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Tansley review

Traits, properties, and performance: how woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant

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Contents

Summary

This review presents a framework for evaluating how cells, tissues, organs, and whole plants perform both hydraulic and mechanical functions. The morphological alterations that affect dual functionality are varied: individual cells can have altered morphology; tissues can have altered partitioning to functions or altered cell alignment; and organs and whole plants can differ in their allocation to different tissues, or in the geometric distribution of the tissues they have. A hierarchical model emphasizes that morphological traits influence the hydraulic or mechanical properties; the properties, combined with the plant unit's environment, then influence the performance of that plant unit. As a special case, we discuss the mechanisms by which the proxy property wood density has strong correlations to performance but without direct causality. Traits and properties influence multiple aspects of performance, and there can be mutual compensations such that similar performance occurs. This compensation emphasizes that natural selection acts on, and a plant's viability is determined by, its performance, rather than its contributing traits and properties. Continued research on the relationships among traits, and on their effects on multiple aspects of performance, will help us better predict, manage, and select plant material for success under multiple stresses in the future.

I. Introduction

Plants accomplish a multitude of tasks through mechanisms that operate at scales from the cell to the whole organism. As the most fundamental attribute of woody plants, xylem tissue is under strong selective pressure to adaptively respond to abiotic and biotic challenges. Consequently, at the cell and tissue levels, the xylem is an exemplar of multiple functionality (Gartner, 1995). But just as an engineered structure's performance depends on both the shape of the structure and the material from which it is made (e.g. a hollow

tube is stiffer than a solid cylinder of the same material and mass), the performance at the level of the organ (e.g. a branch) or the whole plant depends on both the material's properties and the organ or plant's geometric structure. This review explores the underlying mechanisms that allow plants to combine two functions into one plant unit (a cell, tissue, or organ/whole plant). We concentrate on hydraulic and mechanical function, but the framework is valid for other potentially interacting functions within plants. The framework uses the concept of hierarchy among measures (Arnold, 1983; Violle *et al.*, 2007): the pool of relevant morphological traits influences emergent properties, and then the pool of properties influences performance (Fig. 1). Natural selection then acts on aspects of performance (rather than on traits or properties) to result in fitness (Arnold, 1983). This last concept is in peril of being overlooked by specialists who work mainly with a sole performance, or those who read functional trait research (Violle *et al.*, 2007; Poorter *et al.*, 2008; Chave *et al.*, 2009; Wright *et al.*, 2010; Zanne *et al.*, 2010; Reich, 2014) but then assume selection acted on the functional trait rather than the performance that derives from it, and that may be influenced by other traits as well.

This review focuses on the current performance of an existing plant unit, whereas most of the research on multiple functionality has been conducted in the context of evolution. Olsen & Miller (1958) studied the inter-relationships of traits in vertebrate skulls throughout evolution, with the insight that no trait can be interpreted meaningfully independently of other traits. They

assessed the degree of 'morphological integration' (a phrase they coined) by the strengths of the correlations among the traits, often compared across generations. Further research on phenotypic character correlation in parents and offspring has sought to tease apart whether correlations are caused by selection or genetic correlations. In the case of selection, they have gone further to infer which aspects of performance have contributed to fitness (Berg, 1960; Falconer & Mackay, 1960; Pélabon *et al.*, 2011). Research on phenotypic integration has explored areas such as the evolution of trait combinations, phenotypic integration as a constraint versus an adaptation, and the evolution of integration in modular or plastic organisms (Pigliucci & Preston, 2004; Klingenberg, 2008).

A concise terminology will help for the following discussion. We define a *function* as a role that the *plant unit* (a cell, tissue, organ, or whole plant) can fulfill (Table 1). *Performance* is then defined as the quantifiable level at which a plant unit accomplishes a function over a particular period of time (Table 1, Fig. 1). The *traits* of focus here are the features of the plant unit that influence hydraulic or mechanical function and that are relatively time-independent (Table 1, Fig. 1). As such, they can be characterized instantaneously such as under the microscope or with calipers, and they will maintain the same value over the period in which the performance is evaluated. Most of the traits discussed here are morphological, but several of the traits relate to wood chemistry. *Properties* are the measures that emerge from the traits. For example, the information conveyed by the traits 'leaf area' and 'sapwood area' is very different from the information conveyed by the property 'leaf area/sapwood area,' which sheds light on the amount of transpiration area relative to transport ability (Table 1, Fig. 1). *Measure* is an umbrella term to cover all the traits, properties, and aspects of performance. The magnitude of any measure is called its *value* (Table 1). Lastly, we have avoided using the term *integration* because the term is used by some researchers to describe only negative co-variation of traits (tradeoffs), whereas others include positive co-variation (Klingenberg, 2008). It is unclear whether independent traits would be considered integrated, but they are included in the current discussion.

The schematic model indicates how traits influence hydraulic or mechanical properties, or both (Fig. 1). If traits influence both properties, the co-variation of their effects can be positive, negative, or neutral. Moreover, because many traits affect a property, there can be shifts in the relative or actual values of the traits such that there are mutual compensations, and a property's value can remain unchanged. Next, these emergent hydraulic or mechanical properties set the stage for how the plant can perform hydraulically and mechanically, with the actual levels of performance varying also with the environment. As with traits, if properties affect both types of performance, the co-variation of their effects on performance can be positive, negative, or neutral. Again, there can be compensations among the properties to arrive at the same performance value. The diversity of cell, tissue, and gross morphologies that exists in woody plants attests to these compensations: without compensatory adjustments among traits, it is likely that there could be very little variation among viable plants in the same environment because the plants would have 'solved the problems of dual functionality' in only a small number of ways (Niklas, 1997).
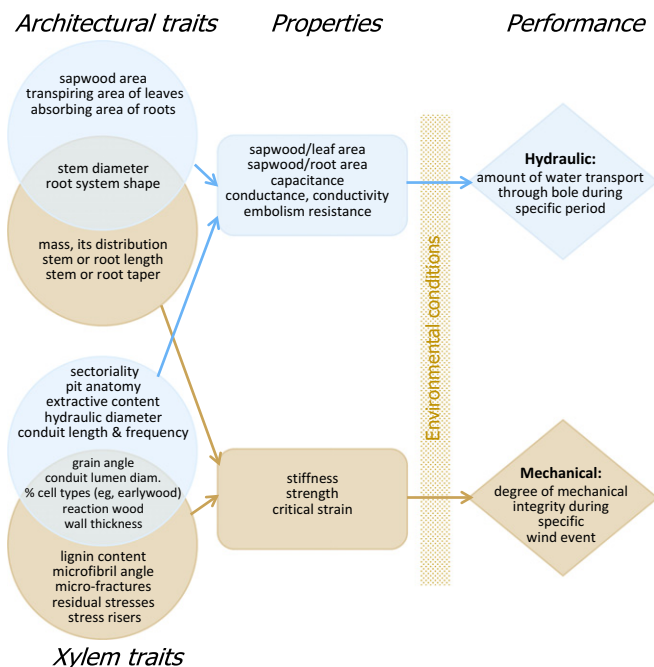
Fig. 1 Effects of architectural and xylem traits on hydraulic and mechanical properties, and their effects on the hydraulic and mechanical performance of a plant unit (cell, tissue, or organ/whole plant) that is faced with a given set of environmental conditions (stresses). Compensatory changes among measures can occur such that a property is unchanged, and compensatory changes among properties can result in the same level of performance. Bubbles show examples of measures that influence hydraulic (blue) and mechanical (brown) traits, properties, and performance. Arrows indicate the direction of influence of the measures.

Table 1 Definitions of terms used

Term	Definition	Examples
Plant unit	A functional unit of a plant; categorized here as cell, tissue, or organ/whole plant (organ and whole plant are discussed together)	Tracheid (cell), sapwood (tissue), root or branch (organ); root system, aboveground plant, or whole plant (organ/whole-plant level)
Function	A role that a plant unit can fulfill	Water transport through a tracheid; maintenance of the stem within a range of angles
Trait	A morphological or chemical measure that does not change over the period in which a performance is assayed	Conduit diameter, microfibril angle, lignin content, earlywood proportion, leaf area, and geometry of the root system
Property	A measure emerging from a combination of traits	Leaf area/sapwood area; specific conductivity; embolism resistance; wood stiffness
Performance	A quantifiable level at which a plant unit accomplishes a function	The amount of water transported per unit time by the bole under specified conditions; the amount of stem deflection under specified wind conditions
Measure	Any trait, property, or performance	(See above)
Value	The numerical value of a measure	Leaf area of $4.0 \, m^2$

A plant will always experience some degree of stress. Even in so-called mild conditions and climates, a plant has the challenge of higher relative drought with increased internal distance from the water-absorbing system. Cells and tissues need to remain intact with forces from water transport and self-weight. And a plant needs to maintain a certain architectural stature to acquire resources and to reproduce. In less equable conditions, stresses will be greater. The perceived stress at a location within a plant depends on its environmental conditions, its properties, and its safety factor (the degree to which it is overbuilt relative to the point at which failure will occur; Domec & Gartner, 2001) for a particular function. If the plant unit performs at a safety factor < 1, it is in the zone called extreme stress (distress), in which processes stop working properly, plant parts may break down, and mortality can occur. At lesser stress levels (eustress), it is possible that the plant unit will exhibit no persistent after-effects (as discussed in Luttge, 2007; Kranner *et al.*, 2010). Fitness may be affected by any level of stress, although it is more likely to be affected at the extreme (distress) end of the spectrum. Because forested lands are likely to be impacted by an increased incidence of extreme events (Allen *et al.*, 2010), it may become even more important for us to understand how the various traits and properties feed into hydraulic and mechanical performance.

This paper begins with a discussion of the approaches used to study how one plant unit can perform dual functions. We then describe mechanisms spread over three spatial scales, for this dual functionality. The review includes a modest entry into the literature to show examples of each of these mechanisms, highlighting cases that show positive, negative, or no co-variance between measures that contribute to hydraulic and/or mechanical performance. Our first aim is to expose the variety of anatomical and biomass configurations that plants use to achieve their multi-functionality, through analyzing the potential arrangement of structures in cells, cells in tissues, and tissues in organs and whole plants. The second aim is to show conceptually how traits, properties and types of performance are related to one another, and the points at which compensation among different measures can occur. The third aim is to bring attention to the fact that dual functionality can be

achieved by positive or neutral relationships between hydraulic and mechanical measures, in addition to negative relationships (trade-offs).

There are three notes to keep in mind. First, the alterations and adjustments in the measures that we discuss refer to the potential range observable among woody plants, and may not represent alternative states in one individual or species. Secondly, the imperfect understanding of a measure's function may lead to errors in how its effects are categorized. Thirdly, at some level, the judgment of whether a measure is hydraulic or mechanical can be semantic and/or subjective. For example, mechanical performance is required for hydraulic performance and so, at the extreme, hydraulic and biomechanical performances are not independent metrics. It is likely that more precise study of given traits will help resolve these last two concerns.

II. Studying dual functionality in plants: some conceptual approaches

1. Choice of research question and experimental design

To design a study to understand: (1) the mechanisms for achieving dual functionality, and (2) the nature of the relationships among traits responsible for this dual functionality, one needs to clarify the actual question, develop an experimental design appropriate to it, and collect data on relevant measures. The resolutions to these tasks are inter-related because the exact question will constrain options, and in many cases it is infeasible to study the measures directly. Therefore, experimental design will be an iterative process, as one starts with a question, a plant system, a set of performance types, or a set of measures, and then clarifies the other parameters.

Specifying the exact question is essential for choosing appropriate plant material. For example, if the question is how woods of extremely different densities differ in a pair of performance measures, then one obviously needs to compare plants with a range of wood densities. Moreover, it will be helpful to clarify where the variation of interest is, such as among or within species, or between or within one geographic region.

Once the question is clarified, plant materials can be chosen, depending on what is available, what is already known about different plants, and whether it may be possible and desirable to limit variation that is unrelated to the target types of performance (e.g. by studying species from only one climate zone, comparing closely related species, or comparing parts within one individual). Material can come from individuals growing in a range of natural habitats (Alder *et al.*, 1996; DeMicco *et al.*, 2008), from different 'contexts' within individual trees (e.g. root systems on the leeward versus the windward side of a tree; Nicoll & Ray, 1996), from control versus manipulated treatments (e.g. irrigation, pruning, or mechanical stimulation; Margolis *et al.*, 1988; Searson *et al.*, 2004; Kern *et al.*, 2005), or from the same individual at different times after perturbation as the plant recovers toward an apparent equilibrium state (e.g. after pruning or topping; Brix & Mitchell, 1983; Spicer & Gartner, 1998a). The focus may be on one species in several sites or treatments, or numerous species or genotypes in common gardens (Wagner *et al.*, 1998; Rosner *et al.*, 2007). Increasingly, there will be opportunities to use study material that is generated from genetic modification affecting developmental pathways, anatomy, or stature (Voelker *et al.*, 2011a,b; Elias *et al.*, 2012; Sengupta & Majumder, 2014), and offering trait combinations in a constant background that have not been available before.

One experimental design is to study how changes in one aspect of performance affect the second aspect of performance, comparing key traits and properties. An example is the comparison of traits that contribute to specific conductivity in several locations that differed in their mechanical loading along buttress roots (Christensen-Dalsgaard *et al.*, 2008). However, few experiments are designed in this manner, and much of the research we encountered focused on only one aspect of performance (e.g. hydraulic redundancy along aridity gradients (Schenk *et al.*, 2008) or mechanical architecture at differing wind exposures (Brüchert & Gardiner, 2006)). While not able to inform our understanding of dual functionality, those studies still can give insight into potential compensations among measures that can occur in that single function.

Another experimental design is to start with hypotheses about the relationship between two aspects of performance and their causal measures in several conditions. If subsequently collected data are not consistent with the hypotheses, then the cause(s) for the deviation from expectation may be sought. For example, two projects asked whether tree height and mass scale according to hydraulic or mechanical principles, by comparing actual architectural data to the predictions that came from mechanical or hydraulic models (Niklas & Spatz, 2004; Niklas, 2007). The mechanical predictions greatly overestimated maximum plant heights whereas the hydraulic predictions were consistent with observations, and the authors were thus able to infer that hydraulic rather than mechanical traits limit tree height. The second project tested a model that predicted the configuration of the most efficient water transport system in stem systems and leaves. Some of the plant material had configurations that were similar to those predicted, so the authors inferred that the system was designed primarily in response to hydraulic requirements. In other plants the configurations departed from predictions, so they deduced that the

water-conducting cells had other important roles, probably biomechanical (McCulloh *et al.*, 2003, 2004, 2009; discussed further in Section III.4).

2. Choice of traits, properties, and performances to study

Because the overarching goal is to learn how two types of performance affect each other as mediated by the traits and properties that are involved, it is essential to choose measures that are relevant for the organism, life stage, and environment in question. Depending on the plant system, it may be necessary to use modeling to generate the predictions (Lichtenegger *et al.*, 1999; Lachenbruch *et al.*, 2011), but in many cases there is sufficient existing knowledge. For example, it is known that compression wood in conifer stems generates a residual stress during development, which contributes to changing the stem's position (Wilson & Archer, 1977; Alméras *et al.*, 2005). But some of the morphological traits associated with compression wood (tracheid length and tracheid diameter distribution across the growth ring) are ones that are likely to affect hydraulic conductance. It would therefore be reasonable to choose an aspect related to hydraulic conductance (such as conductance per unit leaf area at the highest demand period of the day) as the hydraulic performance to follow in relation to the severity of compression wood in a tree (Spicer & Gartner, 1998a,b; Mayr & Cochard, 2003). It would not be particularly meaningful to use an unrelated hydraulic performance measure (such as the water absorption potential of the root system).

3. Proxy measures, with wood density as an example

In many cases, the measure with the strongest effect on a particular performance may not be useful (e.g. it may have insufficient variation) or feasible to study (e.g. it may require an unavailable methodology, or destructive measurements that are not permitted). In such cases, one may be able to estimate the measure's value from a theoretical, causal correlation with other traits. For example, one can estimate specific conductivity – the water volume transported across a cross-sectional area in a given time interval with a given pressure gradient – from the frequency and diameter distribution of vessels in cross-section (Christensen-Dalsgaard *et al.*, 2008). It is important to use such correlations only within the conditions under which the relationship is valid. For example, specific conductivity in conifers depends on several structural features, and not solely tracheid diameter (Pittermann *et al.*, 2006), which helps explain the somewhat counter-intuitive report that, in a conifer species, specific conductivity was correlated strongly with tracheid diameter only in 7-yr-old branches, and not in 20-yr-old branches, three age classes of bole or two age classes of root (Dunham *et al.*, 2008).

Another solution is to choose a proxy (surrogate) measure, which is a measure that is correlated with the level of performance but not necessarily through causality. Wood density is a good example of a proxy measure: it is correlated strongly with a variety of performance measures, it is relatively simple to assay, and many density data are already available. After discussing a few basics about wood density as a proxy measure, we will highlight hydraulic and

mechanical studies that show relationships with wood density, and try to explain the basis for the relationships.

Density is a property, defined as mass/volume. Its value is affected by anatomical and/or chemical traits that affect how much mass is in a given volume (examples shown in red in Fig. 2). Density has no direct effects on hydraulic or mechanical function (red arrows with lines through them; Zanne *et al.*, 2010): statistical relationships exist because some of the traits that affect density also affect hydraulic and/or mechanical properties (Fig. 2). Density does, indeed, have a probable causal relationship with some properties, such as angiosperm decay resistance (Chave *et al.*, 2009), but it also has numerous but very strong relationships with many other measures of plant performance (e.g. growth rate; King *et al.*, 2005; Poorter *et al.*, 2008; Wright *et al.*, 2010). It is entirely appropriate to take advantage of these indirect correlations as long as the proxy is presented as what it is, and the correlation is expected to be valid over the conditions used.

In the following discussions of the mechanisms responsible for wood density's strong correlations with performance, it is useful to introduce the related term void volume. Void volume is the volume of wood that is not cell wall material (MacLean, 1958). The void contains water, gas, or cytoplasm. The xylem cell wall is constructed of material with a relatively constant density of $1.53\ \mathrm{g\ cm^{-3}}$ (dry mass per unit green volume; Stamm, 1929; Kellogg & Wangaard, 1969), so the proportion of wood that is void volume is $1 - (\mathrm{wood\ density}/1.53)$. Given that wood density is the only variable in the previous equation, all woods of the same density have the same void volume.
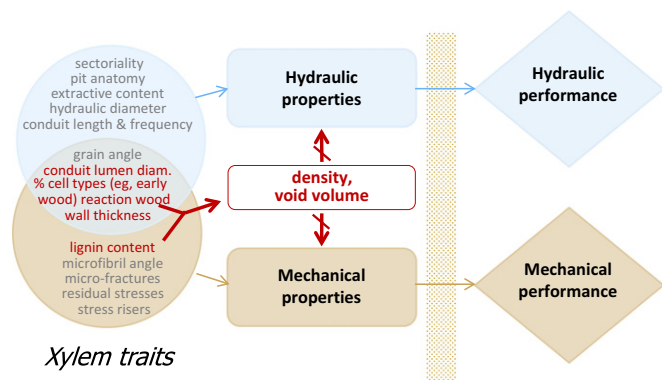
Hydraulics   Wood density is often negatively correlated with specific conductivity (Bucci *et al.*, 2004; Santiago *et al.*, 2004; Pratt *et al.*, 2007). This relationship results from the void volume that is potentially available for water, although it is the manner in which the void is partitioned into conduits that directly affects conductivity (Zanne *et al.*, 2010). This correlation will be strongest in conditions in which: (1) the mean hydraulic diameter of conduits (the diameter that would provide the observed flow if all conduits were that size) is invariant among samples, and (2) the nonconduit

Fig. 2 Density and void volume affect properties primarily through their correlations with traits (red arrows), and not in a direct manner (red arrows with lines through them). Measures affecting hydraulics are shown in blue bubbles, and those affecting mechanics are shown in brown bubbles. Traits contributing to xylem density and void volume are in red.

xylem tissue does not vary in density among samples. These conditions are rarely met. All of the samples in Fig. 3 have very similar density (and thus void volume) and yet vary in lumen proportion by a factor of 6.7, and in theoretical specific conductivity by a factor of 68.

Wood density is often also negatively correlated with capacitance (the amount of stored water released from a volume of wood per MPa change in water potential; Meinzer *et al.*, 2003, 2008; Santiago *et al.*, 2004; Pratt *et al.*, 2007; Scholz *et al.*, 2007). This relationship is also caused largely by void volume, which represents the maximum proportion of the xylem in which water can be stored. The negative correlations of wood density and capacitance will be strongest if all samples have: (1) the same proportional amount of void volume used for storage, and (2) the same resistance to water moving out of storage. Differences in the ease with which water can be extracted from storage (the second condition) can be seen in Fig. 4, in which species from two seasonally dry tropical sites exhibit the same relationship between sapwood wood density and capacitance (dashed line) but species at a wetter site have much greater capacitance for the same wood density (triangles).

Lastly, wood density is often positively correlated with resistance to drought-induced embolism (Hacke *et al.*, 2001; Pratt *et al.*, 2007). This relationship appears to result from the co-evolution of safety factors against mechanical failure and hydraulic failure (Hacke *et al.*, 2001; Jacobsen *et al.*, 2005; Pittermann *et al.*, 2010; Lens *et al.*, 2011). Correlations will be strongest in conditions in which: (1) the strength of the material is invariant among samples, and (2) evolution has resulted in similar risks of hydraulic and mechanical failure. The second condition is most likely to be met if the samples are from locations with similar intrinsic and extrinsic environments within the plant (Section II.1). For example, the relationship is strong among species for small diameter branch material (Hacke *et al.*, 2001) and has proven useful for many studies, but in other contexts the relationship does not hold. Embolism resistance was correlated with density and strength in stems but not in roots in nine Rhamnaceae species (Fig. 5, from Pratt *et al.*, 2007). Similarly, embolism resistance is not correlated with wood density or wood stiffness in corewood versus outerwood (sapwood located near versus far from the pith, respectively) of the trunks of *Pseudotsuga menziesii*, *Pinus ponderosa*, or *Picea abies* (Domec & Gartner, 2002a; Rosner *et al.*, 2006; Domec *et al.*, 2009). Furthermore, Bucci *et al.* (2006) observed lower woody density together with greater resistance to embolism in trees that had been fertilized for 5 yr compared with controls.

Mechanics   Wood density is often positively correlated with many mechanical properties, such as stiffness and strength (Green *et al.*, 1999; Rosner *et al.*, 2007; Niklas & Spatz, 2010). These correlations occur because the density represents the amount of material per unit volume that bears the forces. Correlations will be strongest under two conditions: (1) the materials have the same incidence of micro-failures (microscopic breaks) and/or stress risers (geometric irregularities that cause stresses to concentrate elsewhere), and (2) the materials themselves do not differ mechanically. Stress risers are caused by features such as pore space in the cell wall, pit chambers, large vessels, growth ring boundaries, rays, aggregations of
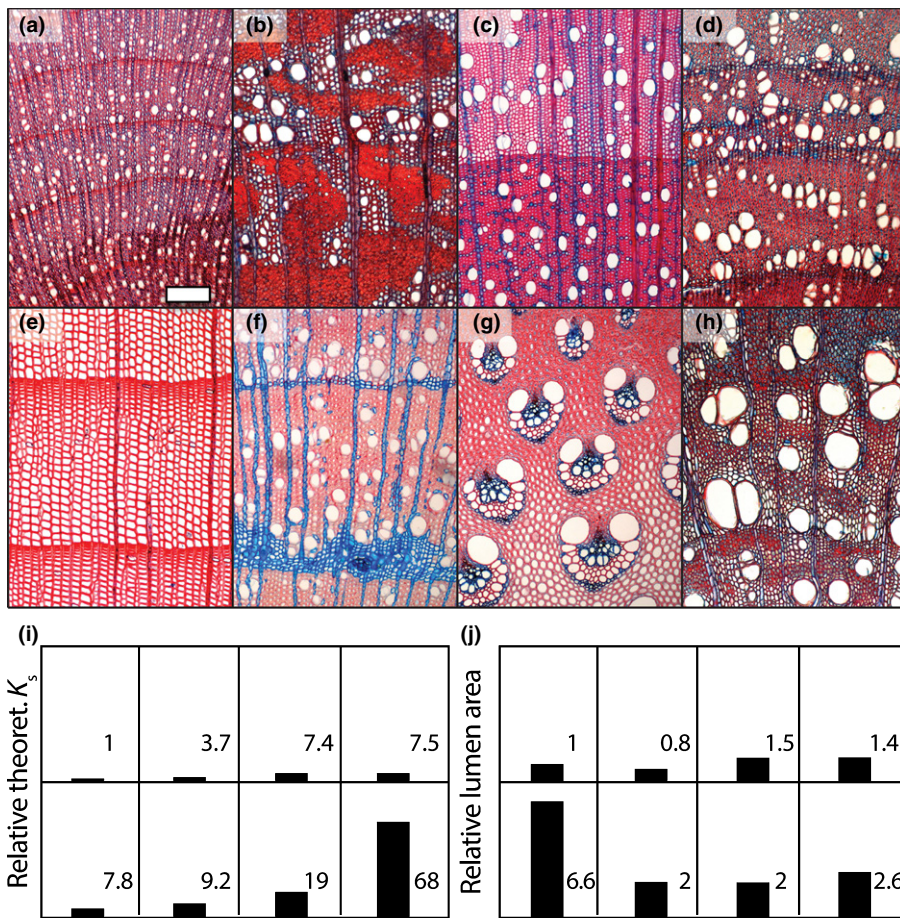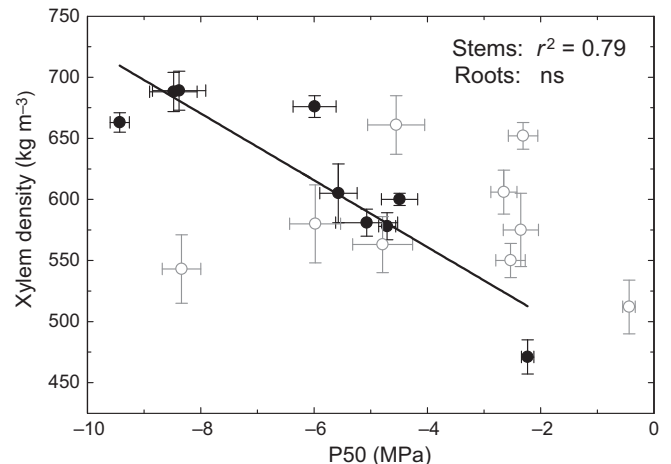
Fig. 3 Woods of similar density can vary greatly in hydraulic and mechanical properties, as illustrated by images and plots. Bar, 100 μm. Density is listed after species name if not 0.60 g cm^{-3}. (a) *Thymus integer* Griseb., (b) *Spartium junceum* L., (c) *Cornus sanguinea* L. (0.61), (d) *Onosma fructicosa* Sm., (e) *Juniperus oxycedrus* L. (0.56), (f) *Convolvulus oleifolius* var. *desertii* Desr. Pamp., (g) *Asparagus acutifolius* L. (0.61), and (h) *Prosopis facta* (Banks et Sol.) Macbride. Plots are arranged in the same species order as the images, and show (i) theoretical specific conductivity (K_s) relative to *T. integer* (whose value was calculated as 6.8×10^{-5} m^2 mPa^{-1} s^{-1}), and (j) proportion of cross-section that is lumen relative to *T. integer* (6.9%). Images are of almost the entire sample tested for density, and thus are representative. Images and density are from Crivellaro *et al.* (2013), with permission.
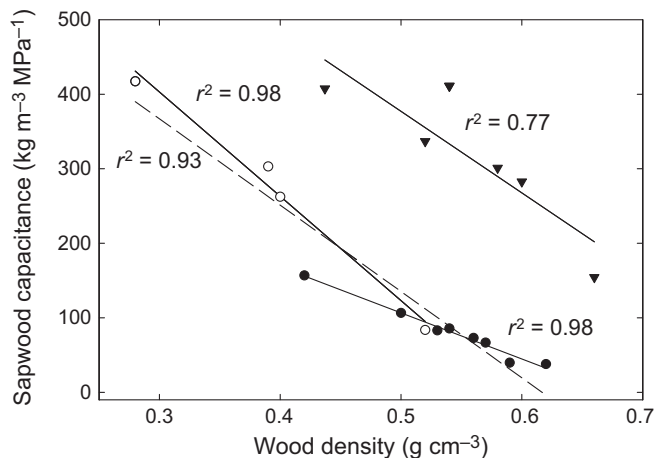
Fig. 4 Capacitance is strongly and negatively correlated with wood density in sapwood of branches from three tropical sites. The relationship was similar within the two drier sites (in Panama and Brazil; dashed regression), but differed markedly between the drier sites and the wetter site (in Panama). Data are from Scholz *et al.* (2007) and Meinzer *et al.* (2008). Closed circles, Cerrado; open circles, seasonally dry secondary forest; triangles, wet old-growth forest.

Fig. 5 Xylem density is a good predictor of embolism resistance for stems (closed circles) but not roots (open circles) of nine species of California chaparral shrubs in the family Rhamnaceae. P50 denotes the xylem water potential at which a sample has lost 50% of its conductivity. From Pratt *et al.* (2007), with permission.

longitudinal parenchyma, resin canals, and branch insertions (knots). In a classic study, Bohannan (1966) showed that small clear wood specimens have much higher stiffness and strength than do larger samples. He inferred that the smaller specimens have a lower likelihood of containing fractures and failures.

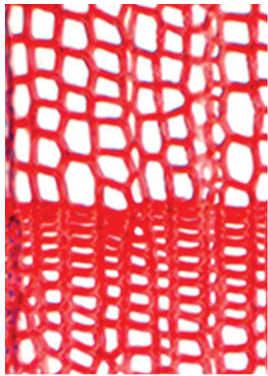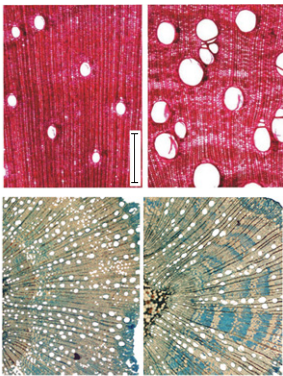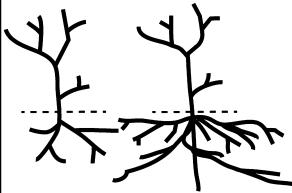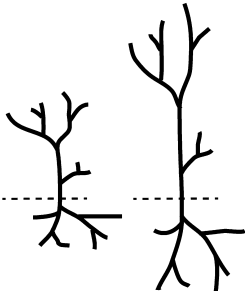The second condition, that the compared specimens have the same mechanical properties, is especially affected by grain angle

(the orientation of xylem cells with respect to the stem's long axis) and microfibril angle (the orientation of the strong, stiff cellulose strands in the cell wall, with respect to the cell's long axis, and usually referring to the S2 cell wall layer only). Wood mechanical properties are strongly anisotropic: for example, wood is 4–12 times stronger in compression when tested perpendicular versus parallel to the grain (Green *et al.*, 1999). Anisotropy is caused predominantly by cell orientation and microfibril angle within the walls of those cells. Even if samples have the same density, they will differ in stiffness and strength if they differ in grain angle (such as normal versus spiral grain; Leelavinichkul & Cherkaev, 2004) or microfibril angle (as is seen comparing wood across the radius of a typical conifer; Zobel & van Buijtenen, 1989; Larson *et al.*, 2001). Differences in wood material properties are implicated in studies in which density does not differ between treatments but wood stiffness and/or wood strength does (Moore *et al.*, 2009). This second condition is also violated if a different proportion of the mass in the compared samples comes from materials that do not bear forces. An example is extractives (secondary compounds soluble in organic solvents, including terpenoids, fatty acids and phenolics), which have very little effect on mechanical properties of green (wet) wood. The quantity and type of extractives vary by species, environment, and location within a tree.

III. Mechanisms influencing dual functionality at different spatial scales

We identify five mechanisms for dual functionality in plants: altering cell morphology, altering the proportion or alignment of different functions within a tissue, and altering the allocation or geometry of tissues and organs within a plant (Fig. 6). The mechanisms that occur at a smaller scale can also occur on top of the mechanisms occurring at larger scales (e.g. cell morphological changes can occur with changes in tissue partitioning). Note that we have grouped organs (branches, shoots, roots, and roots systems) and whole plants together because most of the mechanisms apply to both categories of plant unit. The discussion will illustrate these five mechanisms with brief examples of negative, positive, and neutral co-variation in the hydraulic and mechanical effects that changes in a measure can cause. Further examples are given in Tables 2–6.

Fig. 6 Mechanisms of achieving dual functionality in different plant units: cell, tissue, and organ/whole plant. At the cell level, an example of morphological difference is the cell wall thickness of conifer earlywood (upper) and latewood. At the tissue level, examples of partitioning are the vessel lumen area in a vine axis in wood developed before (left, scale bar = 500 μm) and after it reaches a support (Ménard *et al.*, 2009); and the lack of effect on vessel lumen area of low (left) versus high amounts of tension wood (from the study by Gartner *et al.*, 2003). At the tissue level, an example of alignment is spiral grain. At the organ or whole-plant level, an example of allocation differences is two trees with the same crown size but different root system sizes. At the organ or whole-plant level, an example of geometric differences is two trees with the same biomass, but that differ in that mass's spatial distribution.

Table 2 Examples of the co-variation between hydraulic and mechanical measures that may be mediated by morphological alterations of cells

Co-variation of the dual measures	Example	References
Negative (tradeoffs)	Alterations in conifer tracheids in compression wood change their mechanical performance and some of these alterations (narrower, shorter tracheids with thicker cell walls, different pit morphologies and frequencies) decrease K_s and embolism resistance	Spicer & Gartner (1998a,b); Mayr & Cochard (2003); Burgert *et al.* (2007); Rosner *et al.* (2007); Alméras & Fournier (2009)
	The thicker cell walls of latewood compared with earlywood in conifers are correlated with increased strength and stiffness, but thicker walls have different pit chamber and membrane morphologies that decrease K_s and embolism resistance	Domec & Gartner (2002b); Mott *et al.* (2002)
	Increased embolism (cavitation) fatigue (caused by pit characteristics) may decrease a stem's incidence of internal checking (breakages in the sapwood parallel to the rays) by reducing daily stem diameter variation	Rosner *et al.* (2010)
	Branch wood is usually denser and stiffer than stem wood and has conduits that are shorter and narrower, with smaller pits, lower K_s and higher embolism resistance	Fegel (1941); Hsu *et al.* (2003); Dunham *et al.* (2007); Lintunen & Kalliokoski (2010)
	Plants and plant parts that have higher mechanical demands have higher strength and stiffness but may have lower conduit lumen area or diameter and lower K_s (buttress roots, shrubs/trees versus vines, and trunk at breast height versus tree base versus root)	Gartner *et al.* (1990); Gartner (1991a,b); Chiu & Ewers (1992); Spicer & Gartner (2001); Gallenmüller *et al.* (2001); Dunham *et al.* (2007); Christensen-Dalsgaard *et al.* (2007, 2008); Ménard *et al.* (2009)
Negative (tradeoffs of hydraulics and density)	Tracheids next to the pith have lower K_s than wood farther out because of smaller diameters, but have higher density because more cells fit into a volume and narrow cells have higher cell wall area to lumen ratio	Megraw (1986); Spicer & Gartner (2001)
None (independent)	Altered pit characteristics affect K_s and embolism resistance but not mechanical properties	Hacke *et al.* (2004); Sperry & Hacke (2004); Pittermann *et al.* (2005); Domec *et al.* (2006, 2008); Choat *et al.* (2008)
	Higher extractive content or tyloses in conduits decrease conductivity with no effect on mechanical properties, even though wood density may be increased	Chattaway (1949); Voelker *et al.* (2011a)
	Altered conduit length affects K_s and embolism resistance but not mechanical properties	Comstock & Sperry (2000); Hacke *et al.* (2006); Sperry *et al.* (2006)
	Altered embolism resistance has no correlation with wood density or strength in chaparral species roots, across the radius in conifer trunkwood, and in conifer leaders versus twigs	Domec & Gartner (2002a); Mayr *et al.* (2003); Rosner *et al.* (2006); Pratt *et al.* (2007); Domec *et al.*, (2009)
	Altered microfibril angle causes changes in magnitude and direction of growth stresses in normal wood, compression wood, and tension wood with no effect on hydraulics	Wilson & Archer (1977); Burgert *et al.* (2004); Clair *et al.* (2006); Alméras & Gril (2007)
	Altered microfibril angle changes both critical strain and wood stiffness with no effect on hydraulics	Reiterer *et al.* (1999); Lachenbruch *et al.* (2011)
Positive (mutual benefit)	Because of similar safety factors to implosion and embolism in branch tips of angiosperms and gymnosperms, embolism resistance is positively correlated with increased cell thickness to span ratio as $(t/b)^2$, which itself is correlated with wood density (in some cases; Section II.2)	Hacke *et al.* (2001); Lens *et al.* (2011)

b, tracheid diameter; K_s, specific conductivity; t, double cell wall thickness.

Mechanical effects are listed separately from the effects demonstrated with the proxy property wood density. A caveat for the following is that measures we chose necessarily dictate the nature of the co-variation. For example, wider tracheids may be associated positively with water transport efficiency, but associated negatively with a different hydraulic property, the drought tolerance of a unit of wood (Mayr *et al.*, 2003).

1. Cell morphology: alteration of shape or features within a cell

At the level of the individual xylem cell, the balance between dual functions is achieved through changes in cell features (such as pit frequency or pit geometry), overall cell shape (such as cell lumen diameter or cell wall thickness), and cell inclusions such as gums or gas bubbles (Fig. 6). An example is the wider vessel elements in vines than trees (Gartner *et al.*, 1990), consistent with the lower mechanical constraint in the construction of vine wood because of its lower mechanical demands.

Example with negative co-variation (tradeoffs; Table 2) There are clear hydraulic/mechanical tradeoffs in compression wood compared with normal wood, caused by tracheid morphology. Compression wood tracheids typically develop on the lower side of a leaning conifer stem and generate a residual stress that contributes to the tree's or branch's recovery toward an equilibrium position

Table 3 Examples of the co-variation between hydraulic and mechanical measures that may be mediated by partitioning of tissues

Co-variation of the dual measures	Example	References
Negative (tradeoffs)	A higher proportion of earlywood increases K_s because earlywood has wider vessels and/or tracheids, and it decreases wood strength and stiffness because latewood proportion (which has higher strength and stiffness) necessarily declines	Domec & Gartner (2002a); Mott *et al.* (2002); Domec *et al.* (2008)
	Plant parts that have higher mechanical demands have higher strength and/or stiffness, but may have lower earlywood percentage, higher vessel lumen area, and/or higher sapwood percentage (in outer versus inner portion of the radius in buttress roots, in shrubs/trees versus vines, at tree base versus breast height, and in upper root versus tree base)	Gartner *et al.* (1990); Gartner (1991a,b); Chiu & Ewers (1992); Gallenmüller *et al.* (2001); Dunham *et al.* (2007); Christensen-Dalsgaard *et al.* (2007, 2008); Gould & Harrington (2008); Ménard *et al.* (2009)
Negative (tradeoffs of hydraulics versus density)	Wood density decreases and K_s increases according to a common curve for seven species	Bucci *et al.* (2004)
	Capacitance is negatively correlated with wood density (many examples)	Stratton *et al.* (2000); Meinzer *et al.* (2003, 2008); Santiago *et al.* (2004), Pratt *et al.* (2007); Scholz *et al.* (2007)
	Wood density is negatively correlated with K_s in stems of chaparral shrubs and in different mango (*Mangifera indica*) cultivars	Pratt *et al.* (2007); Normand *et al.* (2008)
None (independent)	Proportion of tension wood presumably has large mechanical effect, but has insignificant effect on K_s, vessel frequency and vessel diameter in *Quercus ilex*	Gartner *et al.* (2003)
	The proportion of the stem that is sapwood alters the ability to transport water but has no effect on mechanics	Långström & Hellqvist (1991); Gartner *et al.* (2004)
	Altered hydraulic needs met by changes that have little or no important effect (e.g. tradeoffs are nonexistent or minor) on density and/or stiffness in chaparral shrubs and *Toxicodendron diversilobum* of two growth forms	Gartner (1991a,b); Wagner *et al.* (1998)
	Altered mechanical demands affect wood stiffness or strength (correlated with fiber lumen diameter, fiber cell wall thickness, and ray percentage) but no effect on K_s in five *Acer* spp	Woodrum *et al.* (2003)
Positive (mutual benefit)	Proportion of libriform fibers is positively correlated with embolism resistance of nearby vessels, and presumably with wood stiffness	Jacobsen *et al.* (2005); Sperry *et al.* (2006)

K_s, specific conductivity.

Table 4 Examples of the co-variation between hydraulic and mechanical measures that may be mediated by cell alignment in tissues

Co-variation of the dual measures	Example	References
None (independent)	Plants with sectoriality have altered conduit connectedness (via intervascular pitting, vessel diameter, and vessel grouping) that can change segmentation without effecting mechanics	Vité & Rudinsky (1959); Carlquist (1984); Larson *et al.* (1994); Ellmore *et al.* (2006); Zanne *et al.* (2006)
Positive (mutual benefit)	Spiral grain increases the stem's ability to distribute water from a patchy resource throughout the canopy and may increase K_s, and will increase the stem's strength in torsion	Vité & Rudinsky (1959); Kubler (1991); Tsehaye & Walker (1995); Skatter & Kucera (1998); Rosner *et al.* (2007); Leelavinichkul & Cherkaev (2004)
	Cable-like construction of some lianas: parenchyma separating cables may act as flexible padding, and should prohibit spread of embolism among 'cables'	Haberlandt (1914); Obaton (1960); Caballé (1993)

K_s, specific conductivity.

(Wilson, 2000; Alméras & Fournier, 2009). After a stem axis changes position, such as by a branch falling off or another tree leaning on it, its newly developed wood has the special morphology of compression wood, which generates a tensile (lengthening) stress in contrast to the compressive (shortening) stress generated by normal wood. The type and magnitude of the forces result mainly from the orientation (up to 45° compared with 0–10° in normal wood) of the relatively inextensible microfibrils that control the direction of swelling during wood development as lignin is deposited into the cell wall (Burgert *et al.*, 2007). Hydraulically relevant morphological differences from normal wood include shorter, narrower tracheids (Panshin & de Zeeuw, 1980) and less frequent bordered pits with smaller pit apertures (Lee & Eom, 1988). These features lead to compression wood's lower specific

Table 5 Examples of the co-variation between hydraulic and mechanical measures that may be mediated by alterations in allocation at the organ or whole-plant level

Co-variation of the dual measures	Example	References
Positive-to-negative continuum (functions have continuum from tradeoffs to no tradeoffs	Degree to which conduit network is optimized for water transport varies, from the least optimized (implying a tradeoff with mechanics) in conifers, then diffuse-porous hardwoods, then ring-porous hardwoods, to the most optimized in lianas and compound leaves (implying no tradeoff), and species with most mechanical support provided by sclerenchyma	McCulloh *et al.* (2003, 2004, 2009); McCulloh & Sperry (2005)
	Degree to which the pipe model (leaf area/sapwood area is constant) is supported, from very strong support (often vines, lianas, some shoots, shrubs, and trees) to not strong support (often shrubs and trees); different relationships in evergreen angiosperms, deciduous angiosperms and gymnosperms	Shinozaki *et al.* (1964a,b); Whitehead *et al.* (1984); Gartner (1991a); Niinemets *et al.* (2006); Ackerly & Donoghue (1998); Pickup *et al.* (2005); Brouat *et al.* (1998)
None (independent)	Altered root morphology and root biomass can have a large effect on tree stability without necessarily affecting the ability to acquire water	Fourcaud *et al.* (2008)
	Stem cross-sectional area scales with the branch cross-sectional area that it supports, according to hydraulic, not mechanical role in *Pinus sylvestris*	Berninger *et al.* (1995)
	Both angiosperm and gymnosperm allocation of leaf mass/mass of supporting primary xylem is closer to mechanical than hydraulic predictions	Taneda & Tateno (2004)
	Branch geometry scales with leaf mass according to mechanical, not hydraulic role in *Picea sitchensis*	Farnsworth & Van Gardingen (1995)

K_s, specific conductivity.

Table 6 Examples of the co-variation between hydraulic and mechanical measures that may be mediated by alterations of geometry at the organ or whole-plant level

Co-variation of the dual measures	Example	References
Negative (tradeoffs)	Axis-splitting avoids spread of embolism among axes, and affects stem integrity and possibly height	Waisel *et al.* (1972); Schenk (1999); Schenk *et al.* (2008)
	A root system optimized for water uptake will have different site-dependent geometry (typically deeper and wider) than a root system optimized for anchorage (typically oriented with respect to wind direction and with more mass close to bole)	Fitter & Ennos (1989); Nicoll & Ray (1996); Hacke *et al.* (2000); Schenk & Jackson (2002); Cucchi *et al.* (2004); Danjon *et al.* (2005); Fourcaud *et al.* (2008)
	Increased wood cross-sectional area near the stem base and in upper roots increases tree stability but is associated with decreased K_s	Spicer & Gartner (2001); Brüchert & Gardiner (2006); Gould & Harrington (2008); Lasserre *et al.* (2009)
	Mechanical perturbations in *Populus trichocarpa × deltoides* cause new growth to have higher strength and stiffness, lower K_s, but more wood such that actual conductance increases	Kern *et al.* (2005)
	Stem cross-sections with more compression wood have wider sapwood that provides partial compensation for compression wood's decreased K_s	Spicer & Gartner (1998a,b); Mayr & Cochard (2003)
None (independent)	Maximum tree height is hydraulically rather than mechanically limited	Delzon *et al.* (2004); Koch *et al.* (2004); Domec & Gartner (2002a); Niklas & Spatz (2004); Domec *et al.* (2008)

K_s, specific conductivity.

conductivity (Spicer & Gartner, 1998a,b; Mayr & Cochard, 2003) and resistance to embolism (Mayr & Cochard, 2003).

Examples without co-variation (independence; Table 2) Wood's hydraulic conductance (similar to conductivity, but not normalized by cross-sectional area) is greatly affected by pit structure (Mayr *et al.*, 2003; Hacke *et al.*, 2004; Sperry & Hacke, 2004; Pittermann *et al.*, 2005; Domec *et al.*, 2006, 2008; Choat *et al.*, 2008), but pit structure has no effect on wood mechanical properties. Moreover, although pit structure can affect the degree of xylem embolism and consequently the mass of water in the stem, models show that the decrease in stem mass attributable to xylem

embolism has no effect on the tree's mechanical stability (Gartner *et al.*, 2004). Also, alterations in cell length can substantially affect conductivity because of the resistance encountered each time water crosses through a pit pair (Comstock & Sperry, 2000; Pittermann *et al.*, 2006; Sperry *et al.*, 2006) and/or through intervessel perforations (Christman & Sperry, 2010), but there is no known impact of conduit length on stem mechanics. For example, tracheid length in conifers is unlikely to affect wood strength given that the tracheid endwalls are infrequent (because tracheids are *c.* 100 times longer than wide), tapered (and so unlikely to be stress risers), and not coincident from tracheid to tracheid.

Likewise, an alteration in cell wall microfibril angle has a direct, causal effect on cell mechanical properties, especially stiffness (Cave, 1969; Groom *et al.*, 2002), critical strain (Reiterer *et al.*, 1999) and growth stresses. Growth stresses in normal wood will put a tension pre-stress in the outer shell of a stem, allowing it to bend farther before it breaks (Boyd, 1972; Gartner, 1997). Growth stresses in compression wood (in conifers), as discussed in the previous paragraph, contribute to cell elongation during development, often pushing a tree toward upright; growth stresses in tension wood (in angiosperms) contribute to cells becoming shorter during development, often pulling (rather than pushing) a tree toward upright (Wilson & Archer, 1977; Clair *et al.*, 2006). We found no evidence that cell wall microfibril angle has any effect on hydraulics. Alméras & Gril (2007) modeled the effect of microfibril angle on the transmission of stress from the water column to the cell wall, and showed relative insensitivity in the range of microfibril angles from 0 to 30°, the most common orientations in xylem.

Example with positive co-variation (mutual benefits; Table 2)
One example of positive co-variation between hydraulic and mechanical measures is embolism resistance and wood mechanical strength and stiffness (assuming wood density is positively correlated with strength or stiffness). Embolism resistance is often strongly correlated with the cell's thickness-to-span ratio $(t/b)^2$, where t is the double wall thickness and b is the mean hydraulic diameter. Natural selection has probably resulted in conduits exhibiting similar risks of failure related to the two properties, mechanical strength to resist conduit implosion (as estimated by $(t/b)^2$), and resistance to embolism (Hacke *et al.*, 2001; Lens *et al.*, 2011). Because wood cell wall material has a constant density (Stamm, 1929), $(t/b)^2$ is positively correlated with wood density. Cases with a positive correlation of wood density and wood stiffness and strength will have an increase in both the hydraulic (embolism resistance) and mechanical performance.

2. Partitioning: alteration of proportion of a tissue dedicated to different functions

Partitioning is the first of the two mechanisms by which tissues can provide dual functionality. Partitioning occurs where one set of cells (e.g. vessel elements) is mainly responsible for one function (e.g. delivery of water), and another set of cells (e.g. the matrix of libriform fibers and parenchyma) is mainly responsible for the other function (e.g. maintenance of the stem's position through support) (Fig. 6; Table 3). If an increase in the volume of cells that provide

one function causes a decrease in the volume of cells providing another function, then there is a tradeoff. If the tissue contains a third volume of cells (e.g. whose function is primarily carbohydrate storage), it is theoretically possible to have independent changes in the first two proportions.

When considering these tissue-based functions, it may be important to question whether tissues function as is assumed in the literature. Cell types were named and described before capabilities existed for testing function in many cases. For example, latewood in conifers is generally assumed to have a mechanical role, but its pattern of water release at decreasing water tensions suggests that it may also have a role in water storage (Domec & Gartner, 2002b). Libriform fibers, assumed to provide mechanical support for the mass above them, may also have a role in strengthening the wood matrix such that nearby vessels have an increased embolism resistance (Jacobsen *et al.*, 2005; Sperry *et al.*, 2006). Parenchyma cells, typically assumed to be involved in storage and/or defense, may increase xylem strength or stiffness (Schniewind, 1959; Woodrum *et al.*, 2003) and may serve as flexible padding to allow a stem of a plant like a liana to twist in the wind, thereby protecting the vessels from breakage (Haberlandt, 1914).

Example with negative co-variation (tradeoffs; Table 3)   A good example of partitioning that shows a tradeoff is seen in hardwood species with ring-porous wood and in coniferous species with an abrupt transition from earlywood to latewood (as opposed to a gradual transition; see Panshin & de Zeeuw, 1980). In these species, the earlywood has the highest conductivity, the latewood confers the greatest wood stiffness, and an increase in one proportion necessitates a decrease in the other. Ring-porous species tend to produce only slightly wider earlywood bands as ring width increases (Paul, 1963; Maeglin & Quirk, 1984). This pattern suggests that trees of these species produce a relatively constant conducting area per unit leaf area (the earlywood), which will maintain a relatively constant leaf-specific conductivity (specific conductivity expressed per unit distal leaf area, rather than per unit stem cross-sectional area). Ring-porous trees that grow faster, therefore, will tend to have stronger wood but lower specific conductivity. In conifers, however, patterns may be more complex, because typically there is a higher earlywood proportion within the crown (Larson, 1969) and latewood is produced earlier in the season toward the tree's base (Funada *et al.*, 1990), and, in one study, there was a stronger correlation of leaf area/sapwood area with total sapwood area than with either earlywood or latewood area (Gartner, 2002).

A second example of a partitioning tradeoff at the tissue level comes from demonstrations of depressed specific conductivity in axes with higher mechanical demands. This pattern usually results from a decrease in the proportion of the tissue's cross-section devoted to transport and an increase in the proportion devoted to support, and is also accompanied by a narrowing of conduits as mechanical demands increase. Such partitioning patterns have been demonstrated in inner versus outer parts of buttress roots (Christensen-Dalsgaard *et al.*, 2007, 2008), in stem xylem of vines versus trees or shrubs (Gartner *et al.*, 1990; Gartner, 1991a,b; Chiu & Ewers, 1992; Gallenmüller *et al.*, 2001; Ménard *et al.*, 2009),

and at breast height versus the trunk base in mature conifer trees (Spicer & Gartner, 2001; Dunham *et al.*, 2007).

Examples without co-variation (independence; Table 3) In the radial-porous species *Quercus ilex*, the vessels made up *c.* 6% of the tissue in 2-yr-old wood, with the other 94% made up of parenchyma and libriform fibers. Plants that were grown with a treatment that increased the amount of tension wood in the stems (from an average of 0% in controls to 15% in the treatment) had an increase in mechanical competence with no significant effects on the proportion of the cross-section that was vessel lumen, or specific conductivity (Gartner *et al.*, 2003; and images in Fig. 6). Likewise, a survey of five *Acer* species (Woodrum *et al.*, 2003) found no correlation between species' conductivity and species' wood stiffness or strength (but see different methodology and conclusions in Lens *et al.*, 2011). The mechanical properties were driven by alterations in libriform fiber morphology and ray proportion, with no effect on the hydraulic properties. A last example involves the proportion of the stem cross-section devoted to sapwood. Higher sapwood area can supply water to a larger leaf area, as suggested by the decrease in sapwood area after trees are pruned (Långström & Hellqvist, 1991). Sapwood proportion, however, does not affect stem mechanics (Gartner *et al.*, 2004).

Example with positive co-variation (mutual benefits; Table 3) Several studies have shown that libriform fibers, whose role is normally associated with wood strength and stiffness, are also associated with higher resistance to embolism, presumably because they add strength to the entire wood matrix which reinforces the wood when it is deformed during transpiration (Jacobsen *et al.*, 2005; Sperry *et al.*, 2006).

3. Alignment: alteration of axial connections of cells within a tissue

Cell alignment is the second mechanism by which tissues can provide dual functionality. Cell alignment can restrict hydraulic function to within the axially aligned sectors in the tissue, but not between them (Fig. 6; Table 4).

Examples without co-variation (independence; Table 4) In plants with a high degree of sectoriality, xylem transport occurs through multiple distinct and restricted pathways (Vité & Rudinsky, 1959; Larson *et al.*, 1994) within the intact entire stem. The high sectoriality confers hydraulic redundancy and a level of safety against the spread of embolism (called vulnerability segmentation) but is linked to reduced specific conductivity (Zanne *et al.*, 2006; Ewers *et al.*, 2007; Loepfe *et al.*, 2007; Schenk *et al.*, 2008; Lens *et al.*, 2011; Brodersen *et al.*, 2012; Martínez-Vilalta *et al.*, 2012). Sectoriality is mediated by the grouping or alignment of vascular tissues, and it is likely that it also relies on different conduit diameters and the nonuniform location and frequency of inter-conduit pitting to keep sectors separate (Carlquist, 1984; Ellmore *et al.*, 2006; Zanne *et al.*, 2006). Unless the stem also exhibits spiral grain there should be no effect of sectoriality on plant mechanical properties (Table 4).

Example with positive co-variation (mutual benefits; Table 4) Spiral grain, in which conducting cells are oriented at a substantial angle from the axial direction, can provide benefits to both hydraulic and mechanical performances under conditions of patchy soil water and asymmetrical wind loads, respectively. With spiral grain and sectoriality, resources ascending from one root can be dispersed to branches on all sides of the tree (Vité & Rudinsky, 1959; Kubler, 1991; Larson *et al.*, 1994). Additionally, saplings of *P. abies* with spiral grain had higher axial specific conductivity than did straight-grained saplings (Rosner *et al.*, 2007). This latter finding probably resulted from a change in the distribution of bordered pits (concentrated at tracheid ends in normal wood, but spread more evenly along the axis in spiral grain) such that total pit resistance decreased. Mechanical benefits of spiral grain include decreased stiffness (Tsehaye & Walker, 1995) and increased strength in torsion (Skatter & Kucera, 1998), both of which help branches and main stems bend and twist in the wind (Kubler, 1991; Skatter & Kucera, 1998). The mechanical benefits appear to occur only at grain angles up to 37° from axial, beyond which the tree's loss of axial wood strength greatly increases the tree's risk of mechanical failure (Leelavinichkul & Cherkaev, 2004).

4. Allocation: alteration of relative proportion of tissues within an organ or plant

Allocation is the first of the two mechanisms by which dual functionality can occur within an organ or a whole plant. Allocation in the present context is the amount of one function relative to another that is located in the organ (such as a branch, root, or shoot) or whole plant (Fig. 6; Table 5). (As such, this mechanism is somewhat similar to partitioning at the tissue level.) A simple example of allocation is leaf area relative to sapwood area. In this case, because sapwood area can be increased (through a reduction in heartwood area) without an increase in stem diameter, a plant with higher leaf area relative to sapwood area can have higher transport efficiency with no requisite change in the mechanical performance. The hydraulic and mechanical performances are independent.

Examples with a spectrum of co-variation (from tradeoff to no tradeoff; Table 5) Several studies show alterations in allocation that lead to a tradeoff between hydraulic and mechanic performances in some cases but not in others. The first example, related to Murray's law, addresses the configuration of the network of xylem tissue used for water transport (McCulloh *et al.*, 2003, 2004, 2009). Lianas and compound leaves have networks that appear close to optimal for water transport, suggesting that their network configurations are not altered for mechanical needs: there are no hydraulic/mechanical tradeoffs. By contrast, trees, and especially those with coniferous or diffuse-porous wood, exhibit network configurations that are farther from optimal for hydraulics, implicating tradeoffs of hydraulic with mechanical functions.

The second example addresses the ratio of transpiring area (leaf area) to conducting area (sapwood area). The pipe model predicts a linear relationship (Shinozaki *et al.*, 1964a). Cases in which data are not consistent with the pipe model suggest that mechanical demands, such as a need for further allocation to stem strength,

explain the inconsistency (Gartner, 1991a). The more difficult interpretation is whether data that support the pipe model demonstrate a lack of hydraulic/mechanical tradeoffs. When a system conforms to the pipe model (Corner, 1949; Shinozaki *et al.*, 1964b; Ackerly & Donoghue, 1998; Brouat *et al.*, 1998; Pickup *et al.*, 2005; Niinemets *et al.*, 2006; McCulloh *et al.*, 2010), we know that the leaf and sapwood areas scale together but we do not know whether the correlations have predominantly hydraulic or mechanical causes (as discussed in Ackerly & Donoghue, 1998). Data interpretation is also made more difficult because the pipe model relies on the relationship of two indirect measures (sapwood area and leaf area) to estimate the properties of interest (stem conductance and tree transpiration). Therefore, other measures that may partially compensate for either sapwood area or leaf area (e.g. timing of water storage and release, degree of sapwood embolism, specific conductivity, timing of transpiration, and leaf phenology) are not taken into account.

Examples without co-variation (independence; Table 5) When trees conform to the pipe model, we presume they are constructed according to hydraulic (and not mechanical) function; in other words, their mechanical performance is presumed to be adequate when they are constructed as dictated by hydraulic principles. Similarly, one study showed that the mass of branch material supported by a stem scaled according to hydraulic, not mechanical rules (Berninger *et al.*, 1995). There are also studies that describe geometric adjustments that are of adaptive value for mechanical performance, with no effect on hydraulic performance. For example, both branch geometry (Farnsworth & Van Gardingen, 1995) and primary xylem mass (Taneda & Tateno, 2004) scale with leaf mass in a manner consistent with mechanical rather than hydraulic performance.

5. Geometry: alteration of the distribution of tissues within an organ or plant

Geometry is the second of the two mechanisms by which dual functionality can be provided by an organ or a whole plant. Geometry for this discussion is the distribution and location of biomass within a plant (Fig. 6; Table 6). A tree with the same aboveground biomass, for example, can have a short wide stem or a tall narrow one.

Example with negative co-variation (tradeoffs; Table 6) Axis-splitting is the phenomenon of a solid stem developing into separate axes. It occurs in a wide range of families, and is particularly common in arid and semi-arid environments (Schenk *et al.*, 2008). The separation of the axes confines water transport or the spread of embolisms to specific zones within the plant, and is referred to as hydraulic or vulnerability segmentation, respectively (Tyree & Ewers, 1991). This physical isolation may give a plant redundancy, and may allow some axes to remain functional while other axes are sacrificed when water becomes scarce, instead of having the entire cross-section (and the whole shoot) develop the critical level of embolism causing death (Schenk, 1999; Schenk *et al.*, 2008). The mechanical properties of split axes are certainly altered by their

Fig. 7 The lobed stem of *Aspidosperma* (Apocynaceae, French Guiana; species unidentified) may confer hydraulic advantage through the redundant and isolated stem sectors, and/or it may confer mechanical advantage by providing the stiffness benefits of a higher second moment of area (like an I-beam) without the biomass investment of an entire (unlobed) stem. The photograph is by Bernard Thibaut.

smaller diameter, which confers a lower second moment of area and thus a lower structural stiffness.

Other forms of axis-splitting or axis isolation have been less extensively studied physiologically. In some species, as plants get larger the stem becomes partially split, giving the appearance of a bundle of parallel but anastomosing stems. In other species, the stems develop prominent radial lobes of various shapes (Fig. 7), circumferential ribbing, or other axial and radial protuberances. We have seen no discussion of the hydraulic or mechanic functions of these geometries, but it is likely that they facilitate a degree of hydraulic and vulnerability segmentation. From a functional perspective, it would seem that there is a continuum of hydraulic and mechanical function from sectoriality (in complete, unseparated stems) through partial axis-splitting, to complete axis-splitting. There are numerous tropical vine species illustrating different points along this continuum (Obaton, 1960; Caballé, 1993).

Another example of a geometric tradeoff is that the optimal shape of a bole, branch, or root will be different for hydraulic than for mechanical function. Stem taper and/or butt swell greatly increase tree stability (Cannell *et al.*, 1988; Lasserre *et al.*, 2009 Moore *et al.*, 2009), but in *Pseudotsuga menziesii* they are associated with a decrease in specific conductivity (Spicer & Gartner, 2001), an increase in sapwood width (Gartner, 2002) and probably an alteration in cell morphology (shorter tracheids; Megraw, 1986). Further, the optimal morphology of a root system should differ depending on the relative hydraulic versus mechanical needs (Fitter & Ennos, 1989). Root systems that are primarily for water uptake typically are deeper and wider and have more root biomass in xeric than mesic sites (Hacke *et al.*, 2000; Schenk & Jackson, 2002). Root systems

that are primarily for anchorage have a higher proportion of mass close to the bole, and more of the roots are orientated parallel to the prevailing winds (Nicoll & Ray, 1996; Cucchi *et al.*, 2004; Danjon *et al.*, 2005; Fourcaud *et al.*, 2008).

Examples without co-variation (independence; Table 6) A number of different lines of research suggest that maximum tree height is more limited by hydraulic than mechanical needs (Delzon *et al.*, 2004; Koch *et al.*, 2004; Niklas & Spatz, 2004; Domec *et al.*, 2008). As trees get taller, the water potential at the top will decline, because of both the hydrostatic gradient (0.01 MPa m^{-1} of height above the ground) and the resistance from the longer path. The reduced water potential in a tall tree's crown will reduce the ability of cells there to fully expand (Koch *et al.*, 2004; Woodruff *et al.*, 2004). Moreover, the pattern of xylem anatomy and embolism resistance is consistent with the hypothesis that height is limited by the ability to transport water, given the need for increasingly embolism-resistant xylem at increasing heights in the tree (Domec *et al.*, 2008).

IV. Conclusions

Among the woody plants, there are many morphological and physiological strategies for survival. This review describes the various alterations of cells, configurations of cells within tissues, and biomass distribution patterns within organs and whole plants that make dual functionality possible. The schematic model indicates that measures can influence hydraulic or mechanical performance, or both, and that there are numerous opportunities for compensatory changes among measures such that there are no alterations at the level above. We have also demonstrated that there can be positive, negative, and no association among measures that influence hydraulic and mechanical performance.

There are still many gaps in our understanding of the mechanisms by which plants of different types and stages respond to stresses. Whereas the very powerful research with functional traits is providing many clues, it is also exposing the need for more mechanistic understanding of the correlational patterns observed, to enable extrapolation to novel environments and plants. We also need much more understanding of how plants perform with respect to stresses, both singly and in combination (Mittler & Blumwald, 2010), including the much understudied physiological effects of pathogens. Further, a plant's response to a stress necessarily depends on its current state, which is a product of its history. We need to explore the importance of the morphological and metabolic legacies of previous conditions; for example, how the previous year's wood anatomy and the current carbohydrate stores affect stress response. Future opportunities will also come from the development of novel trait combinations with molecular biology, and from advances in instrumentation, computational abilities, and statistical techniques.

As anthropogenic changes continue to alter the environments to which today's plants are adapted, it will be increasingly important that this body of information be accessible to other fields (Johnson *et al.*, 2010). Plant breeders will increasingly need information on the traits and trait combinations that need to be maintained in order to produce viable woody plants. Lastly, knowledge of which traits and properties are most influential for survival at different life stages, and under different stress regimes, will help managers choose the species and cultivars that are best suited for different sites and management goals for forested, agricultural and wild lands of the future.

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