VESSEL REDUNDANCY: MODELING SAFETY IN NUMBERS

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SUMMARY

We examined the concept that high vessel number provides xylem safety
and also show that under certain circumstances high vessel number may
increase rather than decrease the probability of mortality. The independ-
ent variable was the number of vessels per organ (redundancy). The de-
pendent variable was the probability of organ death for which we set
three thresholds for catastrophic runaway embolism (50, 75 and 90%
embolism). Results were calculated based upon the probability that any
particular vessel would become embolized (p). When the modeled p was
below the runaway embolism threshold, the safety benefits (decreased
probability of organ death) increased dramatically in going from one to
ten vessels and approached maximum levels of safety in organs with
100 or more vessels. Vessel redundancy conferred the greatest advantage
when p approached, but was less than, the runaway embolism threshold
of the organ. However, when p exceeded the runaway embolism thresh-
old the redundancy relationship was reversed and safety was greatest in
organs with lower vessel numbers. Having greater vessel redundancy
increased the likelihood of an "average" result, *i.e.*, mortality if p is
above the threshold, and survival when p is below the threshold. Model
predictions are discussed in terms of redundancy segmentation, stem split-
ting and various other ecological and evolutionary strategies for plants
exposed to different environmental conditions.

Key words: Plant segmentation, runaway embolism, vessel redundancy,
xylem embolism, r, k and s selection.

INTRODUCTION

Redundancy of vessels or tracheids could confer greater safety of the hydraulic trans-
port stream against failure by offering alternative transport routes when some vessels
become inoperative due to air embolism. Ecological wood anatomists have considered
this as they discussed at length possible tradeoffs between xylem safety and efficiency
(Carlquist 1975, 1977; Baas *et al.* 1983; Zimmermann 1983; Ewers 1985).

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Carlquist's "vulnerability index" (1977) is the mean vessel diameter divided by the vessel frequency per mm^2 of sapwood. Both diameter and frequency predict which species will occur in more arid or freeze-stressed environments. This supports the idea that vessel redundancy may be useful in predicting the relative safety or vulnerability of wood and suggests that there may be distinct advantages to having lesser or greater vessel redundancy which leads to several questions which we seek to address in this paper including: Why don't some plants have roots, stems or leaves with only one, extremely wide vessel? Could narrow stems and roots be riskier due merely to their small vessel number? How much redundancy is sufficient, are there diminishing returns and can there be excess redundancy? Could there be circumstances in which lower redundancy is safer?

Xylem efficiency is a function of both the size and frequency of vessels or tracheids within a given xylem area. However, while there has been a fair amount of attention paid to the role of vessel or tracheid diameter in determining vulnerability to dysfunction (Salleo & Lo Gullo 1986; Hargrave *et al*. 1994; Tyree *et al*. 1994b; Davis *et al*. 1999b; Pittermann & Sperry 2003), little attention has been paid to the impact of vessel redundancy *per se* on xylem safety.

It has been argued that, if vulnerability of vessels is kept constant, increasing the vessel number per xylem area should increase conductivity without impacting safety (Hacke *et al*. 2006). By that "packing strategy" model, safety is predicted by the total pit area per vessel. Thus, when the pit area per vessel remains constant, safety remains constant with increasing vessel number. In the present study, we take a different approach in modeling the safety of the whole organ from a probabilistic perspective.

Although woody plants often operate near the point of catastrophic xylem dysfunction due to embolism, different species vary in their precise safety margin (Tyree & Sperry 1988; Pockman & Sperry 2000). Also, the amount of native embolism in woody plants varies considerably. For instance, amongst 15 species of riparian and upland plants of the Sonoran desert, species averages for native embolism ranged from about 10 to 95% (Pockman & Sperry 2000). Therefore we modeled a similar range of embolism probabilities.

We made various assumptions regarding the probability of vessel dysfunction due to environmental stress and we set three different thresholds for fatal, runaway embolism (*sensu* Tyree & Sperry 1988). The threshold for runaway embolism refers to the situation where the remaining hydraulic conductivity is unable to replace even the small amount of water that is lost when stomates on leaves are closed (cuticular transpiration). This results in extremely low water potentials that lead to 100% embolism and organ death. The exact threshold for a plant in nature will depend on many factors including soil type and the inherent resistance to cavitation of the roots and stems of that species (Sperry *et al*. 1998). Workers often describe species in terms of $-P_{50}$, $-P_{75}$, or $-P_{90}$, that is, the (negative) pressure potential resulting in 50, 75 or 90 percent loss in conductivity due to embolism and so we used those as the thresholds for runaway embolism in our model.

In plants with secondary growth, vessel redundancy could be related to mortality of stems and roots since only a small fraction of narrow root or stem axes will survive

to become wide axes with abundant vessels. The approach we took was to model the probability of organ (root or stem) mortality as a function of the number of vessels in the axis. In a survey of 207 species of southern California plants the vessel frequency per mm^2 ranged from 10.8 in the woodland tree *Quercus chrysolepis* to 1350 in the coastal sage scrub *Romneya coulteri* (Carlquist & Hoekman 1985). To simplify matters, we modeled total vessels, not vessels per mm^2, and the number of vessels ranged from one to 28,000. The actual number of vessels in a plant organ can range from just a few, in a narrow herbaceous axis, up to many hundreds of thousands in a large woody stem or root.

METHODS

Our model included a wide range of possible vessel numbers (from one to 28,000), a wide range of probabilities (*p*) of embolism (0.05 to 0.95), and three thresholds for runaway embolism (50, 75 and 90 %). For simplicity we did not address possible differences with regard to vessel diameter, vessel length, or construction cost of vessels. Our objective was merely to address, from a probabilistic perspective, the role of redundancy *per se* in determining safety from xylem dysfunction. We assumed that embolism formation occurred due to independent random events and that when an organ (stem or root) exceeded a particular embolism threshold, runaway embolism resulted in organ death. The independent variable was the number of vessels per organ, that is, vessel redundancy. The dependent variables were the probability of organ death and the thresholds for catastrophic runaway embolism, which were set at 50, 75 and 90 %. These thresholds can be related to literature results in which the $-P_{50}$, $-P_{75}$, or $-P_{90}$ are used to designate the relative drought tolerance of species.

We used the binomial distribution (Devroye 1986; Kachitvichyanukul & Schmeiser 1988) to calculate the probability of organ death. This distribution gives the probability of having a certain number of 'successes' (in this instance the number of vessels embolized) given the number of trials (in this instance, the total number of vessels). The key assumption, as required by the binomial distribution model, is that all vessels are independent and that the probability that a particular vessel becomes embolized remains constant in a particular trial. The probability, *P*, of getting exactly *k* successes is given by the Binomial Distribution Formula:

$$P[X = k] = \binom{n}{k} p^k (1-p)^{n-k} \qquad \text{Eqn. 1}$$

where *n* = the number of vessels in an organ, *p* = probability that any particular vessel is embolized, and *k* = number of vessels embolized.

In the above equation the Binomial Coefficient is defined as:

$$\binom{n}{k} = \frac{n!}{k!\,(n-k)!} \qquad \text{Eqn. 2}$$

To determine the probability of survival for the organ, we calculated the probability that the number of vessels embolized is less than or equal to the threshold, *K*, the number of vessels embolized that would lead to runaway embolism (calculated by multiplying the critical threshold by the number of vessels). It is assumed that if the num-

ber of embolized vessels, k, is greater than K, runaway embolism and organ death will occur. This probability, $P(k > K)$ is calculated by first taking the sum of Eqn. 1 from 0 to K, $i.e.$ $F(K) = P(k = 0) + P(k = 1) + P(k = 2) \ldots P(k = K)$. This cumulative equation $F(K)$, was used to determine the probability of organ survival throughout this study. The probability of organ death, P, is then calculated as 1.0 – probability of organ survival, or $1-F(K)$.

The various figures in this study show the average or most likely outcomes of simulations. In order to put the conclusions in perspective, we also calculated 95% confidence intervals considering the normal approximation to the binomial distribution. These confidence intervals are given by the equation $P_{death} \pm 1.96 * [p*(1-p)/n]$- (Fig. 1).

<div align="center">RESULTS</div>

When the probability of embolism for an individual vessel (p) was near but less than the runaway embolism threshold, increased redundancy conferred increased safety against organ death (Fig. 1A). Note that vessel number is shown on a log scale to clarify the results for lower vessel number while still illustrating results for vessel numbers up to 10,000. With vessel numbers less than ten, the 95% confidence intervals are quite wide, but this variability decreased considerably as the vessel number approached 100.

The confidence intervals we show are the best approximations, but using a normal distribution to approximate the binomial distribution and to develop confidence intervals is generally considered to be valid only for the higher sample sizes and not with samples sizes less than 10.

When the p was 0.48 and the threshold for runaway embolism was 50%, the probability of organ death declined in going from 100 to 1000 vessels, and approached zero at vessel numbers of several thousand and beyond (Fig. 1A). The probability of organ death zigzagged with even and odd numbers of vessels, as would be expected since the threshold in this simulation was 50%, which results in different probabilities for even versus odd numbers of trials. The magnitude of the zigzag pattern was considerable with vessel numbers less than ten, but it steadily dampened with increasing vessel number.

In contrast to the situation in Figure 1A, where p, the probability of a vessel being embolized, was less than the 50% threshold for runaway embolism, with the same threshold but with the p of embolism set at 0.52 (Fig. 1B), the probability of organ death increased with vessel number. As the number of vessels increased from 100 to 1000, the probability of organ death increased and approached 1.0. Again, the zigzag pattern and the 95% confidence intervals dampened with increased vessel number (Fig. 1B). Thus, when p was above the 50% runaway embolism threshold, the results were a mirror image of those for when p was below the threshold. Therefore, while Figure 1A models the safety advantages of redundancy, Figure 1B models the dangers of excess redundancy.

The advantages and disadvantages to redundancy ($i.e.$ changes in the probability of organ death) over various p values and at three thresholds for runaway embolism (50, 75 and 90%) are shown in Figure 2. For each of these thresholds, the average results are shown assuming p values of 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.75, 0.8, 0.9, and
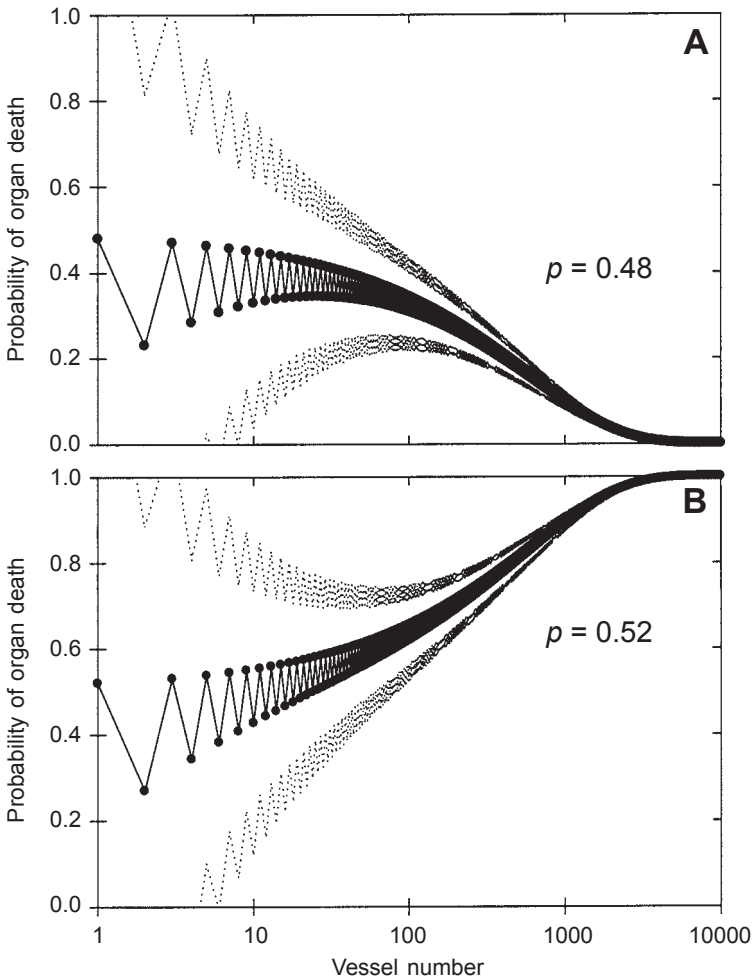
Figure 1. Probability of organ death, with 95 % confidence intervals, as a function of vessel number, assuming a 50 % threshold for runaway embolism, and a probability (*p*) of embolism of an individual vessel of either 0.48 (A) or 0.52 (B). Note that vessel number is reported here on a log scale in this Figure as well as in Figures 2–4.

0.95. For simplicity of presentation we do not show the 95 % confidence intervals in this figure, but they were similar to those shown in Figure 1. That is, they are considerable in magnitude when vessel numbers were less than ten but dampening with increasing vessel number.

When the threshold for runaway embolism was set at 50 %, there was an even-odd zigzag pattern to the probability of organ death, with the odd vessel numbers having higher probability of mortality than the even numbers (Fig. 2A). When the threshold was 75 %, the zigzag pattern corresponded to vessel numbers that were multiples of
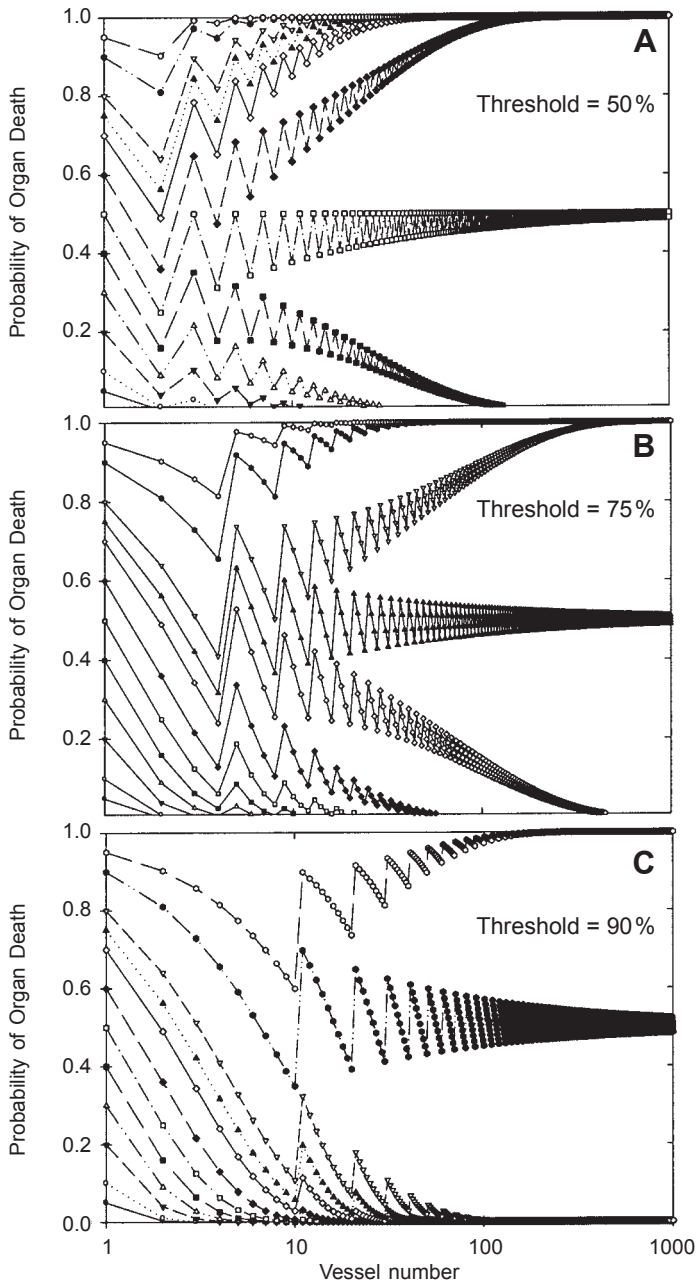
Figure 2. Average probability of organ death as a function of vessel number, assuming a 50% threshold for runaway embolism (A), a 75% threshold (B), or a 90% threshold (C). The probability of embolism in an individual vessel ranged from 0.05 to 0.95 (a different symbol and line is shown for each case) in each of the panels and coincides with the probability of organ death value when the vessel number is equal to one (0.05, 0.1, 0.2, 0.3, *etc*.).

four; with increasing vessel number the probability of death goes down for three consecutive integers, followed by an increase on the fourth integer (Fig. 2B). When the threshold was 90 %, the zigzag pattern corresponded to multiples of ten; there is a downward pattern for nine consecutive integers, followed by an increase. Regardless of the threshold, such patterns consistently repeated but steadily dampened in magnitude with increases in vessel number.

When p was exactly equal to the threshold for runaway embolism, with increasing vessel number the probability of organ death always approached 50 %. This is shown in Figure 2A (50 % threshold) with the line for $p = 0.5$, in Figure 2B (75 % threshold) with the line for $p = 0.75$, and in Figure 2C (90 % threshold) with the line for $p = 0.9$.

When the p value was less than the threshold for runaway embolism, the probability of organ death decreased with increasing vessel number. In contrast, when the p value was greater than the threshold for runaway embolism, the probability of organ death increased with increasing vessel number (Fig. 2).

The redundancy benefit (decreased mortality with increase in vessel number) and the redundancy risk (increased mortality with increase in vessel number) both tended to saturate (approach mortality of either 0.0 or of 1.0) with fairly low vessel numbers when the p value was not close to the threshold for runaway embolism. In contrast, when the p value was closer to the threshold, the redundancy benefit and redundancy risk both required much higher vessel numbers to saturate (Fig. 2). For instance, when the threshold for runaway embolism was 50 %, with a p value of either 0.05 or 0.95, the redundancy benefit, in the prior case, or the redundancy risk, in the latter case, saturated (approached either 0.0 or 1.0) with vessel numbers of less than ten (Fig. 2A). In contrast, also with the 50 % threshold, with a p of either 0.40 or 0.80, the redundancy benefit, in the prior case, and the redundancy risk, in the latter case, did not saturate until vessel numbers approached 100 (Fig. 2A). In the earlier example, also with a 50 % threshold, with p of 0.48 or 0.52, the redundancy benefit (Fig. 1A) and the redundancy risk (Fig. 1B) did not saturate until vessel numbers approached several thousand.

In comparing the situation with an organ having only one vessel versus having two vessels, regardless of the p of embolism, or the threshold for runaway embolism, two vessels always resulted in lower mortality than one (Fig. 1 & 2). For runaway embolism to have occurred in an organ with two vessels, the way the models were designed, it would have required that both of the two vessels became embolized, which was less likely than having one vessel embolized.

To explore what happens when p approaches the threshold for runaway embolism, we plotted the vessel number required for safety (arbitrarily set at the number required to have less than or equal to 0.05 probability of organ death) and the number of vessels that would all but ensure organ death (arbitrarily set at greater than or equal to 0.95 probability of organ death) as a function of p. In this case we set the threshold for runaway embolism at 50 %. The safety advantage of redundancy increased as p got closer to the threshold. The 95 % survivorship (less than 0.05 mortality) was reached with merely one vessel at 0.05 p, but with increasingly higher vessel numbers as p increased, approaching infinity as p rose towards 0.5 (Fig. 3). From the perspective of redundancy risk, or the number of vessels required for 95 % mortality, this occurred with
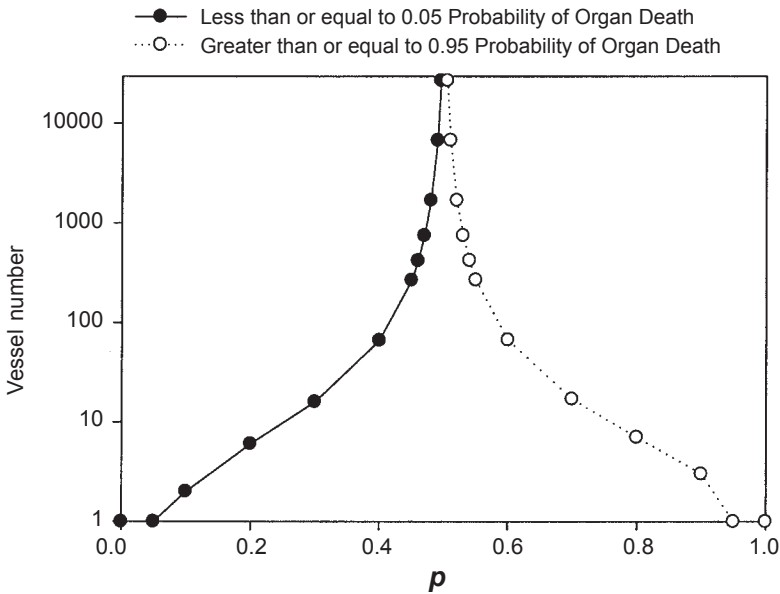
Figure 3. Number of vessels required for less that 0.05 probability of organ death (solid symbols), or for more than 0.95 probability of organ death (open symbols), as functions of the probability that a particular vessel was embolized (p).
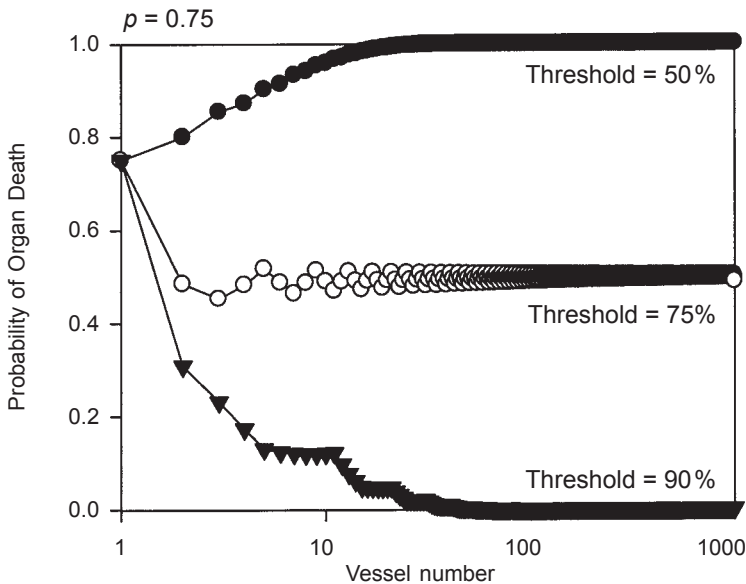

Figure 4. Probability of organ death as a function of vessel number, assuming either a 50 % threshold for runaway embolism (solid circles), a 75 % threshold (open circles), or a 90 % threshold (triangles). The probability of a particular vessel being embolized (p) was kept constant at 0.75. Five point running averages are shown, to dampen the variation in results that occurs with low vessel numbers and to thus clarify the overall trends.

just two vessels when *p* was 0.95. The vessel number required to assure 95 % mortality increased as *p* dropped from 1.0 and it approached infinity as *p* dropped to the threshold level of 50 % (Fig. 3).

For a comparison of results when the *p* value is held constant (*e.g.*, 0.75 in Fig. 4) but with the three different thresholds for runaway embolism, we show the five point running averages, which dampen the zigzag appearance and show general trends more clearly. At *p* of 0.75 and a threshold for runaway embolism of 50 %, increasing vessel number steadily increased the probability of organ death, with probabilities approaching 1.0 at vessel numbers of about 20. With a threshold of 75 % embolism, with increasing vessel number the probability of organ death soon approaches 0.5. With a threshold of 90 % embolism, well above the 0.75 *p*, increases in vessel number show a clear redundancy benefit. That is, there is lower mortality with greater vessel numbers, with the probability of death approaching 0.0 as vessel numbers approach 100 or more.

A more intuitive example of the redundancy model is shown in Figure 5. Here average results are shown for the situation where there is a 75 % threshold for runaway embolism. There are two different means of packaging 100 vessels, namely, one large axis with 100 vessels, or 10 smaller axes with 10 vessels each. In Figure 5A, the probability that an individual vessel is embolized (*p)* was 0.7, whereas in Figure 5B, the *p* was 0.8. In the situation where *p* was less than the threshold for runaway embolism, the single large stem, with higher redundancy, survived, but four out of 10 of the small stems, died (Fig. 5A). In contrast, where *p* was greater than the threshold for runaway embolism, the large stem died while three of the 10 small stems survived (Fig. 5B).

DISCUSSION

The model underestimates the disadvantages of vessel redundancy since construction cost is not considered. Our model thus sets the upper limit to the possible advantages of redundancy and also establishes the minimum disadvantages to redundancy. Also, because of our assumption that vessels within an organ were all equally likely to embolize, we have not taken into account the influence of vessel grouping on probability of embolism of individual vessels (although vessel pairing in general may increase the likelihood of embolism—*i.e.* increase *p*). The frequency of vessel-vessel pits would certainly impact safety in an interesting manner, but it would add a level of complexity beyond the scope of the present study.

Random embolism

The use of random events to explain predictable patterns of cavitation, embolism and organ mortality is not without precedent. Oertli (1971) discussed in detail the probabilities of xylem embolisms arising as random events. More recently, the "pit area hypothesis" which currently best explains the tradeoff between hydraulic efficiency and resistance to water stress-induced embolism, supposes the random placement of the largest pores on pit membranes (Wheeler *et al.* 2005; Choat *et al.* 2005; Hacke *et al.* 2006). Namely, longer and wider vessels, which are more efficient in water conduction, would not inherently be more vulnerable to air seeding were it not for the fact that

they have larger areas of pit membrane. In theory, the larger the total area of pit membrane in a vessel the greater the probability that it will have a least one pore on a pit membrane that would allow air entry at a particular pressure potential gradient. By the definitions of Hacke *et al.* (2006), greater vessel numbers can increase conductivity with no effect on safety, as long as the total pit area per vessel remains constant. In
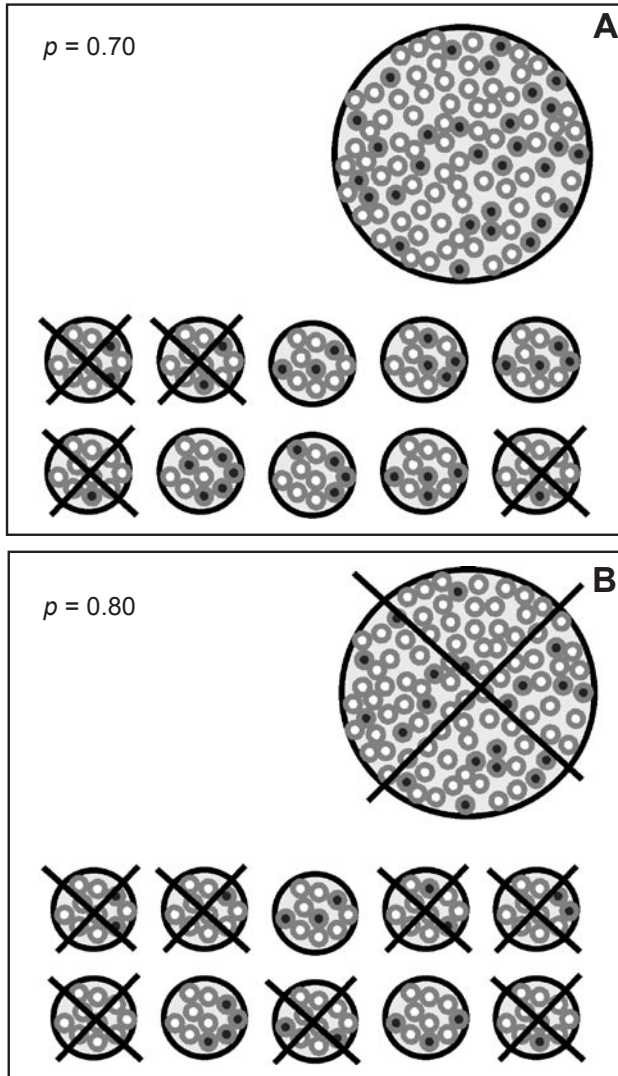

Figure 5. Schematic showing average outcomes for the situation were there is either one large axis with 100 vessels or 10 smaller axes with 10 vessels each. The threshold for runaway embolism was 75% in each case, but the probability that an individual vessel was embolized (*p*) was either 0.7 (A) or 0.8 (B). Open vessels are embolized, while "X" indicates that the axis exceeded the threshold for runaway embolism.

their analysis, the probabilities are explored at the vessel level. In the present study we modeled probabilities at the whole organ level and some interesting properties emerged. With higher redundancy, safety almost never remained constant. Safety either increased or decreased with increasing vessel number unless *p* was exactly equal to the threshold for runaway embolism.

One of the interesting outcomes of the present model is that redundancy benefits or risks are greatly accentuated as thresholds for runaway embolism are approached. Therefore natural selection should impact redundancy of vessels in plants especially as plants colonize new habitats or as global change alters the environmental stress that plants experience, events which may alter the likelihood of embolism.

Two heads are better than one?

The simplest case for redundancy is illustrated by the consistent redundancy benefit of having two vessels rather than one. This "two is better than one" benefit in our models was dependent on the fact that the thresholds for runaway embolism were set at 50 % or higher. In each case the organ could survive if one of the two vessels was conductive. If the thresholds for runaway embolism were set anywhere below 50 %, then it would be a consistent disadvantage to have two vessels rather than one. At another scale, the occurrence of having two redundant organs is widespread in animals. The "two is better than one" redundancy benefit is dependent on the assumption that the organism could survive and reproduce with only one organ (*e.g.*, one ovary, one testicle, one kidney, one lung, one eye, one ear, *etc*.). In the case of animals, the original benefit of having two redundant organs may have been co-opted in many cases by novel functions or by enhanced functioning of two organs working in a coordinated manner (*e.g.*, binocular vision in primates).

The "two is better than one" benefit in our models would rarely apply directly to organ death in plants since plants generally have anywhere from several to many thousands of vessels in an organ. However, at another scale, consider the common occurrence of two metaxylem vessels within the vascular bundles of monocotyledonous plants. Perhaps the functioning of the vascular bundle is dependant on having at least one of the two metaxylem vessels remaining conductive, for instance, to allow the water supply required for phloem conduction.

Redundancy segmentation

By the hydraulic segmentation hypothesis, the distal, more disposable plant parts are more likely to be lost due to hydraulic failure (Zimmermann 1983). This is due, first of all, to the fact that distal parts are usually exposed to more negative water potentials due to their position in the transpiration stream. Hydraulic segmentation is enhanced in some cases by hydraulic constrictions at junctions between plant organs (Sperry 1986; Tyree & Ewers 1991; Meinzer *et al.* 1992; Schulte & Brooks 2003; Lo Gullo *et al.* 2004). Hydraulic segmentation can apply to fine roots as well as to leaves and twigs, since when the soil is extremely dry the water potentials can become lower in the soil than in the plant, and root-stem and root-root junctions become embolized and can then represent hydraulic constrictions (Ewers *et al.* 1992; North *et al.* 1992).

In addition to the segmentation caused by hydraulic gradients, there can be "vulner-ability segmentation", wherein more distal plant parts are inherently more vulnerable to dysfunction at a given water potential (Tyree & Ewers 1991; Tyree *et al.* 1994a; Tsuda & Tyree 1997; Choat *et al.* 2005; Hukin *et al.* 2005). A subset of vulnerability segmenta-tion we can now call "redundancy segmentation", whereby the more distal plant parts are more vulnerable merely due to reduced redundancy of conduits. Consider a tree with a central trunk and many branches and twigs. The trunk would have the greatest vessel redundancy, and the greatest safety, as long as the environmental stress is not too great. Under the same environmental stress, the smaller twigs, with less redundancy, would be more likely by chance to exceed their threshold for runaway embolism (Fig. 5A). In contrast, if the environmental stress exceeded the threshold, the smaller twigs would be at an advantage, assuming they were independent of the large stem (Fig. 5B). In a real tree the branches are hydraulically dependent on the larger stem which bears them. Splitting or some type of hydraulic isolation of portions of the larger stem (see below) would thus be an evolutionary advantage when plants were consistently exposed to extreme hydraulic stress.

It has been argued that drought-induced embolism is one cause of branch die-back (Rood *et al.* 2000; Davis *et al.* 2002), that is, once stems exceed the threshold of run-away embolism, they could quickly become 100 % air blocked. Redundancy segmenta-tion may be useful in explaining patterns of branch and root dieback. For instance, it has been shown that mortality of roots is directly proportional to both root diameter and to water availability in the soil (Gill *et al.* 2002), suggesting a link between number of conduits and probability of conduit embolism (water availability). Similarly, redundancy segmentation may explain patterns of embolism in *Laguncularia racemosa* in which 5 mm diameter stems are much more prone towards embolism than 9 or 14 mm diam-eter stems on the same plant, even when exposed to similar water potentials (Ewers *et al.* 2004). Narrower stems had narrower vessels (hydraulic mean of about 50 μm), which should have made them more resistant to cavitation than the vessels of the larger stems (hydraulic means of 62 to 78 μm). However, the relative lack of redundancy may have caused some of the narrow stems, by chance, to exceed the threshold for runaway embolism, while wider stems remained relatively safe.

The redundancy benefit for wide stems will only occur when the environmental stress is not so severe as to kill the entire plant, that is, when conditions are such that the average p is less than the threshold percentage for runaway embolism. Schenck (1999) reports cases of desert plants in which the stem axis splits to form separate ramets with separate root systems. This may be an advantage in patchy environments where the water stress would be so great that a plant with a single united stem would perish, whereas with separate sectors, one or more sectors may survive. By our model seg-mentation of the main axis should be favored under extreme condition in which the average result would mean death of the main stem. With segmentation of the main stem, one or more segments may survive under extreme drought conditions. By the same logic, under extreme drought conditions, shrubs, with many co-dominant stems, should be favored over trees, with a single trunk. This would explain why some species occur as trees at more mesic sites but as shrubs at xeric sites (Wilson 1995; Martínez & López-Portillo 2003).

Amongst chaparral plants of California, evergreen plants which experience severe summer drought and cool winter rains, there may be tradeoffs between a multi-stemmed and a single stem strategy. Chaparral species are often categorized by their life history strategy with regard to persisting in the landscape following wildfire events. After fire, some species can resprout from a basal root crown following destruction of the above ground plant parts (Keeley 1977; Keeley & Keely 1981; Davis 1989). Such plants can often produce dozens of stems from their root crown following a wildfire, with many of the new stems dying out in their first few years. The probability of a particular stem surviving the first few years after wildfire is low, but some of the stems will survive despite their initial low vessel redundancy. In contrast, other species lack the ability to resprout from the root crown and they can only recruit from seeds following wildfire. Non-sprouters generally have only a single central trunk. It happens that the non-sprouters have much greater resistance to xylem cavitation than do co-occurring congeneric sprouting species (Davis *et al.* 1999a; Jacobsen *et al.* 2007; Pratt *et al.* in press). Perhaps in non-sprouting species, with loss of the genetic basis for the multi-stemmed sprouting strategy, and the lack of ability to split into separate stems, natural selection was towards high resistance to embolism, which would decrease *p* for that species, in order to protect the single central stem.

Ecological strategies

There appear to be tradeoffs between mechanical and hydraulic properties of xylem (Hacke *et al.* 2001; Baas *et al.* 2004; Jacobsen *et al.* 2005; Jacobsen *et al.* 2007) and vessel redundancy should play a role in those tradeoffs. Due to Poiseuille's Law for Ideal Capillaries (see Zimmermann 1983), vessel redundancy improves conductivity only in an additive manner, whereas conductivity is increased in proportion to the fourth power of vessel diameter. Wide and long vessels, with low redundancy, should be the most cost effective means of transporting water, were it not for the fact that wide vessels may weaken the wood to a point that stem breakage or vessel implosion should occur (Hacke *et al.* 2001; Baas *et al.* 2004; Jacobsen *et al.* 2005). In contrast, producing wood with many narrow vessels, especially vessels with thick walls and with associated thick-walled fibers, results in mechanically strong wood. However, it requires much greater carbon expenditure than wood with low redundancy and wide vessels, and it has the added disadvantage that the conductive efficiency may be low (Jacobsen *et al.* 2005; Jacobsen *et al.* 2007).

With global change, in areas experiencing increased water stress levels there should be increased selection for species with greater vessel redundancy and/or more cavitation resistant vessels. This would explain the greater vessel frequency (Carlquist 1975; Baas *et al.* 1983) and greater cavitation resistance found in woody plants from colder and more arid environments (Maharali *et al.* 2004). However, by our redundancy model, when the stress levels exceed what the average hydraulic system of a species can endure, the selection pattern would be completely reversed. Only a small fraction of individuals will survive and those with the least redundancy would have the advantage. This is consistent for instance, with the relatively lower vessel numbers, and higher vulnerability, found in desert annuals and desert vines.

The relative degree of redundancy of vessels could be a part of a suite of characteristics associated with the ecological and evolutionary "strategy" that a species employs. As an example, plants can be characterized as having either a ruderal (r-selected) strategy, a climax community competitive (k-selected) strategy, or a high stress tolerance (s-selected) strategy (Grime 1977). The r-strategy involves the production of many seeds, fast growth rates, and high mortality. The r-selected plants would be expected to have low vessel redundancy. The k-strategy involves fewer, larger seeds, slower growth rates, greater life spans and lower mortality. The k-selected plants would be expected to have moderate redundancy. The s-strategy involves extremely slow growth rates, the greatest life spans and tolerance of the most extreme environmental stress. The s-selected plants should have the highest vessel redundancy. By our model, when plants are exposed to stress levels above the threshold allowing for likely survival of larger plants, rather than stress tolerance, which would select for high vessel redundancy, the better strategy may be to produce many individuals with very low vessel redundancy, increasing the likelihood that a few individuals will beat the odds and survive. That is essentially the r-strategy, which involves stress avoidance rather than stress tolerance, which is best represented by the ephemerals of deserts and other dryland landscapes.

CONCLUSION

The optimal amount of redundancy depends upon the likelihood of embolism occurring in an individual conduit (p) and the threshold for runaway embolism of the organ (root or stem). Organs with a p below the threshold would have a greater survival chance with increased redundancy, while redundancy would hinder the survival of organs with a p greater than the threshold for runaway embolism. There should be different ways to optimize the vessel redundancy for a particular environment and the solution may depend on the ecological and evolutionary background of a species.

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