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Publication Date

2020-10-01

DOI

Peer reviewed

A New Phenomenological Model to Describe Root-Soil Interactions Based on Percolation Theory

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Abstract

In his paper on net primary productivity of terrestrial communities predicted from climatological data, Rosenzweig (1968) argued that variability in productivity is well accounted for by (evapo)-transpiration, and that water from transpiration is, on global scales, the most variable component in the photosynthesis reaction. The goal of this paper is to investigate whether variability in plant growth on local scales and within species is primarily related to transpiration under several scenarios including different terrain curvature, slope aspect, soil characteristics, and climate ranges. We test the hypothesis that this relationship exists because root growth into the surface soil layers (0-2 m) tends to follow paths with minima in resistance, which in turn maximizes water flow and nutrient delivery rates that regulate growth. The set of all connected paths with individual pore-to-pore flow resistances less than a critical, percolating, value forms a cluster with mass fractal dimensionality, d_f. We propose that roots follow paths through the 2D percolation cluster, defining the set of all optimal flow paths, making the 2D value of d_f from percolation relevant to root fractal dimensionality. The tortuosity of such optimal paths as defined in percolation theory should then relate root length to root radial extent, linking the parameters of root tortuosity and plant productivity. Our analysis of large data sets across

species implies that root radial extent and tree height are both proportional to cumulative transpiration until trees approached maximum height, and their growth rates are proportional to the transpiration rate, not to the moisture content. Local variations in tree height as functions of the variables investigated appear generally consistent with deduced variations in transpiration. Here this correlation is investigated more closely in the context of studies addressing individual tree species.

1. Introduction

Plant growth and productivity are influenced by many factors, such as nutrient and light availability, adaptation, competition, soil substrate variability, grazing by herbivores, attacks by various pathogens, and climate variables. Mechanisms that explain observed differences in maximum tree height at different locations and patterns in height growth have eluded ecologists and plant physiologists (Ryan and Yoder, 1997). Clearly, the growth of trees can be restricted by any conditions that limit productivity. We suggest, however, that it may be possible that any of these limiting conditions is expressed through, or reflected by, a reduction in actual transpiration. Already more than a half a century ago, Rosenzweig (1968) argued that variability in productivity is well accounted for by (evapo)-transpiration. Rosenzweig's argument is elegant, though difficult to use predictively, on account of the many interacting factors that influence how much water is actually transpired by any individual plant. Although the physiological responses of plants to water stress, and the associated effects on plant growth, are well-studied on easy to access aboveground tissues, *i.e.*, stems, branches, and leaves (Zhu, 2002; Jaleel *et al*., 2009, Venturas *et al*., 2017), there still remains a paucity of information on how plant growth is modulated by fundamental constraints over plant available soil water that arise from the interaction between roots and soil physical properties. While this interaction provides a basis for our guiding hypothesis, our goal here is

60 to probe available literature for evidence that limitations in transpiration due

61 to variability in a variety of local conditions, such as microclimate, soil

62 conditions, and slope aspect or curvature, are reflected in corresponding

63 reductions in tree height. With this investigation, we hope then to provide

64 motivation for more detailed experimental studies that can isolate the

65 dependence of growth rate on transpiration.

66 The basis for the application of percolation theory approach for explaining

67 how root-soil interactions regulate transpiration was laid by considering

68 limitations on root growth imposed by network properties of the soil (Hunt,

69 2017), and an interfacial constraint between the directed network of a plant

70 and the random network of the soil (Hunt and Manzoni, 2016). Two recent

71 large-scale studies of world data sets on tree growth confirmed the

72 importance of percolation theoretical values of: (a) the two-dimensional

73 optimal path exponent in the time dependence of tree height and (b) root

74 radial extent growth rates, and the two-dimensional value of the percolation

75 mass fractal dimensionality, d_f, to root fractal mass.

76 The goal of the current paper is to investigate whether variability in plant

77 growth on local scales and within species is, in part, related to constraints

78 placed on transpiration by soil structure that can be explained by percolation

79 theory. The scope of the paper is to present the results of testing several

80 scenarios including different terrain curvature, slope aspect, soil

81 characteristics, and climate ranges. Particularly, we addressed the possibility

82 that variability in tree height cited by Ryan and Yoder (1997), as well as

83 several other cases, may be accounted for by a single analytical result for

84 the growth of plants, suggested to be governed by root radial extent (RRE),

85 but also shown to account for plant height (Hunt and Manzoni, 2016; Hunt,

86 2017). Note that the same result for extensional growth rates used here

87 generates as well (Hunt, 2017) the quoted relationship of net primary

88 productivity (NPP) to transpiration, the problem that originally interested

89 Rosenzweig (1968).

2. Critical Literature Review

A literature review of publications on the variability of tree growth showed that multiple factors and processes can affect transpiration, such as soil moisture content, compaction and hydrophobicity, climate, slope aspect, and slope curvature. For example, Popova *et al*. (2016) found that the optimal path selection by roots in the soil is fundamental for resource acquisition. Popova *et al*. (2016) stated that "root apices may direct their growth through cracks or generally follow paths with a low impedance to penetration (Darwin and Darwin, 1897; Hart, 1990; Brown, 1993; Migliaccio and Piconese, 2001; Blancaflor and Masson, 2003; Gilroy and Masson, 2008; Migliaccio *et al*., 2013). These authors provided only empirical data, with no theoretical background: "Although we can evaluate the overall bending response by analyzing the […] tortuosity, quantitative estimates of the contribution of active growth responses relative to passive deflection during root bending in the soil remain lacking."

The root radial extent is related to root length by the tortuosity of the root path through the soil. Hunt and Manzoni (2016) argued that the basis for the prediction of the root radial extent is an analytical result describing the tortuosity of paths in random networks whose total impedance to flow (or, equivalently, growth) is minimized. This constraint constitutes the chief root-soil interaction considered here. In addition to minimizing direct metabolic energy expenditure in the search for water and nutrients, such an optimization also tends to maximize nutrient access.

Clausnitzer and Hopmans (1994) and Somma *et al*. (1998) performed 3-D modeling of the root growth as a function of mechanical soil strength, soil temperature and solute concentration, as well as soil water flow. Hunt *et al*. (2014) and Hunt and Sahimi (2017) indicated that the root tortuosity is based on percolation theory. While percolation theory can be applied to generate flow rates in disordered media (Hunt and Manzoni, 2016), the application of percolation theory in this paper is to evaluate the tortuosity of

120 the optimal paths. To this purpose, the physical soil network is represented

121 as a network of bonds that describe the ease of passage (of fluid, or a root

122 tip) from each pore to its neighbors. In the limit of a strongly heterogeneous

123 medium, optimal paths are defined as having the smallest value of their

124 cumulative resistance. The resulting paths are fractal, with length-dependent

125 tortuosity. Such fractal paths (Hunt, 2017) are compatible with

126 measurements made on root systems (Levang-Brilz and Biondini, 2002),

127 whose results imply that the root length RL is proportional to the RRE to a

128 power larger than 1. The tortuosity can be defined explicitly by writing $RL \sim$

129 RRE^{γ}, with $\gamma \geq 1$. For $\gamma > 1$, a path is always tortuous. For $\gamma = 1$, paths may

130 still be tortuous, but tortuosity is given by a numerical constant independent

131 of scale.

132 Levang-Brilz and Biondini (2002) reported directly RL in terms of root

133 biomass, M, to a non-integral power δ, while RRE was given as M to a

134 different power β. In their notation, $RL = RRE^{\delta/\beta}$, and $\gamma = \delta/\beta$. This formula is

135 lacking the consideration of the dimensionality of flow in the root zone.

136 Although transient soil water flow in the vadose zone is commonly simulated

137 as one-, two-, or three-dimensional spatial pattern, the root water uptake is

138 generally considered simply in the vertical dimension only. Vrugt $et\ al$.

139 (2001) indicated that that for row crops and tree lines, a 2-D representation

140 would be better, and for isolated trees the water uptake can be considered a

141 3-D pattern. A root's search for nutrients will largely be confined to the top

142 meter or so of soil, because horizonation of the soil at this length scale tends

143 to accompany preferred sequestration of nutrients, such as N and, more

144 importantly P, within this layer (Lynch, 1995). Thus, Hunt and Manzoni

145 (2016) chose the quantitative description of optimal paths within a two-

146 dimensional network and the value of D_{opt} for 2D networks. Not surprisingly,

147 whenever plant growth is not strongly water-limited, as it is in desert

148 environments, root growth is indeed mostly confined to the top two meters

149   or so of soil (Fan *et al.* 2017) (or to an even thinner layer, on the order of a

150   half a meter (Gentine *et al.* 2012)).

151   Evapotranspiration is generally a function of the aridity and precipitation P

152   (Budyko, 1958; 1974). Increasing precipitation P tends to increase

153   evapotranspiration in a water-limited environment until the limit when

154   further increases in precipitation may bring an ecosystem into energy-

155   limiting conditions, leading to no further increase in transpiration. Competing

156   with transpiration is the direct evaporation of water from the Earth's surface

157   or from vegetation (interception). What is neither evaporated nor transpired

158   may run off or infiltrate into the subsurface. Thus, P + run-on = $E + T + I$ +

159   run-off, where E is evaporation, and T is transpiration. The actual

160   evapotranspiration, AET, is then just the sum of E and T. One can use the

161   combined AET (global average approximately 65% of precipitation, Lvovitch,

162   1973) to estimate the fraction of the precipitation that infiltrates and runs

163   off. With this approximation, a 10% error in an estimation of AET leads to a

164   19% error in the combined fraction that runs off and infiltrates. However, the

165   focus of this paper is the transpiration. If transpiration is estimated from AET

166   and evaporation, since on average transpiration represents 61% of AET, an

167   error of 10% in evaporation will typically lead to an error of only 6% in

168   transpiration. However, local conditions will vary, and the guidance

169   developed from the average conditions may fail in particular cases.

170   Moreover, variability in the fractions of precipitation infiltrating or running

171   off, particularly due to local topographic effects, will be difficult to ascertain,

172   introducing unknown variability into estimates of the transpiration based on

173   the conservation equation.

174   ## 3. Phenomenological Model

175   The hypothesis of the relevance of percolation theory to root growth would

176   imply that the exponent, γ should be the optimal paths exponent, D_{opt}, *i.e.*, γ

177    $= \delta/\beta = D_{opt,}$ or $RL = RRE^{Dopt}$. For a relatively shallow soil layer, for a 2D flow

178 pattern, the value of $\gamma = 1.21$ can be used, and $RL \sim RRE^{1.21}$ implies that RRE

179 $\sim RL^{0.83}$ where $0.83 = 1/1.21$. Since RL is proportional to time, t, RRE

180 becomes proportional to $t^{0.83}$ (Watt *et al*. 2006; Hunt, 2016). Using the

181 experimental data reported by Levang-Brilz and Biondini (2002, Table A1),

182 Hunt (2017) determined that $\delta/\beta = 1.25 \pm 0.41$ for 55 species of grasses and

183 grassland forbs (after removing 10 outliers differing from 1 by more than a

184 factor 2), which is in accord with the value of $\gamma = 1.21$ for 2-D flow. However,

185 multiple values of δ/β were near 1.43, which corresponds to $\gamma=1.43$ for a 3-D

186 flow pattern.

187 Accordingly, Hunt (2016; 2017), Hunt and Manzoni (2016) proposed to

188 express the tree height x, equal to RRE, versus time as

189
$$x = x_0 \left(\frac{t}{t_0} \right)^{0.83} \tag{1}$$

190 Parameters x_0 and t_0 are empirical parameters characterizing the smallest

191 length and time scales in the pore network. In Eq. (1), x_0 is the smaller value

192 of the characteristic pore or plant xylem diameter, and the ratio x_0/t_0 is

193 defined as the rate of water flow through a pore. Values for the flow

194 parameters used are also compatible (Hunt and Manzoni, 2016) with root-tip

195 extension rates measured by Watt *et al*. (2006) and others. Thus, the root

196 radial extent, x, is less than the product of the root tip extension rate (x_0/t_0)

197 and the time, because the paths followed by the roots through the soil are

198 fractal.

199 For comparison with large databases, such as Biometric and Allometric

200 Database (BAAD) (Falster *et al*. 2015), which do not provide root xylem

201 diameters, a geometric mean root xylem diameter of 10μm (Watt *et al*.,

202 2006; Hunt and Manzoni, 2016) can be estimated for x_0. Moreover, a pore

203 diameter of 10μm produces the most common soil hydraulic conductivity

204 values measured under near saturated conditions (Hunt and Manzoni, 2016).

205 Since xylem diameters (Watt *et al*. 2006) and typical pore diameters each

206 range over two orders of magnitude (Hunt and Manzoni, 2016), the
207 uncertainty in length scale is quite large.

208 The growth curve is often assumed to have a universal functional form,
209 modulated by a factor that reflects the characteristic height reached after a
210 standard time (typically 50 – 100 years) at a given site.

211 While growth curves are not generally given in the form of power laws,
212 applying the more commonly used exponential functions—for example, see
213 Lappi and Bailey (1988, Fig. 1), Biging (1985, Fig. 3), Gonzales *et al.* (2005,
214 Fig. 5) — is reasonably consistent with Eq. (1), except at periods of less than
215 about 6 months. The sigmoidal shape of typical growth curves, not reflected
216 in our scaling relationship, is explained by the tendency for root growth to
217 outpace height growth in the first 6 months or so (Hunt and Manzoni, 2016).
218 Subsequently, up to a height of up to about 40 meters, tree heights and root
219 radial extents are nearly equal to each other (Kalliokoski, 2008; Phillips *et al.*,
220 2014; 2015).

221 An upscaled version of Eq. (1) can be used to present the relationship of Eq.
222 (1) in terms of a plant growing season, t_g, and associated transpiration
223 depth, T_g (Hunt, 2017), given by

224 $$x = T_g \left(\frac{t}{t_g} \right)^{0.83} \qquad\qquad (2)$$

225 On a bilogarithmic plot, a power law has two parameters: the power that is
226 its slope, and the coefficient, *e.g.*, $T_g/t_g^{0.83}$, its intercept. Note, however, that
227 the transpiration rate, given in, *e.g.*, mm/yr, is the ratio, T_g/t_g. Whenever $x_0/$
228 $t_0^{0.83} = T_g/t_g^{0.83}$, Eq. (1) and Eq. (2) are identical (Hunt, 2017).

229 The largest and smallest reasonable values for pore-scale flow times, $t_0 \equiv x_0/$
230 v_0, were shown to predict (nearly) identical values for $x(t)$ as calculated from
231 $T_g(t/t_g)^{0.83}$ using smallest and largest known values for T_g, when the growing
232 season, t_g, was fixed at 6 months (Hunt et al., 2017). This comparison

233 between Eq. (2) and observation was found to hold over time scales

234 consistent with a range of heights of about 1 m to 40 m (Hunt and Manzoni,

235 2016; Hunt, 2017) and for RRE to much greater length scales (up to 10 km in

236 the case of *Posidonia oceanica*).

237 Thus, pore-scale percolation constraints on root growth from the structure of

238 optimal paths through networks constrain growth of individual plants over a

239 significant portion of their lifetimes. But the specific connection between RRE

240 and transpiration implies a key role of the magnitude of transpiration in plant

241 growth. Since Eq. (2) is a power-law with power less than 1, the growth rate,

242 dx/dt, must decline in time, which can be given by:

243 $$\frac{dx}{dt} = 0.83 \left(\frac{x_0}{t_0} \right) \left(\frac{t}{t_0} \right)^{-0.17} = 0.83 \left(\frac{T_g}{t_g} \right) \left(\frac{t}{t_g} \right)^{-0.17} \tag{3}$$

244 where the distinction between the two expressions is less than 20% in the

245 upper and lower bounds (using maximum and minimum transpiration values

246 of 1650 mm and 20 mm, respectively), insignificantly larger than uncertainty

247 in knowledge of transpiration or typical pore-scale flow rates.

248 Eq. (2) implies that plant height is proportional to the growing season

249 transpiration, which coincides with a universal power-law form for the growth

250 curve of trees, and which is modulated by a factor (T_g), strongly dependent

251 on a suite of climatic, biological, and edaphic variables. These two features

252 are in general accord with a century's worth of research into tree growth

253 rates as summarized in the concepts of the growth curve and its companion

254 site index, SI (*e.g.*, Biging, 1985; Lappi and Bailey, 1988; Gonzales *et al.*,

255 2005; Aertsen *et al.*, 2010; Weisskittel *et al.*, 2011).

256 Thus, the present prediction, with the universal power 0.83 providing the

257 shape of the growth curve, and its magnitude, may ultimately replace the

258 traditional formulation for tree growth. Indeed, we show below that 1) growth

259 rates adhere to an exponential function until trees emerge from the canopy,

260 with an upper limit on the exponent of 0.83, and 2) the variability of T_g with

261 topography, soil conditions, slope aspect, and climate may account for a

262 wide range of intra-specific tree growth variability reported in the literature.

263 Direct measurements needed for the evaluation of the root production are:

264 transpiration, tree height, xylem diameter, pore size, and hydraulic

265 conductivity. The direct dependence of Eq. (1) on pore (or xylem) diameter is

266 only to the power of 1 - 0.83 = 0.17, thus, an order of magnitude error in

267 pore diameter produces an error in predicted height only 17% as large, or

268 altogether 50%. The dependence of height in Eq. (2) on transpiration is linear

269 and relative errors in transpiration translate to equal errors in predicted

270 heights. However, T_g is better constrained than pore sizes, though its value is

271 mostly inferred indirectly. Tree height measurements have been a source of

272 significant error, with many experimenters preferring to infer tree heights

273 from allometry and tree diameter measurements. However, due to

274 significant discrepancies between predictions of allometry and observations,

275 we restrict our attention to cases where tree height is measured directly.

276 Since Eq. (1) does not include such variables as the xylem diameter and the

277 pore size, we have not addressed their uncertainty directly, but provided

278 some general arguments below.

279 In the percolation theory of flow through random networks (Sheppard *et al*.,

280 1999), the tortuosity of such paths is not described by a constant. Rather, it

281 is scale-dependent and described by a fractal exponent, defined as D_{opt}. The

282 value of this exponent depends only on the dimensionality of the medium

283 that constrains the path selection (Sheppard *et al*., 1999).

284 We will be analyzing the effectiveness of Eqs. (1)-(3) when compared with

285 actual data for tree heights and growth rates as functions of time. According

286 to these equations, most of the variability in growth rate can be traced to the

287 quantity of water transported, even though the variations in both

288 transpiration across biomes (Box *et al*.,1989) and the variation in xylem

289 diameter across species (Watt *et al*., 2006) amount to about two orders of

290 magnitude. Since, in Eq. (1) the pore-scale t_0 is equal to x_o/v_o, x_o appears

291 both in the numerator and the denominator, generating $x_o/x_o^{0.83} = x_o^{0.17}$. But

292 even when x_o varies over two orders of magnitude, this generates a

293 variability of only a factor $2.2 = 100^{0.17}$ in growth rate. In contrast, v_0 appears

294 only in the ratio x_o/v_o, producing the dependence $v_o^{0.83}$. $100^{0.83}$, the

295 corresponding variability in growth rate, is equal to 46, much larger than 2.2.

296 Equivalently, when the upscaled version Eq. (2) is applied, it is the total

297 water transport, T_g, which provides the greatest influence on plant growth,

298 since growing seasons are typically measured in months, whereas T_g can

299 vary over nearly two orders of magnitude (Box *et al*. 1989). Although we do

300 not ordinarily have any information regarding either pore or xylem

301 diameters, it is seen that, in our phenomenology, the effects of variation in

302 these quantities is secondary to that of the quantity of water transported.

303 Conceptually, in individual cases, we expect x_0 to be given by whichever

304 diameter, pore or xylem, that limits water flow the most.

305 Thomas (1996) noted a proportionality of growth rates to final tree height.

306 This is understandable if, within a species with the same genetic controls,

307 the time for following maximum growth rates does not change from one

308 geographic region to another, but the rate of transformation of solar energy

309 to sugar does. From theory, this is consistent with applying Eq. (3) to

310 different individuals for the same, though variable, t values, and the same t_g

311 values, but with distinct values of T_g. As long as each tree follows Eq. (3), the

312 ratio of their heights will be the ratio of their T_g values. If height growth for

313 both trees ceases at the same time, the ratio of their final heights will also

314 be the same value. Of course, there is individual variability not accounted for

315 by such a formula, *i.e.*, the loss of height of a sapling caused by a branch

316 falling from another tree (Clark and Clark, 2001). Such cases were omitted.

317 Thus, water fluxes available to trees should be equally relevant in

318 determining both their growth rates and final heights.

319 Here, we highlight examples of how transpiration, growth, and stand
320 structure are phenomenologically related to Eq. (1) or Eq. (2). We also
321 address how tree growth rates relate to Eq. (3).

322 In each of the subsections below, we will address the role of total water
323 transport in helping to predict plant growth. Except for the first two, the
324 actual time dependence is neglected. Where the time dependence is
325 neglected, the height of either the dominant or the typical trees accessed is
326 given along a gradient in some quantity (*i.e.*, soil hydrophobicity, climate,
327 curvature) that can be related quantitatively or semi-quantitatively to the
328 transpiration. Where the time dependence is included explicitly, we seek
329 either pore-scale flow rates or total transpiration values that are appropriate
330 to the comparison. For the entire meta-data set in the first case investigated,
331 this corresponds to a range of relevant flow rates across climate zones; for
332 the exceptionally fast-growing trees in the second case, the transpiration
333 value used is the largest documented by Box *et al*. (1989). Here, as
334 elsewhere (Hunt and Manzoni, 2016), we note that the predictive capability
335 of Eq. (1) (or Eq. (2)) for tree height breaks down at larger time scales, from
336 30 years to 100 years. One limiting factor is the "hydraulic limit" (Koch *et al*.,
337 2004) of about 125 m. However, rapidly growing trees may approach the
338 canopy in a much shorter time frame, and we suggest that the chief
339 limitation on growth for trees that have neared or exceeded the canopy is
340 likely not the influence of the physical characteristics of the medium on the
341 roots, but can be a combination of many factors, such as wind, lightning, or
342 co-adaptation to regional characteristics reducing advantages of greater
343 heights.

4. Results: Implications of the Phenomenological Model

345 In this Section, we address a number of published studies where our model
346 of tree growth may find support. As no investigations were actually
347 conducted with the purpose of testing our specific model, though some

348 investigators indeed investigated related hypotheses, we cannot, in general,

349 exclude ambiguity of understanding a model of the tree growth.

350 Nevertheless, the evidence compiled appears to relate to our predictions

351 with regard to both the temporal and transpiration dependences of the tree

352 growth rate.

4.1. Cumulative growth as a function of time

354 Our first comparison (Fig. 1) is with an entire meta-data set (BAAD, Falster *et*

355 *al*. 2015). The data give plant heights over periods of weeks to roughly a

356 century for a range of plant species and climates. In accord with Eq. (1), we

357 use bounds on the typical pore-scale water flux bounds across climate zones

358 from about 240 mm/yr to 20 m/yr to account for the variability of the entire

359 meta-data set for plant heights and ages over the time period of record

360 (Hunt and Manzoni, 2016). Attributing the major variability to flow rates

361 rather than directly to the plant xylem characteristics, we use for all the data

362 the same length scale, chosen equal to a geometric mean xylem diameter of

363 about 10 µm (a range of xylem diameters from 1µm to 100 µm is given by

364 Watt *et al*. 2006).

365 The value of 20 m/yr is roughly consistent with a maximum precipitation, 10

366 m, divided by a typical porosity of about 0.4. At the shortest time scales,

367 measurements for root tip extension rates are accessed, and at time scales

368 larger than hundreds of years, it is the RRE associated with large clones, as

369 evidenced by the existence of surface shoots, and confirmed by genetic

370 comparison. At intermediate time scales, the comparison was with tree

371 heights.

372 In comparison with BAAD, the growing season representation (Eq. 2)

373 provides a more transparent standard. Using for a growing season $t_g = 0.5$ yr

374 and a range of transpirations 20 mm (Namibian desert, Seeley, 1978) to a

375 maximum of 1650 mm (T_g) (tropical savannahs and rainforests, Box *et al*.,

376 1989) generates essentially the same range of plant heights as a function of

377 time as the pore-scale flow rates above, and equally bounds (Hunt *et al.*,

378 2017) the heights of woody plants (Falster *et al.*, 2015) as a function of time,

379 from time scales of weeks to hundreds of years.

380 ## 4.2. Comparison with *Populus deltoides* and *Eucalyptus*

381 ## *regnans*

382 Here, by comparing data with Eq. (2), we address height growth of two

383 specific species within an optimal environment for growth. This allows choice

384 of a single transpiration value rather than a range of transpiration values.

385 *Populus deltoides* and *Eucalyptus regnans* may be the two fastest growing

386 tree species in the world over a period of decades. Fig. 2 provides a

387 comparison of predictions using Eq. (2), with the upper limit of T_g = 1.65 m,

388 with specific tree height and age data for *deltoides* taken from Johnson and

389 Burkhardt (1976), and for *regnans* from Van der Meer *et al.* (1999; 2007),

390 Ryan and Yoder (1997), and Givnish *et al.* (2014). Note that 1.65 m is

391 roughly equal to the total precipitation (between 1.5 m/yr and 2 m/yr,

392 Australian Bureau of Meteorology, 2015) in the region of Australia where *E.*

393 *regnans* grows most rapidly, but this tree species is known to take

394 advantage of virtually all the water available to it. The *Populus deltoides*

395 individuals were measured in the Mississippi flood plain in years following

396 floods that removed all vegetation. Thus, these measurements likely

397 detected transpiration values near an upper known limit.

398 For *Eucalyptus regnans*, with xylem diameter of 200 μm (Petit *et al.*, 2010),

399 using Eq. (2) yields the corresponding pore-scale flow velocity of 0.76 μm/s.

400 For *Populus deltoides*, with xylem diameter 37 μm, the same calculation

401 yields 1.1 μm/s. Bloeschl and Sivapalan (1996) present a figure showing a

402 typical pore scale flow velocity of ca. 1 μm/s. Both inferred values are also in

403 line with the median hydraulic conductivity for soils, about 1 μm/s (Freeze

404 and Cherry, 1979; Clapp and Hornberger, 1978). These values correspond to

405 yearly pore-scale fluxes 30 m/yr, similar to the climatic maximum values of

406 20 m/yr given above. For both comparisons simultaneously, we used a
407 fundamental length scale of 100 μm, very close to the geometric mean of 87
408 μm. A second comparison is with data from Walsh *et al*. (2008), for which the
409 authors provided a portion of the cumulative height growth curves (Fig. 3).

4.3. Comparison with growth rates of *Eucalyptus*

411 According to Eq. (3), tree growth rates should not be constant in time, as
412 assumed in allometric scaling (*e.g.*, Enquist *et al*., 1998; 2007), but
413 correspond to a small negative power, a distinction which should be readily
414 distinguished when comparing with real data. The purpose here is dual: 1) to
415 establish which relationship is more nearly in accord with data trends and 2)
416 to see whether the coefficients assumed for assessing the cumulative height
417 growth as a function of time in the previous section also generate reasonable
418 explicit predictions for the growth rate as a function of time.

419 When assuming a growing season of 6 months and an upper limit on
420 transpired water of around 1650 mm (Box *et al*., 1989), predictions by Eq. (3)
421 compare well with observed growth rates for rapidly growing tree species,
422 such as *Eucalyptus regnans*, *Sequoia sempervirens*, *Sequoiadendron*
423 *giganteum*, or *Metasequoia glyptostroboides* (Fig. 4). Hunt and Manzoni
424 (2016), based on publications by Enquist *et al*. (1998; 2007), showed that
425 existing constant growth-rate predictions from allometric scaling
426 underestimate short-term growth rates by a factor of 10.

427 Note that, like Eq. (2), the growth rate given by Eq. (3) does not hold
428 indefinitely for tree height, though it appears to do so for the RRE of clones
429 (Hunt, 2017), where its predictions generate the size of aspen, spruce,
430 seagrass, as well as growth *rates* of *Armillaria* fungi and other underground
431 root systems of clonal bodies out to length scales of 10 km over 100,000
432 years. When individuals reach the height of the canopy, the competition for
433 light no longer dominates, and growth slows more precipitously or ceases
434 (Hunt and Manzoni, 2016). Further, there appears to be a physiological limit

435 of about 125 m on the height of trees due to hydraulic limitations such as
436 cavitation (Koch *et al*., 2004). The latter limit is visible in the BAAD database
437 in Fig. 1, and the former is evident for *Populus deltoides* in Fig. 2.

438 ## 4.4. Evaluation of the growing rate of the same tree
439 ## species in different geographic regions

440 We evaluated the growing rate of the same tree species in different
441 geographic regions using proxy variables of climate, substrate type (soil or
442 rock), soil characteristics, slope curvature, slope aspect, and tree hydraulic
443 conductivity.

444 Along a rainfall gradient in southeastern Australia, Givnish *et al*. (2012)
445 demonstrate that the heights of the tallest individuals of *E. regnans* are
446 linearly proportional to the ratio of precipitation to potential
447 evapotranspiration, ET_0. Since the transect studied was mostly at equal
448 latitudes (with roughly uniform ET_0), a Budyko (1958; 1974) representation of
449 ET (ET_0) implies that ET may be approximately substituted for P, though the
450 fraction of ET represented by transpiration may vary more significantly. We
451 found that growth curves of Eucalyptus in various locations conform to our
452 scaling prediction (Fig. 3) and the ratio of tallest tree heights from distinct
453 tree populations at any age is the same, compatible with the results of
454 Givnish *et al*. (2012). The uncertainty in this comparison stems mainly from
455 the inexact correspondence of the ratio of transpiration to ET_0 to the ratio of
456 P to ET_0.

457 Ryan and Yoder (1997) stated, "On the eastern slope of the Cascade
458 Mountains in Oregon ponderosa pine soar to 50 m. 30 km farther east, in a
459 drier climate, the same species struggles to attain 10 m." If soils do not vary
460 significantly, and topography is relatively consistent, the proposed change in
461 climate is due, to lowest order, to a contrast in precipitation. According to
462 the PRISM precipitation map of Oregon (Daly *et al*., 1994), the rainfall along
463 the Cascade crest ranges from 175 cm/yr to 400 cm/yr; 25 km to the east,

464   the rainfall contour is 50 cm/yr. The ratio is thus constrained to lie between

465   3.5:1 and 8:1, as measured along the crest from well south of Bend, OR,

466   almost to the Columbia River, a distance of roughly 200 km. The geometric

467   mean of 3.5 and 8 is 5.3, a discrepancy of 6% from the ratio (5) of the

468   heights of mature ponderosa pines from just east of the crest to 25 km

469   further east. The arithmetic mean is 5.75, only 15% off the observed ratio.

470   Oberhuber *et al*. (1998) studied the response of tree growth to dryness,

471   "Response function analysis indicates that at most sites wide rings are

472   significantly associated with high precipitation in April to June and cool

473   conditions in May of the current year…. Limited water availability causes a

474   homogeneous relationship of radial tree growth to climate at all habitats,

475   though site characteristics (slope magnitude, slope aspect, soil depth,

476   vegetation cover) differ substantially." Cool conditions in late spring reduce

477   water loss to direct evaporation, with the associated tendency therefore to

478   increase transpiration. By allometric scaling arguments (Enquist *et al*., 1998;

479   2007), increased diameters correlate strongly with increased tree height,

480   implying that increased transpiration increases height growth.

481   Murphy and Lugo (1986) indicated that in tropical forests with precipitation

482   between 500 mm and 2000 mm per year (geometric mean 1000 mm), tree

483   heights ranged from 10 m to 40 m (geometric mean of 20 m), and tree

484   growth at 1 yr from 1 m to 3 m (geometric mean, 1.7 m). But in tropical

485   forests with greater than 2000 mm precipitation per year, roughly twice as

486   great, the tree heights varied from 20 m to 84 m (geometric mean 41 m),

487   and the growth at 1 yr from 2 m to 5 m (geometric mean 3.2 m). As

488   precipitation increases by a factor 2, so do growth at one year (a factor 1.88)

489   and the final tree heights (a factor 2.05). The general conclusions are

490   independent of comparison scheme (arithmetic or geometric mean, two data

491   points or three), though the exact numbers will vary, of course. These

492   authors cited such a wide spread in values because their work was a meta-

493   study reviewing many separate studies.

4.5. Effect of substrate – soil or rock

494 Trees growing on bare rock present an unusual sight; normally crevices can
495 be located which the trees have exploited for their roots. Yet, even where
496 crevices serve as root pathways, the growth of such trees is typically
497 stunted. Is this also a product of a reduced transpiration? Ryan and Yoder
498 (1997) state, in particular, that "in the front range of the Colorado Rocky
499 Mountains a seed from a 25 m tall ponderosa pine (*Pinus ponderosa*) may fall
500 into a rocky crevice and never grow more than 1-2 m." The geometric mean
501 hydraulic conductivity of unconsolidated sediments at
502 (http://www.aqtesolv.com/aquifer-tests/aquifer_properties.htm, with source
503 Domenico and Schwartz, 1990) is 1.35×10^{-7} m/s (the geometric mean for
504 each sediment type calculated from its maximum and minimum value; the
505 overall geometric mean calculated over the seven sediment types given,
506 likewise for sedimentary and crystalline rocks). But the geometric mean of all
507 the sedimentary rock values cited is 3.03×10^{-9} m/s, smaller by a factor of
508 44. Contrarily, the geometric mean for crystalline rock types is 1.63×10^{-7} m/
509 s, slightly larger than for unconsolidated sediments. However, this sampling
510 includes permeable basalt and fractured rocks, with high permeability due to
511 fractures. Since it is primarily the rock matrix, from which transpired water
512 must come, these two categories should be excluded, as high fracture
513 permeability transports water away from roots. Excluding those two
514 categories, the ratio of the geometric mean of unconsolidated sediments to
515 crystalline rock hydraulic conductivity is 7. The geometric mean of 44 and 7
516 is 18. The ratio of 25 m to $(1 \text{ m} \times 2 \text{ m})^{0.5}$ is also 18. Thus, a reasonable ratio
517 of hydraulic conductivities for permeability-limited flow is the ratio of
518 observed heights, consistent with attributing growth variability to variability
519 in permeability-limited transpiration. Significantly, Freeze and Cherry (1979)
520 report nearly the same spreads of hydraulic conductivity values as quoted
521 above. Thus, trees grow faster and taller on soil than on rock because of its
522 higher hydraulic conductivity and consequent greater transpiration.

4.6. Effect of soil characteristics

Hydrophobicity. Russel and Woolhouse (2012) investigated variability in the height of *Sequoia sempervirens* along a soil characteristic gradient near Cape Mendocino, California USA. Our assertion that hydrophobicity may constrain water uptake, and thus growth, contrasts with that of the authors, who attribute the variation in growth to variable soil chemistry, evinced by the pH gradient.

Trees grow shorter on more acidic soils because they are more hydrophobic, thus reducing water fluxes. Our interpretation is based on the reported correlation between hydrophobicity and soil pH value. The authors state, "The (youngest) terrace [VI] has well-drained soils rich in organic matter and nutrients. The (older, *i.e.*, I - III) terraces where pygmy forest(s) are found contain highly acidic, extremely podzolized soils with a *hydrophobic hardpan*." However, the authors do not report hydraulic conductivity at their site, making it necessary to find data for broadly analogous conditions.

Table 1. Soil characteristics of Cape Mendocino Terraces (Russel and Woolhouse (2012)

Stratum	I	II	III	IV	V	VI
Soil pH	4.8	4.95	4.95	5	5.5	5.95
Canopy Height (m)	2.09	5.64	11.95	21.5	39.6	58.3

While the quoted range of pH values correlates well with height, soil pH correlates equally strongly with hydrophobicity (Lozano *et al*., 2013), lower pH values being associated with more hydrophobic soils. Moreover, de Bano (1971) concluded, "Horizontal infiltration was 25 times slower in water repellent soil than in wettable soil." Similarly, Rowe (1941) found that vertical infiltration was reduced from 8.9 cm /hr to 0.304 cm/hr (by a factor of 29) through periodic chaparral burning, a hydrophobicity interpreted by de Bano and Krammes (2000) as due to coatings of organics on particles. Both

550   values, 25 and 29 are compatible with the ratio (28) of the tree heights in

551   Zone VI to that in Zone I. These growth ratios are similar to the maximum

552   *regnans* height range (20) as well as the ratio of precipitation to pan

553   evaporation along the rainfall gradient in southeastern Australia (Givnish *et*

554   *al*. 2014). Further, Wallis *et al*., 1990 found that infiltration rates varied by a

555   factor 6 over a horizontal distance 10 m between strongly and moderately

556   water-repellent agricultural (Himatangi) sands. This smaller ratio, 6

557   (compared with 28), derived from soils differing only in the degree of water

558   repellency, and is similar to the height ratio (nearly 6) in soils I – III of Russel

559   and Woolhouse (2012). Of course, other aspects of podzolization or high

560   acidity may also inhibit growth of redwoods in zones 1–3.

561   **Compaction.** Tardieu *et al*. (1991) showed that compaction reduced

562   stomatal conductance even though plants on compacted soil showed water

563   relations comparable to those of plants on uncompacted soils." Reductions in

564   stomatal conductance reduce transpiration (*e.g*., Motzer *et al*., 2005). In

565   accord with Kozlowski (1999) who noted that the deleterious effects on the

566   hydraulic properties of soil could be responsible for the diminished plant

567   growth, we hypothesize that the stronger dependence of hydraulic

568   conductivity on pore-size distributions than that of a characteristic pressure

569   is the likely cause of reduced growth rates of plants on compacted soils.

570   Thus, plants grow more slowly on compacted soils because the reduction in

571   pore sizes strongly inhibits flow.

4.7. Topography

573   **Surface Curvature.** Plant growth rates should be positively correlated with

574   local topographic curvature, particularly in areas with more arid climates,

575   because surface run-off tends to collect in hollows, increasing infiltration and

576   thus also transpiration. McNabb (1989) found that yellow poplar (*Tulipifera*

577   *liriodendron*) trees in the southeastern USA averaged 50 m in zones of

578   convergent topography (*i.e*., valley bottoms) but only 35 m in divergent

579   topography (ridgetops). This distinction may be due to variation in water

580 fluxes entering the soil, which provides a limit to water volumes extracted

581 from the soil. Dunne *et al*. (1991) modeled effects of microtopography on

582 stormwater infiltration. In Fig. 16 these authors showed uniform infiltration

583 rates of about 2.5 cm/hr along steeper slopes, independent of position. But

584 with less steep topography, the infiltration rate could increase from 2.5

585 cm/hr along the ridge to over 4 cm/hr towards the bottom of the slope, a

586 ratio exceeding 1.6. The ratio 50 m/35 m is 1.43. Our conclusion is

587 compatible with that of Berges *et al*. (2005), although these authors

588 interpreted topographic variability in terms of soil water, "The effect of

589 topography on site index was consistent with the effect of soil water

590 capacity," and concluded that, "Most site index variance was related to local

591 soil factors and corroborated the hypothesis that sessile oak growth was

592 regulated by the combined influence of soil water and nutrient budgets." The

593 example regarding slope aspect below shows difficulties in general

594 interpretation in terms of water content, however.

595 Oberhuber and Koffler (2000). These authors studied small-scale variability

596 in the growth of trees in a water-limited montane (elevation 750 m) region

597 and produced the following table for tree heights of a post-glacial rockslide

598 region in a dry valley of the Swiss Alps.

599 Table 2. Data related to topography and the tree height (Oberhuber and

600 Koffer, 2000)

Site	Topography	Slope (degrees)	Height (m)
K130	slope	50	4 - 6
K131	hollow	<20	10
K132	plateau	Assumed 0	8
K134	slope	40	4 - 6
K135	hollow	Assumed 0	10
K136	ridgetop	20	5
K 137	toe of slope	<15	13
K138	plateau	Assumed 0	5

601

602 Tree ages, except for K135 (92 years), were between 105 and 153 years,

603 with mean value 125 years and typical variability 15%. Thus, to first order,

604 one can neglect age as a primary factor behind variation in tree height. Sites

605 in hollows and at the toe of the slope have positive curvature, plateaus and

606 mid-slope near zero curvature, ridgetops negative. Tree height decreases

607 with increasing slope, from about 8 m to 6 m for slopes changing from 0 to

608 50 degrees, but R^2 is only 0.15. Slope curvature is likely more important,

609 since regression (not shown) of height on curvature index (1 if positive, -1 if

610 negative, and 0 otherwise) has $R^2 = 0.7$. Here, the ratio of maximum to

611 minimum tree heights, excluding K137 at the toe of the slope, is consistently

612 a factor 2. Inclusion of the site at the toe of the slope, which will also have a

613 significant positive curvature, but intercept even more water, increases the

614 ratio further. Either way, 2 is larger than the tree height ratio (1.43) from

615 McNabb (1989), and the ratio of infiltration rates (> 1.6) of Dunne *et al*.

616 (1991). However, the large slopes and slope differences, and the proclivity to

617 landslides, suggest a greater curvature than observed by McNabb (1989) or

618 modeled by Dunne *et al*. (1991).

619 **Slope aspect.** Tree growth should be inhibited (in the Northern

620 Hemisphere) on southward and westward facing slopes because a greater

621 fraction of *ET* is lost to direct evaporation. Fekedulegn *et al*. (2003)

622 determined that in a mixed hardwood forest in West Virginia at mean

623 elevation about 224 m, and with precipitation 130 cm/yr, there is a strong

624 correlation between the slope aspect and tree height, "Aspect affects the

625 amount and daily cycle of solar radiation received at different times of the

626 year and has a strong influence on the microclimate, especially air

627 temperature, humidity, and soil moisture (Rosenberg *et al*.,1983)." Net

628 radiation on southwestern slopes was 24% higher than on northeastern

629 slopes (Lee and Sypolt, 1974), while tree heights of the four species

630 investigated averaged 17% lower on the southwestern slope. However, the

631 correlation between aspect and soil water *content* was imperfect: "Although

632 it is generally believed that south-facing slopes are drier and soil moisture

633 deficits limit tree growth on these sites, a study by Lee and Sypolt (1974) has

634 shown that, in some years, available soil moisture was not significantly

635 different by aspect in West Virginia." Even when soil moisture content does

636 not vary across aspect, however, increased solar radiation impinging on a

637 southwestern slope will increase evaporation; if the soil moisture content is

638 unchanged, transpiration was less. Mu *et al*. (2011) showed that, worldwide,

639 mean evaporation typically makes up 39% of evapotranspiration, a mean

640 value obtained also for precipitation about 130 cm/yr, appropriate to the site.

641 Mu *et al*. (2011) also state that, for temperate deciduous forests, evaporation

642 is only 33% of evapotranspiration. In the first case, the observed increase of

643 24% would bring evaporation to 48.3%, decreasing transpiration from 61% to

644 51.6%, a reduction of 15%, quite close to the height reductions for yellow

645 poplar (17%), northern red oak (14%), and red maple (15%), though smaller

646 than for chestnut oak (24%). If evaporation is only 33% of

647 evapotranspiration, a 24% increase in evaporation would decrease

648 transpiration by only 12%.

649 Liang *et al*. (2006) studied growth of spruce and junipers at the eastern

650 margin of the Tibetan Plateau. Soil depths on east and west facing slopes

651 were the same. Junipers on the east facing slope reached a height of 10 m,

652 but only 8.5 m on the west, whereas spruce grew to 14 m on the east and 12

653 m on the west). These authors stated, "The west-facing slope experiences a

654 drier microclimate since it receives more solar radiation and hence stronger

655 evaporation of soil water than the east-facing slope (Rosenberg *et al*.,

656 1983)." Whether the results match predictions quantitatively is not

657 addressed in this case as there is an even greater lack of relevant

658 information for assessment than in the previous case.

4.8. Xylem Characteristics and Plant Hydraulic Conductivity

Larger xylem diameters should promote faster growth rates from a reduction in hydraulic resistance and increased transpiration rates. Zach *et al*. (2010) found, "In humid environments, where trees rarely experience severe soil water limitation, the hydraulic system of trees requires a functional architecture for effectively transporting water to the crown despite a comparably low atmospheric evaporative demand for most of the year" (Zach *et al*. 2010). Fig. 5, digitized from Zach *et al*. (2010), demonstrates clear correlation of xylem diameter with tree height. In this case, the strong dependence of hydraulic conductance on xylem diameter together with minimal soil water limitations implies a strong correlation of growth with tree water transport as well. From Fan *et al*. (2012), "In this study, we found xylem anatomical traits were much better predictors of growth rate [and stature] than wood density, which is consistent with their more direct and stronger correlation with hydraulic conductivity." Hubbard *et al*. (2001) offered as title, "Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine." A linear variance of photosynthesis with plant hydraulic conductance, *i.e*., water transport, is consistent with Eq. (2), which implies a linear dependence of height on transpiration.

5. Discussion and Conclusions

A possible application of the present results is to enhanced drought susceptibility of trees in the western continental USA and diminution of water resources. The recent increase in drought mortality may be partly due to higher temperatures, but it certainly also has a component related to higher tree density brought on by a century of fire suppression. At higher densities, less water is available per tree. Drought weakened trees are also more

687 susceptible to pathogens. The increased (dead) tree density is then linked to

688 higher intensity fires with higher risks to encroaching populations. Any

689 theory capable of predicting both tree growth rates in time and the

690 dependence of NPP on transpiration should have relevance to the water

691 balance in a changing environment and thus water resources.

692 If one can reliably predict tree growth patterns on the basis of their water

693 consumption, it should be possible to analyze patterns of fire, tree growth

694 and health, and water resources in concert. Consider that biological

695 productivity has relevance for potential feedbacks to climate change in view

696 of the complex interaction between water resources, transpiration, and

697 productivity. Thus, increases in productivity due to fire suppression practices

698 should contribute to longer-term shallow subsurface water shortages (with

699 correspondingly reduced streamflow) and greater susceptibility of forests to

700 inter-annual to decadal scale climatic fluctuations, which, according to

701 models, should be enhanced in a warming climate. Making such relationships

702 more predictive should help to discern how tree population changes

703 introduced by suppression are responsible for an increased risk of larger

704 conflagrations, as well as how best to reverse impacts of suppression.

705 In order to address the specific input of a forest changing with time, it is

706 necessary to expand the analysis at the beginning. Eq. (2) for RRE (and,

707 thus, also tree height) as a function of time yields, for $t = t_g$, $RRE = T_g$. This

708 result is for a single tree and a single growing season and was used equally

709 for individuals as for ecosystems. First, address complications from

710 advancing age of individual trees, and then use this result as a basis to

711 consider entire tree populations. Using the predicted percolation mass fractal

712 dimensionality in 2D of $d_f = 1.9$, Hunt (2017) suggested that NPP should then

713 be expressed as $NPP = C\ ET^{1.9}$, where C is an, as yet, unknown constant.

714 Extended to longer time intervals, one can write $RRE^{1.9} = [T_g(1$ year) (Age

715 (years))$^{-0.17}]^{1.9}$. This is a decreasing function of time. An additional factor that

716 produces a decrease in time may come from tree thinning with increasing

717   stand age. If tree density is inversely proportional to the square of the RRE,

718   then ecosystem NPP is proportional to $RRE^{-0.1}$, producing a diminishing

719   productivity with increasing tree size. However, in contrast to canopies, tree

720   roots may overlap, implying that the density may be greater than RRE^{-2}.

721   Further, above ground biomass is likely proportional to a larger power of RRE

722   (and tree height) than root biomass, since above-ground tree structures are

723   more nearly expressed in 3D than in 2D. Finally, as trees age, apportionment

724   of transpiration to various functions changes. Nevertheless, the current

725   analysis is generally compatible with Ryan's observation regarding the

726   diminution of productivity of forests with increasing age.

727   In the intermountain west, suppression of fires tends to allow the growth of

728   younger trees and an increased stand density simultaneously. According to

729   the present analysis, both the tendency to a higher density of trees and a

730   translation to a younger population should increase both NPP and, thus, ET

731   demands. Increased ET will strain water resources and long-term water

732   storage, while increasing demand during drought, all of which would be

733   expected to increase drought susceptibility of trees. Thus, extensions of the

734   present framework to address more fully the specific conditions of the

735   western USA may help to quantify drought stresses in a changing climate

736   and thus assess the magnitudes of risks associated with particular

737   management strategies.

738   A single relationship from the scaling of optimal paths from percolation

739   theory accounts for nutrient and transpiration limits on woody plant growth.

740   The conceptual bases of this relationship are consistent with inferences of

741   other recent studies (*e.g.*, Popova *et al*., 2016). Any such spatio-temporal

742   scaling relationship relating tree height to its age (from germination),

743   requires two site-specific parameters, one a spatial scale and one a temporal

744   scale. Here, the length scale is considered the smaller of the soil pore or

745   plant xylem diameter, while the time scale is the ratio of the length scale to

746   the pore-scale flow rate. Since the relationship is a power law, its

747 fundamental constants may be referred to larger scales, such as a growing

748 season and the transpiration during the growing season. The relevance of

749 the transpiration allows reasonable prediction of tree height variability as

750 function of climate, substrate, soil characteristics (including compaction and

751 water-repellency), and topography (slope curvature and aspect), while the

752 sublinear power law explains why tree growth slows with age. These

753 predictions work quite well across a variety of factors that limit tree growth.

754 Thus, the present results may help formulation of more accurate and general

755 plant growth models and help to understand a number of seemingly

756 unrelated puzzles in the ecology literature. But note that a similar hypothesis

757 of hydraulic limitations on tree height was already formulated by Ryan and

758 Yoder (1997).

759 The relative success of the model suggests that it is not directly the soil

760 water potential, or the soil water content, that governs growth rates, but that

761 water flow and coupled transpiration rate determine plant growth. Of course,

762 rapid increase in hydraulic conductivity of a soil with increasing water

763 content provides an important link between these two variables, and the

764 decrease in water potential with increasing water content also makes it

765 easier for plants to draw water from the soil. Thus, the two concepts and

766 their related variables are often well-correlated. One system studied (aspect

767 variations of tree height in Pennsylvania) showed a clearer correlation

768 between transpiration and tree growth than between soil water content and

769 tree growth. While a location may have too much water, it is difficult for a

770 tree to transpire too much, since excess soil moisture implies water storage

771 that exceeds the capacity of a tree to transpire.

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1080 **Figure Captions**

1081 Figure 1. Comparison of Eq. (1) for maximum and minimum flow rates with
1082 Falster BAAD database of woody plant heights as a function of time. The
1083 maximum and minimum flow rates at the pore scale correspond to 20 m/yr
1084 and 24 cm/yr, respectively. The red and blue dots are results of Eq. 2
1085 evaluated at the maximum and minimum transpiration rates, 1650 mm and
1086 20 mm for a growing season of 180 days), and are nearly on the lines
1087 generated by the pore-scale limits. The hydraulic limit of about 125 m (Koch
1088 *et al*. 2004) provides an upper bound to plant height, but not to root radial
1089 extent, which follows the above upper limit down to five minutes for root tip
1090 extension, as well as out to 10,000 years and 10 km, when clones are
1091 included (Hunt and Manzoni, 2016; Hunt, 2017).

1092 Figure 2. Direct comparison of the height of Eucalyptus regnans and Populus
1093 deltoides with Eq. (2) using six months as the growing season and 1650 mm
1094 as the growing season transpiration. Data sources are given in the text.
1095 Deviations from Eq. (2) that set on at about 30-40 yr may be related to
1096 canopy heights of about 50 m.

1097 Figure 3. Data from Walsh *et al*. (2008) regarding Eucalyptus height as a
1098 function of time compared with present scaling function using varying values
1099 of T_g, in accord with varying transpiration rates.

1100 Figure 4. Growth rates as a function of time for several species of rapidly
1101 growing trees compared with the scaling prediction of Eq. 3 with a maximum

1102 flow rate of 20 m/yr, and a fundamental length scale of 10 µm. The most
1103 extreme case considered, *Eucalyptus regnans* can have xylem diameters of
1104 up to 200 µm (Petit, 2010). But the fact that $D_{opt} = 1.21$ is not very different
1105 from 1 leads to only a weak dependence on xylem diameter, and even (200
1106 µm/10 µm)$^{0.21}$, is a factor 1.87. With one exception, the data for growth rates
1107 were already collected from primary sources and reported in Hunt and
1108 Manzoni, 2016; the source there for *Eucalyptus regnans* included Ryan and
1109 Yoder (1997). New in this graph is the value of nearly 6 m/yr for *Eucalyptus*
1110 *regnans* at a fraction of a growing season from Cremer (1975). Angiosperm
1111 and gymnosperm predictions of constant growth rates are from allometry.

1112 Figure 5. Tree height as a function of mean trunk xylem diameter (Data
1113 digitized from Zach *et al*. 2010).

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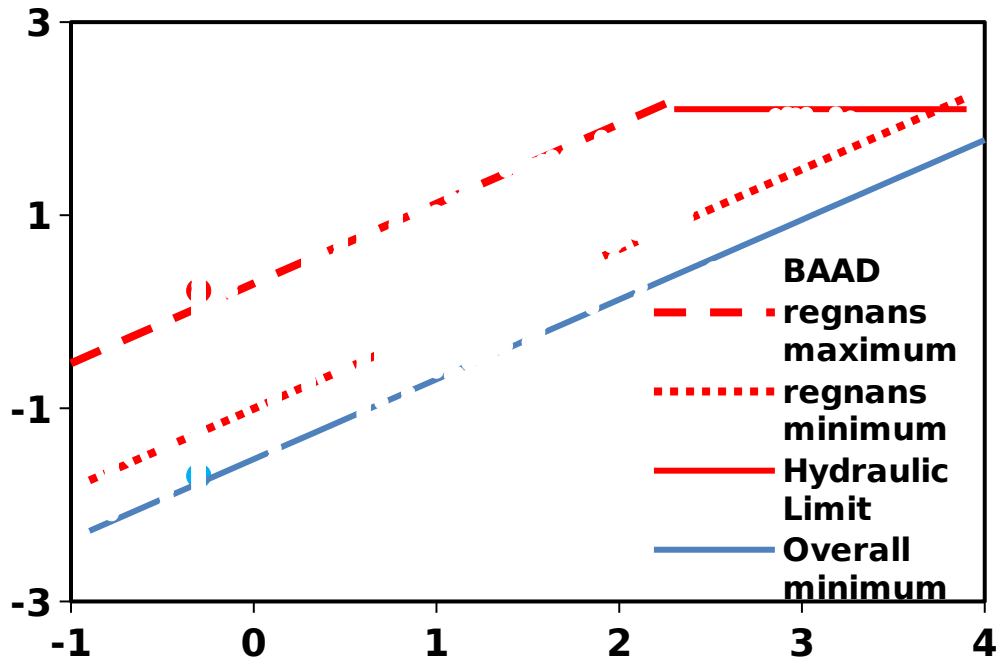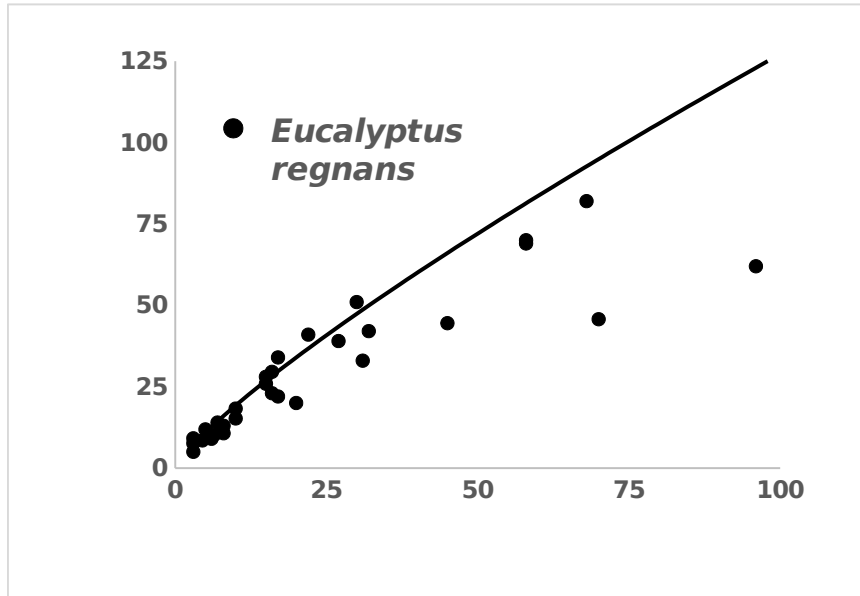1116

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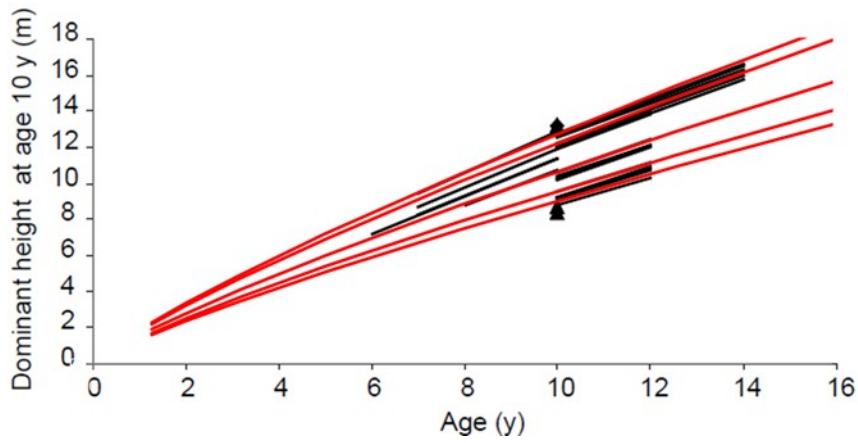1121 **Figures**

1122

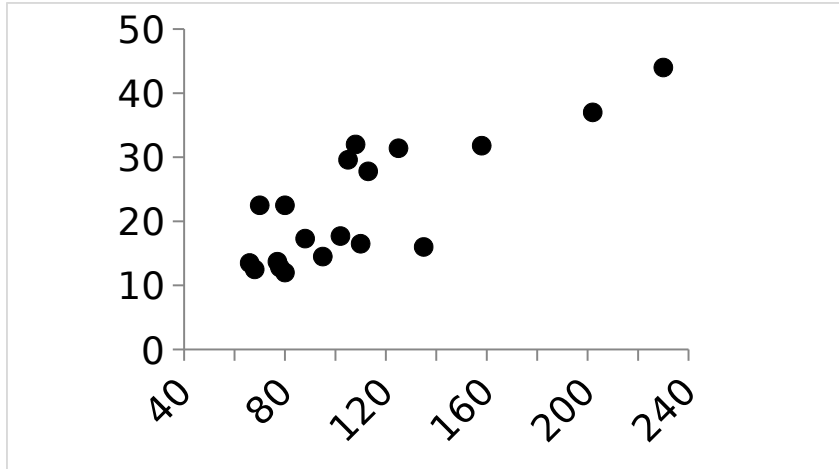1123   Figure 1

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Figure 5.

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