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Recommended Citation
Goldsmith, G.R., M.M. Lehmann, L.A. Cernusak, M. Arend & R.T.W. Siegwolf. 2017. Inferring foliar water uptake using stable isotopes of water. *Oecologia* 184: 763-766.

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Comments

This is a pre-copy-editing, author-produced PDF of an article accepted for publication in *Oecologia*, volume 184, issue 4, in 2017 following peer review. The final publication is available at Springer via DOI: 10.1007/s00442-017-3917-1

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1   **Inferring foliar water uptake using stable isotopes of water**

2

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22

23   **Author Contributions**

24

25   GRG and RS conceived of the project. GRG, MML, and LC performed the research with

26   assistance from MA. GRG analyzed the data and wrote the paper with contributions from all

27   the authors.

28 **Abstract**

29

30 A growing number of studies have described the direct absorption of water into leaves, a

31 phenomenon known as foliar water uptake. The resultant increase in the amount of water

32 in the leaf can be important for plant function. Exposing leaves to isotopically enriched or

33 depleted water sources has become a common method for establishing whether or not a

34 plant is capable of carrying out foliar water uptake. However, a careful inspection of our

35 understanding of the fluxes of water isotopes between leaves and the atmosphere under

36 high humidity conditions shows that there can clearly be isotopic exchange between the

37 two pools even in the absence of a change in the mass of water in the leaf. We provide

38 experimental evidence that while leaf water isotope ratios may change following exposure

39 to a fog event using water with a depleted oxygen isotope ratio, leaf mass only changes

40 when leaves are experiencing a water deficit that creates a driving gradient for the uptake

41 of water by the leaf. Studies that rely on stable isotopes of water as a means of studying

42 plant water use, particularly with respect to foliar water uptake, must consider the effects

43 of these isotopic exchange processes.

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47 **Key words:** fog, isotope dendrochronology, leaf wetting, plant-water relations, stomata

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50

51 **Body of Text**

52

53 Foliar water uptake describes the process by which plants absorb water into their leaves,

54 resulting in a net increase in the mass of water in the leaf. This occurs when saturating

55 atmospheric water vapor conditions result in a driving gradient for water to enter into a

56 leaf that is at a more negative water potential (Simonin et al. 2009; Goldsmith 2013; Vesala

57 et al. 2017). The conditions necessary for this phenomenon are often observed in dew- and

58 fog-affected ecosystems such as coastal Mediterranean ecosystems (Burgess and Dawson

59 2004; Baguskas et al. 2016) and tropical montane cloud forests (Eller et al. 2013; Gotsch et

60 al. 2014; Malhi et al. 2017), where fog (often leading to leaf wetting) serves as an

61 alternative plant water source during the dry season. However, the effects of precipitation

62 events are similar and foliar water uptake has now been described as affecting plant water

63 and carbon relations in > 70 species from a number of different ecosystems (Goldsmith et

64 al. 2013).

65 The capacity for species to do foliar water uptake has frequently been established

66 by means of water isotope labeling experiments (Burgess and Dawson 2004; Breshears et

67 al. 2008; Limm et al. 2009; Eller et al. 2013; Berry and Smith 2014; Berry et al. 2014;

68 Gotsch et al. 2014; Cassana et al. 2015; Eller et al. 2016; Emery 2016; Schwerbrock and

69 Leuschner 2017). This method relies on exposing leaves to a water source that is highly

70 enriched or depleted in heavy isotopes of oxygen or hydrogen compared to that of the

71 xylem source water and measuring for the presence of this label in the leaf. The labeled

72 water is delivered through a simulated fog or leaf wetting event using an ultrasonic fog

73   machine or a simple spray bottle. A shift in the bulk leaf water isotope ratio towards that of

74   the labeled water source is interpreted as foliar water uptake.

75   Water molecules can also exchange back and forth between the leaf and the

76   atmosphere without a net increase in the mass of water in the leaf (Kim and Lee 2011).

77   This occurs when atmospheric vapor pressure (e_a) increases relative to leaf vapor pressure

78   (e_i). As a result, the air to leaf vapor pressure deficit decreases and reduces the driving

79   gradient for water loss from the leaf. Stomata generally open in response to decreasing

80   VPD (Lange et al. 1971), leading to an increase in leaf stomatal conductance (g_s) in the light,

81   even though net transpiration (E) is decreasing to zero. Thus, with the stomata open, but

82   transpiration suppressed due to e_a/e_i reaching unity (i.e. 100% relative humidity), water

83   molecules simply move from the leaf to the atmosphere and vice versa with no net flux.

84   This is akin to isotopic exchange between two pools of water in a closed system (Clark and

85   Fritz 1997). Notably, this changes the isotope ratio of the leaf water, but does not lead to a

86   net increase in the amount of water in the leaf. Thus, it is not possible to distinguish

87   between a change in the leaf water isotope ratio due to foliar water uptake (net gain H_2O)

88   versus a change caused solely by water isotopes simply exchanging back and forth (no net

89   change H_2O) between the leaf and the atmosphere (Figure 1).

90   The effect of the isotope exchange of water across the leaf surface on leaf water

91   isotope ratios at steady state is described by the Craig-Gordon Model (Craig and Gordon

92   1965; Dongmann et al. 1974):

93

94    $$\delta_e = \delta^+ + \varepsilon_k + (\delta_v - \varepsilon_k)\frac{e_a}{e_i} \tag{1}$$

95

96   where the enrichment in leaf water isotopes relative to the source (Δ_e) is a function of

97   equilibrium (ε^+) and kinetic fractionation factors (ε_k), the enrichment in atmospheric water

98   vapor isotopes relative to source water isotopes (Δ_v), and the ratio of ambient air vapor

99   pressure to leaf intracellular vapor pressure (e_a/e_i). Equilibrium fractionation occurs with

100   the phase change of water from liquid to vapor within the stomata, whereas kinetic

101   fractionation occurs with the diffusion of that vapor through the stomata and boundary

102   layer into the atmosphere. Dongmann et al. (1974) notes that when e_a/e_i is at unity, the

103   model simplifies to:

104

105      $$\Delta_e = \varepsilon^+ + \Delta_v \tag{2}$$

106

107   In Eq. 2, the stable isotope ratio of water in leaves is not subject to kinetic fractionation and

108   can be explained solely by a temperature-dependent equilibrium fractionation factor and

109   the difference in atmospheric water vapor isotopes relative to source water isotopes. It is

110   important to note that this theory cannot distinguish between the effects of foliar water

111   uptake versus bi-directional exchange.

112   The exchange of water isotopes between leaves and the atmosphere in the absence

113   of foliar water uptake can be demonstrated experimentally. We exposed leaves from well-

114   watered poplar (*Populus x canescens*) plants growing in a high humidity (~80%) growth

115   chamber to a fog event using water with a depleted oxygen isotope ratio. We excised leaves

116   at full water content, measured the leaf mass, and sealed the petioles from water entry.

117   Leaves were either immediately exposed to fog, or allowed to lose 5 or 10% of their initial

118   mass prior to fog exposure to create a driving gradient for water to enter the leaf through

119   foliar water uptake (n = 1 leaf each from 5 individuals per treatment). Fog was generated

120   using an ultrasonic fog machine (Ultrasonic 3, CIS Products, France) and supplemented by

121   periodic physical spraying for 1 h (i.e. fog leading to leaf wetting). We then quickly and

122   carefully dried the leaf surfaces, re-measured the leaf mass, and sealed the leaf in a glass

123   vial to later measure the oxygen isotope ratios of bulk leaf water via isotope ratio mass

124   spectrometry. We compared the three treatments (0, 5, and 10% mass loss) with the

125   isotope ratio of the source water provided to the plants (for methods, see Online Resource).

126   All data are available in the KNB data repository (Goldsmith et al. 2017).

127   The leaf water isotope ratios of all three treatments shifted towards the depleted

128   isotopic label following fog exposure (Figure 2). However, the leaf mass of the 0%

129   treatment did not change, indicating the exchange of water isotopes even though there was

130   no foliar water uptake. The 5 and 10% treatments recovered some (but not all) of their

131   initial mass, as would be predicted by the establishment of a driving gradient for foliar

132   water uptake. Due to the short duration of the experiment, the leaf water isotope ratios did

133   not converge with the labeled water vapor, as would be predicted by theory and has been

134   observed in other experimental approaches (Kim and Lee 2011).

135   The observation that leaf water isotopes exchange even in the absence of a change

136   in leaf mass is of particular importance if the primary pathway for foliar water uptake is

137   stomata (Burkhardt et al. 2012). However, the pathways for foliar water uptake are not yet

138   fully resolved. There is evidence for water entry through hydathodes, trichomes, fungal

139   hyphae and the cuticle, depending on the species under study (Burgess and Dawson 2004;

140   Oliveira et al. 2014). However, even if the primary pathways were to be something other

141 than the stomata, inferences regarding foliar water uptake could still be confounded by bi-

142 directional exchange through open (or at night, partially open) stomata.

143   There are other analogous applications of water isotope tracers that should also be

144 considered. Branch water uptake directly through bark has been studied by submerging

145 branch segments into labeled water sources; even in the absence of stomata, it is likely that

146 isotopic exchange will occur given sufficient time (Mayr et al. 2014; Earles et al. 2015).

147 Several studies have also used differences between the stable isotope ratios of fog versus

148 soil water to infer the proportional use of these two sources through sampling of xylem

149 water isotope ratios (Berry et al. 2013; Fischer et al. 2016; Fu et al. 2016). Here, it must be

150 assumed that the water in the xylem could come from a combination of the 1) soil water

151 derived from precipitation, 2) drip of intercepted fog water from the plant canopy into the

152 soil, 3) foliar uptake of fog water, or 4) bi-directional exchange of fog water with leaf water.

153 The subsequent incorporation of these water isotopes into plant tissue (e.g. $\delta^{18}O$ of tree

154 rings) has also been proposed as a means of tracing the contribution of fog water to plant

155 water use over time (Hu and Riveros-Iregui 2016); our results may help explain patterns

156 observed in fog-affected environments (Anchukaitis et al. 2008; Zhu et al. 2012).

157   Foliar water uptake remains a real phenomenon. There are a number of different

158 methods to independently establish its existence, including sapflow (Burgess and Dawson

159 2004), dye tracers (Eller et al. 2013), gravimetric approaches (Limm et al. 2009), and plant

160 water potentials (Goldsmith et al. 2013). In fact, many of the research studies cited above

161 combined stable isotope labeling experiments with other methods and thus the results are

162 likely to stand. As no single method is perfect, we recommend that investigators try to use

163 multiple means to establish foliar water uptake wherever possible.

164

Acknowledgements

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269

270 **Figure Legend**

271

272 **Figure 1.** Leaf water isotope ratios can vary due to (a) the effects of transpiration when the

273 ratio of ambient air vapor pressure to leaf intracellular vapor pressure (e_a/e_i) < 1, (b) the

274 effects of transpiration suppression when e_a/e_i = 1, which results in no change in the mass

275 of leaf water and (c) the effects of foliar water uptake when $e_a/e_i \geq 1$, which results in a net

276 increase in the mass of leaf water. The effects of bi-directional exchange of water isotopes

277 between the leaf and the atmosphere observed in (b) cannot be distinguished from the net

278 uptake of water isotopes from the atmosphere in (c).

279

280 **Figure 2.** Changes in (a) the $\delta^{18}O$ of water and (b) the percent change in fresh leaf mass of

281 poplar (*Populus x canescens*) leaves exposed to a fog source water depleted in $\delta^{18}O$ after 0,

282 5, and 10% loss of fresh leaf mass achieved through bench drying (n = 1 leaf each from 5
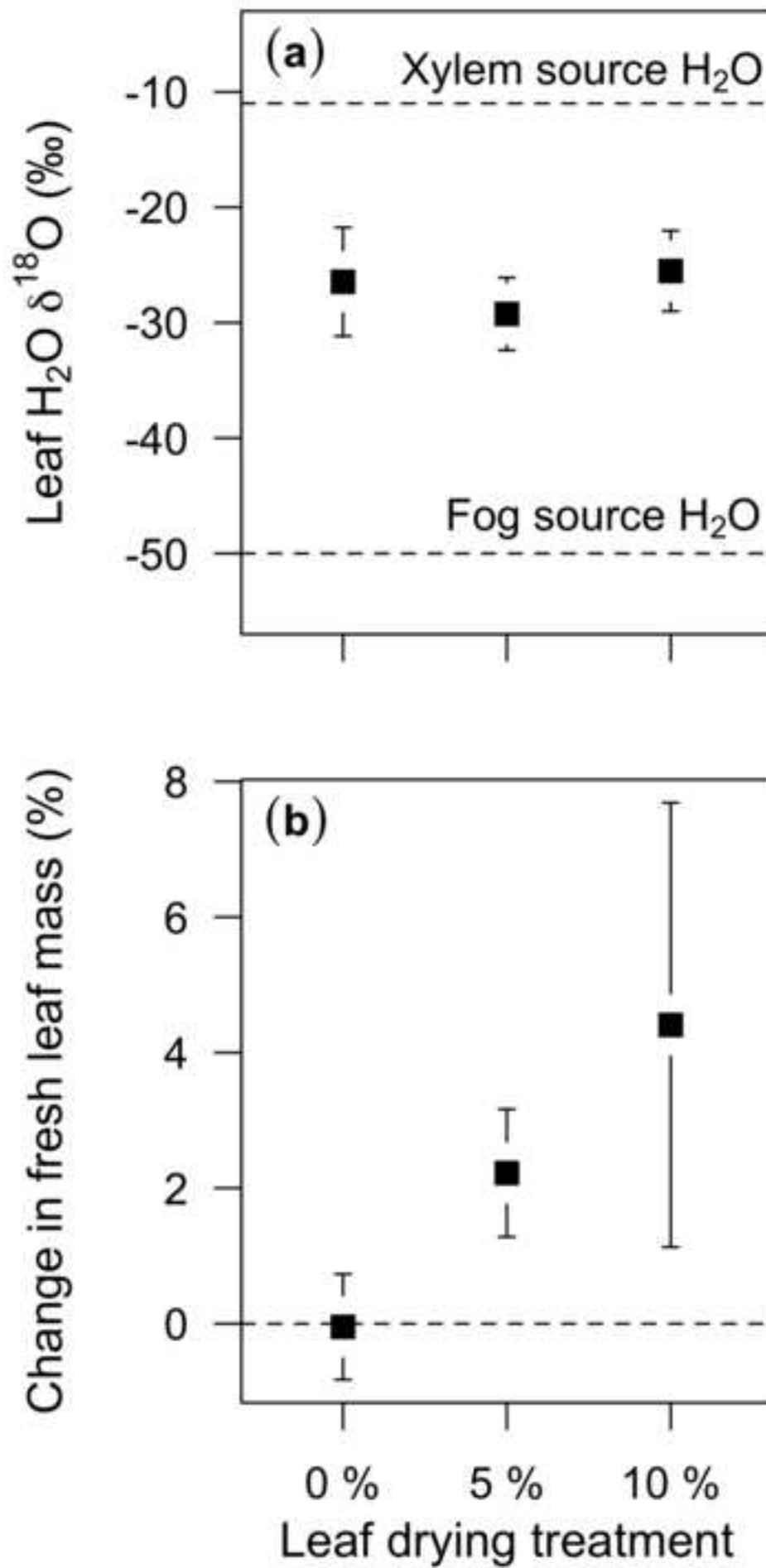
283 individuals per treatment). Data are means ± 1 SD.

Figure 1

Click here to download Figure Goldsmith_Figure1_27Mar17.tiff
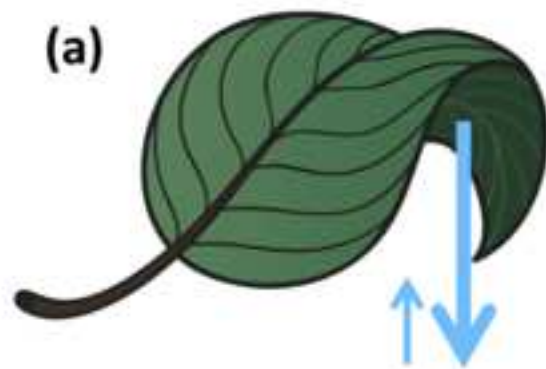
(a) **Transpiration ($e_a/e_i < 1$)**
Net loss H_2O
H_2O isotopes enriched
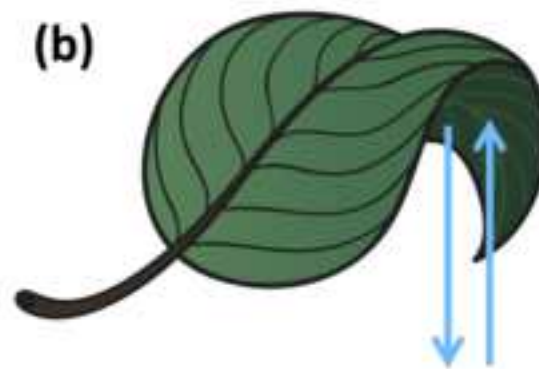
(b) **No transpiration ($e_a/e_i = 1$)**
No net change H_2O
H_2O isotopes exchange
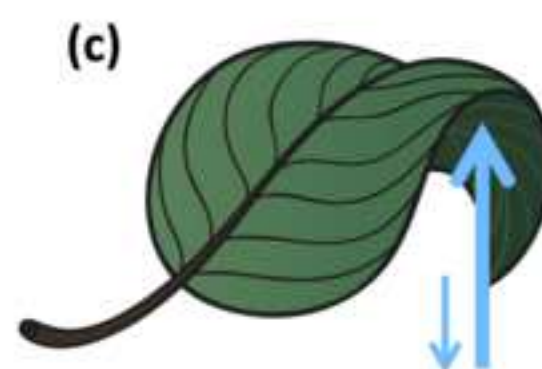
(c) **Foliar water uptake ($e_a/e_i \geq 1$)**
Net gain H_2O
H_2O isotopes taken up

Figure 2

Figure 2

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Supplementary Material

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