

Abstract

Existing one-dimensional non-steady-state leaf water enrichment models are reviewed. They are all subsets of the Farquhar & Cernusak [2005] non-steady-state model by neglecting either varying leaf water volume, or the isotopic gradient between the xylem and the evaporating site, or both. It is shown that the Farquhar & Cernusak non-steady model is based upon advection-diffusion theory in porous media. The full advection-diffusion theory demonstrates that the assumed shape of the leaf isotopic gradient in the Farquhar & Cernusak model, the so-called “brave assumption”, is well met most of the day. It also validates that one effective length is sufficient to describe non-steady-state leaf water enrichment satisfactorily. The one-dimensional leaf water enrichment models were compared to observations in the field. Varying leaf water volume does not seem crucial for a good prediction of leaf water enrichment. We further examined which level of complication in the non-steady-state description is minimally required for different applications of leaf water enrichment. We suggest applications that depend on leaf water enrichment throughout the leaf should take the isotopic gradient from the xylem to the evaporative site into account but can neglect varying leaf water volume. Applications that depend only on leaf water enrichment at the evaporating site, however, are sufficiently described by a non-steady-state model that neglects varying leaf water volume and the isotopic gradient from the xylem to the evaporative site.

Existing One-Dimensional Models

Steady-State (SS)

Craig and Gordon (1965) Steady-state: $R_E = R_s$

$$R_E = \frac{1}{\alpha' \alpha_x (1-h)} (R_s - \alpha' h R_s)$$

$$R_s = \alpha' \alpha_x (1-h) R_s + \alpha' h R_E$$

Non-Steady-State (NSS)

Governing equation $\frac{d(V_L \Delta_L)}{dt} = \frac{g_w w_L}{\alpha' \alpha_x} (\Delta_s^* - \Delta_L)$
 Dongmann et al. (1974) $V_L \frac{d\Delta_L}{dt} = \frac{g_w w_L}{\alpha' \alpha_x} (\Delta_s^* - \Delta_L)$
 Bariac et al. (1990)
 Cernusak et al. (2002) $\frac{d(\Delta_L V_L)}{dt} = \frac{g_w w_L}{\alpha' \alpha_x} (\Delta_s^* - \Delta_L)$
 Farquhar & Cernusak (2005) $\frac{d(\Delta_L V_L)}{dt} = \frac{g_w w_L}{\alpha' \alpha_x} (\Delta_s^* - \Delta_L) - f_{em}$
 This study $V_L \frac{d\Delta_L}{dt} = \frac{g_w w_L}{\alpha' \alpha_x} (\Delta_s^* - \Delta_L) - f_{em}$

Dongmann-style solution

$$\Delta_L(t+dt) = c_1 \Delta_s^*(t+dt) + [\Delta_L(t) - c_1 \Delta_s^*(t+dt)] e^{-\frac{g_w w_L}{\alpha' \alpha_x V_L c_1} dt}$$

Name	V_L	f_{em}	c_1	Reference
Dongmann	constant	1	1	Dongmann et al. [1974] Bariac et al. [1990]
Cernusak	varying	1	$\frac{1}{1 + \frac{\alpha' \alpha_x}{g_w w_L} \frac{dV_L}{dt}}$	Cernusak et al. [2002]
Farquhar $V_{L, const}$	constant	$\frac{1-e^{-\rho}}{\rho}$	f_{em}	This study
Farquhar	varying	$\frac{1-e^{-\rho}}{\rho}$	$\frac{1}{f_{em} + \frac{\alpha' \alpha_x}{g_w w_L} \frac{dV_L}{dt}}$	Farquhar & Cernusak [2005]

with “brave assumption”: $\Delta_L = f_{em} \Delta_s^*$

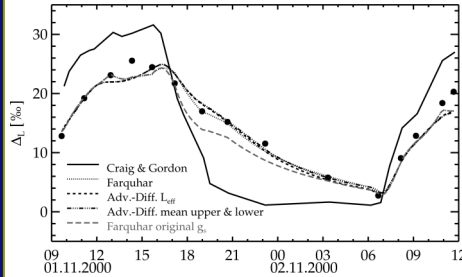
Advection-Diffusion model

PDE $\frac{\partial R}{\partial t} = -v_x \frac{\partial R}{\partial x} + D_x \frac{\partial^2 R}{\partial x^2}$
 BC xylem $v_x(0,t)R(0,t) - D_x \frac{\partial R}{\partial x} \Big|_{x=0} = v_x(0,t)R_s$
 BC stoma $v_x(x_e,t)R(x_e,t) - D_x \frac{\partial R}{\partial x} \Big|_{x=x_e} = v_x(x_e,t)R_e$

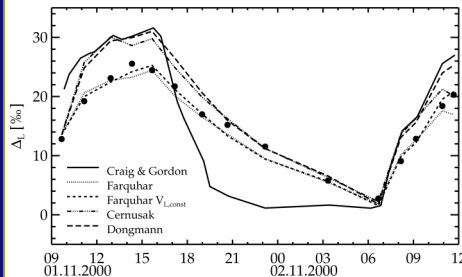
with $v_x(x_e,t) = E/C$ and if leaf water volume V_L variations only change volumetric leaf water content Θ_L

$$\frac{\partial \Theta_L}{\partial t} = -\frac{\partial v}{\partial x}$$

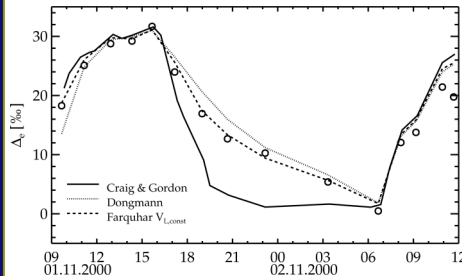
Comparison to Field Data



Comparison of the Farquhar & Cernusak [2005] NSS model (dotted line) and the advection-diffusion model with observed bulk leaf water isotope values for $H_2^{18}O$ of *Lupinus angustifolius* (filled circles, Cernusak et al. [2002]). The dash-triple dot line is the leaf water volume weighted mean of two advection-diffusion equations, one for the upper and one for the lower part of the leaf. The dashed line is the solution of one single advection-diffusion equation with mean leaf parameters determined from measured L_{eff} . The solid line is the Craig & Gordon steady-state solution. The grey long-dashed line is the Farquhar & Cernusak [2005] NSS model with the original value of stomatal conductance g_s at 01.11.2000 17:00h.



Comparison of the different NSS models with observed bulk leaf water isotope enrichment (filled circles). The lines are Dongmann-style solutions of the ODE with large time steps, i.e. calculated only at times of the leaf water measurements (ca. 1.5-4 hours apart).



Isotopic composition at the site of evaporation Δ_s^* . The open circles are calculated from the Δ_L measurements. Only shown are NSS models that neglect varying leaf water volume V_L , because the NSS models with varying V_L (Cernusak, Farquhar) are very similar to the two presented.

Findings & Recommendations

Average of bulk leaf water enrichment Δ_L and enrichment at the evaporative site Δ_s^* of the Dongmann and Farquhar $V_{L, const}$ NSS models weighted by different gas exchange parameters. The Craig & Gordon predictions are also presented. “non” stands for no weighting, A for assimilation, $g_w w_L$ for the one-way H_2O flux from the stomata into the atmosphere, $g_s C_i$ for the one-way CO_2 flux from the stomata into the atmosphere.

	Weighting variable			
	non	A	$g_w w_L$	$g_s C_i$
Δ_L Dongmann	17.0	20.3	18.8	14.8
Δ_L Farquhar $V_{L, const}$	13.8	16.3	15.1	12.0
Craig & Gordon	12.4	20.9	18.8	13.6
Δ_s^* Dongmann	17.0	20.3	18.8	14.8
Δ_s^* Farquhar $V_{L, const}$	16.1	20.7	19.0	14.8

- The theory underlying the Farquhar NSS model and all its variants is the theory of advection and diffusion in porous media.
- The so-called AD model gives not only the temporal evolution of bulk leaf water Δ_L but the temporal evolution at each point in the leaf. It does not need the “brave assumption” of the Farquhar NSS model.
- The AD model in conjunction with observations shows that the “brave assumption” is very well assumed most of the day.
- Taking just one L_{eff} compares startling well with the mean of two separate AD models and the observations.
- One can achieve very satisfying results by assuming fixed leaf water volume V_L . However one should try to get a solid mean leaf water volume V_L estimate that is not biased towards very low or very high leaf water status.
- We recommend the simple Dongmann-style solution for all NSS models.
- Applications that involve leaf water isotopic enrichment at the evaporative site Δ_s^* , the Dongmann NSS model is an expedient choice; e.g. atmospheric water isotopes, atmospheric O_2 (Dole) and CO_2 .
- If the application involves bulk leaf water enrichment Δ_L then the Farquhar $V_{L, const}$ NSS model is advisable; e.g. leaf organic matter such as tree rings.

Keep in mind that these findings and recommendations stem from one single data set in Western Australia, which might not be representative for the whole world.

References

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