

**Across climates and species, higher vapor pressure deficit is associated with wider vessels
for plants of the same height**

running head: VPD and vessel diameter

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Abstract

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While plant height is the main driver of variation in mean vessel diameter at the stem base (*VD*) across angiosperms, climate, specifically temperature, does play an explanatory role, with vessels being wider with warmer temperature for plants of the same height. Using a comparative approach sampling 537 species of angiosperms across 19 communities, we rejected selection favoring freezing-induced embolism resistance as being able to account for wider vessels for a given height in warmer climates. Instead, we give reason to suspect that higher vapor pressure deficit *VPD* accounts for the positive scaling of height-standardized *VD* (and potential xylem conductance) with temperature. Selection likely favors conductive systems that are able to meet the higher transpirational demand of warmer climates, which have higher *VPD*, resulting in wider vessels for a given height. At the same time, wider vessels are likely more vulnerable to dysfunction. With future climates likely to experience ever greater extremes of *VPD*, future forests could be increasingly vulnerable.

Keywords: Adaptation, allometry, climate, ecological wood anatomy, freezing-induced embolism, vapor pressure deficit, xylem embolism, xylem vessels

Introduction

The evaporative demand of the atmosphere, as reflected by vapor pressure deficit (*VPD*), is one of the selective agents acting crucially on plant water relations (Eamus, Boulain, Cleverly & Breshears 2013; Will, Wilson, Zou & Hennessey 2013; Gotsch, Davidson, Murray, Duarte & Draguljić 2017; Lemordant, Gentine, Swann, Cook & Scheff 2018; Aparecido, Woo, Suazo, Hultine & Blonder 2020), yet its effect on the evolution of plant long-distance water transport systems has remained largely unexamined (Bush *et al.* 2008; Isaac-Renton *et al.* 2018). How quickly water evaporates from plant leaves into the atmosphere is a fundamental variable affecting plant productivity worldwide (Stockle & Kiniry 1990; Churkina & Running 1998). High *VPD* often induces stomatal closure (Jones 1992), meaning that high *VPD* is often associated with lowered productivity, even if water is present in the soil (Pugnaire, Serrano & Pardos 1999; Lemordant *et al.* 2018; Anderegg *et al.* 2018). High cuticular water loss exacerbates these effects (Anderegg, Berry & Field 2012). Under drought, high *VPD* often leads to extreme xylem tensions that break the long-distance conductive stream in the wood (secondary xylem), which transports water from roots to leaves (Pugnaire *et al.* 1999; Eamus *et al.* 2013; Will *et al.* 2013; Anderegg & Meinzer 2015; Fontes *et al.* 2018). These are important considerations, because extremes of temperature and *VPD* are only projected to increase in many areas as climates change (Anderegg & Meinzer 2015; Zwieniecki & Secchi 2015; Ficklin &

Novick 2017; Fontes *et al.* 2018; Barkhordarian, Saatchi, Behrangi, Loikith & Mechoso 2019; Sullivan *et al.* 2020).

Because failure of the hydraulic system is implicated as a participant in all climate-change associated forest mortality events to date (Anderegg *et al.* 2016; Adams *et al.* 2017; Choat *et al.* 2018), identifying whether *VPD* shapes the long-distance hydraulic transport system is a priority for understanding the causes of mortality and designing climate change mitigating strategies (Eamus *et al.* 2013). Despite the importance of *VPD*, most studies have regarded moisture availability, especially precipitation, as fundamentally driving the diameters of xylem water conduits (Webber 1936; Baas 1982; Carlquist & Hoekman 1985; Pfautsch *et al.* 2016; Warwick, Hailey, Clarke & Gasson 2017). Xylem conduit (tracheid or vessel) diameter is a key variable because it affects conductive efficiency, and likely vulnerability to failure via the formation of gas embolisms (Cochard & Tyree 1990; Hargrave, Kolb, Ewers & Davis 1994; Davis, Sperry & Hacke 1999; Pittermann & Sperry 2003, 2006; Cobb, Choat & Holbrook 2007; Cai & Tyree 2010; Sevanto, Holbrook & Ball 2012; Anderegg & Meinzer 2015; Brodribb, Bienaimé & Marmottant 2016; Scoffoni *et al.* 2017). In this study, we give evidence to suggest that *VPD* is an important climatic driver of variation in conduit diameter in plant stems across the world's climates.

Although *VPD* seems plausibly a key *climatic* driver, the main driver of conduit diameter variation by far is stem length, so any evaluation of the effect of *VPD* or any other variable on conduit diameter must take stem length into account. As a plant grows taller, the distance

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between roots and leaves, across which water must be moved, increases. The walls of conduits exert friction on the moving water column, and, for a given difference in leaf and soil water potentials, following Poiseuille's Law (Vogel 2003), if conduits do not change in diameter, hydraulic conductance drops as a linear function of conduit length increase. Conduits do not remain uniform, however, with increases in diameter lowering hydraulic resistance as diameter to the fourth power. This means that small increases in diameter are in principle able to maintain conductance constant per unit leaf area as trees grow taller, with the net effect that taller plants have predictably wider conduits (West, Brown & Enquist 1999; McCulloh, Sperry & Adler 2003; Anfodillo, Carraro, Carrer, Fior & Rossi 2006; Meinzer, Lachenbruch & Dawson 2011; Olson *et al.* 2018). This tendency for plant size to predict conduit diameter must be taken into account in understanding how variables such as climate affect conduit diameter. The widespread notion that precipitation is the main driver of variation in conduit diameter (Carlquist 1980; Fahn, Werker & Baas 1983; Baas & Carlquist 1985; Carlquist & Hoekman 1985; Micco, Aronne & Baas 2008; Pfautsch *et al.* 2016; Warwick *et al.* 2017) is due to study of raw rather than height-corrected conduit diameter. In contrast, recent studies show that, once conductive path length (as approximated by plant height or stem length) is taken into account, precipitation has no statistical power to predict residual variation in conduit diameter (Olson *et al.* 2014, 2018; Morris *et al.* 2018). Therefore, the tendency to find wider mean conduit diameters in moister areas is simply because plants are on average taller in moister areas.

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Instead, recent studies (Olson *et al.* 2014, 2018; Morris *et al.* 2018) have shown the unexpected observation that, when taking conductive path length into account, mean annual temperature, not precipitation, is the variable examined explaining the most residual variation in the conduit diameter-stem length relationship (see also He *et al.* 2019). Because temperature is a fundamental driver of *VPD* (Wang, Dickinson & Liang 2012; Monteith & Unsworth 2013; Eamus *et al.* 2013; Ficklin & Novick 2017), these recent results point to the potential role of *VPD* in shaping plant conductive systems.

One way that *VPD* could shape long-distance conductive systems is through selection maintaining carbon acquisition rates across climates that differ in temperature and thus *VPD* (Fig. 1) (cf. Voelker *et al.* 2012). Higher *VPD* exerts greater demand for water at the sites of transpiration. So, for the same carbon acquisition rate, level of hydration, water potential, and stomatal aperture, a plant under high *VPD* requires a greater water supply than one under low *VPD*. Meeting this greater water supply, under conditions of higher mean annual temperature and thus *VPD*, natural selection would favor variants with slightly wider conduits and higher total xylem conductance (Gleason, Butler & Waryszak 2013; Voelker *et al.* 2012 present an analogous argument with regard to variation in CO₂ concentration). This scenario suggests that conductance should keep pace exactly, that is, scale isometrically, with *VPD*. Crucially, such a scenario would be consistent with the association that has been documented in recent studies, in which mean annual temperature is the best predictor of size-standardized vessel diameter (Olson

et al. 2014, 2018; Morris *et al.* 2018), a heretofore unrecognized pattern and one requiring explanation.

Here, we used the most recent dataset examining the conduit diameter-stem length-climate association (Olson *et al.* 2018) to test the notion that *VPD* can account for much of the residual variation in the conduit diameter-stem length relationship. This sampling included flowering plants (angiosperms) from 19 communities from the north and south temperate zones and the lowland and highland tropics. The communities included both frost-prone and frost-free deserts, a Mediterranean climate shrubland, tropical dry forests, tropical savannahs, lowland and highland tropical rainforests, two north temperate deciduous forests, and four elevational treeline ecotones (Table 1). The plants sampled conduct water in vessels, and we examined the causes of variation in species mean height-standardized vessel diameter (\overline{VD}_{stand}) across climates. We give reason to reject the notion that cold selecting for narrow conduits is responsible for the ability of mean annual temperature to predict \overline{VD}_{stand} . Under freezing, narrower conduits are likelier either to resist embolism or for gas bubbles to return into solution (Sevanto *et al.* 2012). Given heritable variation in a population, individuals that all else being equal minimize carbon investment in embolism recovery or resistance should be favored, so selection should favor narrow conduits in freezing prone localities (Langan, Ewers & Davis 1997; Davis *et al.* 1999; Cavender-Bares & Holbrook 2001; Martínez-Vilalta & Pockman 2002; Pittermann & Sperry 2003; Cavender-Bares 2005; Cavender-Bares *et al.* 2005; Stuart, Choat, Martin, Holbrook & Ball 2007; Savage & Cavender-Bares 2013; Zanne *et al.* 2013). However, the ability of temperature

to predict \overline{VD}_{stand} persisted even when we analyzed only the frost-free communities. Instead, we show that potential conductance scales isometrically with VPD , as predicted by the scenario in Fig. 1. Our results provide the first explanation accounting for the \overline{VD}_{stand} – temperature relationship, and explain otherwise enigmatic results, such as finding narrower, rather than the expected wider, conduits in experiments that raise humidity levels (Jasińska, Alber, Tullus, Rahi & Sellin 2015; Sellin, Alber & Kupper 2017).

Methods

The data used (Olson *et al.* 2018) are species means of vessel diameter at the stem base VD , vessel density Vmm^{-2} , and height (“stem length” SL) plus climate data and were calculated based on samples of similar-sized individuals of mature size per species, 3 individuals for 88% of the species, 1-2 individuals for the others, from 19 communities spanning most of the world’s vegetated climates (Table 1). The dataset included only self-supporting habits and vessel-bearing non-monocots. Monocots tend to have higher vessel diameter-stem length Y-intercepts (Olson *et al.* 2014), and non self-supporting plants tend to have wider vessel diameter variances for a given stem length than self-supporting plants (Rosell & Olson 2014). While this variation is of functional significance and thus of great interest, for the purposes of our comparisons, it would introduce additional sources of variation beyond plant size and climate. Excluding monocots and lianas as sources of variation about the Y axis therefore increased our ability to detect the effect of climate on fine differences in intercept between communities.

Community mean plant height and vessel diameter with temperature and precipitation

To test the effects of temperature on the *VD-SL* relationship, we calculated mean values per-community for the 19 communities for *VD*, *SL*, and mean annual temperature (*MAT*) (Table 1). We fit simple linear regressions predicting community mean $\log_{10}VD$ or $\log_{10}SL$ based on *MAT*. We then fit models using community $\log_{10}VD$ - $\log_{10}SL$ residuals, removing the effects of plant height on vessel diameter, against *MAT*, with the expectation that these relationships should have poorer fits than $\log_{10}VD$ -*MAT* or $\log_{10}SL$ -*MAT* relationships alone. By way of contrast, we also fit similar models for mean annual precipitation (*MAP*), because precipitation is often regarded as an important climate variable acting on *VD*. The results to this point underscored the ability of temperature to predict community mean *VD-SL* residuals positively (Fig. 2, Table 2), so we proceeded to test potential causes of this association. These and all other analyses used R v.3.4.3.

Variation in vessel diameter-stem length Y-intercept across climates

To examine the effect of climate on vessel diameter-stem length scaling, we fit multiple linear regression models using all of the data (means for each of the 537 species, not community means). When the same species was collected in more than one community, we treated these as though they were different species (e.g. *Vaccinium myrtillus* Alpine, *V. myrtillus* Temperate Forest), in case the differing climates under which they were growing affected their *VD-SL* relations. We first fit a model predicting $\log_{10}VD$ against $\log_{10}SL$, a “community” categorical

variable with 19 levels, corresponding to the 19 communities sampled, and a $\log_{10}SL$ · community interaction term. This interaction term was non-significant, indicating that vessel diameter scales with SL with the same slope across communities, so we re-fit the model without the interaction term. We then found that the communities differed markedly in their Y-intercepts (Fig. 3), and we present and discuss this final model in the results. We followed a similar procedure for V_{mm}^{-2} .

Does MAT predict \overline{VD}_{stand} because of selection favoring resistance of freezing-induced embolism in cold communities?

We are not aware of any hypothesis that proposes a plausible direct link between VD and MAT . As a result, it seems certain that the tendency for MAT to predict species mean height-standardized vessel diameter \overline{VD}_{stand} is not the result of scaling with MAT per se. Instead, it seems more likely that factors such as VPD or climatic extremes are the relevant selection pressures (Zwieniecki & Secchi 2015), and that these tend to be correlated with the mean values that are available in climate datasets such as WorldClim. One of these climatic extremes that is likely a significant selection pressure are low temperatures. Low temperatures are thought to select for narrow mean conduit diameters because narrow conduits better resist freezing-induced embolism (Cavender-Bares & Holbrook 2001; Pittermann & Sperry 2003; Cavender-Bares 2005; Cavender-Bares *et al.* 2005; Ball, Canny, Huang, Egerton & Wolfe 2006; Sevanto *et al.* 2012; Zanne *et al.* 2013). It could be that selection favoring freezing resistance accounts for the

\overline{VD}_{stand} - MAT relationship and variation in the VD - SL Y-intercept across communities: if selection favors narrower vessels for a given plant size in colder communities, then this process could account for the pattern. To examine this possibility, we first fit a linear regression model predicting $\log_{10}VD$ based on $\log_{10}SL$ plus MAT . We then eliminated the seven communities with minimum temperatures of the coldest month below 5°C (YALE, ESPALP, PATA, SPM, MF, MV, ESPTMP, following the abbreviations in Table 1), and re-fit the models. If the positive association with temperature is the result of selection acting against wide vessels given plant height in freezing-prone localities, then the coefficient associated with MAT in the relationship between mean community vessel diameter and temperature should lose significance when only the frost-free communities are included.

Does temperature predict \overline{VD}_{stand} because of the scaling of plant transpiration rate with vapor pressure deficit?

We then examined the possibility that differences in transpiration rate associated with temperature-induced variation in VPD could underlie the \overline{VD}_{stand} – mean annual temperature association. To calculate vapor pressure deficit VPD , we extracted monthly average relative humidity values at 3 pm for each locality from the CliMond dataset (Kriticos *et al.* 2012) at 10 minutes resolution using `sp` (Bivand, Pebesma & Gómez-Rubio 2013), `raster` (Hijmans 2019) and `dismo`. We used relative humidity values from 3 pm because these should approximate well the maximal evaporative demands that exert the selection pressure postulated to vary across

communities (cf. Gleason, Butler & Waryszak 2013). We used *MAT* to calculate our *VPD* index. *MAT* was important to use because our main aim was to examine the novel and unexplained association between \overline{VD}_{stand} and *MAT* observed in previous studies (Olson *et al.* 2014, 2018; Morris *et al.* 2018). In this way, we estimated *VPD* over the range of temperatures as $e_s - e_a$, where e_s is the saturation vapor pressure (conventionally assumed to represent conditions within the leaf) and e_a the actual vapor pressure, where $e_s = 6.1078 \exp(17.269 \cdot T)/(237.3+T)$ and $e_a = RH/100 \cdot e_s$ (Monteith & Unsworth 2013).

With this information in hand, we then used the following procedure to estimate the effect of *VPD* on vessel diameter. For plants of a given height, those in warmer climates tend to have wider vessels. If this is due to the effect of greater evaporative demand favoring greater transpiration rate, then, all else being equal, conductance should keep with *VPD*. We therefore modeled the way that conductance scales with *VPD* while standardizing for plant height. To do so, we used the model predicting *VD* based on *SL* and community (presented in Table 3) to calculate mean vessel diameters across the height range present in each community, from 1 meter tall to the maximum height per community, in 1 meter increments. We then estimated per-vessel conductance as VD^4 , assuming that flow in a vessel is proportional to radius to the fourth power (Vogel 2003). Because in addition to vessel diameter vessel density also affects bulk conductance, we multiplied VD^4 by vessel density (Vmm^{-2}), also based on the model for vessel density in Table 3. In this way, $VD^4 \cdot Vmm^{-2}$ provides a useful metric for the conductance of a given transectional area of xylem across the height ranges found in the communities studied.

Real plant conduits have many sources of resistance that estimates of this sort do not reflect, including interconduit pit membrane features, internal sculpturing, variation in conduit diameter, and finite conduit length. However, simple capillary assumptions are sufficient to predict the rate of tip-to-base conduit widening, implying that these additional sources of resistance scale in exact proportion to tip-to-base conduit widening (Lazzarin *et al.* 2016; Olson *et al.* 2018, 2020). We then used VPD and SL (together with the interaction term between them) to predict $VD^4 \cdot Vmm^{-2}$, with the prediction that, if the variation in community intercepts of the $VD-SL$ relationship (Fig. 3) is due to the scaling of VD with VPD , then VPD should predict $VD^4 \cdot Vmm^{-2}$ with a slope whose confidence interval includes isometry.

Results

Plant height and vessel diameter scaling with temperature and precipitation: mean community values

Across the 19 communities studied (Table 1), community mean VD was predicted very well by plant height SL ($R^2=0.75$, Table 2). With regard to environmental variables, VD was predicted well by MAT ($R^2=0.59$), less so by MAP ($R^2=0.32$) (Fig. 2a, b, Table 2). SL was predicted about equally by both MAT ($R^2=0.24$) and MAP ($R^2=0.28$) (Fig. 2c, d). In contrast, the associations between $VD-SL$ residuals and MAP and MAT were strikingly different. $VD-SL$ residuals versus MAT retained almost all predictive signal, with an R^2 of 0.46 (Fig. 2e), as compared to the 0.59 with non height-standardized vessel diameter (Fig. 2a). In contrast, $VD-SL$ residuals against MAP

lost all relationship ($R^2=0.02$, regression not significant). These results indicate that vessel diameter is predicted by precipitation only to the degree that plant height is predicted by precipitation, and that all else being equal similar-sized plants in areas of differing precipitation have similar mean vessel diameters (cf. He *et al.* 2019). However, they also indicate that vessel diameter is positively predicted by temperature even when standardizing for plant height.

Variation in vessel diameter-stem length Y-intercept across communities

Our regression models predicting vessel diameter and vessel density based on stem length and community are presented in Table 3. They show that, while *VD* scales with *SL* with the same slope across all communities, there were significant differences in Y-intercept. Figure 3 and Table 3 order the mean community *VD-SL* Y-intercepts from high to low. Figure 3 colors each species according to the mean annual temperature of its community, revealing a clear ranking by temperature, with warmer communities having wider mean vessel diameters when controlling for plant height. Figure 3 illustrates graphically that the effect of temperature is very small compared to stem length. The variance in *VD* across a relatively modest range of plant heights (0.07-32.5 m) was much higher than that associated with a very wide range in community *MAT* (3.2-27.3°C). Though much smaller than that of *SL*, the effect of *MAT* on *VD* was statistically significant, with warmer communities having slightly wider mean vessel diameters when controlling for plant height. Within the warm communities, the savannahs had the widest vessels for a given height. These were followed by the tropical deciduous and rain forests, along with the

frost-free desert, which falls within the tropics at the tip of the Baja California peninsula in Mexico. The lower intercepts include the frost-prone desert, the north and south temperate forests, the highland tropical forest, the California Mediterranean-type chaparral, and all four treeline ecotone communities. There is thus a marked association between \overline{VD}_{stand} and mean annual temperature, and this relationship requires explanation.

Does temperature predict \overline{VD}_{stand} because of selection favoring resistance of freezing-induced embolism in cold communities?

It is often assumed that that freezing selects for narrow vessels independently of plant size because narrow conduits better resist freezing-induced embolism (Zanne *et al.* 2013). This assumption implies that given plants of similar size, those in a cold habitat will have on average narrower vessels than plants in a warm habitat. Vulnerability to freezing clearly can affect species distribution (Langan *et al.* 1997; Davis, Pratt, Ewers & Jacobsen 2007; Stuart *et al.* 2007; Gleason *et al.* 2018), so it does seem possible that selection against wide vessels in areas of freezing risk might be causing the ability that we observed for mean annual temperature to positively predict \overline{VD}_{stand} (Table 4). In our data, *MAT* predicts the average minimum temperature of the coldest month very well (Table 2). This correlation illustrates that it is plausible that *MAT* is correlated with the absolute minimum temperatures (rather than the average minima found in WorldClim) that presumably exert the significant selection pressures shaping conduit diameters via freezing induced embolism (Zwieniecki & Secchi 2015).

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Rejecting our expectation, when we examined only the frost-free communities (excluding the seven freezing-prone communities, with minimum temperatures of the coldest month below 5°C), we still recovered a strong ability of mean annual temperature to predict community \overline{VD}_{stand} even across these warm, mostly lowland tropical and subtropical communities (Table 4). Therefore, while selection favoring resistance of freezing-induced embolism would be consistent with the narrow height-standardized mean vessel diameters (\overline{VD}_{stand}) of the cold communities, it is not sufficient to explain why \overline{VD}_{stand} of the warm communities should be predicted by *MAT*.

Does temperature predict \overline{VD}_{stand} because of the scaling of plant transpiration rate with VPD?

Our estimate of conductance scaled isometrically with *VPD* across the range of heights present in each community (Fig. 4), with the coefficient associated with *VPD* being 1.132 and a confidence interval that included the predicted slope of 1 (0.954, 1.310); (N=291, $R^2=0.72$; $F_{(2,288)}=372.8$, $P<0.001$; slope *SL*: 0.999 (0.913, 1.085); intercept 6.939 (6.756, 7.121)).

Discussion

The scaling of plant conductance with vapor pressure deficit is consistent with the \overline{VD}_{stand} –mean annual temperature relationship

Consistent with Fig. 1, the dependence of vapor pressure deficit (*VPD*) on temperature provides a plausible explanation for the the relationship observed here and in other studies between species mean vessel diameter standardized for plant height (\overline{VD}_{stand}) and mean annual

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temperature (*MAT*) (Olson *et al.* 2014, 2018; Morris *et al.* 2018), not directly but via the effects of temperature on *VPD* (Fig. 4 and the final model presented in Results) (Eamus *et al.* 2013; Gleason *et al.* 2013, 2016). This conclusion is supported by experimental data that remain enigmatic in the absence of a link between \overline{VD}_{stand} and *VPD*. In one experiment, hybrid poplars exposed to free-air humidity enhancement produced *narrower* vessels rather than the wider ones that traditional ecological wood anatomy would expect, in which moister conditions would be expected to favor wider, more vulnerable but more efficient, vessels (Jasińska *et al.* 2015; Sellin *et al.* 2017). Instead, if \overline{VD}_{stand} scales with *VPD*, with conductance keeping pace with atmospheric evaporative demand, then this would explain the production of narrower vessels under enhanced humidity (Jasińska *et al.* 2015; Sellin *et al.* 2017). In addition to showing isometry of conductance with *VPD*, the model predicting *VD* based on *SL* and *VPD* (see final section of Results) also shows isometry of conductance with height, exactly what would be expected if tip-to-base conduit widening is the result of natural selection buffering the effects of resistance caused by increasing conductive pathlength with height growth (Anfodillo *et al.* 2006; Olson *et al.* 2018, 2020). That the results of our conductance-*VPD* estimates coincide strikingly with the predicted isometry does suggest that the role of conduit scaling with *VPD* is one worth exploring in more detail, especially because our analyses clearly reject the freezing hypothesis we tested.

Selection favoring resistance of freezing-induced embolism cannot explain the positive relationship between \overline{VD}_{stand} and mean annual temperature observed in our data

The tendency for plants to have narrower vessels for a given height in colder communities (Fig. 3) would seem congruent with the traditional expectation that selection favors narrow vessels in frost-prone localities independently of stem size. Temperature is traditionally regarded as affecting vessel diameter across communities because it favors narrow vessels (independently of plant size) in freezing-prone localities as a result of narrow vessels better resisting freezing-induced embolism (Zanne *et al.* 2013, 2018; He *et al.* 2019). If this were the case, then excluding freezing-prone communities should have eliminated the \overline{VD}_{stand} -temperature relationship, but it persisted (Table 4). The hypothesis that it is cold favoring narrow vessel diameters independently of plant size that explains the \overline{VD}_{stand} -MAT relationship therefore seems inconsistent with the data.

This conclusion is not to say that selection favoring resistance of freezing induced cavitation is not a major selective force acting on conduit diameter, just that it does not appear sufficient to explain the \overline{VD}_{stand} -MAT relationship. Selection favoring resistance of freezing induced embolism via narrow conduit diameters seems likely to be a potent selective agent on absolute (i.e. not height-standardized) vessel diameters (Zanne *et al.* 2013). If wider conduits are more vulnerable to freezing induced embolism than narrow ones (Cavender-Bares 2005; Pittermann & Sperry 2006; Sevanto *et al.* 2012; Medeiros & Pockman 2014), then in areas of very low temperatures (Ball *et al.* 2006), or very frequent freeze-thaw cycles and short growing

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seasons, selection should favor narrow conduits. Because selection favors a more or less constant relationship between conduit diameter and plant height (Couvreur *et al.* 2018), presumably the result of selection maintaining per-leaf area conductance constant as plants grow taller (Echeverría, Anfodillo, Soriano, Rosell & Olson 2019), then there is a predictable relationship between conduit diameter and plant size. Therefore, if selection favors narrow conduits, then it necessarily does so by reducing plant size (Coomes, Jenkins & Cole 2007; Losso *et al.* 2017; Olson *et al.* 2018; Prendin *et al.* 2018; Gleason *et al.* 2018). This scenario predicts that the areas with the lowest temperatures and the most frequent freeze-thaw events per growing season should have the shortest plants, and this is indeed the case, e.g. tundra and páramo. Similarly, warming climates should relax selection favoring narrow conduits, permitting height increase in tundras, as is being observed throughout the arctic and subarctic (Sturm, Racine & Tape 2001; Gamache & Payette 2004; Devi *et al.* 2008; Berner, Beck, Bunn & Goetz 2013). Therefore, abundant data are congruent with the notion that freezing is a powerful selective agent acting on conduit diameter, but such selection does not appear to explain the pattern that we focus on, the positive $\overline{VD}_{stand-MAT}$ relationship across all climates.

Conclusion: increasing VPD and the need to understand the conduit diameter-vulnerability link

The possibility that vapor pressure deficit VPD is a central selective force reflected in plant hydraulic anatomy has been little explored but does seem congruent with other studies that

implicate *VPD*, rather than temperature *per se*, as a crucial agent of selection on plant hydraulics (Eamus *et al.* 2013; Jasińska *et al.* 2015; Sellin *et al.* 2017). Future climates promise increasing extremes of *VPD*, which in turn exerts strong pressures on plants (Breshears *et al.* 2013; Park Williams *et al.* 2013; Lemordant *et al.* 2018). Much evidence seems to suggest that wider conduits are more susceptible to drought induced embolism (Hargrave *et al.* 1994; Davis *et al.* 1999; Cai & Tyree 2010; Schreiber *et al.* 2016; Lobo *et al.* 2018; Jacobsen, Brandon Pratt, Venturas, Hacke & Lens 2019). However, this point is still controversial and there is no well-established theory regarding the connection between conduit diameter and drought induced embolism the way there is for freezing induced embolism (Pittermann & Sperry 2003, 2006; Sevanto *et al.* 2012). Understanding the link between conduit diameter and drought induced embolism is urgent, however, because if there is such a link, then future climates leading to wider height-standardized conduit diameters therefore implies that future forests will be increasingly vulnerable, exactly when they are being exposed to more extreme climate events likely to provoke embolism and potentially mortality (Breshears *et al.* 2013; Park Williams *et al.* 2013; Eamus *et al.* 2013; Will *et al.* 2013; McDowell & Allen 2015; Zwieniecki & Secchi 2015; Adams *et al.* 2017; McDowell *et al.* 2018; Fontes *et al.* 2018; Isaac-Renton *et al.* 2018; Barkhordarian *et al.* 2019; Sullivan *et al.* 2020).

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Conflict of interest statement

The authors have no conflict of interest to declare.

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Table 1. Communities studied, ordered from high to low mean annual temperature (*MAT*), with geographical coordinates, mean annual precipitation (*MAP*), community mean basal vessel diameter (*VD*), and stem length (*SL*), with ranges in parentheses

Code	Vegetation	Locality	Lat	Lon	MAT (°C)	MAP (mm)	VD (µm)	SL (m)
HS	Tropical	Howard Springs,	-12.452	131.032	27.3	1570	86.9 (20.1, 158.1)	6.7 (0.1, 15.6)
CH	Tropical dry	Chamela dry forest,	19.495	-105.039	26.2	794	81.1 (20.3, 173.5)	7.6 (0.2, 16.1)
DT	Tropical	Daintree rainforest,	-16.109	145.443	25.14	2081.2	85.4 (20.2, 210.3)	12.1 (0.5, 30.8)
SJC	Desert	Queensland, Baja California	23.081	-109.662	23.7	230	49.8 (20, 104.2)	2.8 (0.1, 7.7)
LT	Tropical	Cape, Mexico Los Tuxtlas	18.55	-95.09	23.19	3271.3	103.2 (24.1, 244.3)	14.2 (0.8, 32.5)
CAA	rainforest Tropical dry	rainforest, Veracruz, Fazenda Almas	-7.471	-36.898	22.3	580	59.8 (19.5, 144.5)	5.4 (0.9, 12.6)
NC	Tropical	Barrage de Yaté,	-22.16	166.78	21.6	2112	68.6 (28.0, 115.4)	4.0 (0.7, 8.0)
CERR	Tropical	Botucatu cerrado,	-22.914	-48.503	18.9	1331	60.8 (14.1, 122.8)	2.8 (0.7, 5.4)
SYDSCL	South temperate	Sydney, New South	-33.756	151.104	17.2	1169	42.3 (11.1, 143.6)	4.2 (0.2, 31.3)
NSWRF	Temperate	New South Wales	-33.54	151.223	16.33	1419.5	64.5 (29.6, 198.7)	9.6 (1.3, 25.3)
MV	Desert	Mojave Desert,	34.083	-116.582	16.3	324	32.4 (13.1, 109.5)	1.5 (0.1, 4.9)
SR	Mediterranean	Santa Monica	34.093	-118.656	16.3	516	32.1 (19.8, 88)	2.7 (0.6, 7.1)
A	Highland	Loja, Ecuador	-3.992	-79.159	14.8	1083	23.6 (12.1, 41.1)	1.2 (0.6, 2.9)
SPTEMP	Temperate	Pyrenees foothills,	43.167	-1.6	12.2	1279	44.4 (16.9, 106.5)	6.1 (0.7, 1.8)
YALE	deciduous forest Temperate	Spain Yale Forest,	41.953	-72.122	8.1	1238	51.2 (14.5, 136.1)	10.1 (0.7, 30.1)
SPM	Cold temperate	Sierra San Pedro	31.044	-115.464	7.4	763	27.0 (11.7, 58.9)	1.7 (0.1, 11.2)
MF	treeline ecotone Cold temperate	Mártir, Baja Mount Field,	-42.684	146.589	4.5	1515	30.1 (14.1, 118)	2.0 (0.3, 13.7)
PATA	Cold temperate	Coyhaique,	-45.518	-72.042	4.1	944	26.1 (17.1, 39.6)	1.7 (0.7, 7.7)

ESPALP	Cold temperate treeline ecotone	Pyrenees highlands, Spain	42.761	-0.249	3.2	1263	36.5 (17.3, 88.6)	3.0 (0.4, 7.3)
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Table 2. Regression models involving community mean vessel diameter with plant height and climate variables

Parameters	$\log_{10}VD \sim \log_{10}SL$	$\log_{10}VD \sim MAT$	$\log_{10}VD \sim MAP$	$\log_{10}SL \sim MAT$	$\log_{10}SL \sim MAP$	$\log_{10}VD-SL$ residuals~ MAT	$\log_{10}VD-SL$ residuals~ MAP	Average minimum T of coldest month~ MAT
N, R ²	19, 0.75	19, 0.59	19, 0.32	19, 0.24	19, 0.28	19, 0.46	19, 0.02	19, 0.87
model ANOVA	F _(1,17) =50.47 P<0.001	F _(1,17) =23.99 P<0.001	F _(1,17) =7.822 P=0.012	F _(1,17) =5.47 P<0.05	F _(1,17) =8.01 P<0.05	F _(1,17) =14.16 P<0.005	F _(1,17) =0.358, P=0.558	F _(1,17) =118.08, P<0.001
slope	0.520 (0.366, 0.674)***	0.194 (0.110, 0.277)***	1.5X10 ⁻⁴ (3.8X10 ⁻⁵ , 2.7X10 ⁻⁴)*	0.208 (0.020, 0.396)*	2.6X10 ⁻⁴ (6.6X10 ⁻⁵ , 4.5X10 ⁻⁴)	0.086 (0.038, 0.134)**	2.0X10 ⁻⁵ (- 0.125-0.008) ^{ns}	1.072 (0.863, 1.280)***
intercept	1.368 (1.263, 1.474)***	1.367 (1.217, 1.517)***	1.490 (1.324, 1.657)***	0.266 (-0.070, 0.603) ^{ns}	0.282 (0.007, 0.558)	-0.139 (- 0.226, - 0.053)**	-2.47X10 ⁻² (- 5.0X10 ⁻⁵ , 9.0X10 ⁻⁵) ^{ns}	-1.105 (-1.479, - 0.732)***
figure		2a	2b	2c	2d	2e	2f	

VD , vessel diameter; SL , stem length/ plant height; MAT , mean annual temperature; MAP , mean annual precipitation; T , temperature

Table 3. Models predicting vessel diameter (*VD*) and vessel density (*Vmm⁻²*) based on stem length (*SL*) and a “community” categorical variable using the 537 species of the 19 climatically diverse communities sampled¹.

Parameters	<i>log₁₀VD~log₁₀SL+community</i>	<i>log₁₀Vmm⁻²~log₁₀SL+community</i>
N, R ² _{adj}	537, 0.74	537, 0.63
model ANOVA	F _(19,517) =76.88, P<0.0001	F _(19,517) =45.78, P<0.0001
Slope equality	P=0.066	P=0.233
slope	0.392 (0.361, 0.423)	-0.639 (-0.715, -0.563)
Intercept HS	1.638 (1.577, 1.698)	1.734 (1.585, 1.884)
Intercept NC	1.600 (1.541, 1.658)	2.164 (2.020, 2.309)
Intercept CERR	1.595 (1.543, 1.648)	1.938 (1.810, 2.067)
Intercept CH	1.547 (1.492, 1.601)	1.938 (1.805, 2.072)
Intercept LT	1.543 (1.489, 1.598)	1.803 (1.669, 1.937)
Intercept SJC	1.527 (1.482, 1.572)	2.044 (1.931, 2.156)
Intercept DT	1.511 (1.452, 1.571)	1.952 (1.806, 2.098)
intercept CAA	1.464 (1.415, 1.513)	2.124 (2.003, 2.245)
Intercept MV	1.453 (1.401, 1.504)	2.169 (2.042, 2.295)
Intercept NSWRF	1.434 (1.373, 1.496)	2.190 (2.039, 2.341)
Intercept SYDSCL	1.426 (1.377, 1.476)	2.111 (1.989, 2.232)
Intercept MF	1.413 (1.354, 1.472)	2.269 (2.124, 2.414)

Intercept SPM	1.404 (1.346, 1.462)	2.455 (2.313, 2.597)
Intercept ESPALP	1.400 (1.333, 1.467)	2.481 (2.316, 2.647)
Intercept ESPTEMP	1.362 (1.303, 1.421)	2.552 (2.407, 2.698)
Intercept PATA	1.358 (1.295, 1.421)	2.390 (2.234, 2.545)
Intercept YALE	1.351 (1.293, 1.408)	2.457 (2.317, 2.598)
Intercept SR	1.340 (1.282, 1.399)	2.562 (2.418, 2.707)
Intercept PARA	1.336 (1.275, 1.398)	2.087 (1.935, 2.239)

¹95% confidence intervals are given in parentheses for model estimates. The Brazilian tropical dry forest (CAA) was the reference category against which site intercepts were compared.

Table 4. Regression models predicting *VD* based on *SL* and *MAT*, all and warm communities only

Parameters	<i>log₁₀VD~log₁₀SL*MAT, all communities</i>	<i>log₁₀VD~log₁₀SL+MAT, warm communities only</i>
N, R ² _{adj}	537, 0.70	368, 0.64
model ANOVA	F _(3,533) =410.0, P<0.0001	F _(2,365) =319.2, P<0.0001
interaction test	P=0.010	P=0.470
intercept	1.333 (1.293, 1.372) ^{***}	1.163 (1.070, 1.256) ^{***}
β ₁ <i>SL</i>	0.310 (0.244, 0.376) ^{***}	0.403 (0.366, 0.440) ^{***}
β ₂ <i>MAT</i>	0.075 (0.051, 0.099) ^{***}	0.155 (0.110, 0.200) ^{***}
β ₃ <i>MAT*SL</i>	0.046 (0.011, 0.080) [*]	-

Figure Legends

Fig. 1. Vapor pressure deficit (*VPD*) as a major selective agent acting on plant hydraulic

systems. (a) In a single plant (i.e. keeping plant height and vessel diameter constant), increases in *VPD* reach a point at which water supply does not meet demands and stomata close. (b) Under constant conditions of *VPD*, leaves in plants with excessively narrow vessels would outstrip supply earlier than those with wider vessels. One possible response of selection under such conditions would be for the shoot-root system vessels to be slightly wider in areas of higher average mean annual temperature and therefore *VPD*, a scenario that would account for the $\overline{VD}_{stand} - MAT$ association. \overline{VD}_{stand} = species mean vessel diameter standardized for plant height.

Fig. 2. Taking stem length into account shows that precipitation does not predict vessel

diameter, but temperature does. Plant height is the main driver of variation in vessel diameter, but some of the residual variation is predicted by climate. Points are mean community-level values across the 19 communities studied. (a) Mean community vessel diameter is predicted about equally by mean annual temperature *MAT* as by mean annual precipitation *MAP* (b). Mean community plant height is predicted slightly by *MAT* (c) and poorly by *MAP* (d). Even when removing the effect of plant size, *MAT* retains the ability to predict variance in vessel diameter (e), while none at all remains against *MAP* (n.s. = not significant) (f). Regression details are given in Table 2.

Fig. 3. Temperature and the vessel diameter-stem length relationship. While stem length (*SL*) is clearly the main driver of variation in species mean vessel diameter (*VD*) across communities, temperature also explains some of the variation. Each species is colored according to the mean annual temperature of its community (community abbreviations follow Table 1), with reds indicating warm temperatures, grays intermediate, and blues cooler temperatures. A clear pattern is visible, with species from communities with warmer temperatures tending to have wider mean vessel diameters for a given plant height. This pattern translates into an ordering of community *VD-SL* Y-intercepts in such a way that the warm tropical communities account for the upper half of the communities ordered by Y-intercept, and the cold and temperate frost-prone communities account for the lower half. The ordering on the right of the graph expands the spacing of the Y-intercepts to make their relative distances easier to see.

Fig. 4. Controlling for plant height, estimated conductance scales isometrically with vapor pressure deficit. Points are estimated conductances for the different communities, each of which corresponds to a given vapor pressure deficit *VPD*. Mean conductance is estimated across the entire height range present in each community in 1 m increments, so each community is represented by a column of points. Fitting a model predicting conductance based on plant height and *VPD* (see Results) shows that conductance scales isometrically across the entire height range present, represented here by lines with the same slope corresponding to height categories of 1, 3, 10, and 32 m. This result is congruent with the notion that warmer climates select for slightly

wider vessel diameters for a given plant height as greater transpirational demand requires greater conductance for the same carbon assimilation. VD =vessel diameter, Vmm^{-2} =number of vessels per square millimeter of xylem transection.

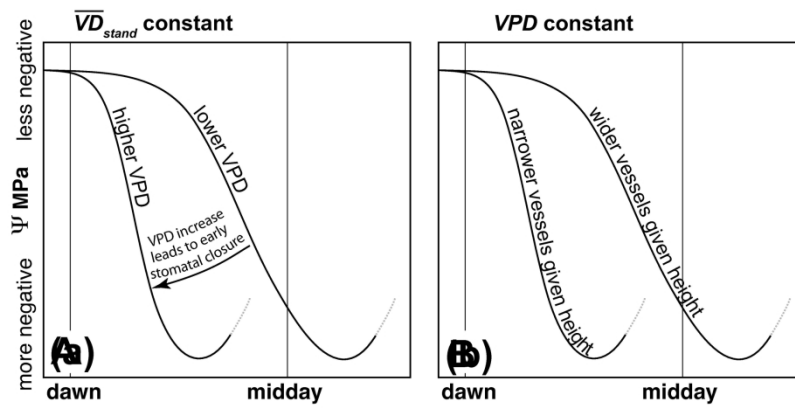


Fig. 1

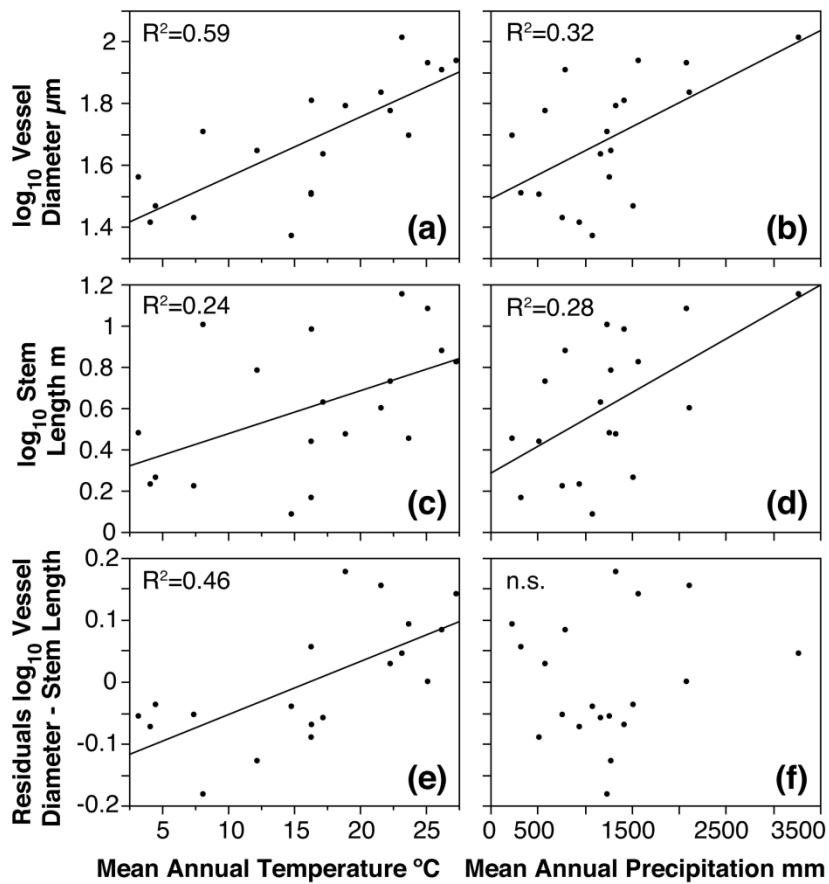


Fig. 2

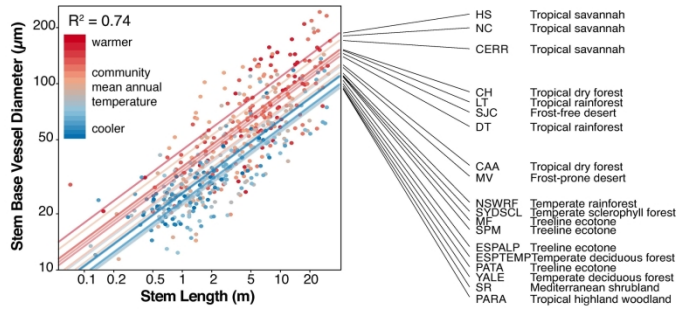


Fig. 3

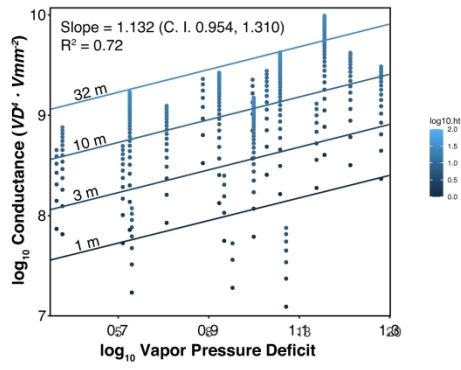


Fig. 4