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Respiration in wood: integrating across tissues, functions and scales

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4 Commentary on Salomón et al. (2019), 'TReSpire – a biophysical TRee Stem respiration
5 model', *New Phytologist.*

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> **Commented [PM1]:** Nichola – Ingrid uses her middle name; her full name is Sarah Ingrid Coughlin.
> I checked: Ingrid is happy with S. Ingrid Coughlin, but if you need both names, then, the S is Sarah.

25 Success in life for any seedling requires the simultaneous acquisition of resources from soil
26 and atmosphere. This must be coupled to an ability to distribute these resources to the
27 points of use above and below ground, and to house the distribution system within resilient
28 woody structures. The cells comprising these lignified structures – roots, stems and
29 branches – need to be constructed, maintained and defended. To do so requires chemical
30 energy which is almost entirely derived from respiration. However, despite the fundamental
31 role woody tissue plays in driving life in most terrestrial ecosystems, it has received much
32 less research attention than has the physiology of its greener counterpart, the leaf. To some
33 extent this difference reflects the challenge of understanding the metabolically distinct
34 tissues and related fluid and solute movements that occur simultaneously in wood.
35 Advanced models of xylem and phloem function and of cambial growth have existed for a
36 few years (e.g., Hölttä et al. ~~2007~~2006, 2010, de Schepper ~~et al.~~& Steppe 2010, Mencuccini
37 et al. 2013), but Salomón et al's new paper (NP page details) takes a notable step forward

38 integrating and advancing these approaches. Their model 'TReSpire' combines
39 representations of the essential properties of both phloem and xylem, the use of phloem-
40 derived sugars to produce irreversible cellular growth, together with the activity and
41 physical properties of associated tissues (e.g., cambium, parenchyma, bark). TReSpire
42 describes the variation in the flux of carbon dioxide (CO_2) from tree bark, its underlying
43 respiratory production by both growth and maintenance processes, and its transport,
44 limited by energy expenditure and the fundamental physical constraints of pH,
45 concentration gradients, stem carbon density and diffusive resistances.

46

47 The flux of CO_2 from woody tissue is thought to comprise up to 40% of total respiration from
48 vegetation (Campioli et al. 2016, Yang et al. 2016). Hence, quantifying how it responds to
49 disturbance or climate has substantial consequences across scales, from the carbon budgets
50 of individual plants to the terrestrial biosphere (Meir & Grace 2002, Reich et al. 2006,
51 Huntingford et al. 2017, West et al. 2019). However, woody tissue respiration has proved
52 difficult to quantify accurately. Most efforts have used chamber-based measurements of
53 CO_2 efflux from tree stems (E_a) usually at 1-2 m above ground, then related these fluxes to
54 sap wood volume, or to tree-size metrics (woody tissue area or volume), and assumed a
55 simplified tree structure to extrapolate to whole trees or stands (Ryan et al. 1997, Meir et al.
56 2017).

57

58 Even before scaling to a whole tree, the physiological signals in E_a require interpretation
59 because they reflect multiple sink and source processes occurring below the outer bark. In
60 addition to cellular respiration, E_a fluxes may be affected by CO_2 carried in the transpiration
61 stream (Levy et al. 1999, Teskey et al. 2008), by biochemical consumption, e.g., through
62 cortical photosynthesis or PEP-carboxylase metabolism (Angert et al. 2012), and by diffusion
63 constraints imposed by tissue properties and stem size (Steppe et al. 2007). Salomón et al.
64 have formalised much of this complexity for the first time in a combined model that fuses
65 bark and xylem hydraulics with two additional sub-models that quantify carbohydrate use in

66 respiratory metabolism and growth, together with the dynamics of phloem unloading and
67 consequent carbon balance.

68 The determination of respiration in Salomón et al.'s model is anchored in the classical
69 growth-maintenance paradigm (Thornley 1970, Amthor 2000). This assumes a constant
70 construction respiration cost for biomass of a given elemental composition, and uses live
71 tissue nitrogen content and temperature to drive short-term responses in maintenance
72 respiration (Cannell and Thornley 2000). The simulated mass balance ultimately links
73 fluctuations in cell turgor and stem diameter all the way through to E_a values (Figs 1,2,
74 Salomón et al., this issue). A key advance is that the processes and storage terms
75 determining E_a can be resolved separately at sub-daily temporal resolution as well as over
76 the longer term. The model outputs are broadly consistent with observations reported
77 elsewhere as well as with the detailed experimental measurements made to test the model.
78 This provides initial confidence in the model outputs, despite the sparse validation data for
79 some variables, such as non-structural carbohydrate concentration.

80

81 Besides a more integrated representation of respiratory processes, TReSpire also aims to
82 reduce some of the uncertainties that still surround stem growth. Irreversible radial growth
83 consists of the processes of cambial cell differentiation, cellular periclinal division, radial
84 enlargement, subsequent wall thickening *via* lignification of the secondary wall and final
85 programmed cell death (Rossi et al. 2006). High-precision dendrometry and/or repeated
86 micro-coring coupled with wood anatomical analysis are generally used to quantify these
87 processes. The first method (also employed here) provides rich time-series of highly time-
88 resolved data. However, at least three processes contribute to the observed
89 shrinking/swelling signals measured by dendrometers at the hourly and daily scale, i.e., bark
90 hydraulic capacitance driven by xylem water potential (Zweifel et al. 2016), radial water
91 transport associated with osmotic changes in bark (de Schepper et al.& Steppe 2010) and/or
92 xylem and irreversible growth. Disentangling these processes has become possible recently
93 (Mencuccini et al. 2017) and these new advances are incorporated in TReSpire. By contrast,
94 micro-coring provides less capacity to resolve processes at the daily scale and is inherently
95 destructive by nature. However, compared to dendrometry, it has significant advantages in
96 its capacity to identify individual phenological phases and thus attribute metabolic costs to
97 each one of them at the seasonal time scale (Rossi et al. 2006; Cuny et al., 2015).

98

99 Because interpreting dendrometry signals at diurnal and seasonal time scales remains
100 challenging, fundamental questions over the relative roles of hydraulic (e.g., turgor) versus
101 metabolic (e.g., carbon supply, carbon demand) variables on the control of wood growth
102 have remained unanswered. The insights provided by TReSpire are exploited to separate the
103 detailed time-dynamics not only of respiratory fluxes but also of the subtending irreversible
104 growth processes. Such an approach has the potential to help address outstanding
105 questions, including the impact of high vapour pressure deficit or reduced soil water
106 availability on the rate of radial growth. Coupled with additional measurements of the rate

107 of photosynthesis and carbohydrate content, it may also shed light on the balance between
108 storage, source-driven and sink-driven processes. Interestingly, the authors report that the
109 stem growth rate (in sucrose equivalents) of a young Norway maple tree was lowest in late
110 afternoon, accelerated during the night and peaked in early morning, remaining relatively
111 high also during the middle part of the day. This finding casts doubts over the generally held
112 view that radial xylem growth occurs only during night-time periods of maximum cellular
113 turgor, but is consistent with growth pattern reports for some *Eucalyptus* species
114 (Mencuccini et al. 2017).

115

116 Some of the key measurements used to calibrate the model included high-resolution stem
117 diameter changes, sap flux and chamber-based E_a fluxes. Given the significance of
118 dendrometric measurements for the present analysis and the interest in establishing
119 dendrometric monitoring networks in carbon cycle studies, it is now a priority to examine
120 the comparability of the widely different approaches employed for this purpose.
121 Dendrometer systems vary widely in their design and capacity to account for radial changes
122 in xylem and bark, among other factors. They also differ depending on whether they
123 measure point radius, diameter and/or circumference changes. Their temperature
124 sensitivity and the significance of temperature and water content changes in various tissue
125 compartments (including potentially the heartwood of large trees) will need to be examined
126 carefully.

127

128 A new overall view is thus presented by Salomon et al. of how respiration can vary hourly in
129 the context of stem hydraulic dynamics and growth, with quantitative account also taken of
130 the effects of changes in the transport of CO_2 in the xylem stream and in the changes in
131 gaseous and dissolved CO_2 concentrations in different tissues. For example, detailed *in situ*
132 measurements have shown that E_a fluxes can often be less than the overall respiration rate
133 (R_s) of underlying cells (Angert et al. 2012, Teskey et al. 2008). TReSpire replicates this
134 mechanistically: over a 24 hr cycle, the modelled ratio of E_a/R_s varies between 0.7 and 1,
135 matching field measurements (Angert et al. 2012, Hilman et 2018). However, this
136 agreement breaks down at sub-daily timescales, where diurnal E_a/R_s ratios are more stable
137 (Hilman et al. 2018) than the modelled outputs, which overestimate E_a at night. A
138 discrepancy of this sort highlights the advantages accrued by comparing a mechanistic
139 model with field data, and points to the need not just to understand additional processes
140 causing the removal of locally respired CO_2 (Angert et al. 2012), but also when different
141 processes might dominate the signals in E_a and R_s.

142

143 TReSpire has only been validated against saplings thus far, and whilst data on E_a remain
144 relatively sparse for all ecosystems (Yang et al 2016), it is clear that the relationship
145 between E_a and woody limb size varies strongly. E_a has often been represented as a function
146 of sapwood volume, outer bark diameter and/or bark surface area (e.g., Ryan et al. 1997,
147 Levy et al. 1998, Chambers et al. 2004), though the increased CO_2 transport associated with

148 the larger sap flux that occurs in bigger trees was recently found to explain much variation
149 in E_a with stem size in one species, *Liridendron tulipifera* (Fan et al. 2017). TReSpire could be
150 used to simulate similar datasets, and in combination with field data, to explore the
151 mechanistic underpinnings of E_a and R_s in large trees under varying environmental
152 conditions (e.g., Metcalfe et al. 2010). Whilst it is unclear how well the classical assumptions
153 of constant cost for different respiration components will hold over large changes in
154 temperature or moisture availability (O'Leary et al. 2019), the integration of hydraulics and
155 respiration in one model may help interpret how respiration varies with limb size and
156 growth conditions.

157

158 To proceed from limb to whole tree, a fine-scale model requires additional information on
159 tree structure. The difficulty of acquiring such data has until now forced a reliance on
160 destructive harvests to enable extrapolation of chamber-based E_a measurements to
161 estimate CO_2 emissions from whole trees. Whilst some of this work has yielded apparently
162 general power-law descriptions of respiration with total biomass (Mori et al. 2010),
163 sensitivity to the power-law exponents is high, and the approach has not yet fitted easily
164 into mechanistic models of tree function. New terrestrial laser scanning methods offer a
165 way to significantly advance how we scale tree physiology from limb to tree, by enabling the
166 rapid high-resolution measurement of full tree structure, for hundreds of trees (Meir et al.
167 2017). Laser-scanning methods are advancing rapidly and will likely deliver tree structural
168 data for large forested areas within a few years, with wide application in ecological and
169 forestry science (Disney et al. 2018).

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171 Moving up further-still in scale, from tree to ecosystem, the integration of such a
172 comprehensive description of tree form with the new mechanistic detail that is embedded
173 in TReSpire should help in specifying the carbon cost and climate-responsiveness of woody
174 tissue respiration at large scale. These kinds of new datasets are urgently needed to
175 examine how land-surface models perform under climate change (*cf*. Huntingford et al.
176 2017). Until now such vegetation models have made the weakly-tested assumption that the
177 respiration of woody tissue can be derived simply from leaf respiration rates, based on
178 biomass, tissue nitrogen concentration and temperature. TReSpire is a new addition to the
179 toolbox needed to determine these key components of the carbon budget of trees and
180 forests, and thereby advance how we understand the fundamental respiration cost of tree
181 size, and how this bears upon land-atmosphere interactions.

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