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Review

Water relations in tree physiology: where to from here?

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We look back over 50 years of research into the water relations of trees, with the objective of assessing the maturity of the topic in terms of the idea of a paradigm, put forward by Kuhn in 1962. Our brief review indicates that the physical processes underlying the calculation of transpiration are well understood and accepted, and knowledge of those processes can be applied if information about the leaf area of trees, and stomatal conductance, is available. Considerable progress has been made in understanding the factors governing stomatal responses to environment, with insights into how the hydraulic conducting system of trees determines the maximum aperture of stomata. Knowledge about the maximum stomatal conductance values likely to be reached by different species, and recognition that stomatal responses to increasing atmospheric vapor pressure deficits are in fact responses to water loss from leaves, provides the basis for linking these responses to information about hydraulic conductance through soil–root–stem–branch systems. Improved understanding in these areas is being incorporated into modern models of stomatal conductance and responses to environmental conditions. There have been significant advances in understanding hydraulic pathways, including cavitation and its implications. A few studies suggest that the major resistances to water flux within trees are not in the stem but in the branches. This insight may have implications for productivity: it may be advantageous to select trees with the genetic propensity to produce short branches in stands with open canopies. Studies on the storage of water in stems have provided improved understanding of fluxes from sapwood at different levels. Water stored in the stems of large trees may provide up to 20–30% daily sap flow, but this water is likely to be replaced by inflows at night. In dry conditions transpiration by large trees may be maintained from stored water for up to a week, but flows from storage may be more important in refilling cavitated xylem elements and hence ensuring that the overall hydraulic conductivity of stems is not reduced. Hydraulic redistribution of water in the soil may make a contribution to facilitating root growth in dry soils and modifying resource availability. We conclude that the field of tree water relations is mature, in the sense that the concepts underlying models describing processes and system responses to change are well-tested and accepted and there are few, if any, serious anomalies emerging. Models are essentially formal statements about the way we think systems work. They are always subject to further testing, refinement and improvements. Gaps in knowledge appear within the framework of accepted concepts and mechanisms research is needed to fill those gaps. The models currently available can be used to scale estimates of transpiration from leaf to landscape levels and predict species responses to drought. The focus in tree water relations has shifted to examine the climatic thresholds at which drought, high temperatures and vapor pressure deficits cause mortality. Tree death may be caused by hydraulic collapse following irreversible cavitation or extremely low water potentials, but recent research indicates that the relative sensitivity of stomatal conductance and whole-plant hydraulic conductance plays a major role in determining plant responses to drought.

Keywords: cavitation, hydraulic pathways, models, plant water relations, review, scientific paradigm, stomata, transpiration.

Introduction

In 1962 Thomas Kuhn published an iconic book, 'The structure of scientific revolutions', which influenced the way several generations of scientists, and historians of science, thought about how scientific research is done and scientific knowledge increases. Kuhn's primary postulate was that most research activity is what he called 'normal science'—research that takes place within a well-recognized and accepted paradigm: a model of reality that provides a framework of theory, results and procedures, accepted by the community of scientists concerned with the field in question. A mature paradigm is likely to provide the basis for adequate descriptions and quantitative models of the system under study; it also provides a guide to the problems to which research should be directed. But, over time, normal science may lead to recognition of increasing anomalies between predicted results and those observed, leading to a paradigm shift—new understanding and new ways of thinking about the field.

Kuhn confined his analyses to the physical sciences, to the crises that developed in relation to some of the most important areas of physics and chemistry and the revolutions that changed them. Somewhat surprisingly, he said nothing about biology, although Charles Darwin's publication of 'The Origin of Species' in 1859 led to one of the greatest of all intellectual upheavals in the history of science. Scientists and naturalists in the mid-19th century struggled to explain species extinctions and the appearance of new species in layers of sedimentary rocks. Competing theories ranged from creationism to Lamarckism (heritability of acquired characteristics). Darwin's ideas about evolution provided an all-encompassing explanation for the accumulating observations on species change and adaptation. Many scientists at the time, as well as clerics, did not accept the theory of evolution, but the Darwinian paradigm, which fits comfortably within Kuhn's structure, still provides an overarching framework for the biological sciences, explaining change, variation and adaptation at every organizational level. The central puzzle of evolutionary theory—the mechanism by which genetic changes are inherited—was solved by the recognition (Watson and Crick 1953) of the double helix structure of DNA. This had immense implications for our understanding of genetics and the mechanisms of heredity that underpins all of molecular biology and biotechnology.

We are concerned, in this paper, to evaluate progress in research on tree water relations, a sub-branch in the field of tree physiology. We do not intend to provide a comprehensive review of the topic but present an overview of tree water relations, showing that the concepts and ideas about mechanisms that define the topic were well established by the early 1980s. This provides the framework—the paradigm—within which the present generation of scientists set their research. There is a large and growing body of work driven by questions arising from recognition of gaps in knowledge that have become apparent in our understanding of the water relations of trees and the effects on

them of changing environmental conditions, but there are no indications of major anomalies, of findings that undermine the overarching paradigm. There is some concern that a proportion of the scarce research resources—which include the abilities and time of able scientists—currently applied to the study of tree physiology is being wasted in work that contributes little or nothing to advancing knowledge. This may be a result of scientific amnesia, caused by lack of awareness of old literature. However, expressing such concerns is always likely to lead to arguments, so an important objective of this paper is to assess whether we have reached the point where returns from additional research on tree water relations are becoming progressively smaller.

There is a tendency, in many branches of science, to follow the reductionist approach and investigate at lower and lower organizational levels the processes that determine responses of organisms, such as trees, or systems, such as plant communities, to stimulus and change. Reductionist research is essential to provide understanding about how organisms or systems function, but detail at a particular (low) level of organization may not contribute greatly to our ability to predict the behavior and responses of the system at higher levels. For example, in the case of tree water relations, it would be difficult to use knowledge about the role of phloem in water storage, or the mechanisms by which xylem vessels are refilled after embolism, to model water use rates and physiological responses of trees or forest canopies to changing environmental conditions over weeks, months or seasons. de Wit (1970) suggested that it is not practical to attempt to model a system across more than two levels of organization, i.e. to attempt to explain observations in terms of processes more than one level down in the organizational hierarchy. Measurement techniques have improved and computer power has increased enormously since 1970, but the point is still valid. Considerable amounts of detail are subsumed in models that predict system responses at progressively higher levels of organization. As the level of synthesis progresses upward, the significance of the processes under study also changes (Passioura 1979).

All models are hypotheses and are likely to include assumptions about some aspects of the system. The assumptions included in, or underlying, the models must be clearly stated and the models should be formulated in such a way that they make testable predictions. If a model is tested and its output is shown to be consistent with empirical data, this does not mean that the model is right; it simply means that it has not yet been shown to be wrong. However, as the range of tests and conditions under which models are tested is increased, confidence in them will also increase. The models widely used in the analysis of tree water relations are, for the most part, based on analogs of Ohm's law, using the concepts of flows across potential gradients, resistances or conductances to describe water movement through the system. They have survived countless tests and provide the framework for our evaluation of the maturity of this area of tree physiology.

We have taken as our starting point (see the next section) seminal papers written in the 1970s and early 1980s, which provide excellent summaries of the theoretical basis, and information then available, about tree water relations. With those as our baseline, we review some of the papers published since that time. In the last part of this paper we indicate areas that seem most likely to be profitable for future research. These include physiological adaptations and the interactions between genetics and tree water relations.

Tree water relations science: historical overview

In 1975 Paul Jarvis published a seminal paper on water transfer in trees—a synthesis of the information available at that time. He outlined the relationships between transpiration rate, resistances to liquid flow, tree leaf area, the sapwood basal area of the trees and leaf water potential. In a major review, written a few years later, [Whitehead and Jarvis \(1981\)](#) recapitulated and expanded on [Jarvis \(1975\)](#). They dealt in detail with: transpiration and water use; water potential gradients and the movement of water through trees as a result of water loss from the foliage; stomatal resistance and the environmental factors affecting that crucially important variable; and resistances to the flow of water through stems, shoots and roots.

The Whitehead and Jarvis paper provides a useful starting point for our discussion because it is a good summary of knowledge and understanding about tree water relations at that time. The paradigm that the paper describes was, in fact, largely established in the 1960s and 1970s. [Slatyer's \(1967\)](#) book ('Plant–water relationships') provided a comprehensive and detailed treatment of underlying theory, including plant–environment interactions, water in soils and discussion of techniques for measuring plant water potential. Slatyer did not deal specifically with trees. Between the later 1960s and 1980s the measurement of water potential was revolutionized by the development of the pressure chamber by [Scholander et al. \(1965\)](#). This instrument was first used to study the diurnal water relations of trees by [Waring and Cleary \(1967\)](#), who used a shotgun to obtain samples, at night, from high in tall trees. The pressure chamber has provided the basis for much of the work on tree water relations since that time. Other areas where there has been considerable progress in the measurement techniques that underlie all experimental work are the development of easy-to-use, accurate, automated porometers of various types, allowing measurement of gas exchange at leaf level, and greatly improved sap flow rate measurements, mainly based on the technique developed by [Granier \(1985\)](#). [Landsberg and Sands \(2011, p 53\)](#) made the comment, in relation to the modern, off-the-shelf, automated gas exchange units, that they have resulted in an avalanche of measurements on a wide range of plants in all sorts of conditions. The comment is a pertinent warning against the uncritical collection of

data without a clear focus on testing some model or theoretical concept.

The Baconian approach to scientific investigation—data collection, tabulation and analysis without a theoretical framework—has long been superseded by the hypothetico-deductive approach, now generally accepted as the basis of scientific method. The fact that most data collection exercises, whether based on experiment or observation of un-manipulated systems, are now carried out within the context of some theoretical concept, which may be quite precise, or rather vague, does not preclude the possibility of surprises: unexpected results and findings. In fact such surprises are more likely when data are collected with the clearly stated intention of testing some hypothesis consistent with currently accepted theory. If the data are consistent with the hypothesis they may add to our knowledge of the system under study. If they do not support the hypothesis they may provide grounds for re-examining it, although the path to complete rejection of established theory is a long one. There is no indication in the literature of significant anomalies in the general framework of theory that underlies tree water relations.

[Whitehead and Jarvis \(1981\)](#) did not deal in any detail with the effects of water potential on stomatal apertures, and hence conductance, but other contributions in that volume ([Kozłowski 1981](#)) did so ([Hinckley et al. 1981](#), [Doley 1981](#), [Landsberg and Jones 1981](#)). They did provide detailed discussion of variations in water potential and the flow of water across potential gradients through the system (tree), focusing on resistances to flow in various parts of the system. Changes in the water content of tree tissues were measured by a number of workers in the 1950s, 1960s and 1970s, but water storage in stems (sapwood) in large trees seems to have been first identified as a significant factor in the seasonal water relations and water balance of conifers by [Waring and Running \(1978\)](#) and [Waring et al. \(1979\)](#). The recognition of capacitance explained why hysteresis occurs in the diurnal variation of leaf water potential in the spring, but not in the fall, if available water stored in sapwood is largely extracted. [Landsberg et al. \(1976\)](#), working with apple trees, were, apparently, the first to describe the movement of water in and out of storage in terms of the capacitance of tissues. The mathematics are reproduced by Whitehead and Jarvis, who concluded their review with some comments on modeling water flow through trees, noting that [Running et al. \(1975\)](#) and [Waring and Running \(1976\)](#) had produced the only then-extant model that included changes in tissue water storage. Whitehead and Jarvis also provided a relatively cursory treatment of soil water, and reviewed the information then available on tree root distribution.

Developments since the 1980s

Transpiration

Information about the flow of water through trees, driven by transpiration, is central to the whole field of tree water relations. We

noted earlier that [Whitehead and Jarvis \(1981\)](#) dealt with transpiration at leaf and canopy level in some detail. The principles and physics of the process were well established in the 1960s: the combination energy-balance mass-transfer equation (the Penman–Monteith equation) first derived by [Penman \(1948\)](#) and subsequently refined and modified by [Monteith \(1965\)](#) is now generally accepted as providing estimates of canopy transpiration rates that are accurate to within the limits imposed by the meteorological and biological data. Details of the algebra involved in deriving the equation, and discussion of the assumptions and implications, can be found in [Monteith and Unsworth \(1990\)](#) (see also [Landsberg and Sands 2011](#)). The meteorological data required as inputs consist of solar radiation, from which net radiation absorbed by the canopy can be derived (it may be measured directly), windspeed and atmospheric vapor pressure. The biological data required are the leaf area index of the canopy, leaf geometry and the canopy conductance, derived from stomatal conductance and canopy leaf area. Transpiration at the canopy level, i.e. from stands or extended areas of forest, can be measured, with varying degrees of accuracy, using sap flow meters set in a number of trees, and then scaling up to stand level on the basis of leaf area per tree (see next paragraph) or eddy covariance measurements, which provide estimates of vapor fluxes from extended areas (see [Williams et al. \(2001\)](#) and [Bonan et al. \(2014\)](#) for examples of the use of those data.)

The most important of the biological variables that determine canopy transpiration rates, and hence the flow of water through the tree stems, are leaf area per stem and the stomatal conductance of the foliage. [Shinozaki et al. \(1964a, 1964b\)](#) developed the pipe model theory, showing that the mass of foliage in the crowns of trees was linearly related to the supporting sapwood. [Grier and Waring \(1974\)](#), [Waring et al. \(1978\)](#) and [Whitehead \(1978\)](#) established linear relationships between sapwood cross-sectional area and leaf area per tree. [Waring et al. \(1982\)](#) proposed that unit area of foliage is serviced by a specific cross-sectional area of sapwood in the crown of the tree. [Shinozaki et al.](#) had assumed that much of the sapwood is non-functional, but [Whitehead et al. \(1984\)](#) demonstrated that all the sapwood remains functional, although conducting efficiency changes: the product of leaf area \times efficiency remains constant. Given these relationships and the number and size of stems in a stand, it is possible to estimate the leaf area index of stands.

[Whitehead and Jarvis \(1981\)](#) discussed the application of the Penman–Monteith equation to forests, and provided a table of transpiration rates from coniferous canopies, as well as references to studies in which the equation was tested. [Stewart \(1984\)](#) listed others, and we note an interesting paper by [Schulze et al. \(1985\)](#) reporting the results of comparing different methods of measuring canopy transpiration from forests, although [Schulze et al.](#) did not test the Penman–Monteith equation.

Pertinent to the matter of scaling water use by tree size, [Hatton and Wu \(1995\)](#), studying Eucalyptus species on two widely different sites in New South Wales, and Queensland, found that, when soils were wet, water use by the trees (flux per stem) was linearly related to leaf area per tree \times intercepted radiation, but as the soils dried, there was a non-linear decline in flux per unit leaf area. Therefore, as Hatton and Wu pointed out, an important implication of their results is that scaling tree community water use by leaf area index will not necessarily produce accurate results when soils are dry. Hatton and Wu did not interpret their results in terms of the effects of hydraulic conductivity and its effects on stomatal conductance (see next section), but they are consistent with those effects.

It follows from the fact that water flux per stem in closed canopies with different stem populations is—particularly when the soil is wet—approximately proportional to leaf area per stem, and the flow of water up each stem will be (more or less) inversely proportional to stem numbers, with concomitant differences in resistances to flow through individual stems. These resistances will, obviously, vary with tree height (see the later section on Hydraulic conductance). There are other resistances to water flow through the system, notably at the soil–root interface: [Landsberg and Sands \(2011\)](#) discussed, briefly, root distribution (see also [Landsberg and Gower 1997](#)) and the factors that influence resistance to water movement into tree root systems, an important area in the field of tree water relations to which we return later in this paper. It is becoming clear that the hydraulic characteristics of the soil–root–stem systems of trees influence tree height, the maximum stomatal conductance realized by the leaves and, possibly, branch length. There has been significant progress, in recent years, both conceptually and in terms of measurements, in the study of these effects and interactions. We return to consider them in some detail later, but must first outline the situation with regard to stomatal conductance.

Stomatal conductance

Stomata, hydraulically linked to the surrounding mesophyll cells, are the organs at the interface between foliage and the atmosphere. Stomatal conductance is the inverse of stomatal resistance, which is a measure of the resistance to diffusion of CO₂ into the leaf or of water vapor molecules out of the cavities behind the stomata. It is a function of the number, size and degree of opening of the stomata in the surface layers of leaves. The degree to which stomata are open or closed is affected by irradiance, atmospheric CO₂ concentrations, atmospheric vapor pressure deficit, by leaf water potential, and ultimately, turgor. Leaf water potential is strongly dependent on the rate of flow through the hydraulic pathways from soil to root and through the conducting systems of the trees. Because of the importance of stomatal functioning and responses to those variables, they have been the subjects of a vast amount of research over many years, starting well before the period (since about 1980) that we are

considering here (e.g., Francis Darwin (1898, pp 577–581), who observed stomata open at night in many species when not limited by water).

Landsberg and Sands (2011) provide a recent review, which is by no means exhaustive but offers a reasonably up-to-date and comprehensive summary of the 'state of the art' in empirical stomatal studies (see pp 61–68). They consider a range of models that include terms describing stomatal responses to all the major variables mentioned above. Models such as those presented by Leuning et al. (1995) and Tuzet et al. (2003) have, arguably, reached the point where further mathematical modifications are unlikely to add significantly to our ability to predict stomatal responses to environmental conditions (but see later comment on the model by Medlyn et al. (2011)). The Leuning et al. model includes the effects of vapor pressure deficits, leaf surface CO₂ concentrations and the within-leaf CO₂ compensation point. It provides a fully coupled solution for CO₂ assimilation and transpiration calculations. Tuzet et al. (2003) incorporated calculations of leaf and soil water potentials, and plant hydraulic resistance, into the Leuning model. New data sets, particularly data collected in the field (as opposed to measurements made under controlled conditions) will lead to different values for some of the empirical parameters included in these models, but are unlikely to lead to the type of model failure that would require complete re-formulation.

An important feature of most of the modern models that describe stomatal responses to changing environmental conditions, including changes in leaf water potential, is the inclusion of values for the maximum stomatal conductance values likely to be reached by different species under the most favorable conditions of light, water availability and temperature. A major conceptual advance, stemming from work of Mott and Parkhurst (1991; cited by Oren et al. 1999) and Monteith (1995), has been the explicit recognition that the widely documented stomatal closure in response to increasing atmospheric vapor pressure deficit is caused by evaporation from the leaves, and is therefore a feedback response to water loss from the leaf tissue (Oren et al. 1999). Changes in the water content of tissues cause changes in leaf water potential, resulting in potential gradients through the soil–plant system. These gradients provide the driving force for water movement through the system, with the result that the water status of plants is determined by the relations between rates of transpiration and rates of water uptake and movement through the soil–plant system. It follows from this that the maximum conductance attained by different species under favorable conditions, and their responses to falling leaf water potential and increasing vapor pressure deficits, will be determined by the hydraulic conductivity of the pathways from soil to leaves.

It seems that relatively few studies on stomatal conductance have taken account of the fact (Tardieu 1993, Tardieu and Simonneau 1998) that plants can be placed in two categories—labeled isohydric and anisohydric—across the continuum of

stomatal regulation of water status. Isohydric plants reduce their stomatal conductance as soil water potential decreases and atmospheric vapor pressure deficits increase, so that leaf water potentials tend to remain relatively constant. Anisohydric species, by contrast, allow midday water potential to decline as the soil dries. Focusing on two species, McDowell et al. (2008) discussed the implications of these strategies for plant survival and mortality during drought; we return to that discussion in the following section dealing with hydraulic conductance, but note here that Martinez-Vilalta et al. (2014) demonstrated that most plants lie on a continuum between these two behaviors. Oren et al. (1999) showed that stomatal sensitivity to vapor pressure deficit (D) is proportional to the magnitude of g_s at low D (≤ 1 kPa), i.e.

$$g_s = g_{Sref} - m \ln D, \quad (1)$$

where g_{Sref} is the value of g_s at $D = 1$ kPa. This serves as a reference conductance, and m is a parameter, the value of which is related to the regulation of leaf water potential by stomata, to prevent cavitation. We would expect different values of m for isohydric and anisohydric tree species.

In a study based on data in the literature, Novick et al. (2009) invoked the relationships between the hydraulic constraints, indicated by leaf area (A_l) and sapwood cross-sectional area (A_s) per tree, and tree height (h), to formulate a simple general relationship between reference stomatal conductance values (g_{Cref}) and these architectural canopy variables. They found that at long time scales, under conditions when light and soil moisture are not limiting, g_{Cref} is approximated by the simple relationship

$$g_{Cref} = 98.2 \frac{A_s}{A_f H} + 37.3, \quad (2)$$

where g_{Cref} is in $\text{mmol m}^{-2} \text{s}^{-1}$, A_s and A_f are in m^2 and H is in m. Equation (2) accounted for 75% of the variance in g_{Cref} . Novick et al. provided detailed discussion of the various factors involved and the caveats associated with the use of the equation, but it provides a useful tool for large-scale modeling. In that application actual, as opposed to reference, values of canopy conductance could be estimated by applying modifying factors to account for the effects of vapor pressure deficits and soil moisture (Waring and Landsberg 2011).

We asserted earlier that empirical models of stomatal conductance have reached the point where further mathematical modifications are unlikely to significantly improve our ability to predict responses to environmental conditions. There is, however, a long-standing theory (Cowan and Farquhar 1977) of the so-called optimal stomatal behavior, which postulates that stomata should act to maximize carbon gain while minimizing water loss by transpiration. This was invoked by Williams et al. (1996), who postulated that stomatal conductance in a mixed deciduous (oak-maple) stand varied so that daily carbon uptake per unit of

foliar nitrogen was maximized in relation to the water available in the canopy. They included estimates of resistances in the soil–root system, and xylem hydraulic resistances, in their model. Calculating leaf and shoot water potentials from tissue capacitance data (capacitance is the change in tissue water content per unit change in water potential), Williams et al. used the idea that the maintenance of a maximally efficient conducting system requires that stomata close as evaporative demand rises, to prevent shoot water potentials falling below some threshold value. Threshold values for stomatal closure were obtained from the literature.

Medlyn et al. (2011) reconciled the Cowan–Farquhar (1977) theory with the empirical approach (Leuning et al. 1995), deriving a new model that provides a framework for interpreting stomatal behavior across species in response to a range of environmental conditions, including rising CO₂. Their model includes a parameter (λ , from Cowan and Farquhar) that describes the marginal water cost of unit carbon gain. Medlyn et al. said: 'By linking the optimal and empirical stomatal models we have identified a new and simple way of estimating λ from measurements of stomatal conductance. We suggest that comparative studies of (such) values of λ across species and soil moisture conditions are likely to bring new insights into adaptation of stomatal behavior and water use strategies.' They consider that the model will improve simulations of vegetation carbon cycling and water use at large scales. The Medlyn et al. model does not include consideration of hydraulic pathways and the effects of water potential on stomatal conductance, but Duursma and Medlyn (2012) developed a model called MAESPA from MAESTRA, a detailed array model of canopy light interception and photosynthesis (Medlyn 2004). Stomatal conductance in MAESPA is calculated from a modified form of the Tuzet et al. (2003) model, which takes into account the responses of stomata to atmospheric vapor pressure deficits and leaf water potential; the algorithms include root water uptake calculations and soil to leaf pathway hydraulics.

More recently Bonan et al. (2014) carried out a complex modeling exercise in which differing formulations of stomatal conductance, modeled at leaf and canopy scales, were evaluated in terms of the performance of different earth system models. Stomatal conductance was simulated using the empirical Ball–Berry model (Ball et al. 1987) and two optimization algorithms, based on the Cowan–Farquhar theory, linked to soil and plant hydraulic controls on maximum rates of water use. Bonan et al. adopted, and modified, the soil–plant–atmosphere model of Williams et al. (1996). The models were tested against canopy flux measurements made at six Ameri-flux forest sites, from which 51 site-years of data were available. Selected baseline parameter values were tested against leaf-scale and canopy scale analyses. Bonan et al. also carried out parameter sensitivity tests. They found that the optimization algorithms gave the best results, particularly during drought periods when plant and soil

hydraulics became increasingly important. The Ball–Berry model provides a closed-form analytical approach that can be combined with empirical dependence on soil moisture or leaf water potential (Duursma and Medlyn 2012). The optimization algorithms and high data demands of the procedures used by Bonan et al. demonstrate the importance of incorporating estimates of hydraulic conductance through the system, and the principle that plants reduce stomatal conductance as needed to regulate transpiration and prevent hydraulic failure. They note the need for numerical parameterizations for future use in models at scales from leaf to canopy to global.

Hydraulic conductance

Because of the dependence of transpiration rates on leaf area, and the relationships between sapwood cross-sectional area and the foliage carried by stems, Whitehead and Jarvis (1981) recognized and demonstrated that there must be considerable differences in the hydraulic efficiency of sapwood from the base to the top of a tree. They noted that the product of sapwood hydraulic conductance and cross-sectional area remained stable from breast height to the base of the live crown. Although they reviewed early work on cavitation, there was not enough information available, at the time, to allow critical evaluation or definitive analysis of the importance and implications of this phenomenon. Recognition of the importance of the hydraulic pathways in more recent years has been driven by the work of Tyree (1988), Tyree and Sperry (1988) and a significant body of work by Sperry (Sperry et al. 1998, Sperry et al. 2002, *inter alia*). In this section we explore the implications of the hydraulic hypothesis which, together with improving data on water storage in stems, and changes in that variable, are the areas of tree water relations where significant progress has been made in recent years.

We do not, here, explicitly consider the role of phloem in stem water storage and hydraulic conductance. In all plants the xylem and phloem occur in close proximity but, in the large body of work on plant hydraulics, the focus has been on xylem and relatively little attention has been paid to phloem. A recent review by Savage et al. (2016) indicates that most of the work on phloem has been concerned with carbon transport, the primary function of phloem. However, they note that phloem may make a significant contribution to stem water storage in trees and also that the influence of xylem water potential on phloem transport may affect drought mortality in trees (McDowell and Sevanto 2010). There is a clear need for more research, focused on the role and importance of phloem in tree water relations per se, but at this time our ability to explain water movement through trees, and tree water relations, at foliage, individual tree, stand and ecosystem level, does not appear to be significantly reduced by the lacunae that currently exist in this area.

Running et al. (1975) had recognized that differences in hydraulic efficiency accounted for the contrasting values of

maximum stomatal conductance between large and small conifers. At that time, the differences in hydraulic conductance between roots, stems and branches were unknown. There has been a considerable body of work, in recent years, investigating differences in conductance between species and between stems, roots and branches. (Note the distinction made by Sperry et al. (2002) between conductivity, which is a property of some part of the water-conducting pathway, and conductance, which applies to the whole flow pathway. Conductivity may vary along the conducting tissue, or in the soil.)

Mencuccini (2003) carried out a meta-analysis of hydraulic conductances in a wide range of tree species: a summary of his findings provides a useful synopsis, now somewhat dated but not out-of-date, of the state of knowledge in this area. The main points were as follows:

- Resistance to water flow in xylem represents only a fraction of the total liquid flow resistance, sometimes quite a minor fraction, but it may play a significant role in regulating physiological responses at the level of leaves and whole plants.
- The capacity to conduct water from soil to leaves is an important factor regulating leaf level gas exchange properties.
- Under conditions of ample soil water whole-plant hydraulic conductance controls the levels of water potential obtained within the plant at any transpiration rate.
- Across 50 species, with a range of different life forms, a large fraction of the variability in stomatal aperture could be accounted for by species-specific hydraulic properties.
- Whole-plant leaf area was significantly related to the subtending hydraulic conductance across species.
- There is convergence in the functional balance between leaf level properties and hydraulic properties.
- There is a relationship between plant size and hydraulic transport capacity—taller organisms require significantly more biomass to achieve similar levels of water transport capacity in comparison with shorter plants.
- There is evidence that hydraulic systems adapt/respond to changes in external stimuli over time. Mencuccini's meta-analysis indicated that decreasing air humidity over time, as well as long-term soil drought, tended to result in long-term increases in measures of plant hydraulic efficiency.

A model by Sperry et al. (1998) predicted that plants tend to optimize their leaf area:root area ratio to achieve optimal regulation of gas exchange. Ewers et al. (2000), provided insights into this: they studied the variation in hydraulic conductivity of *Pinus taeda* trees growing under different conditions of water supply and nutrition. They found that canopy stomatal conductance of fertilized trees was 50% of that of irrigated, unfertilized, trees. This lower conductance was associated with a 50% reduction in leaf-specific hydraulic conductance relative to other treatments, and was significantly less sensitive to changes in vapor pressure deficit. The projected leaf area index of the fertilized trees was

50% higher than that of trees in the control treatment, resulting in an 11% reduction in the sapwood area/leaf area ratio, A_s/A_l . The slope of the relationship between leaf water potential (ψ_s) and transpiration per unit leaf area (E) was significantly steeper for the fertilized trees than for the other treatments, indicating that hydraulic failure in those trees would occur at values of E far lower than in the other treatments, consistent with the conclusion that K_l was much lower in the fertilized trees. Several factors contributed to this: the fertilized trees were taller than those in other treatments as well as having larger leaf areas. Fertilization caused a significant reduction in root mass and surface area, but those roots showed greater resistance to cavitation.

Pataki et al. (1998), in a short-term foliage pruning experiment, showed that stomatal conductance, as inferred from sap flux measurements, increased proportionately to the amount of foliage removed. They concluded that the large increases in canopy stomatal conductance could be attributed to hydraulic effects. Meinzer and Granz (1990) also reported full compensation of water uptake, by sugar cane, down to 40% reduction in leaf area index.

In one of the relatively few studies that included angiosperms as well as coniferous species, Brodribb and Feild (2000) provided further evidence of the fact that better hydraulic conductance ('greater hydraulic supply') allows leaves to realize higher maximum stomatal conductance, which was linked to maximum photosynthetic quantum efficiency. It was, perhaps, helpful that the places where they made their field measurements were wet, and temperatures were very similar. The fluorescence analysis that they used to determine leaf photosynthetic capacity was therefore unlikely to generate errors caused by significant differences in photorespiration. The fact that conifers can maintain equally open stomata with a less steep water potential gradient than is the case for many angiosperms is because the conifers have invested in proportionately more, although less efficient, vascular tissue to supply a reduced amount of foliage. Brodribb and Feild commented that their results may have been very different if their measurements had been made under stressful, rather than optimal, conditions, and that there is convergence (functional overlap) between the two groups of plants.

McDowell et al. (2008) used the steady-state approximation

$$E = K_l(\psi_s - \psi_l - h\rho_w g) \quad (3)$$

to analyze plant responses to soil water potential and rates of water loss (transpiration) from the leaves. In Eq. (3) E is the rate of transpiration, K_l is leaf-specific hydraulic conductance of the soil-plant continuum, ψ_s and ψ_l are soil and leaf water potentials and $h\rho_w g$ is the gravitational pull on a water column of height h and density ρ_w . McDowell et al. analyzed plant responses to E in terms of hydraulic failure—the point at which a critical value (ψ_{crit}) of leaf water potential is reached, at which xylem conduits may cavitate, K_l approaches zero and the plant can no longer

move water. The capacity of plants to withstand drought depends on root density and distribution, and soil type and conditions as well as the hydraulic properties of the xylem conducting system. Hydraulic failure may occur in the soil as well as within plant conducting systems: greater tension is required to pull water through fine-textured soils because of their small pore sizes, so fine-textured soils have lower conductance than sandy soils when water is abundant. However, fine-textured soils retain hydraulic conductance longer and at more negative water potentials than coarse-textured soils because the low conductance of fine soils results in slower water loss to transpiration and drainage.

McDowell et al. (2008) postulated that plant death as a result of drought may be due to whole-plant hydraulic failure, resulting in death by desiccation, or through carbon starvation. The carbon starvation hypothesis predicts that stomatal closure, particularly in isohydric plants, reduces photosynthesis to near zero rates. Continued demand for carbohydrates for respiration depletes reserves, making the plants increasingly susceptible to attack by biotic agents (Waring 1987).

New insights into the regulation of water transport in plants have been provided by Martinez-Vilalta et al. (2014). They analyzed the relationships between midday leaf water potential values and soil water potentials, measured as pre-dawn leaf water potentials, from 83 carefully selected papers. The analysis was based on an equation used by Whitehead et al. (1984)—which followed from relationships presented by Whitehead and Jarvis (1981)—describing the flow of water through trees in terms of whole-plant hydraulic conductance, leaf area and the potential gradients between leaf and soil. Some simple algebraic manipulation led to an expression that allowed Martinez-Vilalta et al. to evaluate the relative sensitivity of transpiration rates and plant hydraulic potentials to declining soil water potential. They were able to conclude that the relative sensitivity of the transpiration rate and plant hydraulic conductance to declining soil water potential is more relevant than either stomatal sensitivity to drought or vulnerability to xylem embolism in determining the temporal dynamics of leaf water potentials. This implies that the development of water potential gradients in plants, in response to declining soil water availability is not determined directly by stomatal sensitivity to drought but by the ratio between this sensitivity and the vulnerability of the plant's hydraulic system (as a result, for example, of xylem embolism).

Several studies have demonstrated that the major resistance to water flux within a tree is not in the stem but in its branches (see Warren and Adams 2000, for detail and discussion). There are genetic differences within species that are worth noting: Walcroft et al. (1996) found no differences in growth among populations of radiata pine when grown in densely planted stands, but when thinned, the populations that produced short branches grew much better than those that did not.

The effects of hydraulic conductivity on the overall patterns of plant growth are illustrated by the hypothesis put forward by

Ryan and Yoder (1997), who proposed that tree height is limited by the supply of water to the leaves. Because water is dragged up trees under tension, and every meter of height growth is equivalent to an increment in gravitational water potential of 0.01 MPa, the taller the tree the higher the tension has to be. Air bubbles are therefore more likely to form in the xylem vessels, causing cavitation and loss of conducting ability. To prevent this taller, older trees have to close their stomata earlier in the day or earlier in a drought; this limits photosynthesis, and so slows tree growth (Landsberg and Sands 2011, p 203). This has been supported by Koch et al. (2004) who, in a study of tall redwoods, showed that leaf turgor decreases with height, growth slows and that maximum tree height varies from site to site, i.e. changes in hydraulic conductance are relative to maximum height on a site; they are not an absolute function of measured height. More recently Ryan et al. (2006) re-visited the hydraulic limitation hypothesis, reviewing 51 studies that measured one or more of the components necessary for testing whether tall trees differ physiologically from shorter, younger trees. They found that, in general, where hydraulic limitations to photosynthesis occurred, there was no evidence that these were sufficient to explain observed declines in wood production with stand age. Ryan and his co-authors suggest that future work on age-related productivity decline should explicitly link leaf or canopy gas exchange with tree and stand growth, and reconsider the common modeling assumption that tree biomass growth is limited by carbon availability.

Studying mortality of large trees in a tropical forest Rowland et al. (2015) found that the most likely cause of death in trees subject to extended drought was hydraulic vulnerability and deterioration. This is not consistent with the carbon starvation hypothesis, although hydraulic breakdown resulted in subsequent, potentially rapid, limitations in carbon uptake. In a global study Bennett et al. (2015) found that drought consistently had a more detrimental impact on the growth of large trees. The results of their survey support the theoretical prediction that greater height and pathlength resistance are likely to make large trees more hydraulically vulnerable and therefore more sensitive to drought. They also point out that large trees, with crowns in or above the canopy, are exposed to higher solar radiation and leaf-air vapor pressure gradients than trees in the relatively buffered understorey. Furthermore, drought-stressed trees are more liable to attack by biotic agents—for example in cases where bark beetles are associated with drought-induced mortality in the coniferous forests of the western United States.

In the highly seasonal environments common across Australia, evergreen Eucalyptus species respond to droughts by leaf shedding, as well as by short-term physiological mechanisms. These ecosystems offer opportunities for studying changes in tree water relations that may provide important general insights into tree water relations. We note, for example, the finding by Prior and Eamus (1999) of positive correlations between pre-dawn

leaf water potential and tree height, in two species, during the dry season but not during the wet season. Prior and Eamus (2000) also found that hydraulic conductance and conductivity, normalized for leaf area, declined as the dry season progressed: seasonal increases in embolism could not account for these declines. Macinnis-Ng et al. (2004), investigating a range of species in the Sydney region, found seasonal differences in minimum leaf water potential and sapwood conductivity, with correlations between xylem embolism, minimum leaf water potential and sapwood conductivity that varied seasonally.

There would clearly be considerable benefits from more studies on trees in strongly seasonal environments, for example across Africa as well as Australia, but the predominance of scientific resources in the northern hemisphere probably means that these are unlikely in the absence of (so far non-existent) highly enlightened attitudes on the part of science funding agencies.

Storage and capacitance

Since the establishment by Waring and Running (1976) and Waring et al. (1979) of the importance of water storage in the stems of large trees, there has been a large body of work, on a range of species, examining storage and capacitance. Storage is a measure of the amount of water stored in a tree, or in particular tissues (roots, stems, branches, foliage). Capacitance is defined as the change in tissue water content with change in potential. The concept provides the basis for analyzing the movement of water into and out of tissues. Scholz et al. (2011) have reviewed the literature dealing with these concepts, and their implications. Collating data from a number of studies they were able to demonstrate a linear relationship between tree size and the daily use of stored water; they also found that trees with higher capacitance tend to exhibit higher (less negative) minimum branch water potential than trees with lower intrinsic capacitance. An interesting point emerging from the review is the fact that specific capacitances in angiosperms and conifers span a similar range of values, despite dramatic differences in wood anatomy. Scholz et al. comment on the factors that have to be taken into account when modeling water fluxes in and out of stored tissue, noting that transient responses to water flow can be predicted from the time constant associated with step changes in transpiration rate. Phillips et al. (2004) used a bulk resistance–capacitance model to describe the hydraulic characteristics of *Pinus abies* and *P. taeda* trees in which flow rates were measured with sap flux sensors, together with a coupled hydraulic–stomatal physiology model to evaluate the role of stomatal conductance in regulating the observed sap flow responses. Chuang et al. (2006) proposed a porous media model that leads to a mass-conserving partial differential equation that describes the spatial-temporal dynamics of a tree hydraulic system and connects sap flux to transpiration. This approach leads to complex mathematics and can only be applied

when sap flux data are available. Landsberg and Sands (2011, pp 209–211) provide a complete set of solved equations, based on pools and resistances, for simulation of the time course of leaf water potential and storage tissue water content.

The most detailed study, so far, of water movement in and out of storage in response to transpiration losses from the foliage is that by Čermák et al. (2007), who studied flow patterns in three very large (57 m tall) Douglas fir trees, placing sap flow sensors in the stems at 4 m and 51 m, and in branches at 46, 51 and 56 m. They calculated the amount of stored water in the sapwood and other tissues at the measurement heights and, by following the fluxes, lags in water potential and recovery in water content overnight, reconfirmed that the most important reservoir for water storage resides in the lower part of the stem, which, on clear days, supplied about 20% to daily transpiration. Čermák et al. demonstrated that daily withdrawal of water from lower stem sapwood of large trees can help buffer the lower strata of foliage against early stomatal closure. The more exposed upper strata of foliage, however, has much smaller storage reserves to draw upon, and may become isolated from the lower part, experience irreversible cavitation, and as a result, dieback. In dry conditions transpiration by large trees may be maintained from stored water for up to a week (Čermák et al. 2007) but flows from storage may be more important in refilling cavitated xylem elements and hence ensuring that the overall hydraulic conductivity of stems is not reduced.

Soil moisture and wide-scale hydrologic modeling

The central role and importance of soil moisture to plant water use and the growth patterns of plants has been known—and quite well understood—for at least 70 years. Information about the amount of water available in the root zone of plants is essential as a basis for calculating water balances and plant water status, but uncertainties associated with that information pose a major problem in relation to broad-scale modeling. The theoretical basis of the water-holding capacity of soils is well established (see Slatyer (1967) for a detailed treatment; Landsberg and Gower (1997) for a summary treatment with special reference to forest water requirements, including discussion on root depths and distribution), but spatial variations in soil depth and properties, and the exploitation of soils by roots, are tremendous. Nepstad et al. (1994), studying evergreen and deciduous forests in Brazil, showed that the property ‘evergreen-ness’ was related to deep roots (up to 20 m) that accessed soil water stored during wet years, which provided a buffer against the droughts that occur in association with El Niño/La Niña weather cycles. Hacke et al. (2000) showed that, because the roots of *P. taeda* are restricted to the top layer (about 0.35 m) of soil, three weeks without rain are likely to reduce transpiration to one-third the rate that would occur under the same atmospheric conditions with wet soil.

Over large areas it is possible, in principle, to estimate the amount of water available in the soil using remote sensing. Following a wet period, vegetation surface temperatures rise as the amount of available water is reduced and transpiration rates fall. The temperature rise can be identified by satellite-mounted instruments and used to produce vegetation dryness indices that correlate with the depletion of water from surface soils. Repeated observations over rainless—or very low rainfall—periods, following enough rain to fill soil profiles, can be used to track the temperature changes and from those, and calculations of transpiration rates, the amount of available water in the underlying soils can be estimated. Clearly, such studies must include survey information on soil types and ground-based information on climate and the vegetation. This approach holds out the possibility of providing data at the level of pixels that may allow analysis of the spatial variation in available soil water.

Two recent review-type papers demonstrate that the body of theory describing water movement from soil to roots, driven by transpiration and modified by soil water content, is adequate to describe tree water use across landscapes, including the development of drought and its effects on trees, despite the inevitable errors and uncertainty associated with spatial variations in soil properties and available soil water.

The paper by [Breda et al. \(2006\)](#) used established, well-accepted models and published measurements to describe the hydrology and tree water relations at nine European forest sites during the severe European drought that occurred in the summer of 2003. The authors calculated the time course of water extraction by the trees, using the Penman–Monteith equation, data on stand structure, leaf area index and soil water in the root zones. They estimated vulnerability to drought-induced cavitation as the xylem tension at which 50% loss of stem hydraulic conductivity occurred, citing [Mencuccini's \(2003\)](#) review (discussed above) as indicating that plant hydraulic conductance is a plastic (adaptable) property, affected by drought, although they did not provide direct evidence for such adaptation. Breda et al. did not have direct measurements of soil water content to corroborate their results, but evaluated the effects of drought on tree growth in terms of leaf-shedding patterns, drought-induced mortality and the delayed effects of drought on wood, leaf and fruit production. When the water available in the soil is exhausted stomata remain closed and, without the cooling effects of transpiration, high temperatures (above 50 °C) can prove lethal ([Teskey et al. 2015](#)) and induce premature leaf shedding. Breda et al. also considered drought-induced tree mortality. Their study illustrates the importance of the inter-specific diversity of the coupling between hydraulic architecture in trees and stomatal control of transpiration. It also demonstrated the value of knowing the relative availability of water in the root zone.

[Waring and Landsberg \(2011\)](#) provided a brief review of the factors linking water use by vegetation with atmospheric conditions, including the effects of leaf–air vapor pressure deficits,

and the effects of water potential gradients, on canopy conductance. We considered the effects of canopy structure, including tree height, as well as the effects of nutrition, temperature and atmospheric CO₂ concentrations on canopy conductance. We also evaluated the use of remote sensing: structural features of vegetation, as well as most of the climatic variables required to drive the Penman–Monteith equation, can be obtained at daily resolutions (or better) from a range of weather satellites. Leaf pigment changes associated with stand nutritional status, and leaf water content changes that may be caused by drought, are also discernable using remote sensing. Waring and Landsberg commented that ‘The central point (that) we have been making throughout this paper is that, given information about the canopy structure of vegetation, and adequate weather data—among which precipitation amounts and patterns are probably the most important variables—we can estimate water use with considerable accuracy with a series of landscape-linked models. Within the Penman–Monteith equation, the canopy conductance term describes the interaction between canopies and the atmospheric environment, so our ability to derive accurate values for that term is central to our ability to estimate transpiration rates by ecosystems.’

We note that both the [Breda et al.](#) and the [Waring and Landsberg](#) studies illustrate the point made in our introductory section, where we cited [Passioura \(1979\)](#): ‘As the level of synthesis progresses upward, the significance of the processes under study also changes’. [Passioura's](#) comment refers to the fact that detailed knowledge of processes at low organizational levels, for example at the cell or organ level, is likely to become increasingly less relevant as we move upwards and attempt to describe or simulate the responses of systems at higher levels. In relation to soil moisture, we have detailed knowledge of the physics of water movement through soils, and can calculate rates of water movement through them, provided the soils are homogeneous. But we have only limited ability to make accurate calculations of the rate of water movement in any particular direction in soils where the water-holding properties vary with depth, and spatially. That ability is limited even further when we introduce into the soils plant–root systems, with their enormous variation in root characteristics and root length density. Therefore, as in any modeling exercise, we make approximations based on our knowledge of the physics and guided by the best available information. That will vary depending on the scale we are working at. For small experimental plots in the field, detailed information is likely to be available and detailed calculations of water potentials in plant root zones are feasible, leading to estimates of root zone that can be matched to measurements of plant water potential, stomatal conductance and water use. As the spatial scale increases, knowledge of soil water–root interactions is likely to become progressively less precise, and we have to resort to estimates based on ‘lumped’ information about soil properties in the region of interest. Detailed knowledge of tree

water relations is subsumed in models that predict responses at high levels of system organization. Nevertheless, understanding of the processes involved at low organizational levels (e.g., leaves, tissues, etc.) is needed to guide the estimates and approximations that have to be made when considering higher levels of organization. This is particularly relevant at the ecosystem level. The argument applies to various aspects of tree water relations.

Hydraulic redistribution of water by tree roots

Dawson (1993) pioneered the experimental demonstration of hydraulic redistribution (he called it 'hydraulic lift')—the process by which tree roots take up water from deep within the soil profile and redistribute measurable amounts near the surface. The amounts involved are sufficient to aid the survival of neighboring shallow-rooted plants. Burgess et al. (1998, 2001) confirmed Dawson's findings and observed that the process leads to redistribution of water both upward and downward. They re-named it 'hydraulic redistribution', and commented that it may be significant in maintaining root viability, facilitating root growth in dry soils and modifying resource availability. The amounts of water involved are not likely to make significant contributions to transpiration or be significant in drought avoidance. The major mechanism by which trees prevent salt accumulation at the ground surface, from saline groundwater, is transpiration, which removes enough water to keep the water tables down and prevent salt transfer associated with the capillary rise of water into the topsoil. However, the downward redistribution of fresh water from shallow soil horizons, into saline groundwater at lower levels by deep-rooted trees, may help explain the role those trees play in preventing salt formation at the ground surface. (We note, in passing, that neither Dawson nor Burgess et al. referred to the fact that hydraulic redistribution was predicted by a mathematical analysis of water movement through plant roots by Landsberg and Fowkes (1978; see their Figures 4 and 5). Landsberg and Fowkes commented that there is no reason to believe that reverse flow (from roots to soil) does not occur, although it had never (at that time) been observed. It (reverse flow) is 'likely to be transient as the development of a small damp region round the root would immediately reduce the root-soil gradient.')

Conclusions

This brief survey of progress and developments in the topic of tree water relations—itsself a sub-discipline within the field of tree physiology—has led us to the conclusion that the topic is scientifically mature: most of the work being done on the topic field is 'normal science', aimed at filling in gaps and solving puzzles arising from the accepted paradigm. There are few, if any, indications that serious anomalies are emerging from the literature on the subject.

It seems, from comments made by a reviewer of this paper, that the statement above is open to misinterpretation and misunderstanding. To clarify, we return the reader to our opening paragraph: 'normal science' is research that takes place within a well-recognized and accepted paradigm—a model of reality that provides a framework of theory, results and procedures, accepted by the community of scientists concerned with the field in question. A mature paradigm is likely to provide the basis for adequate descriptions and quantitative models of the system under study; it also provides a guide to the problems to which research should be directed. That is not to say that everything we think we know about tree water relations, including transpiration from leaves and canopies, tree hydraulics, stomatal functioning and responses to and interactions with environmental conditions, is correct in terms of the facts and the mechanisms involved. The system is immensely complex and there will always be inaccuracies, variations between species, locations and variations under different conditions. But it does say that there is no sign of a revolution, of findings that strike at the heart of our understanding and ability to simulate the behavior of systems at a given level—say the water relations of individual trees—in terms of the processes at lower organizational levels. Of course there is much still to be learned. The interactions between phloem and xylem, and their effects on tree water relationships, have not yet been described in any detail; the differences between species, in terms of those relationships, are largely unknown. Yet it seems unlikely that findings in this area will bring into question the whole of the tree water relations paradigm.

In some areas we may be seeing limiting returns on effort expended; in others we are probably seeing real progress, particularly, perhaps, in work on plant hydraulic conductance and the interactions between it, plant life forms, nutrition and adaptation (see Mencuccini's (2003) review). It is perhaps surprising that there has, as yet, been no follow-up to Mencuccini's work on acclimation in terms of the hydraulic pathways in trees. However, the very interesting paper by Martinez-Vilalta et al. (2014) brings new insights into this area and undoubtedly provides a platform from which many studies will be launched. (That paper provides an excellent example of innovative research on problems indicated by the prevailing paradigm, but which do not constitute serious anomalies in relation to it.) The focus on isohydric and anisohydric species in the paper by McDowell et al. (2008) was, to some extent, called into question by the work of Martinez-Vilalta et al.; there are likely to be significant differences between species in their stomatal sensitivity to drought and the ratio between this sensitivity and the vulnerability of the plants' hydraulic systems. However, there is certainly need for more research into the hydraulically based mechanism of drought-induced tree mortality that McDowell et al. proposed, with its implications for carbon balance and resistance to insect attack.

There are various facets of tree water relations that we have not discussed in our treatment so far but, for completeness, we

include them among the following points, on which we base our assessments of some of the areas that we think require particular attention. Accepting that our views are subjective and open to (no doubt considerable) argument, we suggest that the major findings from the past 50 years of research in tree water relations have included:

- A great deal of information about the factors governing stomatal apertures, and hence conductance, transpiration and, of course, photosynthesis. Unfavorable temperatures, vapor pressure deficits and (soil) drought limit stomatal conductance and photosynthetic capacity, gross primary production and above-ground growth. The size of leaves affects the boundary layer conductance. In still air, large leaves with closed stomata, exposed to direct radiation, are likely to experience lethal temperatures. [Oren et al. \(1999\)](#) provided an enlightening discussion about stomatal sensitivity and the feedbacks between g , and tissue water potential. Future research on stomatal behavior and responses to environmental factors is likely to include increased focus on hydraulic pathways and conductances. It also seems likely that, where good quality supplementary measurements are available, there will be increasing use of iterative procedures ([Williams et al. 1996](#)) and optimization algorithms ([Bonan et al. 2014](#)) to develop the empirical relationships between soil moisture, soil to leaf hydraulic pathways and atmospheric conditions that will be needed for wide-scale hydrological modeling.
- Greatly improved understanding of the interactions between the hydraulic conducting systems of trees and maximum achievable stomatal conductance. There has been considerable effort devoted to establishing water potential thresholds, or fluxes, that cause cavitation, and explaining why those thresholds vary with wood properties and change with environmental conditions. The whole area of resistances to water flow through soil–root systems, as well as tree conducting systems, merits much more attention.
- Tree structure follows function, e.g. wood anatomy and morphology vary with species and site. Tall trees require adequate plumbing: the interactions between wood structure and properties and hydraulic characteristics clearly warrant more research attention.
- All mature trees—in which height growth has slowed, or halted—have lower vigor than young trees with shorter branches and relatively more efficient plumbing. The problem of age-related productivity decline was not solved by [Ryan and Yoder \(1997\)](#), as [Ryan et al. \(2006\)](#) recognized. Their comment, quoted earlier (“that future work on age-related productivity decline should explicitly link leaf or canopy gas exchange with tree and stand growth, and consider whether tree biomass growth is limited by carbon availability”), provides a useful pointer to future priorities.
- Stored water buffers diurnal variation in water use (short term). It may also contribute to the ability of trees to withstand drought. There are some preliminary indications ([Savage et al. 2016](#)) that the interactions between phloem and xylem tissues may influence the ability of trees to withstand drought. [Klein et al. \(2014\)](#) showed that species with more storage do better in semi-arid areas than those with limited storage. In general, the effects of drought have become progressively better quantified, showing differences between the vulnerability of roots, stems and branches.
- Branch length may be important. Recognition that much of the resistance to water flow to the foliage is associated with branch length, not stem height, provides an explanation for the fact that thinning in genetically different populations of pine is likely to lead to different growth responses, even if, without thinning, branches were all short and no genetic differences were expressed.
- We can scale estimates of transpiration from leaf to landscape levels, predict changes in species composition if areas become more drought-prone and establish links between controls on transpiration and feedback to climatic conditions, which may range from those above bogs in Canada to those above Amazon rainforests. We understand the role trees play in preventing salt accumulation at the soil surface where saline groundwater occurs. Uncertainties about spatial variations in soil water-holding characteristics and tree rooting depths, and hence the amount and distribution of available soil water across landscapes, must reduce confidence in predictions of water use. Future work should include more investigations into the water stored in soils, not only from the point of view of the sometimes arbitrary criteria of soil physics but also with attention to the interactions between soil type and wetness, tree species and tree–root systems: how much water can tree–root systems extract under varying conditions (see, for example, [Nepstad et al. 1994](#)). A good example of the type of study that should be done, in as many areas as possible, was provided by [Nepstad et al. \(2004\)](#). They used weather data, soil survey data providing information about soil physical characteristics, vegetation information and geographical information systems to model water balances over large areas of Amazon forest. They tested their results by observations and measurements in the field.

Many of the models of various aspects of tree water relations developed by 1975 still work, and are now generally accepted for practical use in hydrology and ecology without additional testing (which is not to say that there should not be additional testing). There will no doubt be continued refinement of those models, particularly in the case of stomatal conductance, as we noted above. However, the focus in tree water relations has shifted to examine the thresholds, in terms of climatic events, at which drought, high temperatures and vapor pressure deficits

cause mortality. The most likely causes of (natural) tree death appear to be whole-plant hydraulic failure and subsequent physiological shut-down (Rowland et al. 2015, Bennett et al. 2015). However, insect attack, disease and animal browsing (Cohen et al. 2016, Dannell et al. 2003) are also major causes of tree death, since carbon starvation renders the plants more susceptible, particularly to insect attack. The challenge is to predict which species or clone will be best adapted to changing conditions.

We need to develop a theoretical foundation that will help to predict the competitive advantage that one species (genotype) might have over another when encountering different intensities of drought. Perhaps the most fruitful future opportunities for tree physiologists lie at the fringe of the field, in interactions with geneticists, insect/disease physiologists and ecologists working on the effects of climate change.

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Conflicts of interest

None declared.

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