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2 **Water relations in tree physiology: where to from here?**

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10

11 **Abstract**

12

13 **We look back over 50 years of research into the water relations of trees, with the**
14 **objective of assessing the maturity of the topic in terms of the idea of a**
15 **paradigm, put forward by Kuhn in 1962. Our brief review indicates that the**
16 **physical processes underlying the calculation of transpiration are well**
17 **understood and accepted, and knowledge of those processes can be applied if**
18 **information about the leaf area of trees, and stomatal conductance, is available.**
19 **Considerable progress has been made in understanding the factors governing**
20 **stomatal responses to environment, with insights into how the hydraulic**
21 **conducting system of trees determines the maximum aperture of stomata.**
22 **Knowledge about the maximum stomatal conductance values likely to be**
23 **reached by different species, and recognition that stomatal responses to**
24 **increasing atmospheric vapor pressure deficits are in fact responses to water loss**
25 **from leaves, provides the basis for linking these responses to information about**
26 **hydraulic conductance through soil-root-stem-branch systems. Improved**
27 **understanding in these areas is being incorporated into modern models of**
28 **stomatal conductance and responses to environmental conditions. There have**
29 **been significant advances in understanding hydraulic pathways, including**
30 **cavitation and its implications. A few studies suggest that the major resistances**
31 **to water flux within trees are not in the stem but in the branches. This insight**
32 **may have implications for productivity: it may be advantageous to select trees**
33 **with the genetic propensity to produce short branches in stands with open**
34 **canopies. Studies on the storage of water in stems have provided improved**
35 **understanding of fluxes from sapwood at different levels. Water stored in the**
36 **stems of large trees may provide up to 20-30% daily sap flow, but this water is**
37 **likely to be replaced by inflows at night. In dry conditions transpiration by large**
38 **trees may be maintained from stored water for up to a week but flows from**
39 **storage may be more important in refilling cavitated xylem elements and hence**
40 **ensuring that the overall hydraulic conductivity of stems is not reduced.**

41 **Hydraulic redistribution of water in the soil may make a contribution to**
42 **facilitating root growth in dry soils and modifying resource availability.**

43

44 **We conclude that the field of tree water relations is mature, in the sense that the**
45 **concepts underlying models describing processes and system responses to change**
46 **are well-tested and accepted and there are few, if any, serious anomalies**
47 **emerging. Models are essentially formal statements about the way we think**
48 **systems work. They are always subject to further testing, refinement and**
49 **improvements. Gaps in knowledge appear within the framework of accepted**
50 **concepts and mechanisms research is needed to fill those gaps. The models**
51 **currently available can be used to scale estimates of transpiration from leaf to**
52 **landscape levels and predict species responses to drought. The focus in tree-**
53 **water relations has shifted to examine the climatic thresholds at which drought,**
54 **high temperatures and vapor pressure deficits cause mortality. Tree death may**
55 **be caused by hydraulic collapse following irreversible cavitation or extremely**
56 **low water potentials, but recent research indicates that the relative sensitivity of**
57 **stomatal conductance and whole plant hydraulic conductance plays a major role**
58 **in determining plant responses to drought.**

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

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64 **Water relations in tree physiology: where to from here?**

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66 **Introduction**

67

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

81

82 Kuhn confined his analyses to the physical sciences, to the crises that developed in
83 relation to some of the most important areas of physics and chemistry and the
84 revolutions that changed them. Somewhat surprisingly, he said nothing about biology,
85 although Charles Darwin’s publication of ‘The Origin of Species’ in 1859 led to one
86 of the greatest of all intellectual upheavals in the history of science. Scientists and
87 naturalists in the mid-19th century struggled to explain species extinctions and the
88 appearance of new species in layers of sedimentary rocks. Competing theories ranged
89 from creationism to Lamarckism (heritability of acquired characteristics). Darwin’s
90 ideas about evolution provided an all-encompassing explanation for the accumulating
91 observations on species change and adaptation. Many scientists at the time, as well as
92 clerics, did not accept the theory of evolution, but the Darwinian paradigm, which fits
93 comfortably within Kuhn’s structure, still provides an overarching framework for the
94 biological sciences, explaining change, variation and adaptation at every

95 organizational level. The central puzzle of evolutionary theory — the mechanism by
96 which genetic changes are inherited — was solved by the recognition (Watson and
97 Crick 1953), of the double helix structure of DNA. This had immense implications
98 for our understanding of genetics and the mechanisms of heredity that underpins all of
99 molecular biology and biotechnology.

100

101 We are concerned, in this paper, to evaluate progress in research on tree-water
102 relations, a sub-branch in the field of tree physiology. We do not intend to provide a
103 comprehensive review of the topic but present an overview of tree water relations,
104 showing that the concepts and ideas about mechanisms that define the topic were well
105 established by the early 1980s. This provides the framework — the paradigm —
106 within which the present generation of scientists set their research. There is a large
107 and growing body of work driven by questions arising from recognition of gaps in
108 knowledge that have become apparent in our understanding of the water relations of
109 trees and the effects on them of changing environmental conditions, but there are no
110 indications of major anomalies, of findings that undermine the overarching paradigm.
111 There is some concern that a proportion of the scarce research resources – which
112 include the abilities and time of able scientists — currently applied to the study of tree
113 physiology is being wasted in work that contributes little or nothing to advancing
114 knowledge. This may be a result of scientific amnesia, caused by lack of awareness of
115 old literature. However, expressing such concerns is always likely to lead to
116 arguments, so an important objective of this paper is to assess whether we have
117 reached the point where returns from additional research on tree water relations are
118 becoming progressively smaller.

119

120 There is a tendency, in many branches of science, to follow the reductionist approach
121 and investigate at lower and lower organizational levels the processes that determine
122 responses of organisms, such as trees, or systems such as plant communities, to
123 stimulus and change. Reductionist research is essential to provide understanding
124 about how organisms or systems function, but detail at a particular (low) level of
125 organization may not contribute greatly to our ability to predict the behavior and
126 responses of the system at higher levels. For example, in the case of tree water
127 relations, it would be difficult to use knowledge about the role of phloem in water

128 storage, or the mechanisms by which xylem vessels are refilled after embolism, to
129 model water use rates and physiological responses of trees or forest canopies to
130 changing environmental conditions over weeks, months or seasons. de Wit (1970)
131 suggested that it is not practical to attempt to model a system across more than two
132 levels of organization, i.e. to attempt to explain observations in terms of processes
133 more than one level down in the organizational hierarchy. Measurement techniques
134 have improved and computer power has increased enormously since 1970, but the
135 point is still valid. Considerable amounts of detail are subsumed in models that
136 predict system responses at progressively higher levels of organization. As the level
137 of synthesis progresses upward, the significance of the processes under study also
138 changes (Passioura 1979).

139

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

152

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

160

161 **Tree-water relations science: historical overview**

162

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

172

173 The Whitehead and Jarvis paper provides a useful starting point for our discussion
174 because it is a good summary of knowledge and understanding about tree water
175 relations at that time. The paradigm that the paper describes was, in fact, largely
176 established in the 1960s and '70s. Slatyer's (1967) book ("Plant-water relationships")
177 provided a comprehensive and detailed treatment of underlying theory, including
178 plant-environment interactions, water in soils and discussion of techniques for
179 measuring plant water potential. Slatyer did not deal specifically with trees. Between
180 the later 1960s and 1980 the measurement of water potential was revolutionized by
181 the development of the pressure chamber by Scholander et al. (1965). This instrument
182 was first used to study the diurnal water relations of trees by Waring and Cleary
183 (1967), who used a shotgun to obtain samples, at night, from high in tall trees. The
184 pressure chamber has provided the basis for much of the work on tree water relations
185 since that time. Other areas where there has been considerable progress in the
186 measurement techniques that underlie all experimental work are the development of
187 easy-to-use, accurate, automated porometers of various types, allowing measurement
188 of gas exchange at leaf level, and greatly improved sap flow rate measurements,
189 mainly based on the technique developed by Granier (1985). Landsberg and Sands
190 (2011, p. 53) made the comment, in relation to the modern, off-the-shelf, automated
191 gas exchange units, that they have resulted in an avalanche of measurements on a
192 wide range of plants in all sorts of conditions. The comment is a pertinent warning
193 against the uncritical collection of data without a clear focus on testing some model or
194 theoretical concept.

195

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

210

211 Whitehead and Jarvis (1981) did not deal in any detail with the effects of water
212 potential on stomatal apertures, and hence conductance, but other contributions in that
213 volume (Kozłowski, 1981) did so (see Hinckley et al., Doley, Landsberg and Jones).
214 They did provide detailed discussion of variations in water potential and the flow of
215 water across potential gradients through the system (tree), focusing on resistances to
216 flow in various parts of the system. Changes in the water content of tree tissues were
217 measured by a number of workers in the 1950s, 1960s and 1970s, but water storage in
218 stems (sapwood) in large trees seems to have been first identified as a significant
219 factor in the seasonal water relations and water balance of conifers by Waring and
220 Running (1978) and Waring et al. (1979). The recognition of capacitance explained
221 why hysteresis occurs in the diurnal variation of leaf-water potential in the spring, but
222 not in the fall, if available water stored in sapwood is largely extracted. Landsberg et
223 al. (1976), working with apple trees, were, apparently, the first to describe the
224 movement of water in and out of storage in terms of the capacitance of tissues. The
225 mathematics are reproduced by Whitehead and Jarvis, who concluded their review
226 with some comments on modeling water flow through trees, noting that Running et al.
227 (1975) and Waring and Running (1976) had produced the only then-extant model that
228 included changes in tissue water storage. Whitehead and Jarvis also provided a

229 relatively cursory treatment of soil water, and reviewed the information then available
230 on tree root distribution.

231

232 **Developments since the 1980s**

233

234 **Transpiration**

235

236 Information about the flow of water through trees, driven by transpiration, is central
237 to the whole field of tree-water relations. We noted earlier that Whitehead and Jarvis
238 (1981) dealt with transpiration at leaf and canopy level in some detail. The principles
239 and physics of the process were well established in the 1960s: the combination
240 energy-balance mass-transfer equation (the Penman-Monteith equation) first derived
241 by Penman (1948) and subsequently refined and modified by Monteith (1965), is now
242 generally accepted as providing estimates of canopy transpiration rates that are
243 accurate to within the limits imposed by the meteorological and biological data.
244 Details of the algebra involved in deriving the equation, and discussion of the
245 assumptions and implications, can be found in Monteith and Unsworth (1990) (see
246 also Landsberg and Sands 2011). The meteorological data required as inputs consist
247 of solar radiation, from which net radiation absorbed by the canopy can be derived (it
248 may be measured directly), windspeed and atmospheric vapor pressure. The
249 biological data required are the leaf area index of the canopy, leaf geometry and the
250 canopy conductance, derived from stomatal conductance and canopy leaf area.
251 Transpiration at the canopy level, i.e. from stands or extended areas of forest, can be
252 measured, with varying degrees of accuracy, using sap flow meters set in a number of
253 trees, and then scaling up to stand level on the basis of leaf area per tree (see next
254 paragraph) or eddy covariance measurements, which provide estimates of vapor
255 fluxes from extended areas (see Williams et al. (2001); Bonan et al. (2014) for
256 examples of the use of those data.)

257

258 The most important of the biological variables that determine canopy transpiration
259 rates, and hence the flow of water through the tree stems, are leaf area per stem and
260 the stomatal conductance of the foliage. Shinozaki et al. (1964a, 1964b) developed the
261 pipe model theory, showing that the mass of foliage in the crowns of trees was
262 linearly related to the supporting sapwood. Grier and Waring (1974), Waring et al.

263 (1977) and Whitehead (1978), established linear relationships between sapwood
264 cross-sectional area and leaf area per tree. Waring et al. (1982) proposed that unit area
265 of foliage is serviced by a specific cross-sectional area of sapwood in the crown of the
266 tree. Shinozaki et al. had assumed that much of the sapwood is non-functional, but
267 Whitehead et al. (1984) demonstrated that all the sapwood remains functional,
268 although conducting efficiency changes: the product of leaf area x efficiency remains
269 constant. Given these relationships and the number and size of stems in a stand, it is
270 possible to estimate the leaf area index of stands.

271

272 Whitehead and Jarvis (1981) discussed the application of the Penman-Monteith
273 equation to forests, and provided a table of transpiration rates from coniferous
274 canopies, as well as references to studies in which the equation was tested. Stewart
275 (1984) listed others, and we note an interesting paper by Schulze et al. (1985)
276 reporting the results of comparing different methods of measuring canopy
277 transpiration from forests, although Schulze et al. did not test the Penman-Monteith
278 equation.

279

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

290

291 It follows from the fact that water flux per stem in closed canopies with different stem
292 populations is — particularly when the soil is wet — approximately proportional to
293 leaf area per stem, the flow of water up each stem will be (more or less) inversely
294 proportional to stem numbers, with concomitant differences in resistances to flow
295 through individual stems. These resistances will, obviously, vary with tree height (see
296 the later section on hydraulic conductances). There are other resistances to water flow

297 through the system, notably at the soil-root interface: Landsberg and Sands (2011)
298 discussed, briefly, root distribution (see also Landsberg and Gower, 1997) and the
299 factors that influence resistance to water movement into tree root systems, an
300 important area in the field of tree water relations to which we return later in this
301 paper. It is becoming clear that the hydraulic characteristics of the soil-root-stem
302 systems of trees influence tree height, the maximum stomatal conductance realized by
303 the leaves and, possibly, branch length. There has been significant progress, in recent
304 years, both conceptually and in terms of measurements, in the study of these effects
305 and interactions. We return to consider them in some detail later, but must first outline
306 the situation with regard to stomatal conductance.

307

308 **Stomatal conductance**

309

310 Stomata, hydraulically linked to the surrounding mesophyll cells, are the organs at the
311 interface between foliage and the atmosphere. Stomatal conductance is the inverse of
312 stomatal resistance, which is a measure of the resistance to diffusion of CO₂ into the
313 leaf or of water vapor molecules out of the cavities behind the stomata. It is a function
314 of the number, size and degree of opening of the stomata in the surface layers of
315 leaves. The degree to which stomata are open or closed is affected by irradiance,
316 atmospheric CO₂ concentrations, atmospheric vapor pressure deficit, by leaf water
317 potential, and ultimately, turgor. Leaf water potential is strongly dependent on the rate
318 of flow through the hydraulic pathways from soil to root and through the conducting
319 systems of the trees. Because of the importance of stomatal functioning and responses
320 to those variables, they have been the subjects of a vast amount of research over many
321 years, starting well before the period (since about 1980) that we are considering here
322 (e.g., Francis Darwin (1898, pp 577-581), who observed stomata open at night in
323 many species when not limited by water).

324

325 Landsberg and Sands (2011) provide a recent review, which is by no means
326 exhaustive but offers a reasonably up-to-date and comprehensive summary of the
327 'state of the art' in empirical stomatal studies (see pp. 61-68). They consider a range
328 of models that include terms describing stomatal responses to all the major variables
329 mentioned above. Models such as those presented by Leuning et al. (1995) and Tuzet
330 et al. (2003) have, arguably, reached the point where further mathematical

331 modifications are unlikely to add significantly to our ability to predict stomatal
332 responses to environmental conditions (but see later comment on the model by
333 Medlyn et al. (2011)). The Leuning et al. model includes the effects of vapor pressure
334 deficits, leaf surface CO₂ concentrations and the within-leaf carbon dioxide
335 compensation point. It provides a fully coupled solution for CO₂ assimilation and
336 transpiration calculations. Tuzet et al. (2003) incorporated calculations of leaf and soil
337 water potentials, and plant hydraulic resistance, into the Leuning model. New data
338 sets, particularly data collected in the field (as opposed to measurements made under
339 controlled conditions) will lead to different values for some of the empirical
340 parameters included in these models, but are unlikely to lead to the type of model
341 failure that would require complete re-formulation.

342

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

361

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

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

$$375 \quad g_s = g_{sref} - m \ln D \quad (1)$$

376
 377 where g_{sref} is the value of g_s at $D = 1$ kPa. This serves as a reference conductance,
 378 and m is a parameter, the value of which is related to the regulation of leaf water
 379 potential by stomata, to prevent cavitation. We would expect different values of m
 380 for isohydric and anisohydric tree species.

381
 382 In a study based on data in the literature, Novick et al. (2009) invoked the
 383 relationships between the hydraulic constraints, indicated by leaf area (A_l) and
 384 sapwood cross-sectional area (A_s) per tree, and tree height (h), to formulate a
 385 simple general relationship between reference stomatal conductance values (g_{Cref})
 386 and these architectural canopy variables. They found that at long time scales, under
 387 conditions when light and soil moisture are not limiting, g_{Cref} is approximated by the
 388 simple relationship

$$389 \quad g_{Cref} = 98.2 \frac{A_s}{A_l H} + 37.3 \quad (2)$$

391
 392 where g_{Cref} is in $\text{mmol m}^{-2} \text{s}^{-1}$, A_s and A_l are in m^2 and H is in m. Equation (2)
 393 accounted for 75% of the variance in g_{Cref} . Novick et al. provided detailed discussion
 394 of the various factors involved and the caveats associated with the use of the equation,
 395 but it provides a useful tool for large-scale modeling. In that application actual, as

396 opposed to reference, values of canopy conductance could be estimated by applying
397 modifying factors to account for the effects of vapor pressure deficits and soil
398 moisture (see Waring and Landsberg, 2011).

399

400 We asserted, earlier, that empirical models of stomatal conductance have reached the
401 point where further mathematical modifications are unlikely to significantly improve
402 our ability to predict responses to environmental conditions. There is, however, a
403 long-standing theory (Cowan and Farquhar 1977) of so-called optimal stomatal
404 behavior, which postulates that stomata should act to maximize carbon gain while
405 minimizing water loss by transpiration. This was invoked by Williams et al. (1996),
406 who postulated that stomatal conductance in a mixed deciduous (oak-maple) stand
407 varied so that daily carbon uptake per unit of foliar nitrogen was maximized in
408 relation to the water available in the canopy. They included estimates of resistances in
409 the soil–root system, and xylem hydraulic resistances, in their model. Calculating leaf
410 and shoot water potentials from tissue capacitance data (capacitance is the change in
411 tissue water content per unit change in water potential), Williams et al. used the idea
412 that the maintenance of a maximally efficient conducting system requires that stomata
413 close as evaporative demand rises, to prevent shoot water potentials falling below
414 some threshold value. Threshold values for stomatal closure were obtained from the
415 literature.

416

417 Medlyn et al. (2011) reconciled the Cowan-Farquhar (1977) theory with the
418 empirical approach (Leuning et al. 1995), deriving a new model that provides a
419 framework for interpreting stomatal behavior across species in response to a range of
420 environmental conditions, including rising CO₂. Their model includes a parameter (λ
421 , from Cowan and Farquhar) that describes the marginal water cost of unit carbon
422 gain. Medlyn et al. said: “By linking the optimal and empirical stomatal models we
423 have identified a new and simple way of estimating λ from measurements of
424 stomatal conductance. We suggest that comparative studies of (such) values of λ
425 across species and soil moisture conditions are likely to bring new insights into
426 adaptation of stomatal behavior and water use strategies.” They consider that the
427 model will improve simulations of vegetation carbon cycling and water use at large
428 scales. The Medlyn et al. model does not include consideration of hydraulic pathways

429 and the effects of water potential on stomatal conductance, but Duursma and Medlyn
430 (2012) developed a model called MAESPA from MAESTRA, a detailed array model
431 of canopy light interception and photosynthesis (Medlyn, 2004). Stomatal
432 conductance in MAESPA is calculated from a modified form of the Tuzet (2003)
433 model, which takes into account the responses of stomata to atmospheric vapor
434 pressure deficits and leaf water potential; the algorithms include root water uptake
435 calculations and soil to leaf pathway hydraulics.

436

437 More recently Bonan et al. (2014), carried out a complex modeling exercise in which
438 differing formulations of stomatal conductance, modeled at leaf and canopy scales,
439 were evaluated in terms of the performance of different earth system models.
440 Stomatal conductance was simulated using the empirical Ball-Berry model (Ball, et
441 al. 1987) and two optimization algorithms, based on the Cowan—Farquhar theory,
442 linked to soil and plant hydraulic controls on maximum rates of water use. Bonan et
443 al. adopted, and modified, the soil-plant atmosphere model of Williams et al. (1996).
444 The models were tested against canopy flux measurements made at six Ameri-flux
445 forest sites, from which 51 site-years of data were available. Selected base-line
446 parameter values were tested against leaf-scale and canopy scale analyses. Bonan et
447 al. also carried out parameter sensitivity tests. They found that the optimization
448 algorithms gave the best results, particularly during drought periods when plant and
449 soil hydraulics became increasingly important. The Ball-Berry model provides a
450 closed-form analytical approach that can be combined with empirical dependence on
451 soil moisture or leaf water potential (see Duursma and Medlyn, 2012). The
452 optimization algorithms and high data demands of the procedures used by Bonan et
453 al. demonstrate the importance of incorporating estimates of hydraulic conductance
454 through the system, and the principle that plants reduce stomatal conductance as
455 needed to regulate transpiration and prevent hydraulic failure. They note the need for
456 numerical parameterizations for future use in models at scales from leaf to canopy to
457 global.

458

459 **Hydraulic conductance**

460

461 Because of the dependence of transpiration rates on leaf area, and the relationships
462 between sapwood cross-sectional area and the foliage carried by stems, Whitehead

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

476

477 We do not, here, explicitly consider the role of phloem in stem water storage and
478 hydraulic conductance. In all plants the xylem and phloem occur in close proximity
479 but, in the large body of work on plant hydraulics, the focus has been on xylem and
480 relatively little attention has been paid to phloem. A recent review by Savage et al.
481 (2016) indicates that most of the work on phloem has been concerned with carbon
482 transport, the primary function of phloem. However, they note that phloem may make
483 a significant contribution to stem water storage in trees and also that the influence of
484 xylem water potential on phloem transport may affect drought mortality in trees
485 (McDowell and Sevanto, 2010). There is a clear need for more research, focused on
486 the role and importance of phloem in tree-water relations *per se*, but at this time our
487 ability to explain water movement through trees, and tree water relations, at foliage,
488 individual tree, stand and ecosystem level, does not appear to be significantly reduced
489 by the lacunae that currently exist in this area.

490

491 Running et al. (1975) had recognized that differences in hydraulic efficiency
492 accounted for the contrasting values of maximum stomatal conductance between large
493 and small conifers. At that time, the differences in hydraulic conductance between
494 roots, stems and branches were unknown. There has been a considerable body of
495 work, in recent years, investigating differences in conductance between species and
496 between stems, roots and branches. (Note the distinction made by Sperry et al. (2002)

497 between conductivity, which is a property of some part of the water-conducting
498 pathway, and conductance, which applies to the whole flow pathway. Conductivity
499 may vary along the conducting tissue, or in the soil.)

500

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

505 • resistance to water flow in xylem represents only a fraction of the total liquid flow
506 resistance, sometimes quite a minor fraction, but it may play a significant role in
507 regulating physiological responses at the level of leaves and whole plants;

508 • the capacity to conduct water from soil to leaves is an important factor regulating
509 leaf-level gas exchange properties;

510 • under conditions of ample soil water whole plant hydraulic conductance controls the
511 levels of water potential obtained within the plant at any transpiration rate;

512 • across 50 species, with a range of different life forms, a large fraction of the
513 variability in stomatal aperture could be accounted for by species-specific hydraulic
514 properties;

515 • whole plant leaf area was significantly related to the subtending hydraulic
516 conductance across species;

517 • there is convergence in the functional balance between leaf level properties and
518 hydraulic properties;

519 • there is a relationship between plant size and hydraulic transport capacity – taller
520 organisms require significantly more biomass to achieve similar levels of water
521 transport capacity in comparison to shorter plants;

522 • there is evidence that hydraulic systems adapt/respond to changes in external stimuli
523 over time. Mencuccini's meta-analysis indicated that decreasing air humidity over
524 time, as well as long-term soil drought, tended to result in long-term increases in
525 measures of plant hydraulic efficiency.

526

527 A model by Sperry et al. (1998) predicted that plants tend to optimize their leaf
528 area:root area ratio to achieve optimal regulation of gas exchange. Ewers et al. (2000),
529 provided insights into this: they studied the variation in hydraulic conductivity of *P.*
530 *taeda* trees growing under different conditions of water supply and nutrition. They

531 found that canopy stomatal conductance of fertilized trees was 50% of that of
532 irrigated, unfertilized, trees. This lower conductance was associated with a 50%
533 reduction in leaf-specific hydraulic conductance relative to other treatments, and was
534 significantly less sensitive to changes in vapor pressure deficit. The projected LAI of
535 the fertilized trees was 50% higher than that of trees in the control treatment, resulting
536 in an 11% reduction in the sapwood area/leaf area ratio, A_s / A_l . The slope of the
537 relationship between leaf water potential (ψ_l) and transpiration per unit leaf area (E)
538 was significantly steeper for the fertilized trees than for the other treatments,
539 indicating that hydraulic failure in those trees would occur at values of E far lower
540 than in the other treatments, consistent with the conclusion that K_l was much lower
541 in the fertilized trees. Several factors contributed to this: the fertilized trees were taller
542 than those in other treatments as well as having larger leaf areas. Fertilization caused
543 a significant reduction in root mass and surface area, but those roots showed greater
544 resistance to cavitation.

545

546 Pataki et al. (1998), in a short-term foliage pruning experiment, showed that stomatal
547 conductance, as inferred from sap flux measurements, increased proportionately to the
548 amount of foliage removed. They concluded that the large increases in canopy
549 stomatal conductance could be attributed to hydraulic effects. Meinzer and Granz
550 (1990) also reported full compensation of water uptake, by sugar cane, down to 40%
551 reduction in leaf area index.

552

553 In one of the relatively few studies that included angiosperms as well as coniferous
554 species, Brodribb and Feild (2000) provided further evidence of the fact that better
555 hydraulic conductance ('greater hydraulic supply') allows leaves to realize higher
556 maximum stomatal conductance, which was linked to maximum photosynthetic
557 quantum efficiency. It was, perhaps, helpful that the places where they made their
558 field measurements were wet, and temperatures were very similar. The fluorescence
559 analysis that they used to determine leaf photosynthetic capacity was therefore
560 unlikely to generate errors caused by significant differences in photorespiration. The
561 fact that conifers can maintain equally open stomata with a less steep water potential
562 gradient than is the case for many angiosperms is because the conifers have invested
563 in proportionately more, although less efficient, vascular tissue to supply a reduced

564 amount of foliage. Brodribb and Feild commented that their results may have been
 565 very different if their measurements had been made under stressful, rather than
 566 optimal, conditions, and that there is convergence (functional overlap) between the
 567 two groups of plants.

568

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

570

$$571 \quad E = K_l(\psi_s - \psi_l - h\rho_w g) \quad (3)$$

572

573 to analyze plant responses to soil water potential and rates of water loss (transpiration)
 574 from the leaves. In equation (3) E is the rate of transpiration, K_l is leaf-specific
 575 hydraulic conductance of the soil-plant continuum, ψ_s and ψ_l are soil and leaf water
 576 potentials and $h\rho_w g$ is the gravitational pull on a water column of height h and
 577 density ρ_w . McDowell et al. analyzed plant responses to E in terms of hydraulic
 578 failure — the point at which a critical value (ψ_{crit}) of leaf water potential is reached,
 579 at which xylem conduits may cavitate, K_l approaches zero and the plant can no longer
 580 move water. The capacity of plants to withstand drought depends on root density and
 581 distribution and soil type and conditions as well as the hydraulic properties of the
 582 xylem conducting system. Hydraulic failure may occur in the soil as well as within
 583 plant conducting systems: greater tension is required to pull water through fine-
 584 textured soils because of their small pore sizes, so fine-textured soils have lower
 585 conductance than sandy soils when water is abundant. However, fine-textured soils
 586 retain hydraulic conductance longer and at more negative water potentials than
 587 coarse-textured soils because the low conductance of fine soils results in slower water
 588 loss to transpiration and drainage.

589

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

596

597

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

616

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

623

624 The effects of hydraulic conductivity on the overall patterns of plant growth are
625 illustrated by the hypothesis put forward by Ryan and Yoder (1997), who proposed
626 that tree height is limited by the supply of water to the leaves. Because water is
627 dragged up trees under tension, and every meter of height growth is equivalent to an
628 increment in gravitational water potential of 0.01 MPa, the taller the tree the higher
629 the tension has to be. Air bubbles are therefore more likely to form in the xylem
630 vessels, causing cavitation and loss of conducting ability. To prevent this taller, older

631 trees, have to close their stomata earlier in the day or earlier in a drought; this limits
632 photosynthesis, and so slows tree growth (Landsberg and Sands, 2012, p. 203). This
633 has been supported by Koch et al. (2004) who, in a study of tall redwoods, showed
634 that leaf turgor decreases with height, growth slows and that maximum tree height
635 varies from site to site, i.e. changes in hydraulic conductance are relative to maximum
636 height on a site; they are not an absolute function of measured height. More recently
637 Ryan et al. (2006) re-visited the hydraulic limitation hypothesis, reviewing 51 studies
638 that measured one or more of the components necessary for testing whether tall trees
639 differ physiologically from shorter, younger trees. They found that, in general, where
640 hydraulic limitations to photosynthesis occurred, there was no evidence that these
641 were sufficient to explain observed declines in wood production with stand age. Ryan
642 and his co-authors suggest that future work on age-related productivity decline should
643 explicitly link leaf or canopy gas exchange with tree and stand growth, and reconsider
644 the common modelling assumption that tree biomass growth is limited by carbon
645 availability.

646 Studying mortality of large trees in a tropical forest Rowland et al. (2016) found that
647 the most likely cause of death in trees subject to extended drought was hydraulic
648 vulnerability and deterioration. This is not consistent with the carbon starvation
649 hypothesis, although hydraulic breakdown resulted in subsequent, potentially rapid,
650 limitations in carbon uptake. In a global study Bennett et al. (2015) found that
651 drought consistently had a more detrimental impact on the growth of large trees. The
652 results of their survey support the theoretical prediction that greater height and
653 pathlength resistance are likely to make large trees more hydraulically vulnerable and
654 therefore more sensitive to drought. They also point out that large trees, with crowns
655 in or above the canopy, are exposed to higher solar radiation and leaf-air vapor
656 pressure gradients than trees in the relatively buffered understorey. Furthermore,
657 drought-stressed trees are more liable to attack by biotic agents — for example in
658 cases where bark beetles are associated with drought-induced mortality in the
659 coniferous forests of the western United States.

660

661 In the highly seasonal environments common across Australia, evergreen eucalyptus
662 species respond to droughts by leaf-shedding, as well as by short-term physiological
663 mechanisms. These ecosystems offer opportunities for studying changes in tree water

664 relations that may provide important general insights into tree water relations. We
665 note, for example, the finding by Prior and Eamus (1999) of positive correlations
666 between pre-dawn leaf water potential and tree height, in two species, during the dry
667 season, but not during the wet season. Prior and Eamus (2000) also found that
668 hydraulic conductance and conductivity, normalized for leaf area, declined as the dry
669 season progressed: seasonal increases in embolism could not account for these
670 declines. Macinnis-Ng et al. (2004), investigating a range of species in the Sydney
671 region, found seasonal differences in minimum leaf water potential and sapwood
672 conductivity, with correlations between xylem embolism, minimum leaf water
673 potential and sapwood conductivity that varied seasonally.

674

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

680

681 **Storage and capacitance**

682

683 Since the establishment by Waring and Running (1976) and Waring et al. (1979) of
684 the importance of water storage in the stems of large trees, there has been a large body
685 of work, on a range of species, examining storage and capacitance. Storage is a
686 measure of the amount of water stored in a tree, or in particular tissues (roots, stems,
687 branches, foliage). Capacitance is defined as the change in tissue water content with
688 change in potential. The concept provides the basis for analyzing the movement of
689 water into and out of tissues. Scholz et al. (2011) have reviewed the literature dealing
690 with these concepts, and their implications. Collating data from a number of studies
691 they were able to demonstrate a linear relationship between tree size and the daily use
692 of stored water; they also found that trees with higher capacitance tend to exhibit
693 higher (less negative) minimum branch water potential than trees with lower intrinsic
694 capacitance. An interesting point emerging from the review is the fact that specific
695 capacitances in angiosperms and conifers span a similar range of values, despite
696 dramatic differences in wood anatomy. Scholz et al. comment on the factors that have
697 to be taken into account when modeling water fluxes in and out of stored tissue,

698 noting that transient responses to water flow can be predicted from the time constant
699 associated with step changes in transpiration rate. Phillips et al. (2004) used a bulk
700 resistance-capacitance model to describe the hydraulic characteristics of *Pinus abies*
701 and *Pinus taeda* trees in which flow rates were measured with sap flux sensors,
702 together with a coupled hydraulic-stomatal physiology model to evaluate the role of
703 stomatal conductance in regulating the observed sap flow responses. Chuang et al.
704 (2006) proposed a porous media model that leads to a mass-conserving partial
705 differential equation which describes the spatial-temporal dynamics of a tree
706 hydraulic system and connects sap flux to transpiration. This approach leads to
707 complex mathematics and can only be applied when sap flux data are available.
708 Landsberg and Sands (2011, pp. 209-211) provide a complete set of solved equations,
709 based on pools and resistances, for simulation of the time course of leaf water
710 potential and storage tissue water content,

711

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

729

730 **Soil moisture and wide-scale hydrologic modeling**

731

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

749

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

762

763 Two recent review-type papers demonstrate that the body of theory describing water
764 movement from soil to roots, driven by transpiration and modified by soil water
765 content, is adequate to describe tree water use across landscapes, including the

766 development of drought and its effects on trees, despite the inevitable errors and
767 uncertainty associated with spatial variations in soil properties and available soil
768 water.

769

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

790

791 Waring and Landsberg (2011) provided a brief review of the factors linking water use
792 by vegetation with atmospheric conditions, including the effects of leaf-air vapor
793 pressure deficits, and the effects of water potential gradients,
794 on canopy conductance. We considered the effects of canopy structure, including tree
795 height, as well as the effects of nutrition, temperature and atmospheric CO₂
796 concentrations on canopy conductance. We also evaluated the use of remote sensing:
797 structural features of vegetation, as well as most of the climatic variables required to
798 drive the Penman-Monteith equation, can be obtained at daily resolutions (or better)
799 from a range of weather satellites. Leaf pigment changes associated with stand

800 nutritional status, and leaf water content changes that may be caused by drought, are
801 also discernable using remote sensing. Waring and Landsberg commented that ‘The
802 central point (that) we have been making throughout this paper is that, given
803 information about the canopy structure of vegetation, and adequate weather data—
804 among which precipitation amounts and patterns are probably the most important
805 variables—we can estimate water use with considerable accuracy with a series of
806 landscape-linked models. Within the Penman–Monteith equation, the canopy
807 conductance term describes the interaction between canopies and the atmospheric
808 environment, so our ability to derive accurate values for that term is central to our
809 ability to estimate transpiration rates by ecosystems.’

810

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

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

839

840 **Hydraulic redistribution of water by tree roots**

841

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

865

866 **Conclusions**

867

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

874

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

897

898 In some areas we may be seeing limiting returns on effort expended; in others we are
899 probably seeing real progress, particularly, perhaps, in work on plant hydraulic

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

915

916 There are various facets of tree water relations that we have not discussed in our
917 treatment so far but, for completeness, we include them among the following points,
918 on which we base our assessments of some of the areas that we think require
919 particular attention. Accepting that our views are subjective and open to (no doubt
920 considerable) argument, we suggest that the major findings from the past 50 years of
921 research in tree water relations have included:

922

923 • a great deal of information about the factors governing stomatal apertures, and
924 hence conductance, transpiration and, of course, photosynthesis. Unfavorable
925 temperatures, vapor pressure deficits and (soil) drought limit stomatal conductance
926 and photosynthetic capacity, gross primary production and above-ground growth. The
927 size of leaves affects the boundary layer conductance. In still air, large leaves with
928 closed stomata, exposed to direct radiation, are likely to experience lethal
929 temperatures. Oren et al. (1999) provided an enlightening discussion about stomatal
930 sensitivity and the feedbacks between g_s and tissue water potential. Future research
931 on stomatal behavior and responses to environmental factors is likely to include
932 increased focus on hydraulic pathways and conductances. It also seems likely that,

933 where good quality supplementary measurements are available, there will be
934 increasing use of iterative procedures (see Williams et al, 1996) and optimization
935 algorithms (see Bonan et al. 2014) to develop the empirical relationships between soil
936 moisture, soil to leaf hydraulic pathways and atmospheric conditions that will be
937 needed for wide-scale hydrological modeling;

938 • greatly improved understanding of the interactions between the hydraulic
939 conducting systems of trees and maximum achievable stomatal conductance. There
940 has been considerable effort devoted to establishing water potential thresholds, or
941 fluxes, that cause cavitation, and explaining why those thresholds vary with wood
942 properties and change with environmental conditions. The whole area of resistances
943 to water flow through soil-root systems, as well as tree conducting systems, merits
944 much more attention.;

945 • tree structure follows function, e.g. wood anatomy and morphology vary with
946 species and site. Tall trees require adequate plumbing: the interactions between wood
947 structure and properties and hydraulic characteristics clearly warrant more research
948 attention;

949 • all mature trees — in which height growth has slowed, or halted — have lower vigor
950 than young trees with shorter branches and relatively more efficient plumbing. The
951 problem of age-related productivity decline was not solved by Ryan and Yoder (1997)
952 as Ryan et al. (2006) recognized. Their comment, quoted earlier (‘that future work on
953 age-related productivity decline should explicitly link leaf or canopy gas exchange
954 with tree and stand growth, and consider whether tree biomass growth is limited by
955 carbon availability’), provides a useful pointer to future priorities;

956 • stored water buffers diurnal variation in water use (short term). It may also
957 contribute to the ability of trees to withstand drought. There are some preliminary
958 indications (Savage et al. 2016) that the interactions between phloem and xylem
959 tissues may influence the ability of trees to withstand drought. Klein et al. (2014)
960 showed that species with more storage do better in semi-arid areas than those with
961 limited storage. In general, the effects of drought have become progressively better
962 quantified, showing differences between the vulnerability of roots, stems and
963 branches;

964 • branch length may be important. Recognition that much of the resistance to water
965 flow to the foliage is associated with branch length, not stem height, provides an

966 explanation for the fact that thinning in genetically different populations of pine is
967 likely to lead to different growth responses, even if, without thinning, branches were
968 all short and no genetic differences were expressed;
969 • we can scale estimates of transpiration from leaf to landscape levels, predict
970 changes in species composition if areas become more drought-prone and establish
971 links between controls on transpiration and feedback to climatic conditions, which
972 may range from those above bogs in Canada to those above Amazon rainforests. We
973 understand the role trees play in preventing salt accumulation at the soil surface where
974 saline ground water occurs. Uncertainties about spatial variations in soil water
975 holding characteristics and tree rooting depths, and hence the amount and distribution
976 of available soil water across landscapes must reduce confidence in predictions of
977 water use. Future work should include more investigations into the water stored in
978 soils, not only from the point of view of the sometimes arbitrary criteria of soil
979 physics but also with attention to the interactions between soil type and wetness, tree
980 species and tree root systems: how much water can tree root systems extract under
981 varying conditions. (see, for example, Nepstad et al., 1994). A good example of the
982 type of study that should be done, in as many areas as possible, was provided by
983 Nepstad et al. (2004). They used weather data, soil survey data providing information
984 about soil physical characteristics, vegetation information and geographical
985 information systems to model water balances over large areas of Amazon forest. They
986 tested their results by observations and measurements in the field.

987

988 Many of the models of various aspects of tree water relations developed by 1975 still
989 work, and are now generally accepted for practical use in hydrology and ecology
990 without additional testing (which is not to say that there should not be additional
991 testing). There will no doubt be continued refinement of those models, particularly in
992 the case of stomatal conductance, as we noted above. However, the focus in tree-
993 water relations has shifted to examine the thresholds, in terms of climatic events, at
994 which drought, high temperatures and vapor pressure deficits cause mortality. The
995 most likely causes of (natural) tree death appear to be whole-plant hydraulic failure
996 and subsequent physiological shut-down (see Rowland et al. 2016; Bennett et al.
997 2015). However, insect attack, disease, and animal browsing (Cohen et al. 2016,
998 Dannell et al. 2003) are also major causes of tree death, since carbon starvation

999 renders the plants more susceptible, particularly to insect attack. The challenge is to
1000 predict which species or clone will be best adapted to changing conditions.

1001

1002 We need to develop a theoretical foundation that will help to predict the competitive
1003 advantage that one species (genotype) might have over another when encountering
1004 different intensities of drought. Perhaps the most fruitful future opportunities for tree
1005 physiologists lie at the fringe of the field, in interactions with geneticists,
1006 insect/disease physiologists and ecologists working on the effects of climate change.

1007

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1009

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1016

1017 **Conflicts of interest**

1018 None declared

1019

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1023

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