

Lawrence Berkeley National Laboratory

LBL Publications

Title

Test of model of equivalence of tree height growth and transpiration rates in percolation-based phenomenology for root-soil interaction

Permalink

<https://escholarship.org/uc/item/5xp371gz>

Authors

Hunt, AG

Faybishenko, B

Powell, TL

Publication Date

2022-03-01

DOI

10.1016/j.ecolmodel.2021.109853

Copyright Information

This work is made available under the terms of a Creative Commons Attribution-NonCommercial License, available at <https://creativecommons.org/licenses/by-nc/4.0/>

Peer reviewed

1 Test of model of equivalence of tree height growth and transpiration rates in 2 percolation-based phenomenology for root-soil interaction

3
4 A. G. Hunt¹, B. Faybishenko², and T. L. Powell²

5 ¹Wright State University, ²Lawrence Berkeley National Laboratory

7 Introduction

8 We recently introduced a phenomenological model to represent root-soil interactions that accounts
9 for variability in tree growth on local scales and within species (Hunt et al., 2020). Here, using
10 publicly available datasets, we examine the developed model to provide additional empirical
11 evidence, which also gives novel insight into two particular tree species, *Eucalyptus regnans* and
12 *Eucalyptus sieberri*. In particular, we discovered two novel aspects of the model: a power-law time
13 dependence with a different power-law exponent than usually heretofore applied, and apparently
14 a direct equivalence of results for transpiration and growth rates. Also, although our original
15 expectation was that growth and transpiration were merely proportional, comparison of the entire
16 BAAD data set (Falster et al. 2015) for tree height with our model (Hunt et al. 2020, Fig. 1) already
17 suggested approximate equality of these disparate measurements (volume/area, height). In the
18 present manuscript we find further evidence for equivalence of the two measurements and provide
19 additional theoretical basis for a model assumption regarding constancy of sap flow rates.

20 Conceptual Approach and Mathematical Model

21 The pore space of soils is well modeled by a network with at least some random characteristics
22 using methods of percolation theory (Sahimi, 1991, 1994; Stauffer and Aharony; 1994). The pore
23 necks represent the greatest resistances, and water flow tends to be concentrated along paths with
24 the least cumulative resistance (Hunt et al. 2013). These paths, whenever they intersect with
25 nutrient sources, will also carry fluxes thereof (Hunt and Manzoni, 2015). It is thus conjectured
26 that roots will also follow such paths, both for reasons of minimizing energy expenditure, and on
27 account of an increased likelihood of locating nutrient sources (Hunt and Manzoni, 2015). This
28 argument is the product of the understanding that the growth of a directed network (tree root system)
29 into a random network (the soil) is best understood in a network theory (Hunt and Manzoni, 2015),
30 a perspective that is completely distinct from the more typical approach of embedding roots in a
31 continuum (Koch et al. 2018) imbued with 40+ property parameters generated from capillary
32 bundle models.

33 In the current paper, the developed model is applied specifically to the Eucalyptus ecosystems of
34 southeastern Australia's Yarra Ranges, which are located in regions of high precipitation and
35 relatively abundant water resources, but where fire plays vital role. After fire, seeds stored in
36 woody capsules at the crowns of trees fall to the ground, where they germinate by the dozens per
37 square meter (Vertessey et al. 2001). Under intense competition for sunlight and water, seedlings

38 and mature trees grow as rapidly as possible. Under such conditions, because of competition for
 39 nutrients and water within the soil, the pore network likely provides the strongest limits on growth.
 40 By the time trees reach 80 meters in height, the number of survivors per hectare has been reduced
 41 from hundreds of thousands to near one.

42 In our conceptual approach, the growth of trees is proposed to be restricted primarily by constraints
 43 imposed by root searches for resources (such as water and nutrients), and the soil root growth paths
 44 are generally characterized by a minimum cumulative impedance. Based on the concept of
 45 percolation theory, the soil flow path network is fractal, and, thus, tortuous. The tortuosity is
 46 defined through an exponent that is proposed to relate the actual root length L to the root radial
 47 extent (RRE). The exponent is known as the optimal path exponent (Porto et al., 1997) and is found
 48 from simulations on large networks.

49 The results of data analysis presented in this paper show that the model of paths of minimal
 50 resistance involves a single parameter characterizing tortuosity that takes on only two values, one
 51 is for root systems confined to a thin near-surface layer, and the other one is for a more isotropic
 52 and deeper soil-root layer. The RRE has been previously shown to be equivalent to tree height (H)
 53 over length scales from about 1 m to 40 m (Hunt and Manzoni, 2015, and data sources therein).
 54 The actual root length (L) can be defined in terms of the optimal paths' exponent, D_{opt} , given by
 55 (Hunt et al., 2020)

$$56 \quad L \sim RRE^{D_{opt}}$$

57 To apply this relationship for predicting the tree height as a function of time, it is necessary to
 58 provide length and time scales and a value for D_{opt} . Taking into account the conventional
 59 understanding that for most trees the root systems are shallow--usually <2 m depth (Hunt and
 60 Manzoni, 2015; Hunt, 2017; Hunt et al., 2020), the relevant tortuosity of the paths was suggested
 61 to be described by the two-dimensional (2D) optimal paths exponent of 1.21 (Sheppard et al.,
 62 1999). This value is justified by arguing that a resource search in the shallow subsurface is largely
 63 confined to paths restricted to form in two dimensions. However, trees growing under water-
 64 limited conditions or trees with exceptionally high transpiration demand might have deeper root
 65 systems and a nearly isotropic water sourcing. In such cases, one could expect that the root system
 66 would follow optimal paths in three dimensions (3D) with an exponent of 1.43 (Sheppard et al.
 67 1999).

68 The relationship for the RRE can then be given by

$$69 \quad RRE = x_0 \left(\frac{t}{t_0} \right)^{1/D_{opt}} \quad (1)$$

70 where t is the time since germination, x_0 is a pore-scale distance, and $t_0 = x_0/v_0$, with v_0 being a
 71 pore-scale flow rate.

72 An upscaled version of relationship (1) and the equivalence of H to RRE can be used to write the
 73 expression for long-term prediction of H (Hunt and Manzoni, 2015; Hunt et al. 2020).

$$74 \quad H = T_g \left(\frac{t}{t_g} \right)^{1/D_{opt}} \quad (2)$$

75 where T_g is interpreted as the transpiration during a growing season, and t_g is the duration of a
76 growing season.

77 The procedure for determining H from Equation (2) outlined below implies an application of
78 stepwise upscaling by assigning the declining rate of increase either directly to H , while holding
79 T_g as the value of the transpiration for the *first* year growing season, or assigning the decline to T_g
80 as a function of time.

81 In the following, we approximate n years of time, t_n as nt_g , use T_n for the transpiration over the
82 entire n years, while approximating the value of T_g for the growing season as appropriate for the
83 entire first year; these approximations could produce discrepancies when transpiration demand is
84 high outside the growing season. A further upscaled version of Equation (2) would then read, $H =$
85 $T_n (t/nt_n)^{1/D_{opt}}$. If we substitute $t = nt_g$ directly into Equation (2), however, the result is $H = T_g n^{1/D_{opt}}$.
86 Thus, $T_n = T_g n^{1/D_{opt}}$. H has the same value in both cases. The identical result is obtained if one
87 simply notes that, for the given t -dependence, H will not change at any t as long as $T_n/(t_n)^{1/D_{opt}} =$
88 $T_g/(t_g)^{1/D_{opt}}$ for all n .

89 Now, the expression for the rate of tree growth dH/dt can be given by

$$90 \quad \frac{dH}{dt} = \frac{1}{D_{opt}} \frac{T_g}{t_g} \left(\frac{t}{t_g} \right)^{\left(\frac{1}{D_{opt}} - 1 \right)} = \frac{1}{D_{opt}} \frac{T_g}{t_g} n^{\left(\frac{1}{D_{opt}} - 1 \right)} = \frac{1}{D_{opt}} \frac{T_n}{t_n} = \frac{1}{D_{opt}} \frac{T_n}{nt_g} \quad (3)$$

91 In accord with the discussion above, the fourth expression yields the transpiration *rate* over the
92 tree lifetime, T_n/nt_g . But the second expression yields for an n^{th} year transpiration T_g times $n^{(1/D_{opt})-1}$
93 ¹ divided by the growing season length, t_g . For the growth rate in the n^{th} year, Equation (3) yields
94 the product of the rate in the first year, T_g/t_g and the factor, $n^{(1/D_{opt})-1}$. Thus, the rate of tree growth
95 declines in time because the transpiration declines in time. In other words, the added height in the
96 first year is T_g , and the rate of height increase is T_g/t_g , but in subsequent years, the transpiration
97 and, as a consequence, the tree growth is reduced by the factor given by

$$98 \quad \left(\frac{t}{t_g} \right)^{\left(\frac{1}{D_{opt}} - 1 \right)} \quad (4)$$

99 Thus, a graph of either the tree growth, or a graph of transpiration, as a function of time is expected
100 to conform to a power-law with the power exponent of $(1/D_{opt} - 1)$, and the intercept equals the
101 transpiration rate in the first year. For $D_{opt} = 1.21$ (for 2D), $1/D_{opt} - 1 = -0.17$, while for $D_{opt} =$
102 1.43 (for 3D), $1/D_{opt} - 1 = -0.301$.

103 Data sources

104 Our search for data was constrained by the publicly available datasets. Very little tabulated data
105 for growth rates of *Eucalyptus* species are readily available in the literature. We found four values
106 for *Eucalyptus regnans* from three separate sources. The growth rate data used in the current paper
107 were obtained from publications by Cremer (1975), Ryan and Yoder (1997), Vertessy et al. (2001)

108 and Givnish et al. (2014). While the growth data appear to be reliable, there is no indication, *a*
109 *priori*, of consistency in the environmental and ecological conditions, under which the trees were
110 growing. The transpiration and growth data for *Eucalyptus regnans* from Vertessy et al. (2001) are
111 for overstory trees growing in uniform stands that range in age from about 15 years to 300 years,
112 with the area of each stand having been clear-cut or burned at a known date. The overstory trees
113 were reported to have self-thinned into a state with little light limitation. Simultaneous
114 measurements of transpiration were taken from the understory *Pomaderris aspera* (hazel) trees.
115 Additional measurements included interception and leaf litter evaporation. Vertessy et al. (2001,
116 Figure 7) illustrated the changes with time of the mean annual understory transpiration, mean
117 annual soil and litter evaporation, mean annual rainfall interception, and mean annual water. Sap
118 flow velocities (Vertessy et al. 2001) were measured directly by using sap flow loggers at multiple
119 locations in the xylem at breast height at intervals of 20 minutes for each tree. Measurements were
120 repeated on multiple trees for time periods between 5- and 60-days during spring and summer.
121 Vertessy et al. (2001) found average values for each age group. Distinctions between sap flow
122 rates at different ages were found by to have no statistical significance in either the mountain ash
123 or hazel trees. All field measurements were taken from the Maroondah catchments, which are
124 located approximately 80 km northeast of Melbourne, Australia.

125 Cremer (1975) documented a height growth of 50cm in the first 30 days, for a rate of just over 600
126 cm/yr. Ryan and Yoder (1997) stated, “A young mountain ash (*Eucalyptus regnans*) growing east
127 of Melbourne may grow 200–300 cm per year in height. By 90 years of age, height growth has
128 slowed to 50 cm yr⁻¹. By 150 years, height growth has virtually stopped, although the tree may live
129 for another century or more.” Givnish et al. (2014) documented growth of 20 cm yr⁻¹ even at the
130 age of 300 yrs.

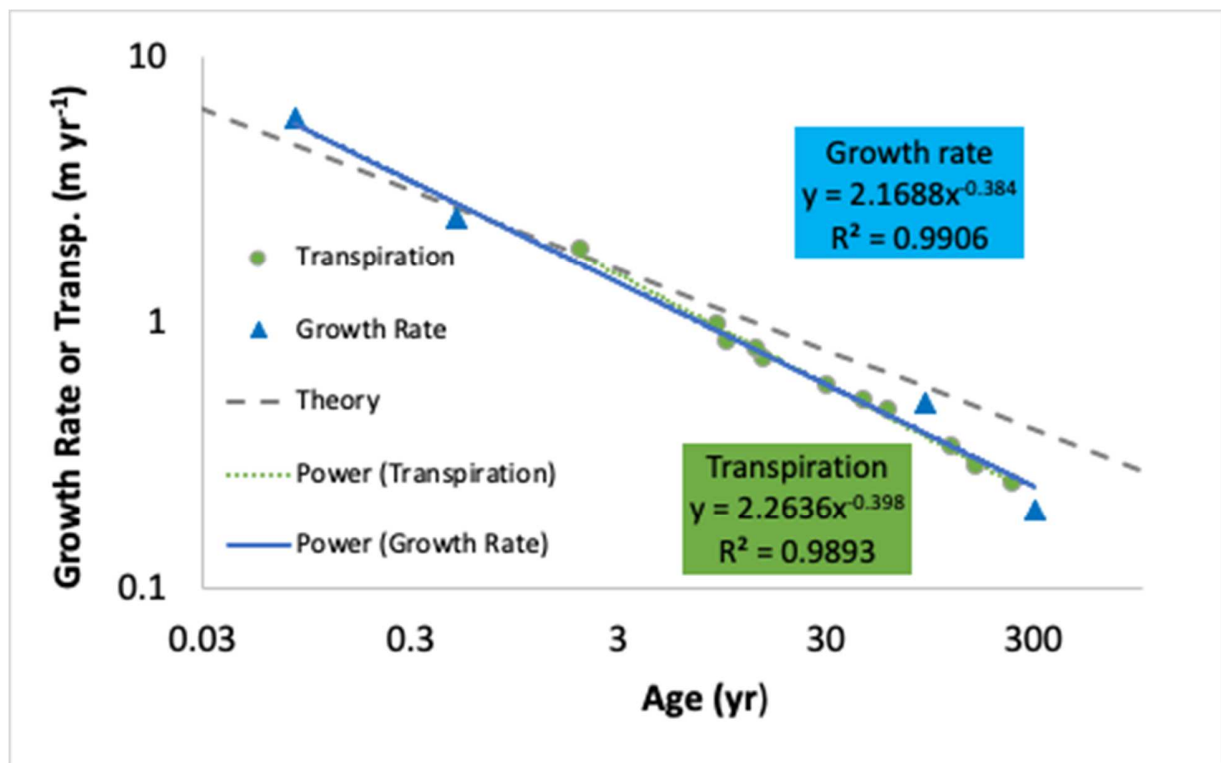
131 Transpiration rates of *Eucalyptus regnans* and *Eucalyptus sieberri* in the central highlands of
132 Victoria, southeastern Australia, were obtained from Vertessy et al. (2001), who provided six
133 experimental data points, and Roberts et al. (2001), who contributed three data points. For the study
134 area given in these papers, the annual precipitation ranges from 120 cm yr⁻¹ at lower elevations to
135 280 cm yr⁻¹ at the higher elevations. For the Maroondah catchments studied, Vertessy et al. (2001)
136 use as an average precipitation 180 cm yr⁻¹ to constrain their data. We used an average precipitation
137 of 200 cm yr⁻¹ to calculate an approximate upper bound for T_g/t_g from Equation (3). By simple water
138 conservation arguments (Budyko, 1958), the annual transpiration rate, T_g/t_g , of an ecosystem such
139 as a forest, except in relatively narrow riparian zones, cannot ordinarily exceed the annual
140 precipitation.

141 Givnish et al. (2014) found that the maximum heights of *Eucalyptus* trees along a climate gradient
142 were proportional to the ratio of precipitation to pan evaporation, from heights of 4 m to over 80
143 m. Ryan and Yoder (1997) have noted a proportionality between early growth rates and final
144 heights of trees.

145 Results of Data Analysis

146 Growth rates and transpiration rates are graphed in Figure 1 for the theoretical 3D prediction ($D_{opt} =$
 147 1.43, and the power-law exponent is -0.301) and empirical data. Figure 1 shows that the power-law
 148 fits both of these two different variables—the growth rate and transpiration rate with slightly different
 149 exponents of -0.384 and -0.398, respectively, and numerical prefactors that differ only by 4%. The
 150 R^2 values are both high, 0.991 and 0.989, respectively. A power-law exponent of a combined dataset
 151 of both growth and transpiration rates is -0.391, with the $R^2=0.992$, exceeding the theoretical value
 152 of -0.301 for the 3D prediction. Lacking unambiguous guidance in a process of significant complexity,
 153 the numerical prefactor of the theoretical prediction was chosen as 220 cm yr^{-1} in accord with the
 154 corresponding values from the fits of the experimental data.

155
 156



157

158 Figure 1. Comparison of the power-law function based on the 3D optimal paths exponent with
 159 power-law functions of empirical transpiration and tree height growth rates over the age of even-
 160 aged stands. The extreme height growth rates (600 cm yr^{-1} at ca. 1 month, and 20 cm yr^{-1} at 300
 161 years for individual trees are taken from Cremer (1975) and Givnish et al. (2014); the other two
 162 height growth rates are values cited by Ryan and Yoder (1997). The transpiration values are
 163 derived from long-term measurements of sap area index and sap velocities of multiple trees
 164 (Vertessy et al., 2001).

165

166 The 3D optimal paths exponent and empirical exponents give a better prediction of the decay of
 167 the growth and transpiration rates with age than does the 2D exponent, which is in accord with the
 168 suggestion that *Eucalypts* have a deep root structure, rather than one confined mostly to the top
 169 meter or two of soil. Nevertheless, early growth rates exceed the prediction and suggest that at
 170 young ages, *Eucalypts* access nearly all the water available, a result that is compatible with the
 171 conclusions of Vertessy et al. (2001) regarding the strongly negative influence young *Eucalyptus*
 172 forests have on water resources, when stem separations are still less than stem heights.

173 Very young *Eucalypts* of uniform age (Vertessy et al., 2001; Roberts et al., 2001) may take nearly
 174 all the water available. Note that according to Figure 6 of Vertessy et al. (2001) the total ecosystem
 175 evapotranspiration, which at young ages is traceable primarily to *Eucalyptus regnans*, approach
 176 180 cm yr⁻¹ at about of 5-10 years age. This is important, since eucalypts are known to be “thirsty”
 177 trees with a dimorphic root system that can extend to bedrock (Knight, 1999), which supports the
 178 notion of the 3D structure of the eucalypts root system and a corresponding 3D value of D_{opt} . It is
 179 also remarkable that the power-law time dependence of two ecological variables plotted as one
 180 (not shown) produces an R² value as high as 0.99 over a time scale from 30 days to 300 years.

181 It is instructive to discuss the transpiration and growth rates functions given by Vertessy et al. (2001)
 182 with the temporal dependence of the Sapwood Area Index (SAI, defined as the sapwood area within
 183 a hectare, ha) (Vertessy et al. 2001; Roberts et al. 2001), as the SAI relates closely to
 184 evapotranspiration (Benyon et al., 2015) and influences streamflow, which is defined as the annual
 185 volume of water leaving a stream catchment divided by the area of the catchment. Benyon et al.
 186 (2015) reported an initial rise in SAI with time following clear-cutting, with SAI declining with age
 187 at later times. Benyon et al. (2015) also found that sap velocity did not vary across stands and sites.
 188 The decline over time in stand-level transpiration of the *Eucalyptus* forests reported by Roberts et
 189 al (2001) and Vertessy et al (2001) is thus attributed to a decline in sapwood area as the forests age,
 190 which is a consequence of the cumulative effects of tree thinning by about 9 years. In view of
 191 measurements of sap velocities that were consistent over time, a transpiration flux, proportional to
 192 the product of a velocity and a cross-sectional area, should scale roughly as the sapwood area.
 193 Vertessy et al. (2001) reported in their Eq. (4) that the SAI declined according to the stand age, t ,
 194 as

$$195 \quad SAI = 37.5t^{-0.44}m^2ha^{-1} \quad (5)$$

196 An analogous result, but with an exponent of -0.51, was obtained by Roberts et al., (2001), similar
 197 to the temporal dependence of transpiration in Figure 1.

198 Vertessy et al. (1991) use Equation (5) to predict experimental transpiration through multiplication
 199 by their experimentally determined sap flux of 691 m³/m². We summed arithmetically the annual
 200 transpiration values as calculated from Equation (5) through multiplication by the sap flux and
 201 conversion of hectares to m². The results were 14.9 m after 11 years and 86.3 m after 200 years.
 202 One can compare these values with the statement (Vertessy et al., 2001), “At the 11-year-old site,
 203 the mountain ash trees were 15-m tall and very closely spaced. By the time the forest is over 200
 204 years old, the trees exceed 80 m in height and large gaps of up to 80 m in width are formed [through
 205 self-thinning] in the canopy.” Thus, Vertessy et al.’s (2001) best estimate of cumulative

206 transpiration over 15- and 200-year periods differs from their observed tree heights by 0.67% and
207 less than 7.5%, respectively. It follows that the relationship between RRE and L also applies to
208 RRE and sapwood area, an important parameter in process-based models.

209 The developed power-law function for transpiration depends on the overall root architecture, which,
210 in turn, depends on the type of soil, including the physical and mineralogical properties of soil, clay
211 content of soil, soil structure (anisotropy) and associated water retention properties, and not only
212 on the variability of adaptation strategies between species. More general discussions of factors
213 influencing root architecture, however, are outside the scope of this communication.

214

215 Conclusions

216 In the process of investigating the relevance to *Eucalyptus* species of our phenomenological model
217 for tree growth in terms of transpiration, we discovered two novel aspects of the model: an
218 apparently direct equivalence of transpiration and growth rates, and that the power-law time
219 dependence exceeds not only a 2D system power-law exponent, but also that for the model of
220 optimal (minimal) resistance in 3D. The first result was a little surprising, since we had not
221 necessarily expected a closer correspondence than a proportionality. Yet, values deduced for
222 transpiration rates at specific field sites in SE Australia and growth rates cited more generally in
223 the literature corresponded rather closely over a wide range of time scales. Moreover, cumulative
224 transpiration and tree heights at the same sites and times (11 years and 80 years) matched within a
225 few percent. Consequently, decline in tree growth with age appears to be unrelated to changes in
226 sap velocities, but rather, to changes in sapwood index, SAI, defined as the cross-sectional area of
227 the trees within a given area divided by that area. If the relationship proves more broadly applicable,
228 it would be valuable in several respects. First, it would be possible to predict stand height over a
229 period of time up to 300 years with knowledge of the first year's transpiration alone (provided it
230 was representative of climate averages). Consequently, it might also be possible to predict the
231 effects of known climate change on growth rates and final tree heights. Finally, an important direct
232 application of the developed simple semi-empirical model is that it can be used to inform the
233 parameterization of sapwood area or complex root architecture schemes in process-based forest
234 models that represent plant hydrodynamics (e.g., Fisher et al. 2018, Kennedy et al. 2019,
235 Mirfenderesgi et al. 2019).

236

237 Acknowledgments

238 Critical review comments and suggestions given by the reviewers are very much appreciated. BF
239 and TP research was partially supported by the NGEE-Tropics and Deduce projects, funded by the
240 U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research,
241 and Office of Advanced Scientific Computing under contract DE-AC02-05CH11231.

242

243 **References**

- 244 Benyon, R. G., P. N. J. Lane, D. Jaskierniak, G. Kuczera, and S.R. Haydon (2015), Use of a
 245 forest sapwood area index to explain long-term variability in mean annual evapotranspiration and
 246 streamflow in moist eucalypt forests, *Water Resour.Res.*, 51, 5318–5331
 247 10.1002/2015WR017321.
- 248 Box, E.O., B.N. Holben, and V. Kalb. 1989. Accuracy of the AVHRR vegetation index as a
 249 predictor of biomass, primary productivity, and net CO₂ flux. *Vegetatio* 80:71–89.
 250 doi:10.1007/BF00048034.
- 251 Budyko, M.I. The Heat Balance of the Earth's Surface; Translated 1958 by N. A. Stepanova; US
 252 Dept. of Commerce, Weather Bureau: Washington, DC, USA, 1956.
- 253 Cremer, K. W., 1975, *Australian Journal of Botany*, 23(1) 27 - 44
- 254 Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, Farrior CE, Holm JA,
 255 Hurtt GC, Knox RG, Lawrence PJ, Lichstein JW, Longo M, Matheny AM, Medvigy DM,
 256 Muller-Landau HC, Powell TL, Serbin SP, Sato H, Shuman JK, Smith B, Trugman AT, Viskari
 257 T, Verbeeck H, Weng E, Xu C, Xu X, Zhang T, Moorcroft PR, 2018, Vegetation demographics
 258 in Earth System Models: A review of progress and priorities. *Global Change Biology*, 24, 35-54,
 259 doi: 10.1111/gcb.13910.
- 260 Givnish, T. J., C. Wong, H. Stuart-Williams, 2014, Determinants of maximum tree height in
 261 Eucalyptus species along a rainfall gradient in Victoria, Australia, *Ecology*, 95 (11): 2991-3007.
- 262 Hunt, A. G., 2017, Spatio-temporal scaling of vegetation growth and soil formation: Explicit
 263 predictions, *Vadose Zone Journal* doi:10.2136/vzj2016.06.0055
- 264 Hunt, A.G., Faybishenko, B., and T.L. Powell, 2020, A new phenomenological model to
 265 describe root-soil interactions based on percolation theory, *Ecological Modelling*, 433 (1)
 266 109205 <https://doi.org/10.1016/j.ecolmodel.2020.109205>.
- 267 Kennedy, D., Swenson, S., Oleson, K. W., Lawrence, D. M., Fisher, R., Lola da Costa, A. C.,
 268 Gentine, P. 2019, Implementing plant hydraulics in the Community Land Model, version 5.
 269 *Journal of Advances in Modeling Earth Systems*, 11, 485–513. doi: 10.1029/2018MS001500
- 270 Knight JH (1999) Root Distribution and water uptake patterns in Eucalypts and other species In:
 271 The way trees use water. Ed. Landsburg J.
- 272 Koch, G.W., Sillett, S.C., Jennings, G.M., Davis, S.D., 2004. The limits to tree height. *Nature*
 273 428, 851-854.
- 274 Koch, T., Heck, K., Schröder, N., Class, H. and Helmig, R., 2018. A new simulation framework
 275 for soil-root interaction, evaporation, root growth, and solute transport, *Vadose Zone J.*
 276 17:170210. doi:10.2136/vzj2017.12.021.

- 277 Mirfenderesgi G, Matheny AM, Bohrer G, 2019, Hydrodynamic trait coordination and cost-
278 benefit trade-offs throughout the isohydric-anisohydric continuum in trees. *Ecohydrology*,
279 12:e2041, 1-16. Doi: 10.1002/eco.2041.
- 280 Petit, G., S. Pfautsch, T. Anfodillo, and M. A. Adams. 2010. The challenge of tree height in
281 *Eucalyptus regnans*: when xylem tapering overcomes hydraulic resistance. *New Phytologist*
282 187:1146–1153.
- 283 Phillips, C.J., Marden, M., Suzanne, L.M., 2014. Observations of root growth of young poplar
284 and willow planting types. *New Zealand Journal of Forestry Science* 44: 15
285 <https://doi.org/10.1186/s40490-014-0015-6>.
- 286 Phillips, C.J., Marden, M., Suzanne, L.M., 2015. Observations of “coarse” root development in
287 young trees of nine exotic species from a New Zealand plot trial. *New Zealand Journal of*
288 *Forestry Science* 45, 1-15.
- 289 Porto, M., Havlin, S., Schwarzer, S., and Bunde, A. 1997. Optimal paths in strong disorder and
290 shortest path in invasion percolation with trapping, *Phys. Rev. Lett.* 79 (21) 4060-4062.
- 291 Roberts, S., Vertessy, R., and Grayson, R., 2001. Transpiration from *Eucalyptus sieberi* (L.
292 Johnson) forests of different age, *Forest Ecology and Management* 143: 153-161.
- 293 Ryan, M. and B. J. Yoder, 1997, Hydraulic limits to tree height and growth: What keeps trees
294 from growing beyond a certain height? *Bioscience* 47(4), 235-242.
- 295 Sheppard, A.P., M.A. Knackstedt, W.V. Pinczewski, and M. Sahimi, 1999, Invasion percolation:
296 new algorithms and universality classes, *J. Phys. A: Math. Gen.* **32**: L521–L529.
- 297 Stone, E.L., Kalisz, P.J., 1991. On the maximum extent of tree roots. *Forest Ecology and*
298 *Management* 46, 59-102.
- 299 Tng, D. Y. P., G. J. Williamson, G. J. Jordan, and D. M. J. S. Bowman. 2012. Giant eucalypts –
300 globally unique fire-adapted rain-forest trees? *New Phytologist* 196: 1001 – 1014.
- 301 Vertessy, R., Watson, F. G. R., and O’Sullivan, S. K., 2001, Factors determining relations
302 between stand age and catchment water balance in mountain ash, *Forest Ecology and*
303 *Management* 143: 153-161.
- 304
- 305
- 306