1999), there is a distinct short-term physiological advantage in cavitation. Hence, optimal tradeoffs between transpiration rate, size of the conducting structure, its vulnerability to cavitation and climate could be determined. According to the model presented, water released by cavitation can play a significant role in buffering the water balance of plants, but unlike other water storage mechanisms (Tyree & Zimmermann 2002), cavitation affects the water potential and gas exchange capacity of trees in two ways. Cavitation leads to a loss of hydraulic conductance, causing a decrease in xylem water potential but it also has a capacitive effect because of the water freed to the transpiration stream. The positive effect of the latter increases in importance compared with negative effect of the former at least when: (1) the ratio of the total amount of water in xylem conduits to transpiration rate increases (i.e.  $G$  increases); (2) the ratio between the volume of water freed to whole plant hydraulic conductance loss increases; (3) cavitation occurs closer to leaves; or (4) the timescale for the refilling of the embolized conduits decreases.

When  $G$  is large, the xylem conduits act like a 'water reservoir' in addition to their role as a conducting system

and losses in hydraulic conductance caused by cavitation are not so critical to the water balance of a plant compared to the capacitive effect on a short timescale. This ratio can also be expressed as the transit time of water molecules through the xylem conduit system. For example, if  $G = 10$ , this means that it will take 10 d for the average water molecule to reach the evaporative surfaces in the leaves after it is taken up by the roots, provided that all water molecules are transported without delay or lateral exchange through the whole xylem pathway. The transit time is a useful parameter to estimate the scaling of the capacitive effect of cavitation as many measurements of transit times can be found in the literature. For example Perks, Irvine & Grace (2002) found the transit time of water molecules to be on average 12 d under normal field conditions for 41-yr-old Scots pine trees, whereas during drought transit times it was in excess of 6 weeks. Meinzer *et al.* (2006) observed transit times ranging between 2.5 and 21 d in 13.5 to 58 m coniferous species. Our simulation results indicate that within such a range of transit times, the capacitive role of cavitations is significant.

According to the metabolic scaling theory (West, Brown & Enquist 1999), transpiration scales to the power of three-fourths of total plant volume, and this was indeed found to be a good approximation (Meinzer *et al.* 2005). Therefore the scaling factor of water in xylem conduits to transpiration rate will generally increase with tree size, and the capacitive effect of water freed by cavitation will be larger in larger trees. Similarly, the water storage capacity in general increases with increasing tree size (e.g. Phillips *et al.* 2003). Meinzer *et al.* (2005) also found that for a given size, angiosperms transported considerably greater quantities of water than conifers. Therefore the capacitive effects of cavitation would be expected to be larger for conifer trees compared with angiosperm trees of the same size. The

importance of cavitation as capacitance in relation to elastic capacitance of living tissue is also expected to differ among groups and species. In conifers, the proportion of living cells is small so their capacitive effect should be correspondingly minor. In angiosperms living cells are typically more abundant so their capacitive role would be expected to be larger. For example, if living tissue with an elastic modulus of 30 MPa would be equal in volume to xylem conduit volume then a 1 MPa decrease in turgor pressure would free the same amount of water from the living cells as the cavitation of approximately 3% (= 1 MPa/30 MPa) of xylem conduits.

The ratio of water freed by cavitation to whole plant hydraulic conductance loss is also of high significance. In the model, Eqn 10 describes the ratio of water released to the transpiration stream to the increase in PLC locally, but at the whole tree level the situation is more intricate. For example, if cavitation occurred axially in an uneven fashion creating a 'hydraulic bottle neck' somewhere along the whole xylem translocation pathway, then less water could be freed per unit loss of whole plant hydraulic conductance. In theory, the beneficial effects of cavitation would be comparatively higher in those parts of the hydraulic pathway comprising a small part of the total resistance to sap flow but a large part of the total water volume available. In this type of compartment much water could be freed to the transpiration stream for a small loss of whole tree hydraulic conductance. A typical example would be the trunk of a tall tree, which includes only a minor part of the total resistance but holds much water in the xylem conduits. The techniques used in measuring vulnerability to cavitation have for a long time been limited to small-diameter wood segments, so little information is available on cavitation rates in trunks or plants larger than 2 cm in diameter (but see Domec & Gartner 2001 and Choat *et al.* 2005 for exceptions). Domec & Gartner (2001) found the trunks of mature Douglas fir trees to be operating at water potentials near the point of cavitation induction, whereas Choat *et al.* (2005) found distal regions of mature sugar maples to be more vulnerable to cavitation than the trunk. The time factor is also important in considering the effects of cavitation. The longer the time without refilling, the more important the conductive effect will be relative to the capacitive effect.

During drought, water freed by cavitation has an especially large importance on the water balance of plants as the loss in transpiration in relation to water in the xylem conduits is much smaller compared with a non-drought case. Furthermore, the plant functioning is affected very little by the loss in xylem hydraulic conductance provided that most of the hydraulic resistance is in the soil and a decrease in xylem conductance contributes very little to a decrease in the total hydraulic pathway conductance (e.g. Duursma *et al.* 2008). It is interesting to note that in the simulation results presented during drought, the water potential in the plant remained for a long time in the water potential range where most of the cavitation occurs, that is, around the water potential corresponding to the PLC<sub>50</sub>. The behaviour of the model in the drought conditions is dependent on the

parameters describing soil type, root size and density and tree density in Eqns 12 to 17. Sensitivity analysis to the parameters was not performed because of the large number of individual parameters.

Because of the water freed by cavitation, no tree larger than a small sapling is expected to run into runaway cavitation during short time periods. This implies that the stomata need not necessarily act immediately in response to changes in the atmospheric drivers for transpiration to avoid runaway cavitation. Therefore, at least larger trees do not necessarily operate near to the point of catastrophic xylem dysfunction caused by runaway cavitation (Tyree & Sperry 1988), as it would appear from steady-state xylem translocation and cavitation models and from comparisons between measured xylem water potentials and vulnerability curves. Cavitation itself prevents further cavitation at a short time scale because of its effect on releasing tension in the transpiration stream.

One reason why the capacitive effect of cavitation has remained so unnoticed could be that small plants are typically used in experiments where the effects of induced cavitation on plant water relations are studied (e.g. Sperry, Alder & Eastlack 1993; Hubbard *et al.* 2001). And maybe even more importantly, cavitation is typically induced only in a minor part of the hydraulic pathway and hence the amount of water freed is small compared with the loss in whole plant hydraulic conductance. However, Sperry *et al.* (1993) did notice a transient increase in stomatal conductance immediately after cavitation induction and this was proposed to be caused by the water freed by cavitation.

Theoretically, the extra carbon gain caused by the capacitive effect of cavitation could be compared with the carbon costs of refilling embolized conduits. There is clearly a metabolic cost to embolism refilling (e.g. Stiller, Sperry & Lafitte 2005; Lovisolo & Schubert 2006), which has not been quantified. If this metabolic cost turned out to be lower than the extra gain in carbon caused by short term cavitation, it could be formulated that cavitation and refilling cycles would actually be an adaptive mechanism to increase carbon gain. It is reasonable to argue that it is a good strategy for a plant to maintain high stomatal conductance at times of high irradiance, that is, during good conditions for photosynthesis, by freeing water to transpiration by cavitation, if the loss in hydraulic conductance can be repaired over a short time interval. Diurnal cavitation and refilling cycles have been observed in various studies and some have even documented embolism repair during the day under high water tensions (e.g. Canny 1997; Zwieniecki & Holbrook 1998; Bucci *et al.* 2003). If the observed diurnal trends in the diurnal embolism cycles are not artefacts of the method used (cryogenic scanning electron microscopy), and all of the water from the cavitating conduits is instantaneously released to the transpiration stream, then the capacitive effect of cavitation can play an enormous role in the water balance of these plants, and their water use can be highly decoupled from the steady-state water transport capacity during peak transpiration (Sperry *et al.* 2008).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** The relationship between *PLC* and the relative amount of air in the xylem conduits with varying values of *A* according to Eqn S4.

**Figure S2.** Xylem water potential at the top of the model tree during one day for various vulnerabilities to cavitation with the ratio of total water in xylem conduits to daily transpiration equal to ten and living tissue included. Inset: percent loss of conductivity (*PLC*) during 1 d for various vulnerabilities to cavitation with the ratio of total water in xylem conduits to daily transpiration equal to 10 (a).

**Figure S3.** Xylem water potential at the top of the model tree for various vulnerabilities to cavitation with the ratio of total water in xylem conduits to daily transpiration equal to 10 with different forms of Eqn 10. Inset: percent loss of conductivity (*PLC*) during 1 d for various forms of Eqn 10.

**Appendix S1.** Addition of surrounding living tissue.

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