Stable water isotopes in halophyte plants

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Mangrove forests distributions of the world (Giri et al. 2011) via Mangroves (Alongi 2008)
Unique physiological structure for adapting to special habitats!

Mangrove plant

Marilyn C. Ball (1988)

Krauss et al. (2013)

Salt gland

Thick leaf cuticle

Aerial root
Special physiological structure with unusual water relations!

Ellsworth, 2007
Isotopic enrichment of Leaf water \( (\Delta^{18}O = ^{18}O_{\text{leaf water}} - ^{18}O_{\text{xylem water}}) \)

Stomatal pore size and density in mangrove leaves and artificial leaves: effects on leaf water isotopic enrichment during transpiration

Leonel da Silveira Lobo Stemberg\(^{A,B}\) and Lynn M. Manganiello\(^A\)

![Diagram showing stainless steel, sponge, and Plexiglass](Image)
Only 3 species

Effects of stomatal density and leaf water content on the $^{18}O$ enrichment of leaf water

Leticia Larcher, Ikuko Hara-Nishimura and Leonel Sternberg

<table>
<thead>
<tr>
<th>STOMAGEN</th>
<th>Transgenic lines</th>
<th>Transpiration</th>
<th>$\Delta_L$</th>
<th>$\Delta_L/\Delta_e$</th>
<th>$\phi$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low stomatal density</td>
<td>(ST-RNAi)</td>
<td>2.32 ± 0.06c</td>
<td>6.2 ± 1.5a</td>
<td>0.45 ± 0.11a</td>
<td>1.97 ± 0.71a</td>
</tr>
<tr>
<td>Wild-type</td>
<td>(CS60000)</td>
<td>3.00 ± 0.02b</td>
<td>6.7 ± 0.7a</td>
<td>0.51 ± 0.05a</td>
<td>1.55 ± 0.30a</td>
</tr>
<tr>
<td>High stomatal density</td>
<td>(ST-OX)</td>
<td>3.50 ± 0.11a</td>
<td>6.5 ± 0.7a</td>
<td>0.55 ± 0.06a</td>
<td>1.38 ± 0.30a</td>
</tr>
</tbody>
</table>

Cuntz et al. (2009): $\Delta_L$ is not influenced by habitats
Is leaf isotopic enrichment in mangroves different from freshwater plants?

Is the difference common presence?

Is the difference related to leaf traits?
Isotopic enrichment of Leaf water \( \Delta^{18}O = ^{18}O_{\text{leaf water}} - ^{18}O_{\text{xylem water}} \)

4 times for field campaign
5 sites in south of China
15 mangrove species (total 28)
16 land species
Isotopic enrichment of Leaf water \( \Delta^{18}O =^{18}O_{\text{leaf water}} - ^{18}O_{\text{xylem water}} \)

Water isotopic discrimination of mangrove leaves are very different from freshwater plants!

(Liang et al. 2017)
Fewer stomata for mangroves
Fewer and larger stomata for mangroves

Aegiceras corniculatum
Kandelia obovata
Melaleuca Viridiflora
Streblus asper
Stomata

- Grasses
- Monocot
- Fossil leaves
- Mangroves
- Freshwater tropical forest
- Tibetan and Mongolian grassland species
Stomata

- Mangroves
- Semi-mangrove
- Freshwater

Log (Δ18O%) vs Stomatal density (mm⁻²)

Log (Δ18O%) vs Guard cell length (µm)
**Succulence**

*Higher water content*

![Graph showing leaf water per area (mol m\(^{-2}\)) for different types of plants: Mangroves, Semi-mangrove, Freshwater. The graph includes a box plot and a linear regression model with the equation \(y = 101.676 + 0.725\) and \(R^2 = 0.875\). The data source is Mantovani (1998).*
Succulence

![Graph showing relationship between leaf water per area and isotopic signature.]

- Mangroves
- Semi-mangrove
- Freshwater

![Graph showing relationship between leaf water per area and stomatal density.]

- Log (Stomatal density mm⁻²)
- Leaf water per area (mol m⁻²)
Theory

Bulk leaf water: \[ \Delta_{ls} = \frac{1 - e^{-p}}{p} \] (1)

Evaporative water: \[ \Delta_{es} = \varepsilon^+ + \varepsilon_k + (\Delta_v - \varepsilon_k)h_L \] (2)

Efficient mixing path length: \[ P = \frac{E_L}{D_C} \] (3)

Transpiration: vein

Evaporative site

Stomata
$L = e^{-0.7612 \times E + 7.0522}$
Theory-sensitivity analysis

**E variation**

![Graphs showing E variation with different modeled and observed Δ¹⁸O values.]

**L variation**

![Graphs showing L variation with different modeled and observed Δ¹⁸O values.]

Theory-sensitivity analysis
Lower transpiration

Mangroves | Semi-mangrove | Freshwater
---|---|---

longer L

Mangroves | Semi-mangrove | Freshwater
---|---|---
\[ L = \left( \frac{\sum_{i=1}^{n} \frac{A_E}{A_{mi}}}{k} \right) + \frac{A_E}{A_S} j^{-\varphi}, \]

Eqn 16

### Theory-Correlation analysis

Table 2. Correlation coefficients of factors related to both leaf anatomical traits and leaf water enrichment

<table>
<thead>
<tr>
<th>Item</th>
<th>LWC</th>
<th>LMA</th>
<th>LS</th>
<th>SL</th>
<th>E</th>
<th>$h_L$</th>
<th>$w_i$</th>
<th>T</th>
<th>$g$</th>
<th>$\Delta_L/\Delta_e$</th>
<th>P</th>
<th>L</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Delta_L$</td>
<td>-0.64</td>
<td>-0.59</td>
<td>0.65</td>
<td>-0.55</td>
<td>0.63</td>
<td>-0.07</td>
<td>-0.09</td>
<td>-0.09</td>
<td>0.60</td>
<td>0.89</td>
<td>-0.87</td>
<td>-0.79</td>
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<tr>
<td>LWC</td>
<td>0.68</td>
<td>-0.67</td>
<td>0.66</td>
<td>-0.63</td>
<td>-0.09</td>
<td>-0.11</td>
<td>-0.10</td>
<td>-0.45</td>
<td>-0.47</td>
<td>0.53</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td>LMA</td>
<td>-0.64</td>
<td>0.68</td>
<td>-0.62</td>
<td>-0.25</td>
<td>-0.07</td>
<td>-0.07</td>
<td>-0.47</td>
<td>-0.53</td>
<td>0.60</td>
<td>0.69</td>
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<td></td>
</tr>
<tr>
<td>LS</td>
<td>-0.69</td>
<td>0.60</td>
<td>0.15</td>
<td>0.22</td>
<td>0.23</td>
<td></td>
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<td></td>
<td>0.53</td>
<td>0.52</td>
<td>-0.55</td>
<td>-0.63</td>
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<tr>
<td>SL</td>
<td>-0.51</td>
<td>-0.03</td>
<td>-0.26</td>
<td>-0.25</td>
<td>-0.37</td>
<td>-0.37</td>
<td>0.45</td>
<td>0.54</td>
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<tr>
<td>$E$</td>
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<td>0.19</td>
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<td>0.11</td>
<td>0.86</td>
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<td>0.65</td>
<td>-0.65</td>
<td>-0.79</td>
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<tr>
<td>$h_L$</td>
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<td>-0.09</td>
<td>-0.04</td>
<td>0.31</td>
<td>0.21</td>
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<td></td>
<td>-0.13</td>
<td>-0.17</td>
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<tr>
<td>$w_i$</td>
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<td>-0.17</td>
<td>0.23</td>
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<tr>
<td>T</td>
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<td>0.23</td>
<td>0.07</td>
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<tr>
<td>$g$</td>
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<td></td>
<td></td>
<td>0.71</td>
<td>-0.68</td>
<td>-0.73</td>
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<tr>
<td>$\Delta_L/\Delta_e$</td>
<td></td>
<td></td>
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<tr>
<td>P</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td>-0.93</td>
<td>-0.84</td>
<td></td>
</tr>
</tbody>
</table>

leaf water content per area (LWC), leaf mass (dry) per area (LMA), stomatal density (LS), transpiration (E), relative humidity ($h_L$), leaf temperature ($T$), stomatal conductance ($g$), the mole fraction of (light) water vapor in the intercellular ($w_i$), the ratio of the isotope enrichment of bulk leaf water to that of the evaporative water ($\Delta_L/\Delta_e$), Pécl et number ($P$), effective mixing path length ($L$) with species-specific leaf water isotopic enrichment ($\Delta_L$). Bold numbers indicated that the correlation coefficients reached the significance level at $p<0.05$. 
Schematic diagram of underlying mechanism lowering leaf water isotopic enrichment of mangroves than adjacent non-mangrove plants. The values beside the paths were the standardized (0~1) path coefficients, which were only shown for the significant effects. (Note that logarithm of all variables was used).
1. Our research built the relationship between leaf traits and L which is hardly measurable.

2. Our research imply models involving leaf water enrichment models should cautiously be used in the plants with special leaf traits in other water-limited ecosystem.

3. Climate reconstruction

\[ \Delta_{es} = \varepsilon^+ + \varepsilon_k + (\Delta_v - \varepsilon_k)h_L \]

\[ \Delta_{cs} = \Delta_L (1 - p_{cx}p_x) + \varepsilon_o \]

\[ M_{c_a} \frac{d\delta_a}{dt} = F_{oa} (\delta_o - a_w - \delta_a) + F_{aw}a_w + \Omega (\delta_i - \delta_a) + A_{\Delta_A} + F_{an} (\delta_{an} - \delta_o) \]
Background atmosphere 
\((\delta^{18}O \approx -22 \, \text{‰})\)

**Steady state**
- Transpired water – midday 
  \((\delta^{18}O \approx -9 \, \text{‰})\)

**Non-steady state**
- Transpired water – morning 
  \((\delta^{18}O \approx -20 \, \text{‰})\)
- Transpired water – late afternoon 
  \((\delta^{18}O \approx -10 \, \text{‰})\)

- Leaf water 
  \(\delta^{18}O \approx 15 \, \text{‰}\)
- Xylem water 
  \(\delta^{18}O \approx -9 \, \text{‰}\)
- Soil evaporation 
  \(\delta^{18}O \approx -35 \, \text{‰}\)

- Precipitation 
  \(\delta^{18}O \approx -9 \, \text{‰}\)
- Soil water 
  \(\delta^{18}O \approx -9 \, \text{‰}\)
Terrestrial water fluxes dominated by transpiration

Scott Jasechko¹, Zachary D. Sharp¹, John J. Gibson², S. Jean Birks², Yi Yi², & Peter J. Fawcett²

Partitioning ET

ET = T + E

Schlesinger & Jasechko, 2014

f = \frac{\delta_{ET} - \delta_E}{\delta_T - \delta_E}

Jasechko, et al., 2013
How to reduce the uncertainty of calculating $\delta_T$?

Is the $T/ET$ in mangrove ecosystem lower?
We monitored separately (every 10 mins) the isotope composition of
1. water vapor above canopy as reference air
2. licor6400 exhaust
3. water vapor below canopy
Y = 1.04X + 2.81; \( R^2 = 0.99 \), P < 0.01
Combining Licor _picarro

**Theory**

**Mass conservation**

\[ sE = u_o w_o - u_e w_e \quad (1) \]

**Flux conservation**

\[ u_o = u_e + sE \quad (2) \]

**Heavier isotope conservation**

\[ \delta_T sE = \delta_p u_o w_o - \delta_A u_e w_e \quad (3) \]

\[ \delta_T = \frac{\delta_p w_o - \delta_A w_e + (\delta_A - \delta_p) w_o w_e}{w_o - w_e} \quad (4) \]
1. $\delta^{18}O_T$ presented a bimodal pattern

2. caused by temporary stomatal closure
Method 1: CG model

Assumption: Mixing uniform leaf water

\[ \delta_T = \frac{\alpha^+ \delta_V - h_L \delta_V - \varepsilon^+ - (1 - h_L)\varepsilon_k}{(1 - h_L)(1 + \varepsilon_k/1000)} \] (6)
Method2: CG_P model (including peclect effect)

Assumption: leaf water is overwhelmed by evaporation site and source water

\[ \delta_T = \frac{\alpha^+ \delta_e - h_L \delta_V - \varepsilon^+ - (1 - h_L) \varepsilon_k}{(1 - h_L)(1 + \varepsilon_k/1000)} \quad (14) \]

\[ \Delta_L = \frac{1 - e^{-p}}{p} \quad (15) \]

\[ P = \frac{E_L}{D_C} \quad (16) \]

\[ L = e^{-0.7612 \cdot E + 7.0522} \quad (17) \]
Method 3: FC model

Assumption: leaf water excluding main vein

Leaf lamina water content (\( W \text{ mol m}^{-2} \)) balance

\[
\frac{d(W)}{dt} = J - T_r \quad (11)
\]

Heavier isotope conservation

\[
\frac{d(R_l W)}{dt} = R_X J - R_T T_r \quad (12)
\]

\[
\delta_T = \delta_X - \frac{1}{T_r} \frac{d(W \Delta_l)}{dt} \quad (13)
\]
Method 4: steady-state assumption

\[ \delta_T = \delta_X \]
Modelling Results

12.10

12.11

12.12

\[ \delta_t (\%o) \]

-30
-20
-10
0
10:00 12:00 14:00 16:00

12.10

CG_P model

Measured

12.11

12.12

10:00 12:00 14:00 16:00
What factors drive $\delta_T$ variation?

its variation mainly was drove by stomatal conductance, leaf temperature and air humidity.
1. The $\delta^{18}O_T$ presented a bimodal pattern caused by stomatal closure during 2:00~4:00 PM, and its variation mainly was drove by stomatal conductance and leaf temperature;

2. The $\delta^{18}O_T$ deviated from isotopic steady state throughout most of the days, when $E$ is not high enough.

3. Modified CG model including peclet effect and FC model are both suitable to simulate $\delta^{18}O_T$ of mangrove leaves.