Plant hydraulics and vegetation height response to climate

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The height of vegetation cover is perhaps the single most ecologically influential biotic variable worldwide, but the cause of variation in maximum vegetation height is still enigmatic (Niklas 2007). It is clear that moister areas with more moderate temperatures support taller maximum heights, but the mechanistic cause of the link between moisture, temperature, and height is still debated (Burgess and Dawson 2007, Moles et al. 2009, cf. MacColl 2011). Identifying this link is not only essential to understand the ecology of plant height, but also because it will permit informed management of the responses of maximum vegetation height under climate change. Such changes are currently being observed as areas become drier, moister, or warmer (Devi et al. 2008, Hoffmann and Sgrò 2011, Clifford et al. 2013). This project brings together plant researchers from Australia, North and South America, and Europe, to test their recent hypothesis regarding the link between moisture, temperature, and vegetation height. Below we briefly outline the hypothesis and the methods we will use to test it, with the aim of identifying the forests most sensitive to climate change world wide.

Hypothesis summary (detail given below)
The water-conducting conduits in a tree become predictably wider as one moves from the highest twig toward the base of the trunk. Therefore, increase in tree height inevitably involves wider conduits basally. However, wider conduits are also more vulnerable to breakage of the conductive stream. The water availability and freezing regimes at any given site determine the maximum conduit diameter that is viable and therefore maximum vegetation height. Alterations to water or temperature regimes, as via anthropogenic climate change, should therefore produce predictable vegetation height responses.

Hypothesis background and details

Tip-to-base conduit widening: theoretical predictions and empirical confirmation

Our hypothesis emerges from recent collaborative work between our labs, and has to do with the conduits that conduct water from roots to leaves. Theoretical work by Anfodillo (Petit and Anfodillo 2009), building on West et al. (1997, 1999, also Enquist 2002, 2003, McCulloh et al. 2003) suggests that conduits should widen slightly from the tip of a plant to the base. As a tree gets taller, the conductive path becomes longer, so if conduits remain the same diameter then a linear increase in friction and therefore decrease in conduction should result. However, if conduits widen slightly from tip to base, then the amount of conduit wall in relation to water volume is decreased, and friction is lessened (Sperry et al. 2006).

Remarkably, the right rate of tip-to-base conduit widening should theoretically be able to maintain hydraulic resistance constant, even as a tree grows from a tiny seedling to a forest giant. This predicted increase can be described by the formula $CD \propto SL^{0.2}$, which means that conduit diameter (*CD*) should be proportional to stem length (*SL*), with the power being the "widening exponent," describing how fast or slow conduits widen from the stem tip. Conduit diameter-stem length exponents < 0.2 (slow widening=high hydraulic resistance) or well above 0.2 (rapid widening=risk of breakage of the conductive stream and redundant network fluid volume) will tend to be selected against, leading to large samples converging on the 0.2 exponent (Petit and Anfodillo 2009). This theoretical prediction is being borne out to a remarkable degree by empirical work in our labs (e.g. Olson et al. 2014). Our work strongly suggests that, at least across flowering plants, conduits do indeed widen exactly following the 0.2 exponent. Our sampling has stretched across six continents and virtually all flowering plant orders, habits, and habitats. Even lianas, with their stems sometimes hundreds of meters long, follow this rule (Rosell and Olson 2014). This universal pattern contradicts the traditional view of plant hydraulic adaptation.

Our work has rejected the traditional view of how natural selection acts on plant conduit diameter. Plant adaptation in the face of drought and height growth hinges on avoidance of gas embolism in water conduits (Burgess and Dawson 2007). Plants transport water from the soil via their roots through small conduits under negative pressure (Tyree and Ewers 1991, Sperry et al. 2006). With increased water stress, excessive negative pressure can break the streams of water, disabling the conduit with a gas embolism and impeding photosynthesis or even killing the plant (Tyree et al. 1994, Cai and Tyree 2010). Narrow conduits resist embolism effectively, because of their high wall surface area for water adhesion relative to the water volume they contain (Salleo and Lo Gullo 1986, Hargrave et al. 1994, Wheeler et al. 2005, Hacke et al. 2006, Cai & Tyree 2010, Christman et al. 2010, Carlquist 1975, 2001, Savage et al. 2010). Wide conduits, in contrast, conduct water with less energy input because they have more conductive volume per unit friction-inducing wall area. However, this lower wall area per unit water volume means that there is less surface for adhesion, and thus breakage of the stream is more likely. The traditional view is therefore that, regardless of plant size, narrow conduits should be favored in dry areas and wide conduits in wet ones (Carlquist 1975, Tyree et al. 1994). Our data conclusively reject this hypothesis and show that plants everywhere, from desert to rainforest, tropics to tundra, have conduits that widen at a similar rate. As a result, desert plants have a similar average conduit diameters as similar-sized rainforest ones. This universal pattern has profound implications for how plants are expected to respond to changes in climate, e.g. increased drought.

Conduit widening, plant height limitation, and drought

Given that a predictable rate of conduit widening means that conduit diameter necessarily increases with plant height, then excessive height growth would lead to conduits that exceed the maximum mean diameter required for avoidance of embolism. In response, plants approaching their maximum heights permitted by embolism risk likely slow apical growth. Given this potential mechanism, then variation in maximum vegetation height is a necessary consequence across environments. To the extent that they limit maximum mean conduit diameter, any change in water or frost regime should also be associated with changes in height. If these assumptions are correct, then the contribution of the conduit-stem size relationship to limiting maximum vegetation height emerges as a deductive outcome. If the 0.2 widening rate really is universal across plants, it can provide a basis for prediction of plant response to climate change world-wide. Producing a global perspective means filling in important gaps, and it is here that Western Australia has a key role.

The importance of Western Australia

Understanding the global relationship between climate, whole plant size, and anatomical structure requires sampling that is as wide as possible, across plant phylogenetic, habital, and climatic diversity. Sampling in Western Australia will provide crucial elements missing from current sampling. Some additional detail is given here regarding these elements.

1. Climatic diversity

Western Australia provides a remarkable climatic gradient. By sampling 7 sites between Shark Bay and Walpole, it is possible to cover a nearly sixfold difference in precipitation. This climate diversity is essential to understand the changes that occur in plant structure in response to drought.

2. Eucalypts

The first sampling priority at each site will be to collect samples from the non-threatened eucalypts. There has been recent controversy in the scientific literature over whether eucalypts behave differently from all other plants known in their anatomical response to drought. It is very important to test this notion, because it will show whether the phenomenon we are studying is truly global, as we suspect. To understand the climate-vessel-plant size relation, it is important to span as wide as possible a range in plant sizes. The span from tiny mallees in the north to the southern giant species offers an unparalled range of sizes.

3. Unique lineages

The second priority will be to sample representatives of phylogenetic lineages that are poorly represented in our current sampling. For example, Dasypogonales is not represented at all in our dataset. The tree mistletoe *Nuytsia* is the only representative of the lineage sister to all remaining Santalaceae. The southwest Australian *Callitris* species appear to represent a unique clade within Cupressaceae. The phylogenetic coverage provided by sampling these and other unique lineages maximizes the generalizability of our results.

4. Life forms and anatomical modes: successive cambia

Some growth forms and anatomical stem constructions are important to sample. Because they are occur in Western Australian drylands, it will be important to sample species with successive cambia. Most woody plants have a single vascular cambium, just under the bark. The vascular cambium produces wood to the inside and phloem, the tissue that moves the sugars produced in the leaves, to the stem and roots. Species with successsive cambia instead have cambia throughout the stem. For various reasons, if our hypothesis is correct, the relationship between plant size and vessel diameter should be slightly different between plants with conventional cambia and those with successive cambia. Species with successive cambia include *Nuytsia* plus Chenopodiaceae.

5. Life forms and anatomical modes: vestured pits

Many dryland plants have special structures called vestures, on the pits that communicate between water-conducting vessels. These structures seem likely to help in resisting drought, but their role is controversial. They are particularly common and varied in Myrtaceae, so sampling in the north, particularly Kalbarri, would sample one species per genus in the area to provide a broad picture of variation in these structures.

6. Life forms and anatomical modes: tracheid bearing plants

Most flowering plants conduct water in tubes called vessels, whereas other plants, mostly conifers, conduct water through cells known as tracheids. Regardless of their structural differences, tracheids should still widen at a similar rate as in flowering plants. To test this notion, we will examine tracheid diameter in the context of stem length across all major tracheid-bearing lineages in a variety of habitats. Finding that the 0.2 exponent is constant across all or most plant lineages will strengthen the notion that it provides a basis for predicting plant response to climate change and understanding the factors that limit plant height. Along these lines, we will collect tracheid-bearing conifers and monocots.

7. Twig samples: the importance of terminal vessel diameter

Adaptation to water availability, in addition to embolism resistance, also involves insuring that all parts of a tree crown receive a similar amount of water. At present, it is not entirely clear how this occurs (Ambrose et al. 2009). Regulation of stomata, the pores in leaves, is certainly part of the picture (Tyree and Ewers 1991). However, because lower branches are closer to the base and therefore are fed by a conductive stream of shorter length and thus lower resistance, it would be expected that lower branches should get a disproportionate amount of the total water supply per unit leaf area (Burgess et al. 2006, Ambrose et al. 2009). If this were the case, then lower branches would grow at the expense of height growth and trees would not grow well in height. Trees the world over do manage to grow vigorously in height, so somehow this inter-branch competition is overcome and even the tallest braches do receive water. Our work suggests that widening of terminal conduits must be involved.

A relation known as Poiseuille's Law illustrates how increases in conduit length l diminish flow rate Q, but that small increases in conduit radius r are sufficient to counteract this drop: $Q = \Delta P/l \cdot \pi r4/8\mu$, where $\Delta P/l$ = the drop in pressure per unit of conduit length, and μ=the fluid viscosity (Tyree and Ewers 1991; Zwieniecki et al. 2001; Bettiai et al. 2012). This is why small increases in r toward the base of a plant are sufficient to maintain Q constant as l increases. By the same token, small increases in r at the *tip* of a stem in the context of a constant rate of tip-to-base conduit widening would also lead to higher Q. A positive relationship between distance from the base of the plant (the length of stem intervening between the ground and a leaf) would mean that taller leaves are fed by wider conduits. Wider conduits imply lower resistance. In this way, comparable flow could be assured to all leaves.

Our results to date seem congruent with this prediction. In interspecific studies, plant height or liana length predicted average vessel diameter at the tips of stems in flowering plants (Fig. 1A), and tracheid diameter in a limited selection of conifers (Fig. 1B). It is essential to understand how within-individual patterns of conduit size lead to interspecific patterns. Because it gives ready access to twig tips of very tall trees, it would be ideal to sample small twig segments (the last 7 cm or so) of twigs from the Tree Top Walk in Nornalup-Walpole National Park. Finding that terminal conduits do generally widen predictably with height would be a major corroboration of the idea that patterns of conduit widening are central in the adaptation of plants to water availability, and therefore for the use of this information in constructing a mechanistic understanding of the expected vegetation response to climate alterations.

Methodological considerations

Sampling is designed to minimize damage to wild populations.

1. Complementarity between sites

The list of species to be collected contains some species that are listed multiple times because they occur at more than one site. They only will need to be collected at one site, but are listed here multiple times to make sure that it will be possible to sample them at least once.

For the non-eucalypts, multiple species per genus are listed in some cases, especially at Kalbarri. Our sampling only requires one species per genus of the non-eucalypts, but several species were listed in the attempt to cover the species likely to be present at the sampling site. In this way, fewer species will be sampled than those listed.

2. Minimizing sampling damage to natural populations

The traditional approach for collecting wood samples involves cutting down whole trees; we instead use minimally invasive sampling techniques. The figures below illustrate the sampling protocol for removing wood samples. If such sampling is deemed too invasive, increment cores can be taken under the advice of local land managers. Only about 5 cm of the outer xylem is needed, so these cores are very shallow. Cores permit vessel diameter measurements, our minimum necessary data, but do not allow for detailed anatomical preparations, so it would be ideal for the project whenever possible to collect wood wedges.

3. Hygiene

Phytophthora and *Quamblaria* are affecting some plant communities in WA, and while transmission plant-to-plant is unlikely using our methods, we make sure to clean our collecting gear between plants with bleach.

Conclusion

In summary, this project aims to test a novel hypothesis regarding the global causes of plant vulnerability to drought. It is based on the observation that water-conducting conduits in a tree become predictably wider as one moves from the highest twig toward the base of the trunk. Therefore, increase in tree height inevitably involves wider conduits basally. However, wider conduits are also more vulnerable to breakage of the conductive stream. The water availability and freezing regimes at any given site determine the maximum conduit diameter that is viable and therefore maximum vegetation height. Alterations to water or temperature regimes, as via anthropogenic climate change, should therefore produce predictable vegetation height responses. Sampling along the remarkable climatic gradient, plant size range, and unique phylogenetic lineages of Western Australia will provide key elements in testing this hypothesis.

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Details of the collection

All species except for twig collections from Tree Top Walk, Nornalup-Walpole

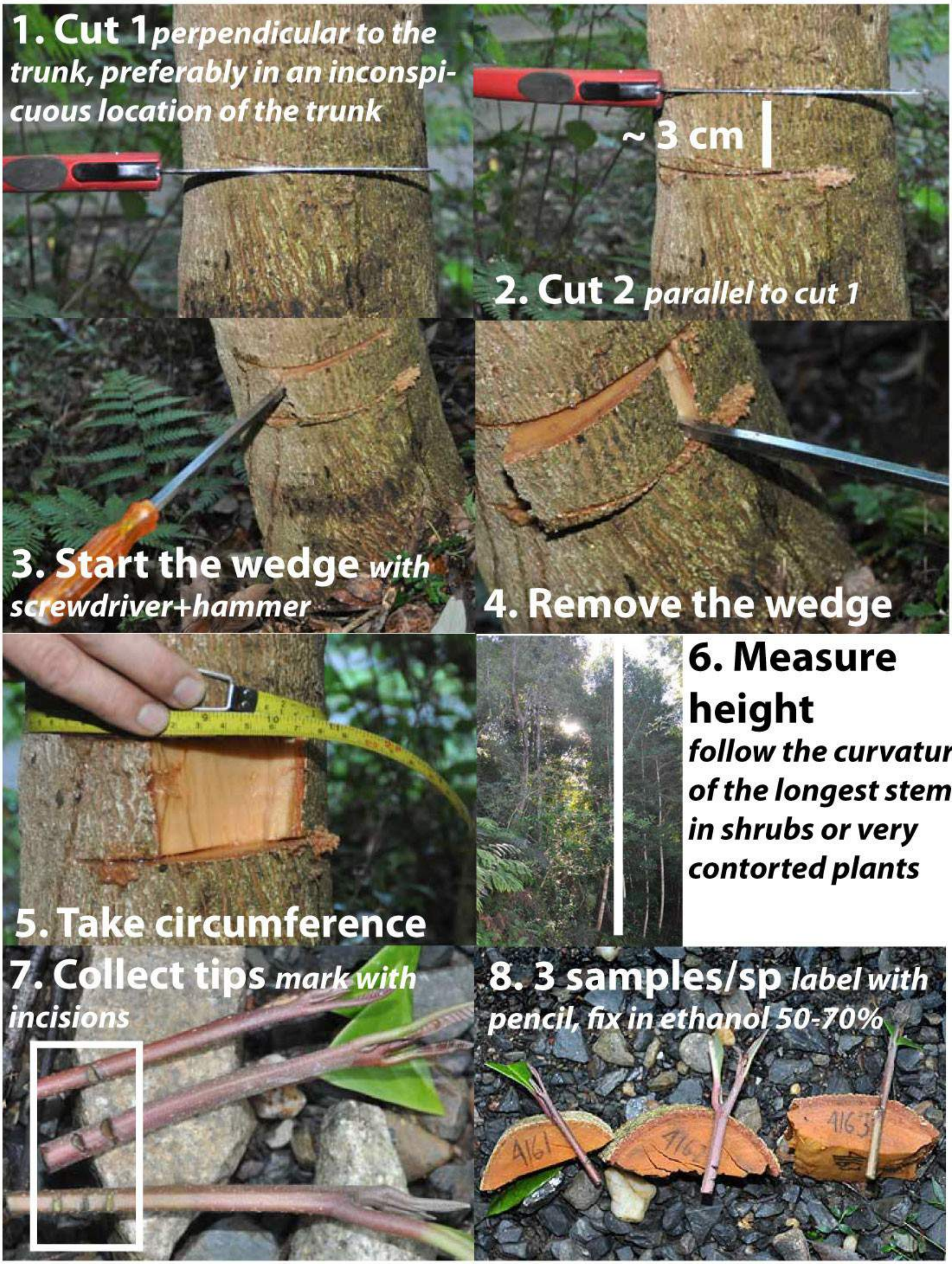
Materials to be taken	wood sample from base plus terminal twig sample
Quantity to be taken	1 base and 1 apex sample from 3 individuals per species
Method of collection	2 parallel saw cuts (please see figures on subsequent 2 pages)
Where specimens will be lodged	spirit collection, National Herbarium of Mexico

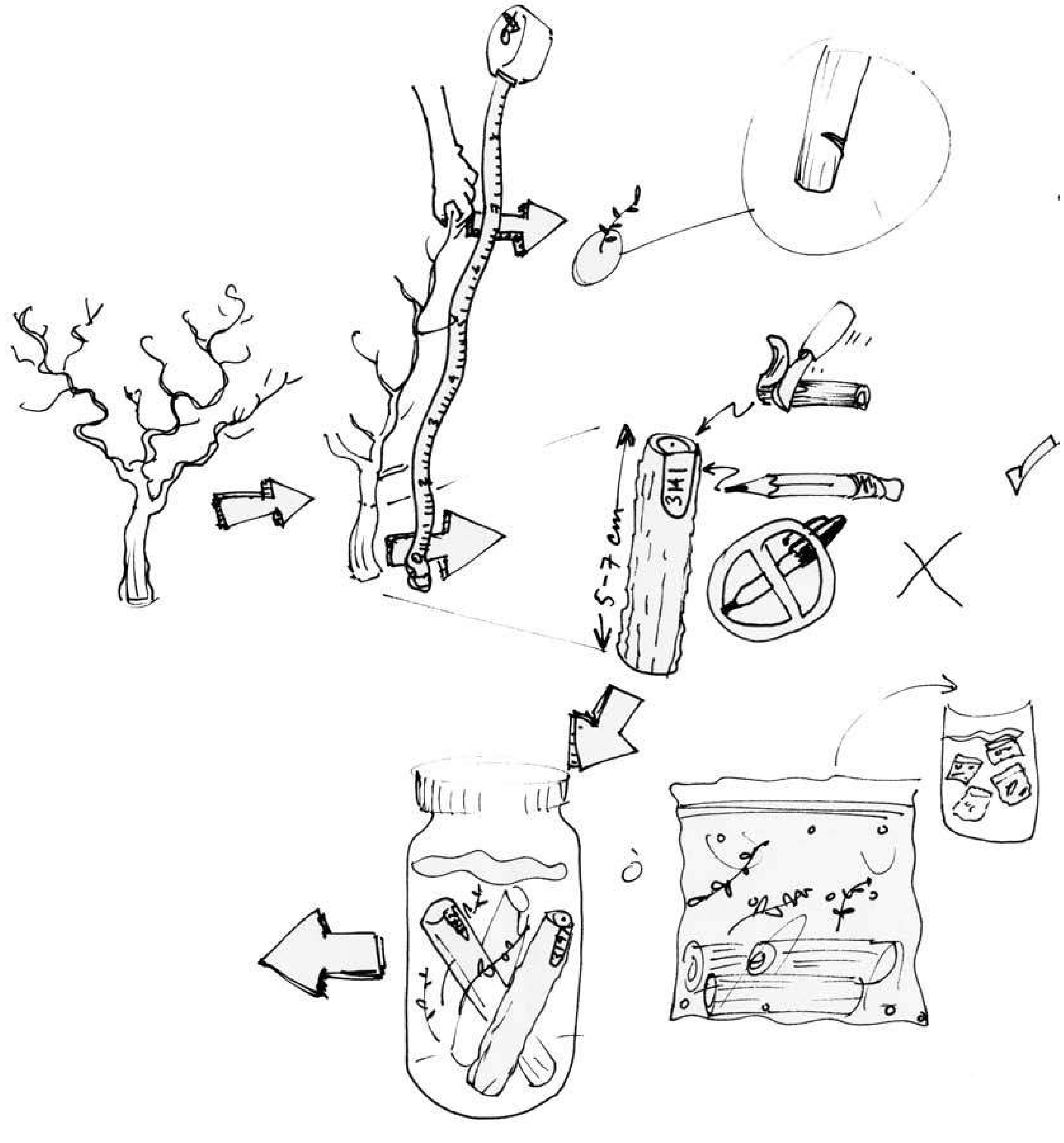
Twig collections from Tree Top Walk, Nornalup-Walpole

Materials to be taken	terminal twig samples, approximately 7 cm of terminal twig with 2-3 leaves
Quantity to be taken	20-30 twigs
Method of collection	measurement of distance to trunk and to ground (to estimate conductive path length) with laser rangefinder; terminal twigs can usually be pinched off by hand or clipped with secateurs
Where specimens will be lodged	spirit collection, National Herbarium of Mexico

Procedure for sampling from trees

wood wedges were cut slightly larger than usual to make the photos clear




5-7 cm
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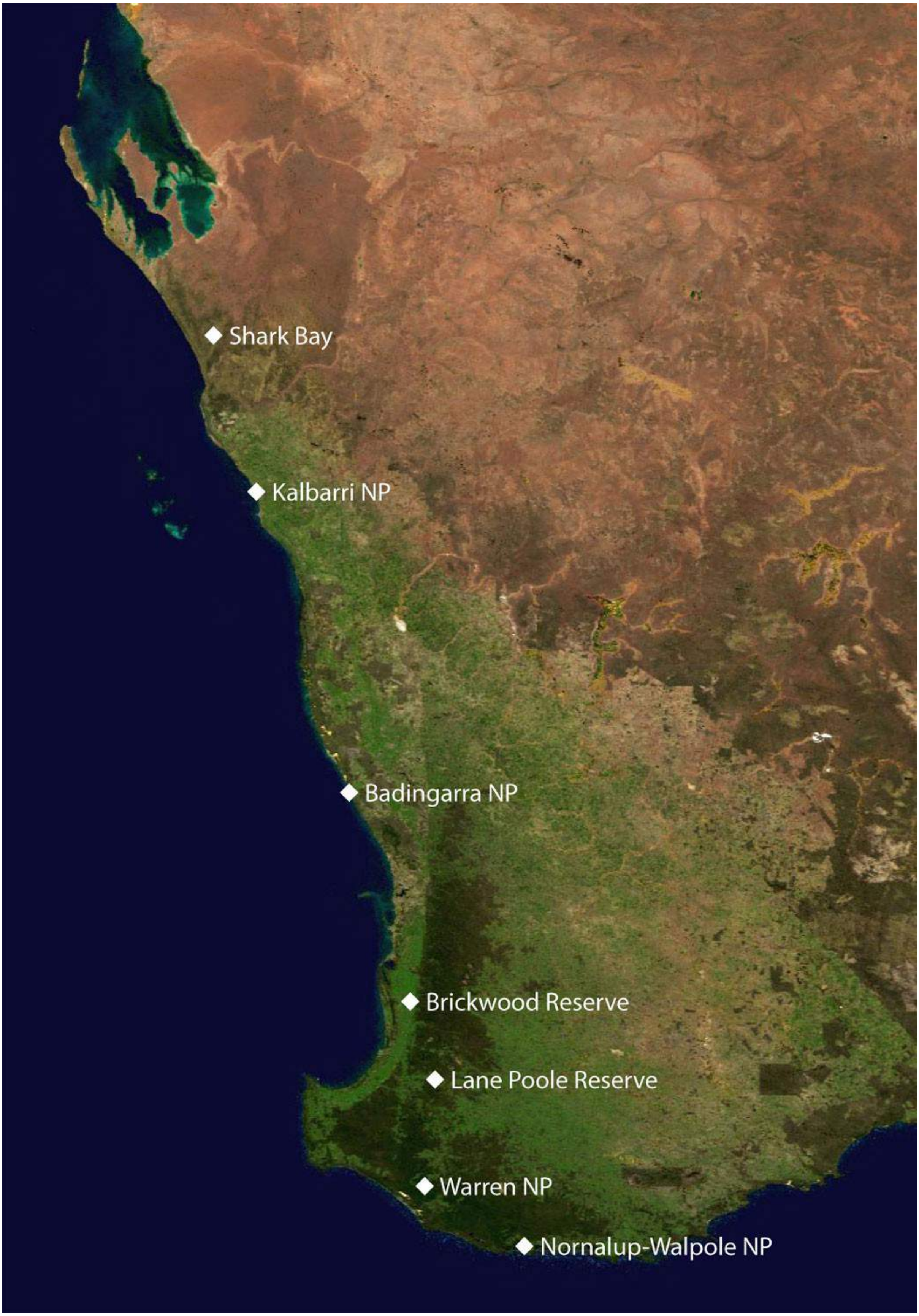
Map of N-S collecting locality transect



Outreach and contact information: I carry copies of the following flyer to distribute to landowners and any other interested party

Drought and wood

why are plants dying worldwide?

As global weather becomes more erratic, droughts are causing many trees to die all over the world. This is worrisome because trees are so important. Trees provide wood, oxygen, improve soil quality, help regulate global climate, and provide wildlife habitat. Even though they are so important, scientists are still not sure exactly what causes them to die from drought.

In our research team, which includes researchers from Australia, North and South America, Asia, and Europe, we think we know why. The cause has to do with the tiny tubes that plants use to transport water- as plants become taller, the tubes become wider, maintaining efficiency. But wider tubes are also more vulnerable to air bubbles that break the conductive stream, killing the leaves.

We are collecting plants all over the world to figure out how and why plant size, climate, and wood make trees and shrubs vulnerable. Our results will identify the most vulnerable plants and allow measures to be taken to save them. We also hope to guide the development of more drought resistant crop plants. We appreciate any help you can provide.

Please get in touch!
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Tasmanian mountain ash, *Eucalyptus regnans* water-conducting tubes