

## Review

# Vulnerability to drought-induced cavitation in poplars: synthesis and future opportunities

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## ABSTRACT

**Vulnerability to drought-induced cavitation is a key trait of plant water relations. Here, we summarize the available literature on vulnerability to drought-induced cavitation in poplars (*Populus* spp.), a genus of agronomic, ecological and scientific importance. Vulnerability curves and vulnerability parameters (including the water potential inducing 50% loss in hydraulic conductivity,  $P_{50}$ ) were collected from 37 studies published between 1991 and 2014, covering a range of 10 species and 12 interspecific hybrid crosses. Results of our meta-analysis confirm that poplars are among the most vulnerable woody species to drought-induced cavitation (mean  $P_{50} = -1.44$  and  $-1.55$  MPa across pure species and hybrids, respectively). Yet, significant variation occurs among species ( $P_{50}$  range: 1.43 MPa) and among hybrid crosses ( $P_{50}$  range: 1.12 MPa), within species and hybrid crosses (max.  $P_{50}$  range reported: 0.8 MPa) as well as in response to environmental factors including nitrogen fertilization, irradiance, temperature and drought (max.  $P_{50}$  range reported: 0.75 MPa). Potential implications and gaps in knowledge are discussed in the context of poplar cultivation, species adaptation and climate modifications. We suggest that poplars represent a valuable model for studies on drought-induced cavitation, especially to elucidate the genetic and molecular basis of cavitation resistance in Angiosperms.**

**Key-words:** *Populus*; genetic variation; interspecific hybrids; phenotypic plasticity; pure species; trade-offs; water deficit; xylem anatomy.

## INTRODUCTION

In vascular plants, long-distance water transport occurs in xylem conduits under tension (i.e. negative pressure) as a result of water evaporating at the surface of the leaf mesophyll cell walls (Tyree & Zimmermann 2002). This places xylem conduits under the threat of cavitation, that is, a phase change of water from liquid to vapour. Drought-induced cavitation events take place in the bordered pits at the interface between water-filled and air-filled conduits when the xylem tension overcomes the capillary forces holding water

in the pit membrane pores (Sperry & Tyree 1988; Tyree & Sperry 1989). This leads to embolized (non-functional) conducting elements and decreased hydraulic conductivity, limiting leaf gas exchange and ultimately threatening plant survival (McDowell *et al.* 2008). During the last 25 years considerable knowledge has been gained with regard to the anatomical, physiological and ecological aspects of vulnerability to drought-induced cavitation in woody plants (e.g. Tyree & Sperry 1989; Hacke & Sperry 2001; Hacke *et al.* 2004; Maherali *et al.* 2004; Sperry & Hacke 2004; Choat *et al.* 2008, 2012). The number of species characterized has steadily increased and comparisons among species from a wide range of habitats have indicated that vulnerability to cavitation is related with the range of water stress experienced *in situ* (Kolb & Sperry 1999; Hacke *et al.* 2000; Pockman & Sperry 2000; Sperry 2000; Jacobsen *et al.* 2007; Pratt *et al.* 2007). Studies conducted at the tree level have recently demonstrated that xylem loss-of-function represents a direct limit to drought resistance and recovery (Brodribb & Cochard 2009; Brodribb *et al.* 2010; Barigah *et al.* 2013; Urli *et al.* 2013). Furthermore, recent data suggest that all forest biomes are equally vulnerable to hydraulic failure and actually operate with a tight safety margin, explaining why drought-induced forest die-offs do not only occur in arid regions (Choat *et al.* 2012). Vulnerability to drought-induced cavitation is therefore regarded as a key trait for plant water relations, which may have shaped plant communities and which might be important for the adaptive potential of species in a global change context (Lamy *et al.* 2014).

Poplar species (*Populus* spp.) represent an attractive and valuable forest resource under temperate latitudes for the paper industry and biomass production (Karp & Shield 2008; Dillen *et al.* 2011). The genus is genetically, morphologically and ecologically diverse, with about 30 species widely distributed over the northern hemisphere at temperate latitudes (Eckenwalder 1996). Most of them are considered as vegetational pioneers and much of the interest in planting poplar lies in their inherently high growth rates, which is nevertheless counterbalanced by their large water requirements and their high drought sensitivity. Drought-induced physiological responses in poplars have therefore been extensively studied, although most studies have focused on traits involved in acclimation processes under moderate drought such as radial

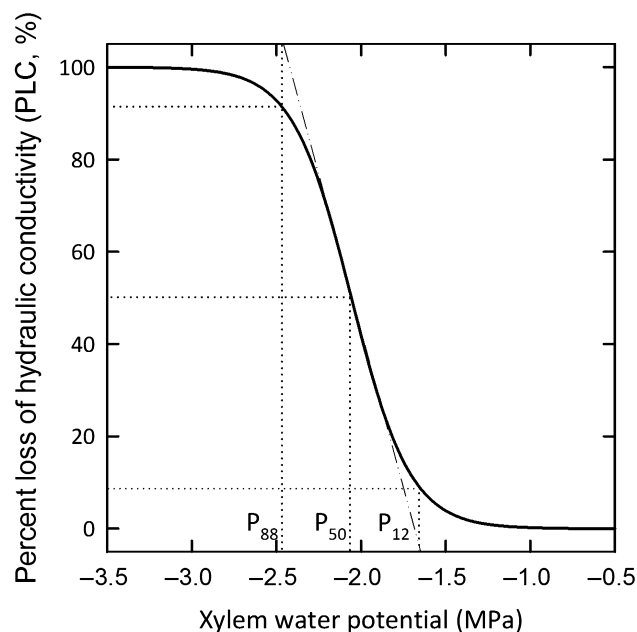
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growth dynamics (e.g. Bogeat-Triboulot *et al.* 2007; Giovannelli *et al.* 2007), modulation of leaf structure, gas exchange and photosynthetic water-use efficiency (WUE) (e.g. Marron *et al.* 2002, 2003; Monclus *et al.* 2006, 2009; Larchevêque *et al.* 2011; Broeckx *et al.* 2014), shifts in root/shoot carbon ratios and anatomical adjustments (e.g. Van Splunder *et al.* 1996; Ibrahim *et al.* 1997; Bogeat-Triboulot *et al.* 2007; Fichot *et al.* 2009). These studies have demonstrated that substantial genetic variations occur among poplars that can be exploited for understanding the genetic and molecular basis of drought acclimation and for the selection of more drought-tolerant genotypes (Street *et al.* 2006). However, traits that help setting functional limits and recovery thresholds under severe drought, such as resistance to cavitation, should also be considered especially with the increased probability of more frequent and more intense drought episodes associated with the ongoing global changes. Data on drought-induced cavitation have already been reported for poplars and several studies have recently illustrated the interest in accounting for cavitation resistance in poplar breeding (Cochard *et al.* 2007; Fichot *et al.* 2010, 2011; Schreiber *et al.* 2011). Yet we lack a comprehensive view of our present knowledge at the genus level.

The goal of this paper was to provide a synthesis of the vulnerability to drought-induced cavitation in one of the most studied tree genera, namely poplar. We first present the extent of variations occurring both within and between pure species and interspecific hybrids. We continue with a review of the variations among organs and environmental-induced acclimation including the effects of irradiance, nutrients, CO<sub>2</sub>, temperature and water availability. Additional insights into how vulnerability to drought-induced cavitation is related to pit membrane ultrastructure, xylem structure and function, leaf physiology and growth performance, are then provided. We conclude by identifying the existing gaps in knowledge and proposing future research opportunities. This review is primarily addressed to the growing community of poplar physiologists and geneticists. However, over the last 15 years, poplars have emerged as model species for the study of molecular tree biology that has been accompanied by the impressive development of genomic-related tools (Bradshaw *et al.* 2000; Jansson & Douglas 2007). Such a model therefore also offers interesting possibilities to gain additional insights into the genetics and genomics of resistance to drought-induced cavitation in Angiosperms.

## METHODS AND GENERAL CHARACTERIZATION OF THE REVIEWED STUDIES

The vulnerability to drought-induced cavitation is usually assessed through vulnerability curves (VCs) representing the course of embolism (most of the time measured as the percent loss of hydraulic conductivity) as a function of xylem tension ( $P_x$ ). These curves typically show a sigmoid shape (Fig. 1). Different techniques have been developed to generate VCs since they were first proposed by Sperry & Tyree (1988). Their principles, advantages and potential pitfalls have recently been critically reviewed (Cochard *et al.* 2013).



**Figure 1.** Example of a typical (sigmoidal) vulnerability curve and of vulnerability estimates.  $P_{12}$ ,  $P_{50}$  and  $P_{88}$  represent values of xylem tension (MPa) at which 12, 50 and 88% of xylem hydraulic conductivity is lost. Redrawn from Domec & Gartner (2001).

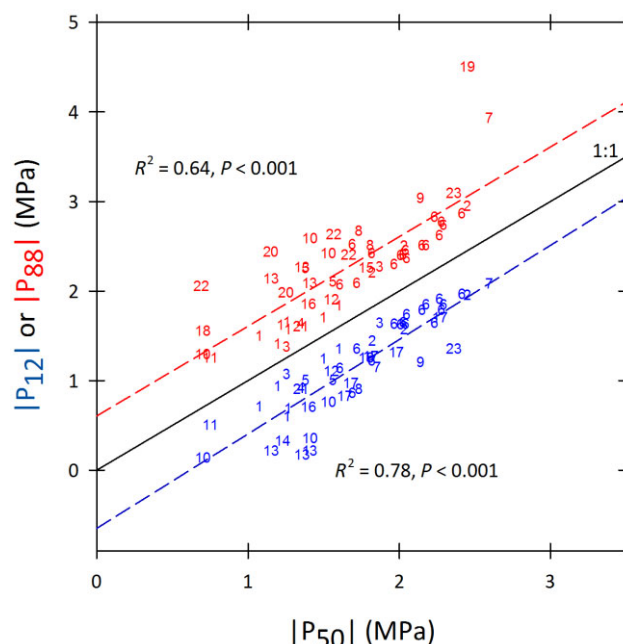
From VCs, several parameters can then be estimated and used for comparing xylem resistance to drought. The value of  $P_x$  inducing 50% loss of conductivity ( $P_{50}$ ) is by far the most commonly used index of cavitation resistance (Fig. 1). As a complement, the threshold xylem tension corresponding to the onset of cavitation is sometimes derived and used in the context of stomatal regulation (Sparks & Black 1999; Meinzer *et al.* 2009). This threshold (the air entry point,  $P_e$ ) can be estimated from the x-intercept of a tangent passing through the inflexion point of a sigmoid curve fitted to the data, and corresponds numerically to the xylem tension provoking 12% loss of conductivity ( $P_{12}$ ) (Domec & Gartner 2001) (Fig. 1). The xylem tension inducing full hydraulic failure can similarly be estimated at the other extreme of the VC and numerically corresponds to the xylem tension provoking 88% loss of conductivity ( $P_{88}$ ) (Domec & Gartner 2001) (Fig. 1). Finally, the slope of the VC can be derived from the linear part of the VC; the steeper the slope, the smaller the range of xylem tensions over which conductivity is lost (Pammenter & Vander Willigen 1998).

Literature searches of the vulnerability to cavitation within the *Populus* genus were conducted in peer-reviewed journals using the *ISI Web of Science* citation database. Papers reporting VCs or vulnerability estimates were retained to form the core of the database for our analysis. Other papers reporting data on native state embolism without vulnerability estimates were considered as additional information and used for further discussion. Values of  $P_{12}$ ,  $P_{50}$  and  $P_{88}$  from stems, branches, petioles, leaf midribs and roots were either directly collected from the text or tables when available or extracted

from digitized figures using standard image analysis software. For each paper, values were then averaged per organ, per species/hybrid cross and per treatment. So, one paper reporting on different species or organs could contribute to multiple observations (e.g. Hukin *et al.* 2005). When the vulnerability was assessed using different techniques for the same organ, values were averaged across methodologies to yield one single value.

A total of 37 publications (from 1991 to now) were found to report estimates of vulnerability to cavitation, covering a range of 10 pure species and 12 hybrid crosses. The  $P_{50}$  values could be extracted from 36 out of the 37 studies (Table 1), the exception being the study of Sparks & Black (1999) where only  $P_e$  values were available. Values of  $P_{12}$  and  $P_{88}$  could be extracted from 21 studies. Considering the individual data per species (Table 1), about one-half was obtained from young plant material (potted cuttings and seedlings of less than 5 months) grown under controlled conditions (growth chambers and greenhouses). The other half was obtained from field grown plants, either growing in field plantations, in botanical gardens or in natural stands. There was however a distinct imbalance when comparing pure species and hybrids. More than 75% of the observations were issued from greenhouse experiments for hybrids against 27% only for pure species. This is most likely explained by the fact that selected cultivars are readily available as clonal material making them convenient for controlled studies. VCs based on ultrasonic acoustic detection were reported only once (Hacke & Sauter 1996). Other techniques were more evenly represented (Table 1).

Questions about the reliability, validity and comparability of the different methods used to construct VCs have been raised (see Cochard *et al.* 2013). Although VCs are typically sigmoidal ('s' shape), exponential curves ('r' shape) have been reported depending on the methods; this phenomenon being particularly exacerbated in species with long vessels (Choat *et al.* 2010; Cochard *et al.* 2013). However, this issue was considered to be minor within the framework of our meta-analysis for the following reasons. First, vessels in poplars are generally short, typically less than 15 cm (Zimmermann & Jeje 1981; Hacke & Sauter 1996; Cai *et al.* 2010; Schreiber *et al.* 2011). Then, studies that have compared techniques head-to-head and using poplars all showed a very good agreement with methodological differences always less than 0.25 MPa (Sperry *et al.* 1991; Cochard *et al.* 1992, 1996; Tyree *et al.* 1992; Pockman *et al.* 1995; Li *et al.* 2008). Finally, VCs should be more or less sigmoidal and symmetrical if the deviation from  $P_{50}$  for  $P_{12}$  and  $P_{88}$  is comparable (see Fig. 1). We therefore plotted values of  $P_{12}$ ,  $P_{50}$  and  $P_{88}$  that we retrieved on poplars (Fig. 2). Across all data (obtained on different species and with different methods),  $P_{12}$  and  $P_{88}$  were linearly and significantly related to  $P_{50}$  ( $R^2 = 0.78$  and  $0.64$ , respectively,  $P < 0.001$ ; Fig. 2), with an average offset from  $P_{50}$  equal to 0.56 MPa for  $P_{12}$  and 0.61 MPa for  $P_{88}$  (Fig. 2); in addition, the slopes of the  $P_{12}$  versus  $P_{50}$  or  $P_{88}$  versus  $P_{50}$  relationships were not significantly different from the 1:1 line (one sample test for linear regression slopes,  $P > 0.100$ ) (Fig. 2). This indicated that most of the VCs pub-



**Figure 2.** Relationships among different vulnerability estimates ( $P_{12}$ ,  $P_{50}$  and  $P_{88}$ ) in poplars. Data below the 1:1 line correspond to the relationship between  $P_{12}$  and  $P_{50}$ ; data above the 1:1 line correspond to the relationship between  $P_{88}$  and  $P_{50}$ . Data points are genotypic means and refer to different publications. 1: Arango-Velez *et al.* 2011; 2: Awad *et al.* 2010; 3: Cai & Tyree 2010; 4: Cochard *et al.* 1992; 5: Cochard *et al.* 1996; 6: Fichot *et al.* 2010; 7: Hacke *et al.* 2001a; 8: Hacke & Sauter 1995; 9: Hacke & Sauter 1996; 10: Hukin *et al.* 2005; 11: Lambs *et al.* 2006; 12: Leffler *et al.* 2000; 13: Li *et al.* 2008; 14: Lo Gullo & Salleo 1992; 15: Plavcová & Hacke 2011; 16: Pockman & Sperry 2000; 17: Schreiber *et al.* 2011; 18: Secchi & Zwieniecki 2010; 19: Sperry *et al.* 1991; 20: Tognetti *et al.* 1999; 21: Tyree *et al.* 1992; 22: Tyree *et al.* 1994a; 23: Urli *et al.* 2013.

lished for poplars were sigmoidal and that the different methods used to establish VCs were not a confounding factor in our analysis.

## VARIATIONS AMONG PURE SPECIES AND INTERSPECIFIC CROSSES

The focus of this part is placed on  $P_{50}$  values from above-ground woody tissues (stems and branches) for which there are most data. We acknowledge that conclusions inferred from species means obtained across different studies should be treated cautiously because of (1) the unequal representation of the different species studied (see below) and (2) potential confounding effects including differences in the origin and the age of the plant material or in growth conditions (see Table 1). However, the reviewed and synthesized data provide a valuable snapshot and some patterns are relevant to further improve our knowledge of poplar biology.

### $P_{50}$ variations among pure species

A total of 10 pure species have been documented so far in terms of  $P_{50}$  (Table 1, Fig. 3a), accounting for about one-third

**Table 1.** Xylem vulnerability to drought-induced cavitation within the *Populus* genus estimated as the xylem tension inducing 50% loss in hydraulic conductivity ( $P_{50}$ , MPa)

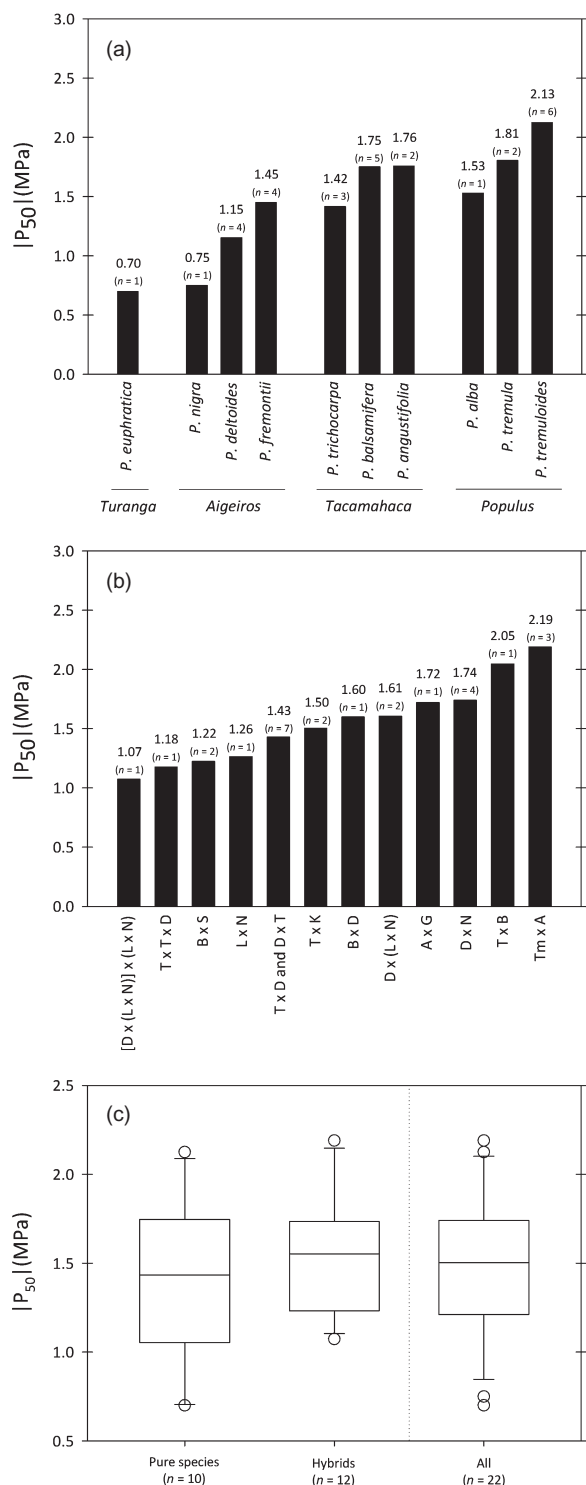
Species	Tissue type	Growth conditions	Plant material	No. of genotypes	Tree age	VC method	$ P_{50} $	Reference <sup>a</sup>
Pure species								
<i>P. alba</i>	Stem	GH	Clonal, potted cuttings	1	2–4 months	AP	1.53	[1]
<i>P. angustifolia</i>	Branch (current year)	NS	Individual mature trees	–	–	BD	1.66	[2]
	Branch (1–2 years)	NS	Individual mature trees	–	–	CE	1.85	[3]
<i>P. balsamifera</i>	Branch (current year)	NS	Individual mature trees	–	–	BD	1.57	[2]
	Branch (current year)	BG	Individual mature trees	–	>15 years	BD	1.77	[4]
	Branch (current year)	BG	Individual mature trees	–	>15 years	UAEs	2.14	[5]
	Stem	GH	Clonal, potted cuttings	1	3 months	CA	1.50	[6]
	Branch	NS	Individual mature trees	–	Mature	CE	1.78	[7]
<i>P. deltoides</i>	Branch (current year)	NS	Individual mature trees	–	–	AP, BD	1.35	[8]
	Branch (current year)	BG	Individual mature trees	–	10 years	BD	1.23	[9]
	Stem + branches (current year)	GH, BG	Clonal, potted scions + individual mature trees	–	–	BD, PD	1.35	[10]
<i>P. euphratica</i>	Branch (current year)	NS	Individual mature trees	–	–	BD	0.69	[2]
<i>P. fremontii</i>	Stem	GH	Clonal, potted cuttings	1	2–4 months	AP	0.70	[1]
	Branch (n.a.)	NS	Individual mature trees	–	–	AP, CE	1.55	[11]
	Branch (current year)	NS	Individual mature trees	5	23–30 years	AP	1.55	[12]
	Branch (current year)	NS	Individual mature trees	–	–	AP	1.40	[13]
	Branch (1–4 years)	NS	Individual mature trees	–	–	AP, CA, CE	1.31	[14]
<i>P. nigra</i>	Branch (n.a.)	NS	Individual mature trees	–	–	AP	0.75	[15]
<i>P. tremula</i>	Branch (3–5 years)	NS	Individual mature trees	–	–	BD	1.25	[16]
	Branch (n.a.)	NS	Individual mature trees	–	–	CA	2.36	[17]
<i>P. tremuloides</i>	Branch (several years)	NS	Individual mature trees	–	–	AP, BD	2.58	[18]
	Branch (n.a.)	NS	Individual mature trees	–	–	AP	2.75	[19]
	Branch (1–2 years)	NS	Individual mature trees	–	–	CE	2.60	[3]
	Stem	GH	Potted seedlings	–	4 months	CA	1.87	[20]
<i>P. trichocarpa</i>	Branch (2–3 years)	FP	Clonal, mature trees	6	11 years	CE	2.27	[21]
	Stem	GC	Potted seedlings	–	20 weeks	CE	0.68	[22]
	Stem	GH	Clonal, potted cuttings	1	4 months	PD	1.65	[23]
	Stem (current year)	FP (coppice)	Clonal, coppiced trees	2	10 years rootstocks	CA	1.90	[24]
	Stem	GH	Clonal, potted cuttings	1	4–5 months	PD	0.70	[25]
Hybrids								
<i>P. alba</i> × <i>P. grandidentata</i>	Stem	GH	Clonal, potted <i>vivo</i> plants	1	4 months	AP	1.72	[26]
<i>P. balsamifera</i> × <i>P. deltoides</i>	Stem	GH	Clonal, potted cuttings	1	3 months	CA	1.60	[6]
<i>P. balsamifera</i> × <i>P. simonii</i>	Stem	GH	Potted seedlings	–	4 months	CA	1.25	[20]
	Stem	GH	Clonal, potted cuttings	1	3 months	CA	1.19	[6]

<i>P. deltoides</i> × <i>P. nigra</i>	Stem	GH	Clonal, potted cuttings	1	4 months	AP, PD	1.56	[27]
	Stem	GH	Clonal, potted cuttings	1	4 months	PD	1.40	[23]
	Stem (current year)	FP (coppice)	Clonal, coppiced trees	2	10 years rootstocks	CA	2.05	[24]
	Stem (current year)	FP (coppice)	Clonal, coppiced trees	8	3 years rootstocks	CA	1.95	[28]
	Stem	GH	Clonal, potted cuttings	1	3 months	CA	1.26	[6]
<i>P. laurifolia</i> × <i>P. nigra</i>								
<i>P. tremula</i> × <i>P. alba</i>	Stem	GH	Clonal, potted <i>in vitro</i> plants	1	2–3 months	CA	1.82	[29]
	Stem (2 years)	FP	Clonal, planted trees	1	2 years	AP	2.70	[30]
	Stem	GH	Clonal, potted <i>in vitro</i> plants	1	5 months	CA	2.05	[31]
	Stem (current year)	FP (coppice)	Clonal, coppiced trees	1	10 years rootstocks	CA	2.05	[24]
<i>P. trichocarpa</i> × <i>P. balsamifera</i>	Stem	GH	Clonal, cuttings, sand culture system	4	3 months	PD	1.32	[32]
<i>P. trichocarpa</i> × <i>P. deltoides</i> (and <i>vice versa</i> )	Stem	GH	Clonal, potted cuttings	2	4 months	PD	1.38	[23]
	Stem	GH	Clonal, potted cuttings	1	4–5 weeks	CE	1.67	[33]
	Stem	GC	Clonal, potted cuttings	1	14 weeks	CE	1.51	[34]
	Branch (2–3 years)	FP	Clonal, mature trees	2	16 years	CE	1.64	[21]
	Stem	GC	Clonal, potted cuttings	1	12 weeks	CE	1.38	[35]
	Stem	GC	Clonal, potted cuttings	1	11 weeks	CE	1.42	[36]
<i>P. trichocarpa</i> × <i>P. koreana</i>	Stem	GH	Clonal, potted cuttings	1	4 months	AP, PD	1.59	[27]
	Stem	GH	Clonal, potted cuttings	1	2–4 months	AP	1.41	[1]
	Stem	GH	Clonal, potted cuttings	2	4 months	PD	1.18	[23]
<i>P. trichocarpa</i> × <i>P. deltoides</i>	Stem	GH	Clonal, potted cuttings	2	3 months	CA	1.23	[6]
<i>P. deltoides</i> × ( <i>P. laurifolia</i> × <i>P. nigra</i> )	Branch (2–3 years)	FP	Clonal, mature trees	1	11 years	CE	1.98	[21]
[ <i>P. deltoides</i> × ( <i>P. laurifolia</i> × <i>P. nigra</i> )] × ( <i>P. laurifolia</i> × <i>P. nigra</i> )	Stem	GH	Clonal, potted cuttings	1	3 months	CA	1.07	[6]

*P*<sub>50</sub> values are from stems and branches.

<sup>a</sup>References: [1] Hukin *et al.* 2005; [2] Tyree *et al.* 1994a; [3] Hacke *et al.* 2001a; [4] Hacke & Sauter 1995; [5] Hacke & Sauter 1996; [6] Arango-Velez *et al.* 2011; [7] Plavcová & Hacke 2011; [8] Cochard *et al.* 1992; [9] Lo Gullo & Salleo 1992; [10] Tyree *et al.* 1992; [11] Pockman *et al.* 1995; [12] Leflier *et al.* 2000; [13] Pockman & Sperry 2000; [14] Li *et al.* 2008; [15] Lambs *et al.* 2006; [16] Tognetti *et al.* 1999; [17] Urii *et al.* 2013; [18] Sperry *et al.* 1991; [19] Sperry & Sullivan 1992; [20] Cai & Tyree 2010; [21] Schreiber *et al.* 2011; [22] Way *et al.* 2013; [23] Harvey & Van Den Driessche 1999; [24] Cochard *et al.* 2007; [25] Secchi & Zwieniecki 2010; [26] Coleman *et al.* 2008; [27] Cochard *et al.* 1996; [28] Fichot *et al.* 2010; [29] Awad *et al.* 2010; [30] Voelker *et al.* 2011; [31] Awad *et al.* 2012; [32] Harvey & Van Den Driessche 1997; [33] Hacke *et al.* 2010; [34] Hacke *et al.* 2011; [35] Plavcová & Hacke 2012; [36] Plavcová *et al.* 2013.

AP, air pressurization; BD, bench dehydration; BG, botanical garden; CA, cavitron; CE, centrifuge; FP, field plantation; GC, growth chambers; GH, greenhouse; NS, natural stand; PD, *in situ* plant dehydration; UAEs, ultrasonic acoustic emissions; VC, vulnerability curve.



**Figure 3.** Genetic variation in resistance to cavitation (as assessed through  $P_{50}$  from stems and branches) in poplar: (a) means for pure species; (b) means for hybrid crosses; (c) box plots for pure species and hybrids based on species/hybrid crosses means from (b) and (c). For (a) and (b), the number of studies conducted on each species/hybrid cross is indicated in parentheses; the numbers in parentheses in (c) refer to the number of species or hybrid crosses considered. Abbreviations: A, *P. alba*; B, *P. balsamifera*; D, *P. deltoides*; G, *P. grandidentata*; K, *P. koreana*; L, *P. laurifolia*; N, *P. nigra*; S, *P. simonii*; T, *P. trichocarpa*; Tm, *P. tremula*.

of the total number of poplar species and representing four botanical sections out of the six comprised by the genus (Eckenwalder 1996). The three most important sections for forestry and breeding (Dickmann & Kuzovkina 2008), that is *Aigeiros*, *Populus* and *Tacamahaca*, were equally represented with three species each (Fig. 3a). The fourth section *Turanga* was represented by one species only (Fig. 3a). There were however disparities between species in terms of their representation (Table 1). So far, *P. tremuloides* has been the most studied (six studies) followed by *P. balsamifera* (five studies), *P. deltoides* and *P. fremontii* (four studies each), *P. trichocarpa* (three studies), *P. angustifolia* and *P. tremula* (two studies each) and *P. euphratica*, *P. nigra* and *P. alba* (one study each). Thus far, North American species (*P. tremuloides*, *P. balsamifera*, *P. deltoides*, *P. fremontii*, *P. trichocarpa* and *P. angustifolia*) have been overall more examined than their Eurasian congeners (*P. alba*, *P. euphratica*, *P. nigra* and *P. tremula*).

The grand mean  $P_{50}$  across the 10 species averages reached  $-1.44$  MPa ( $\pm 0.15$  SE) confirming that the genus *Populus* comprises species that are among the most vulnerable temperate woody plants to drought-induced cavitation (see the compiled database of 167 species in Maherali *et al.* 2004). This trend is generally attributed to their pioneering behaviour and their frequent riparian occurrence. Similarly high levels of vulnerability have also been found for their close willow counterparts (*Salix* spp.) with  $P_{50}$  typically higher than  $-1.50$  MPa (Cochard *et al.* 1992; Pockman *et al.* 1995; Pockman & Sperry 2000; Wikberg & Ögren 2004, 2007). However, it is worth noting that based on species means, our data revealed an interspecific range of variation of 1.43 MPa between extreme species means (Fig. 3a,c), and even more than 2 MPa when considering extreme individual studies only (Table 1). Therefore, although poplars are overall highly vulnerable to cavitation, there are significant differences among species that may be related to their specific ecological range.

So far, *P. tremuloides* appears to be the least vulnerable with a mean  $P_{50}$  of  $-2.13$  MPa. With the exception of only one recent study reporting a very high  $P_{50}$  on young seedlings (i.e.  $-0.68$  MPa; Way *et al.* 2013), the lowest  $P_{50}$  values have been consistently reported for this species (up to  $-2.75$  MPa; Table 1). Contrary to most other species investigated, *P. tremuloides* frequently occurs in non-riparian zones and upland sites (Rood *et al.* 2007) that may explain the rather high resistance to cavitation that has been observed (Schreiber *et al.* 2011). On the other side, *P. euphratica* appears to be the most vulnerable with a  $P_{50}$  of  $-0.70$  MPa. This species occurs typically in semi-arid areas with a very high evaporative demand with a distribution area extending through the Middle East to central and western Asia (Dickmann & Kuzovkina 2008). However, even if *P. euphratica* clearly shows adaptation to hot and saline environments (Chen & Polle 2010; Ma *et al.* 2013), this species is not intrinsically drought tolerant (Hukin *et al.* 2005; Bogeat-Triboulot *et al.* 2007). Its occurrence in dry environments is mainly enabled by its phreatophytic behaviour allowing permanent access to deep water tables (Gries *et al.* 2003).

Studies on riparian cottonwoods from the *Aigeiros* and *Tacamahaca* sections accounted for two-thirds of the total observations made on pure species (Table 1; Fig. 3a). Cottonwoods are particularly adapted to dynamic river valley floodplains (see Rood *et al.* 2003 for a review) although species-specific ecophysiology has been noted depending on their geographic distributions, climatic optimum and river dependency (Rood *et al.* 2003). For instance, *P. deltoides* and *P. fremontii* usually occur in semi-arid environments (Rood *et al.* 2000) whereas cottonwoods from the *Tacamahaca* section occur in cooler and wetter climates (Rood *et al.* 2003). However, the patterns of  $P_{50}$  observed among North American cottonwoods (Fig. 3a) did not match this general idea since *P. balsamifera* and *P. angustifolia* were found to be the most resistant with  $P_{50}$  close to  $-1.75$  MPa while *P. deltoides* was the most vulnerable with a mean  $P_{50}$  of  $-1.15$  MPa (Table 1; Fig. 3a). Direct comparisons between *P. angustifolia*, *P. balsamifera*, *P. trichocarpa* and *P. deltoides* have confirmed this trend with *P. deltoides* as the most vulnerable species (Tyree *et al.* 1994a; Rood *et al.* 2000).

### $P_{50}$ variations among hybrid crosses

Interspecific hybridization has been the basis of most poplar breeding programmes (Stettler *et al.* 1996) because it frequently results in positive heterosis within  $F_1$  hybrids for growth performance, tree architectural components and related leaf traits (e.g. Stettler *et al.* 1988; Hinckley *et al.* 1989; Braatne *et al.* 1992; Bradshaw & Stettler 1995; Li & Wu 1997; Marron *et al.* 2006, 2007, 2010; Dillen *et al.* 2009a,b). So far,  $P_{50}$  values have been reported for a total of 12 different hybrid crosses (Table 1; Fig. 3b). However, as for pure species, not all crosses have been equally studied. In this regard, *P. trichocarpa*  $\times$  *P. deltoides* (including the reverse cross *P. deltoides*  $\times$  *P. trichocarpa*) and *P. deltoides*  $\times$  *P. nigra* have received more attention (Table 1; Fig. 3b) most likely because of their high commercial importance in Europe and North America. The grand mean  $P_{50}$  across the different hybrids averaged  $-1.55$  MPa ( $\pm 0.10$  SE) with a range of variation reaching 1.12 MPa based on extreme means (1.63 MPa when considering individual extreme values) (Table 1; Fig. 3b,c).

The three most resistant hybrid crosses from Fig. 3b (*P. tremula*  $\times$  *P. alba*, *P. trichocarpa*  $\times$  *P. balsamifera* and *P. deltoides*  $\times$  *P. nigra*) consistently outperformed the average resistance of their respective pure species (Fig. 3a). This raises the question of possible heterosis for cavitation resistance. However, the direct comparison of hybrid performance relative to the parental pure species would require the systematic characterization of both parents and offspring, but none of the reviewed studies has directly addressed the question.

### $P_{50}$ variations within species and hybrid crosses

The first report on natural poplar populations concerned *P. trichocarpa* (Sparks & Black 1999). The authors showed that, when compared under greenhouse conditions, cuttings

originating from two populations of the wet American west coast (Hoh and Nisqually river basins) exhibited less negative air entry points ( $P_e = -0.71$  and  $-1.32$  MPa, respectively) than cuttings originating from two populations of inner, drier climates (Palouse and Yakima river basins;  $P_e = -1.55$  and  $-1.67$  MPa, respectively). In addition, values of  $P_e$  among individuals were much variable within the two vulnerable populations from coastal sites while they were highly conserved within the two more resistant populations from inland sites. This first study therefore indicated that (1) within-population and between-population variations for cavitation resistance can occur even in highly vulnerable riparian species such as poplars and (2) the selection of resistant individuals is more effective under a stronger environmental pressure. Since then, small but significant differences in cavitation resistance have also been noted among *P. trichocarpa* and *P. tremuloides* genotypes (Cocharde *et al.* 2007; Schreiber *et al.* 2011) (see Table 2). However, the extent of variations occurring both within and between poplar natural populations remains surprisingly less documented in terms of number of genotypes or populations as compared with other recent large-scale phenotyping studies conducted on, for example, maritime pine (Lamy *et al.* 2011), Scots pine (Martínez-Vilalta *et al.* 2009; Sterck *et al.* 2012) or European beech (Wortemann *et al.* 2011).

Variations within hybrid crosses have also received attention although it has been mostly limited to hybrids between the three species: *P. deltoides*, *P. trichocarpa* and *P. nigra* (see Table 2). Noteworthy, the largest range of variation has been recorded among eight unrelated *P. deltoides*  $\times$  *P. nigra* cultivars, with  $P_{50}$  differences reaching 0.8 MPa between extreme genotypes (Fichot *et al.* 2010, 2011). It is very likely that the process of interspecific hybridization enables generating larger variations than what is observed within pure species, but once again the question of transgressive segregation for cavitation resistance remains to be directly addressed.

### Shape of the VCs

Besides mean resistance to cavitation, the shape of the VC is an important parameter as it determines the range of water potentials over which xylem hydraulic conductivity is lost. However, the slope parameter was only seldom (three studies) reported with VCs. We therefore assumed that it should be at least partly reflected in the difference between  $P_{12}$  and  $P_{88}$  (for which data were more numerous); smaller differences indicating steeper slopes (see Fig. 1). In addition, VCs should be more or less symmetrical if the deviation from  $P_{50}$  for  $P_{12}$  and  $P_{88}$  is comparable (see Fig. 1). Across all data, values of  $P_{12}$  and  $P_{88}$  were linearly and significantly related to values of  $P_{50}$  ( $R^2 = 0.78$  and  $0.64$ , respectively,  $P < 0.001$ ; Fig. 2), with an average offset from  $P_{50}$  equal to 0.56 MPa for  $P_{12}$  and 0.61 MPa for  $P_{88}$  (Fig. 2). The slopes of the  $P_{12}$  versus  $P_{50}$  or  $P_{88}$  versus  $P_{50}$  relationships were not significantly different from the 1:1 line (one sample test for linear regression slopes,  $P > 0.100$ ) (Fig. 2). Therefore, poplars differ primarily in terms of absolute resistance rather in the shape of VCs.

**Table 2.** List and synthesis of studies conducted on cavitation resistance at the infraspecific level in poplar pure species and interspecific hybrids

Species/hybrids	Tissue type	Growth conditions	Plant material	No. of genotypes, populations and replicates	Age	Main findings	Reference
<i>P. fremontii</i>	Branch (current year)	NS	Individual mature trees	5 genotypes from 1 population (New Mexico, USA, Rio Grande river) – 3 branches per genotype	23–30 years	No significant difference between the five genotypes	Leffler et al. 2000
<i>P. tremuloides</i>	Branch (2–3 years)	FP	Clonal, mature trees	2 genotypes × 3 provenances (British Columbia, Canada; Alberta, Canada; Minnesota, USA) – 8 replicates per genotype	11 years	$P_{50}$ varies between –2.05 and –2.44 MPa between extreme genotypes but no significant differences are evidenced between provenances.	Schreiber et al. 2011
<i>P. trichocarpa</i>	Stem	GH	Potted cuttings	5 genotypes × 4 populations (Washington state, USA – Hoh, Nisqually, Palouse and Yakima river basins) – 1 cutting per genotype, that is, no replicate	1 year	Cuttings from the two populations of the wet American west coast are more vulnerable (mean $P_e = -0.71$ and –1.32 MPa) than cuttings from the two populations of inner, drier climate (mean $P_e = -1.55$ and –1.67 MPa). Variations among genotypes (cuttings) are more pronounced within populations of coastal wet sites than within populations of inner dry sites.	Sparks et al. 1999
<i>P. deltoides</i> × <i>P. nigra</i>	Stem (current year)	FP (coppice)	Clonal, coppiced trees	2 commercial genotypes – 5 replicates per genotype	10 years rootstocks	$P_{50} = -1.87$ and –1.94 MPa	Cochard et al. 2007
	Stem (current year)	FP (coppice)	Clonal, coppiced trees	2 commercial genotypes	10 years rootstocks	$P_{50} = -1.91$ and –2.18 MPa	Cochard et al. 2007
	Stem (current year)	FP (coppice)	Clonal, coppiced trees	8 commercial genotypes	3 years rootstocks	$P_{50}$ varies between –1.60 and –2.41 MPa between extreme genotypes.	Fichot et al. 2010, 2011
<i>P. trichocarpa</i> × <i>P. deltoides</i>	Stem	GH	Clonal cuttings, sand culture system	4 commercial genotypes	3 months	$P_{50}$ varies between –1.21 and –1.48 MPa between extreme genotypes.	Harvey & Van Den Driessche 1997
	Stem	GH	Clonal, potted cuttings	2 commercial genotypes	4 months	$P_{50} = -1.25$ and –1.50 MPa	Harvey & Van Den Driessche 1999
<i>P. deltoides</i> × ( <i>P. laurifolia</i> × <i>P. nigra</i> )	Stem	GH	Clonal, potted cuttings	2 commercial genotypes	3 months	$P_{50} = -1.21$ and –1.26 MPa	Arango-Velez et al. 2011

FP, field plantation; GH, greenhouse; NS, natural stand.



Actually, poplars tend to exhibit sigmoidal and rather symmetrical VCs, with cavitation events evenly distributed on each side of the inflexion point and occurring within a narrow range of water potentials (ca. 1.20 MPa on average).

## WITHIN-TREE VARIATIONS AND ENVIRONMENTALLY INDUCED ACCLIMATION

### Within-tree variations

It has been hypothesized that leaves and small terminal branches are more vulnerable to cavitation than larger parts of the plant resulting in the shedding of expendable distal organs during the early steps of drought episodes. This 'vulnerability segmentation' would be part of a strategy in order to maintain a favourable water balance by reducing the transpirational demand, such that organs representing years of growth and carbon investment (as the stem) are preserved (Tyree & Ewers 1991; Tyree *et al.* 1993; Rood *et al.* 2000). Although poplars are highly susceptible to drought, vulnerability segmentation does not seem to be a general rule. Leaf mid-ribs and petioles were more vulnerable than stems in *P. alba* or *P. trichocarpa* × *P. koreana* (Hukin *et al.* 2005) while no significant differences were observed in other cases such as in *P. euphratica* or *P. deltoides* × *P. nigra* (Cochard *et al.* 1996; Hukin *et al.* 2005). The opposite pattern with stems being more vulnerable than petioles or leaves has been reported for *P. balsamifera* and *P. tremuloides* (Hacke & Sauter 1996; Way *et al.* 2013). The different patterns observed probably reflect species-specific optimizations of the hydraulic pathway in relation to the ecological habitats of the species.

Conflicting patterns have also been reported for roots. For instance, roots of *P. balsamifera* were at least 0.5 MPa more vulnerable than petioles and shoots (Hacke & Sauter 1996). In *P. alba* and *P. trichocarpa* × *P. koreana*, roots appeared less vulnerable than leaves and as vulnerable as stems (Hukin *et al.* 2005). Interestingly, the only case where roots have been found significantly more resistant than both shoots and leaves is in the phreatophyte *P. euphratica* (Hukin *et al.* 2005). Considering the importance of root suckering for habitat colonization in this species, especially after periods of stress (Sharma *et al.* 1999), the lower vulnerability of roots may be part of a survival strategy.

Vulnerability to cavitation may also depend on the developmental stage. Early experiments on *P. tremuloides* branches demonstrated that vessels from the outer growth ring were still functional when vessels of the older xylem were mostly embolized (Sperry *et al.* 1991). This increased vulnerability of older vessels was associated with increased leakiness of the inter-conduit pit membranes due to their partial degradation. Later work on *P. tremuloides* and *P. angustifolia* provided new insight into this observation (Hacke *et al.* 2001a). Cavitation-refilling cycles can weaken the vessels through pit membrane stretching or rupture and make them thus more prone to cavitate in the future (Hacke *et al.* 2001a). This phenomenon of cavitation 'fatigue' has been proposed to explain the differences of vulnerability between younger and older xylem for field-grown trees.

Differences in vulnerability along the plant's main axis are another example of developmental plasticity in poplar. In *P. alba* and *P. euphratica*, the apical (younger) region of the main stem was less vulnerable than the basal (older) ones (Hukin *et al.* 2005), highlighting the importance of maintaining water transport to the apical meristem (see also Cochard *et al.* 1996). A similar pattern has been recently reported for a hybrid genotype of *P. alba* × *P. glandulosa* (Leng *et al.* 2013). This vertical gradient has been attributed to possible differences in the dimensions and the physical properties of the xylem vessels such that mature vessels of the basal regions would be larger and longer and thus more prone to embolism (Hukin *et al.* 2005; Leng *et al.* 2013). Ultrastructural data are however lacking. In addition, contradictory results have been recently reported for *P. trichocarpa* × *P. deltoides* with distal parts being on average 0.6 MPa more vulnerable (Plavcová & Hacke 2012). These last mentioned authors demonstrated that the increased vulnerability of apical segments was in this study not directly linked to their juvenility as primary xylem was not less resistant to embolism than secondary xylem.

When trying to explain why leaves of *P. tremuloides* were more resistant than the stem, Way *et al.* (2013) hypothesized that embolism repair may be easier in stems than in leaves. This would explain why leaves in this species would be overbuilt in terms of safety. Besides root pressure, the active refilling of xylem conducting elements while xylem is still under tension has been hypothesized (for reviews see Nardini *et al.* 2011; Zwieniecki & Secchi 2014). In poplar, recent findings have suggested that vessel refilling by surrounding parenchyma cells does occur and involves the up-regulation of genes encoding water transport facilitators (aquaporins) and carbohydrate metabolic pathways (Secchi & Zwieniecki 2010, 2011; Secchi *et al.* 2011). Results on *P. alba* × *P. glandulosa* also indicated that aquaporin expression was at least partly positively correlated with differences in the loss of conductivity along the stem (Leng *et al.* 2013), suggesting that differences in vulnerability among organs might be somehow related to the organs' ability to repair embolism. This hypothesis deserves further attention as the validity of cavitation/repair cycles has been recently questioned (Cochard & Delzon 2013; Wheeler *et al.* 2013; see also Sperry 2013).

### Environmentally induced acclimation

Resistance to drought-induced cavitation may respond to changes in environmental conditions provided the time lapse for acclimation is sufficient for the production of newly acclimated xylem conduits. Most studies conducted on poplar have used clonal hybrids under treatment and controlled conditions (see below), thereby allowing the identification of the phenotypic component *per se*. The factors investigated thus far include nutrient availability, irradiance, increased atmospheric CO<sub>2</sub> concentration, increased air temperature and water availability.

### Nutrient availability

Poplar shows considerable plasticity in response to the availability of inorganic nutrients, especially nitrogen (N) (Cooke

*et al.* 2005), and changes in the resistance to cavitation are an example of physiological adjustment. To date, the effect of N availability on cavitation resistance has been primarily documented and high N-fertilized poplar saplings have been shown to be consistently more vulnerable (Harvey & van den Driessche 1997, 1999; Hacke *et al.* 2010; Plavcová & Hacke 2012; Plavcová *et al.* 2013). Increased vulnerability is likely associated with increased porosity of the vessel pit membranes (Harvey & van den Driessche 1997). Other nutrients assessed so far encompass phosphorus (P) and potassium (K). Additional P supply has the potential to reduce cavitation vulnerability, especially at high N concentrations (Harvey & van den Driessche 1997), whereas K seems to have no clear effects (Harvey & van den Driessche 1999).

### Irradiance

Lower irradiance is typically associated with a lower evaporative demand and lower transpiration rates. This generally translates into a decreased need for water transport and reduced likelihood of cavitation occurrence. As xylem safety features are costly and shaded plants have limited carbon resources, shaded plants are therefore more vulnerable to cavitation (Cochard *et al.* 1999; Barigah *et al.* 2006; Schoonmaker *et al.* 2010). Evidence from *P. trichocarpa* × *P. deltoides* suggests that this general pattern holds in poplar (Plavcová *et al.* 2011).

### Atmospheric CO<sub>2</sub> concentration ([CO<sub>2</sub>]<sub>atm</sub>)

Many studies have already tried to understand how plants respond to increasing [CO<sub>2</sub>]<sub>atm</sub> in the framework of global change (see reviews by Ceulemans & Mousseau 1994; Norby *et al.* 1999), but the effects on plant hydraulics remain largely under-represented as compared with growth- or photosynthesis-related traits (but see Domec *et al.* 2009; Vaz *et al.* 2012; Locke *et al.* 2013; Rico *et al.* 2013). Because increased [CO<sub>2</sub>]<sub>atm</sub> generally reduces the demand placed on transpiration (Tricker *et al.* 2005), a shift towards less resistant xylem might be expected. In poplar, only one study has so far reported cavitation resistance under different [CO<sub>2</sub>]<sub>atm</sub> and no significant difference was observed between control and elevated CO<sub>2</sub> trees (Tognetti *et al.* 1999). This study was conducted on mature *P. tremula* trees occurring close to a natural CO<sub>2</sub> spring in central Italy (daytime CO<sub>2</sub> concentrations varying between 500 and 1000 ppm). Surprisingly, free air CO<sub>2</sub> enrichment experiments, in which poplars have been largely used as model tree species (see Liberloo *et al.* 2009 for a review), have not addressed this specific issue.

### Temperature

Besides rising [CO<sub>2</sub>]<sub>atm</sub>, global change is also projected to increase air temperature and vapour pressure deficit. The effects of higher growth temperature on tree hydraulic characteristics are conflicting (Maherali & DeLucia 2000a,b; Thomas *et al.* 2004; Phillips *et al.* 2011), but recent evidence on trembling aspen seedlings suggests that cavitation resist-

ance can be influenced by elevated temperatures (Way *et al.* 2013). High-temperature acclimated seedlings (+5 °C above ambient temperature) had significantly more vulnerable leaves than controls (*ca.* 0.5 MPa on average). Interestingly, stems were equally vulnerable in both treatments, suggesting that thermal acclimation of cavitation resistance is organ dependent.

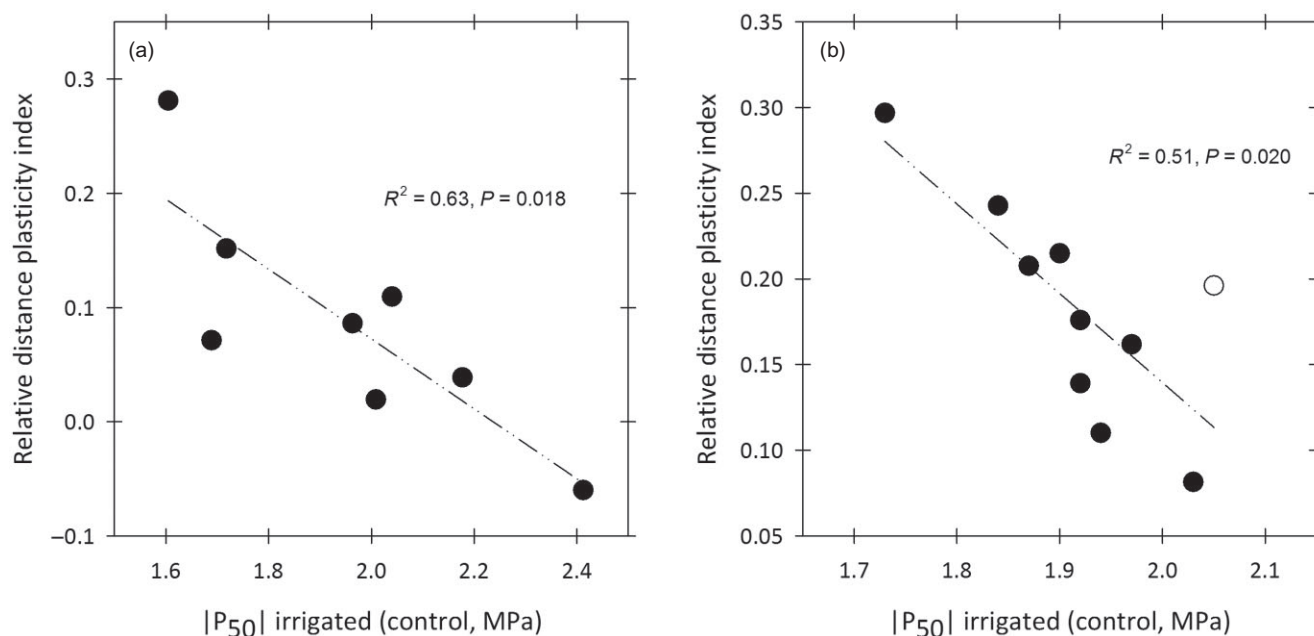
### Water availability

Surprisingly enough, direct evidence for drought-induced acclimation of cavitation resistance is rather recent (Ladjal *et al.* 2005; Holste *et al.* 2006; Beikircher & Mayr 2009). So far, data on poplar are limited to a few hybrid genotypes. Both greenhouse-controlled experiments (Awad *et al.* 2010, 2012; Plavcová & Hacke 2012) and common garden tests (Fichot *et al.* 2010) have suggested a similar response: acclimated trees generally exhibit a safer xylem. This response mainly results from a shift of VCs towards more negative xylem pressures, the slope being poorly affected (Awad *et al.* 2010; Fichot *et al.* 2010). Differences in *P*<sub>50</sub> of up to 0.75 MPa have been reported between control and treated plants (Awad *et al.* 2012; Plavcová & Hacke 2012). However, the effect of drought has been sometimes reported as not significant (Fichot *et al.* 2010; Plavcová & Hacke 2012). One reason for this is that poplars are very sensitive to water deprivation and the acclimation of xylem structure and function therefore needs to be investigated under long-lasting, but moderate, drought conditions so that growth cessation is prevented and xylem acclimation promoted (Fichot *et al.* 2009). Otherwise, the amount of xylem produced under treatment conditions may be too small to see any significant change (Plavcová & Hacke 2012). A second reason is that the acclimation response seems to be genotype dependent, that is, there is some degree of genetic variation in phenotypic plasticity (Fichot *et al.* 2010). A re-analysis of the data from Fichot *et al.* (2010) suggested that the amplitude of the response is negatively related with intrinsic cavitation resistance (i.e. cavitation resistance under control conditions; Fig. 4) and the same pattern could be observed when re-analysing data from *P. tremula* × *P. alba* transgenic lines subjected to drought (Awad *et al.* 2012) (Fig. 4). In other words, the less resistant to cavitation under control conditions, the more prone to acclimation in response to drought.

## ECOPHYSIOLOGICAL CORRELATES OF CAVITATION RESISTANCE: FROM XYLEM ULTRASTRUCTURE TO PHYSIOLOGICAL PERFORMANCE

### Ultrastructural determinism of cavitation resistance

As predicted from the air-seeding mechanism and the capillary equation, the risk of embolism spreading is directly tied to pit membrane porosity, larger pores being predicted to air seed at lower pressure differences (see Choat *et al.* 2008). The ultrastructure of the pit membrane is therefore central in setting vulnerability thresholds. The differences evidenced in



**Figure 4.** Relationship between intrinsic resistance to cavitation ( $P_{50}$  control irrigated) and the amplitude of phenotypic variation in  $P_{50}$  in response to drought (relative distance plasticity index, RDPI). The RDPI has been proposed as a simple index to quantify phenotypic plasticity (Valladares *et al.* 2006) and corresponds to the phenotypic distance between individuals of the same genotype placed in different environments divided by the highest of the two phenotypic values. Higher y-values indicate a higher plastic response. Data points represent genotypic means: (a) data from Fichot *et al.* (2010) on eight *P. deltoides*  $\times$  *P. nigra* genotypes; (b) data from Awad *et al.* (2012) on wild-type *P. tremula*  $\times$  *P. alba* genotype 717-1B4 (open symbol) and nine transgenic lines (lignin deficient, closed symbols). Note that when excluding the wild type in panel (b),  $R^2 = 0.85$ .

cavitation resistance across poplar species (see above) suggest that significant variation exists in bordered pit characteristics, especially in pit membrane porosity. Descriptions of the fine structure of bordered pits in poplar have been, however, restricted to a few number of species/genotypes so far. Poplar pit membranes are typically thin (between 100 and 300 nm thick; Jansen *et al.* 2009; Plavcová & Hacke 2011; Plavcová *et al.* 2011; Capron *et al.* 2014), appearing fragile and most often porous when observed with scanning electron microscope (SEM), with resolvable pores sometimes up to more than 200 nm in diameter (Harvey & van den Driessche 1997; Jansen *et al.* 2009; Ali Ahmed *et al.* 2011; Plavcová & Hacke 2011; Plavcová *et al.* 2011). Based on the capillary equation, a pore of 200 nm in diameter gives a theoretical threshold for cavitation at  $-1.44$  MPa, which fits overall rather well with the mean  $P_{50}$  reviewed here. Pores are, however, not always resolvable (Sperry *et al.* 1991; see also Plavcová & Hacke 2011). In addition, porosity estimates derived from SEM observations must be treated with caution. Sample preparation involves drying plant material, which is supposed to alter the ultrastructure of the pit membrane via stretching. Plavcová & Hacke (2011) showed that different sample preparation techniques for poplar xylem, in this case air drying versus ethanol drying, can indeed lead to different results.

Pit membranes are generally seen as modified primarily cell walls made of multiple layers of cellulose microfibrils embedded in a matrix of hemicelluloses, pectins and struc-

tural proteins (see Choat *et al.* 2008). The porosity of pit membranes is therefore supposedly fine-tuned by its biochemical nature. Perfusion experiments on *P. tremula* stem segments with selective hydrolase solutions have shown that hemicelluloses and wall proteins do not play a significant role in setting the vulnerability threshold (Dusotoit-Coucaud *et al.* 2014); cellulose and pectins are however critical components for pit membrane functioning (Dusotoit-Coucaud *et al.* 2014). Further, immunolabelling experiments in *P. balsamifera* have revealed the presence of two distinct chemical domains in the pit membrane: the main central part of the pit membrane within which pectins and calcium were not detected, and the annulus region corresponding to the marginal membrane region within which pectins and calcium colocalized (Plavcová & Hacke 2011; Plavcová *et al.* 2011). In this configuration, pectins are supposed to play a key role in vulnerability to cavitation through the pectin-rich annulus region by controlling the mechanical strength and the deflection of the central pit membrane (Plavcová & Hacke 2011). Experiments combining optical, electronic and atomic force microscopy have recently confirmed the importance of pit membrane physical deflection with the increasing pressure difference across vessels of *P. deltoides*  $\times$  *P. nigra* (Capron *et al.* 2014). To what extent differences in the pit membrane biochemistry and in the physics of bordered pits can explain differences in resistance to cavitation across poplar species is unknown. However, we know that substantial variation in pit membrane pectin properties has already been reported

across species of the *Lauraceae* family (Gortan *et al.* 2011) and even across *Vitis* genotypes (Sun *et al.* 2011).

Reduced lignification has been associated with decreased resistance to cavitation in several poplar transgenic lines (Coleman *et al.* 2008; Voelker *et al.* 2011; Awad *et al.* 2012). This effect may sometimes be indirectly related to modified xylem mechanical properties and increased propensity to conduit wall collapse (Coleman *et al.* 2008). However, lignins may also play a direct role in the pit membrane chemistry. Several authors have detected lignin contents in the pit membrane of different species (Boyce *et al.* 2004; Schmitz *et al.* 2008). Lignins could thus participate to pit membrane functioning by either influencing its rheological (deformation) properties or by directly influencing the physics of air seeding because of its hydrophobic nature (Plavcová & Hacke 2011; Voelker *et al.* 2011; Awad *et al.* 2012).

### Xylem trade-offs and anatomical indices of cavitation resistance

It has long been thought that an efficient xylem for water transport comes at the cost of being more vulnerable to hydraulic failure (Zimmermann 1983; Tyree *et al.* 1994b). A physiological basis to this has been proposed through the rare pit hypothesis (Wheeler *et al.* 2005; Christman *et al.* 2009). This trade-off is, however, far from being universal and results on poplars are heterogeneous. Within individual poplar genotypes smaller conduits tend to be less vulnerable to cavitation (Hacke & Sauter 1995, 1996; Harvey & van den Driessche 1997; Awad *et al.* 2010; Cai & Tyree 2010; Cai *et al.* 2010; Hacke *et al.* 2010). Yet, data obtained under contrasting growth conditions for the same genotype have indicated that even at the individual level, phenotypic acclimation can partly uncouple xylem safety from conducting efficiency (Plavcová & Hacke 2012). In addition, results from individual studies are also conflicting; some have supported the trade-off (Harvey & van den Driessche 1997, 1999; Sparks & Black 1999) while others have not (Cochard *et al.* 2007; Fichot *et al.* 2010; Schreiber *et al.* 2011). Factors such as variations in pathway redundancy, vessel lengths or the fraction of vessel surface area occupied by pits (Cai *et al.* 2010) partly contribute to weaken the relationship when transferring from within-genotype data to cross-genotypes or cross-species comparisons. In addition, the scale at which relationships are studied is also important. The trade-off may or may not be detected depending on the traits used to estimate water transport efficiency (e.g. vessel diameters of stem segments, xylem- and leaf-specific hydraulic conductance of stem segments, whole-plant hydraulic conductance) (Fichot *et al.* 2010, 2011).

Xylem conduits must be also adequately reinforced to cope with the internal loads arising from the negative sap pressures and to avoid cell wall collapse, resulting in a general trade-off between xylem safety and xylem mechanical reinforcement (Hacke *et al.* 2001b; Jacobsen *et al.* 2005). However, as for the trade-off between safety and efficiency, results published on poplars are highly dependent on plant material, on growth conditions and on study scales. Signifi-

cant correlations between cavitation resistance, thickness-to-wall span ratio (a proxy for conduit resistance to wall collapse, see Hacke *et al.* 2001b) and wood density have been noted, but only within individual genotypes and across different treatments (Awad *et al.* 2010; Plavcová *et al.* 2011; Plavcová & Hacke 2012). In this case, however, the relationship observed may primarily reflect covariation among traits in response to treatment factors rather than a direct functional link. Other studies across closely related genotypes or different poplar species have not shown significant relationships (Cochard *et al.* 2007; Awad *et al.* 2010, 2012; Fichot *et al.* 2010; Schreiber *et al.* 2011).

The variable relationships observed across poplars between cavitation resistance, water transport efficiency and mechanical reinforcement suggest that these xylem functions can be, to a certain extent, decoupled. From a practical point of view, it is therefore not realistic to use simple traits such as vessel diameters or wood density as reliable indices for large-scale screenings of cavitation resistance in poplar. However, the thickness of the cell wall separating clustered vessels (the double-vessel wall thickness) deserves additional attention as a potential anatomical surrogate. This trait has indeed been tightly associated with xylem safety (trees with a thicker double wall being more resistant) in both *P. deltoides* × *P. nigra* and *P. tremula* × *P. alba* suggesting it might be of general application in poplar (Awad *et al.* 2010; Fichot *et al.* 2010). The reason for this relationship probably relates to covariation between cell wall thickness and pit membrane thickness; increased pit membrane thickness being associated with reduced porosity and therefore increased resistance to cavitation (Jansen *et al.* 2009).

### Cavitation resistance and leaf physiology

As drought develops, stomata close to prevent the induction of excessive embolism (Jones & Sutherland 1991; Cochard *et al.* 2002). One might expect a tight dynamic stomatal control in highly vulnerable species with steep VCs such as poplars. However, recent findings on a set of six hybrid and one balsam poplar genotypes have indicated that differences in stomatal sensitivity in response to drought are far from being systematically linked to differences in resistance to stem xylem cavitation (Arango-Velez *et al.* 2011). Older studies on *P. trichocarpa*, *P. trichocarpa* × *P. koreana* (cv. Peace) and *P. euphratica* had already shown that at least in these species stomata may not efficiently control the development of embolism (Cochard *et al.* 1996; Sparks & Black 1999; Hukin *et al.* 2005). Substantial variation occurs between and within poplar species/hybrids in their ability to regulate  $\Psi_{\text{leaf}}$  and stomatal conductance during soil drying (Schulte *et al.* 1987; Ceulemans *et al.* 1988; Braatne *et al.* 1992; Tschaplinski *et al.* 1994; Silim *et al.* 2009), reflecting species ecological preferences and the origin of populations (Sparks & Black 1999; Silim *et al.* 2009). Therefore, stomatal control for the avoidance of embolism may not be the only rule in poplars and other factors may contribute to embolism tolerance.

Safety margins (i.e. the difference between the xylem water potential at the onset of cavitation and the minimum xylem water potential experienced *in planta*) are also expected to be small for highly vulnerable species such as poplars and conserved if leaves operate at the edge in order to maximize gas exchange. Yet, safety margins in poplars have been shown to vary depending on the prevailing environmental conditions (water availability, evaporative demand) (Hacke & Sauter 1995; Fichot *et al.* 2010; Arango-Velez *et al.* 2011) and, under comparable conditions, between genotypes from the same hybrid cross (Fichot *et al.* 2010), from different hybrid crosses (Schreiber *et al.* 2011) or from different populations (Schreiber *et al.* 2011). Margins of up to almost 1 MPa have been reported for some genotypes while others seem to operate close to the limits (Fichot *et al.* 2010; Schreiber *et al.* 2011). The functional significance of such variable safety margins remains unknown but once again this probably reflects genotype- and species-specific hydraulic designs, translating into different growth and water-use strategies during water shortage.

The relationship between xylem safety and WUE has seldom been addressed in poplars, but findings suggest no clear relationship (Fichot *et al.* 2010, 2011; Schreiber *et al.* 2011) in line with the conflicting trends observed on other woody species (Kocacinar & Sage 2003; Maherali *et al.* 2006; Ducrey *et al.* 2008; Martínez-Vilalta *et al.* 2009). From a practical point of view this is particularly interesting for poplars, which are supposedly great water spenders and highly vulnerable to drought, because this suggests that cavitation resistance and WUE might be improved independently. WUE is a dynamic trait, influenced by the environment, and primarily reflecting the economics of leaf gas exchange within functional boundaries. In contrast, cavitation resistance is an intrinsic property of the xylem tissue setting the upper functional limit and not modular at least in the short term. There is therefore no straightforward physiological reason for xylem safety to be directly related to WUE. The direction and the strength of the relationship will depend on (1) how stomatal conductance and photosynthetic capacities are related to each other and to what extent each trait can drive variations in WUE under a given environment and (2) the extent and the way cavitation resistance can be coordinated with other aspects of whole-plant hydraulics that constrain leaf water fluxes (Fichot *et al.* 2010, 2011).

### Cavitation resistance, growth performance and drought resilience

Increased resistance to cavitation is supposedly costly in terms of carbon allocation because of the necessity to build a denser wood with thicker cell walls (Hacke *et al.* 2001b), explaining the frequent trade-off observed with biomass yields at least at the interspecific level (Wikberg & Ögren 2004; Ducrey *et al.* 2008). Although this trade-off has been evidenced across five poplar genotypes from different hybrid crosses (Cochard *et al.* 2007) positive or no significant relationships have been reported depending on genetic backgrounds and environmental conditions (Harvey & van den

Driessche 1997; Fichot *et al.* 2010, 2011; Arango-Velez *et al.* 2011; Schreiber *et al.* 2011). In other words, increased resistance to cavitation may neither come systematically at the expense of decreased growth nor systematically confer a competitive advantage, at least under optimal or moderate drought conditions. Because cavitation resistance can be partly uncoupled from growth, there may be some room for improving both drought resistance and growth performance in poplar.

There is growing evidence that stem hydraulic failure is a causal factor of tree and forest mortality (Brodribb & Cochard 2009; Brodribb *et al.* 2010; Choat *et al.* 2012; Nardini *et al.* 2013; Urli *et al.* 2013) including in poplars (Anderegg *et al.* 2012, 2013; Barigah *et al.* 2013). The mortality threshold in angiosperms seems to be close to 90% of stem embolism (Barigah *et al.* 2013; Galvez *et al.* 2013; Urli *et al.* 2013). However, even after massive embolism and complete leaf and stem desiccation, some poplar trees (*P. tremula* and *P. tremuloides*) are sometimes able to resprout once drought is alleviated (Lu *et al.* 2010; Urli *et al.* 2013). This highlights the need to also account in future studies for the below-ground compartment and possible xylem refilling. In addition, hydraulic failure may also interact with carbon starvation (McDowell *et al.* 2011) depending on drought duration and intensity (Hartmann *et al.* 2013; Mitchell *et al.* 2013). For seedlings of *P. tremuloides* and *P. balsamifera*, severe drought leading to more than 80% loss of hydraulic conductivity by the end of the first growing season directly impaired carbon accumulation in the roots (Galvez *et al.* 2013). This hampered root survival over winter and therefore prevented resprouting the next season, which led to seedling death. Additional research accounting for the temporal and the multi-tissue dynamics of water and carbon relations is therefore needed; this will help understand the fine mechanisms involved in poplar mortality and the possibly different strategies among poplar species.

### GAPS IN KNOWLEDGE AND RESEARCH OPPORTUNITIES

Our analysis clearly indicates that significant variation can be expected in cavitation resistance among poplar species. However, the number of species studied so far remains limited and their unequal representation in the literature hinders firm conclusions to be drawn regarding direct comparisons between species or botanical sections. Only 10 pure species have been characterized for their resistance to drought-induced cavitation (*P. alba*, *P. angustifolia*, *P. balsamifera*, *P. deltoides*, *P. euphratica*, *P. fremontii*, *P. nigra*, *P. tremula*, *P. tremuloides* and *P. trichocarpa*). Although these are the most commonly known species and are of particular importance for silvicultural use, approximately two-thirds of the *ca.* 30 poplar species still remain to be documented. It is very likely that some part of the natural variation occurring for cavitation resistance among *Populus* spp. therefore is still unknown. The characterization of these 'missing' species would thus complete the picture at the genus level and would help reveal possible trends with species phylogeny and life history.

Our meta-analysis did not reveal clear differences in cavitation resistance between pure species and interspecific hybrids (Fig. 3). However, thus far, the largest range of infraspecific genotypic variation has been reported for interspecific hybrids of the same cross (*P. deltoides* × *P. nigra*) raising the question of transgressive segregation for cavitation resistance (Fichot *et al.* 2010). To our knowledge, heterosis for cavitation resistance has not been explored in any plant species yet. Considering both the large natural genetic variation available and the ease for controlled pollination and hybridization, the genus *Populus* stands as an ideal model for such studies. This would help confirm whether gains in resistance can be truly expected from hybrids.

In a changing world with stochastic extreme droughts, the importance of survival for species fitness may become increasingly important and in this context cavitation resistance may be a key trait (Choat *et al.* 2012). Quantifying the extent of genetic and environmental variations for this trait may therefore be central to understand the evolutionary processes that have shaped the structure of populations and to predict their adaptive potential in response to global change. Recent findings obtained on *Pinus pinaster* Aiton. and *Fagus sylvatica* L. have indicated that most of the genetic variation resides within populations, variation between populations being limited as well as phenotypic plasticity (Corcuera *et al.* 2011; Lamy *et al.* 2011, 2014; Wortemann *et al.* 2011). This has led to the hypothesis that resistance to drought-induced cavitation is a canalized trait and that facing drought through xylem cavitation-related traits may have limited adaptive potential (Lamy *et al.* 2011, 2014). Based on the available literature, we do not know whether this conclusion applies to *Populus* spp. because of the limited number of genotypes and/or populations studied so far. However, poplar species represent an interesting model as a whole to target the question because of their generally extensive and varied natural range (DiFazio *et al.* 2011). Not all species have been subjected to the same past selective pressures. Therefore different patterns might be expected between riparian species (typically cottonwoods) for which drought is not expected to be a strong selective pressure, and other species occurring in upland drier habitats (e.g. *P. tremula* and *P. tremuloides*). Similarly, not all poplar species will face the ongoing climate modifications at the same risks. Further work in this research area would be clearly valuable for both our understanding of poplar ecology and of the importance of cavitation resistance in woody plant evolution.

Our assessment of previous studies also shows that cavitation resistance is a plastic trait, at least in response to nitrogen fertilization, irradiance, temperature and water availability, which is not unexpected given the pioneering and opportunistic strategy of poplars. However, many of the studies we examined were limited to a few (hybrid) genotypes. Therefore, the extent (limit) to which cavitation resistance can acclimate and, most importantly, the extent of genetic variation in phenotypic plasticity (genotype × environment interactions, G×E), remain to be uncovered. G×E should be taken into account not only in the context of tree

adaptation (Pigliucci 2005) but also in the context of large-scale deployment of stable cultivars (Aspinwall *et al.* 2014). Findings on hybrid poplars have indicated that G×E can occur for cavitation resistance in response to drought-induced acclimation (Fichot *et al.* 2010) and it is very likely that it is so in response to other environmental factors. In addition, the apparent trade-off observed between intrinsic cavitation resistance and the propensity to acclimate in response to drought (Fig. 4) deserves to be tested across different poplar genetic backgrounds as well as in other woody plant species and calls for further work to unravel its underlying physiological and genetic basis.

From a practical point of view, perhaps the most central question is whether cavitation resistance is a relevant criterion for future poplar breeding programmes. Genotype selection for enhanced survival under extreme drought may have limited interest *per se* because the water potentials corresponding to hydraulic failure ( $P_{ss}$ , typically lower than  $-2$  MPa) are, in most cases, unlikely to be reached at planting sites favourable to poplar growth. Alternatively, as embolism development is generally coupled to leaf stomatal regulation, selecting for increased cavitation resistance may indirectly result into a higher tolerance to moderate water deficits via sustained gas exchange and delayed drought effects. However, previous work on poplars has shown that the link between stomatal sensitivity to drought and cavitation resistance can be variable (Arango-Velez *et al.* 2011; see the above discussion on cavitation resistance and leaf physiology) suggesting different strategies in embolism avoidance depending on genetic backgrounds. Likewise, relationships between resistance to cavitation and other key functional traits such as WUE or growth potential also seem variable. More efforts should therefore go towards the characterization of more species, hybrid crosses and genotypes in field conditions and under contrasting environments. Future research should also adopt a better integrated approach by systematically combining measurements at different scales (tissue, organ and whole-plant levels) and explicitly addressing the possible trade-offs between cavitation resistance, phenotypic plasticity and other traits of agronomic importance in poplar cultivation such as wood quality, growth performance, WUE or leaf rust resistance. A clear understanding of the covariation between these components will be a key step forward in assessing the relevance of resistance to drought-induced cavitation in poplar breeding.

The research avenues proposed above imply the characterization of a large number of individuals, and therefore represent a considerable challenge. This should be facilitated thanks to the availability of methods that now allow more rapid and accurate phenotyping of cavitation resistance (Cochard 2002; Cochard *et al.* 2005), although this step still represents the main bottleneck of large-scale cavitation studies. The development of time- and cost-effective high-throughput tools for phenotyping cavitation resistance is therefore highly desirable, especially if we have to combine phenotypic data with genomics (Furbank & Tester 2011) (see below). However, our review indicates that the use of simple and easily measurable morpho-physiological traits as reliable

predictors of cavitation resistance is unlikely, at least in poplars, which is not unexpected given the complex ultrastructural determinism of this trait in angiosperms. Because cavitation resistance is somehow controlled by the chemical composition of pit membranes, the potential and relevance of near-infrared reflectance spectrometry (NIRS) could be tested in future studies. For instance, this technique has already proven effective in the prediction of complex  $^{13}\text{C}$  and  $^{15}\text{N}$  isotopic signatures of plant tissues (Kleinebecker *et al.* 2009).

Finally, the last 15 years have seen poplars definitely emerging as model species for molecular studies of processes inherent to perennial woody angiosperms (Bradshaw *et al.* 2000; Jansson & Douglas 2007). This has been accompanied by an extensive array of genetic, genomic, functional genomic and other molecular data (e.g. Brunner *et al.* 2004; Tuskan *et al.* 2006; Kelleher *et al.* 2007; Sjödin *et al.* 2009; Slavov *et al.* 2012; McKown *et al.* 2014), thereby highlighting the great potential of poplars for phenotype-genotype studies. As a consequence, poplars represent a valuable model in the perspective of dissecting the genetic architecture of and identifying the genes underlying resistance to drought-induced cavitation in angiosperm trees.

## CONCLUSIONS

Poplars are among the most vulnerable woody plants to drought-induced cavitation. Yet, our assessment of studies conducted thus far on poplars clearly indicates that there is significant variation among species and hybrid crosses, within species and hybrid crosses, as well as in response to environmental factors. Such variation has important implications for plant functioning during water deficit, especially in the case of vulnerable species as poplars, and therefore might be manipulated for the improvement of drought tolerance. We have, however, identified several gaps in knowledge and we stress the need for additional and more integrated research. Finally, we argue that research on poplars may complete our knowledge of the functional and ecological significance of drought-induced cavitation, and may also serve answering unresolved questions such as heterosis for cavitation resistance. Most importantly, poplars represent a valuable model in the perspective of elucidating the genetic architecture and the molecular determinism of this key trait in Angiosperms.

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