BIOPHYSICAL ANALYSIS OF PLANT GAS EXCHANGE AND RECONSTRUCTION OF PALAEOCLIMATE

STAATLICHES MUSEUM FÜR NATURKUNDE STUTTGART
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Introduction

Goal

Reconstruction of palaeo-CO_2 (C_a) from stomatal densities ν of fossil plant leaves.

FIGURE 1: Robert Kidston and David Thomas Gwynne-Vaughan share a pipe over fossils from the Rhynie cherts (ca. 1920).

Model input

(i) Anatomic data of fossil leaves.
(ii) Photosynthesis parameters, in case of fossils to be taken from living descendants or relatives (photosynthetic biochemical parameters are comparatively conservative).

Model output

$\nu(C_a)$-curves of the long-term variation of stomatal density which allow to infer palaeo-CO_2 (C_a) from the stomatal density (ν) of fossil plant leaves.

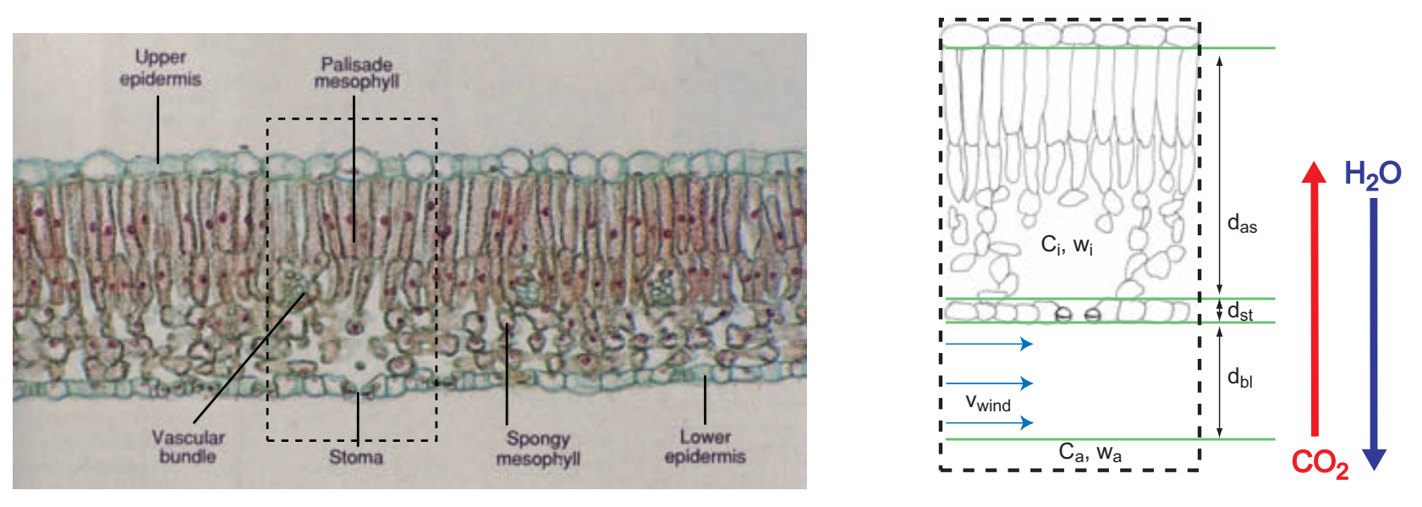

FIGURE 2: Cross section through a leaf, diffusional currents and morphological parameters.

Background

1. Land plants are under pressure to maximise assimilation and to minimise transpiration.
Since transpired H_2O molecules leaving the leaf and CO_2 molecules entering it use the same leaf openings ("stomata") land plants face a hunger vs. thirst dilemma.

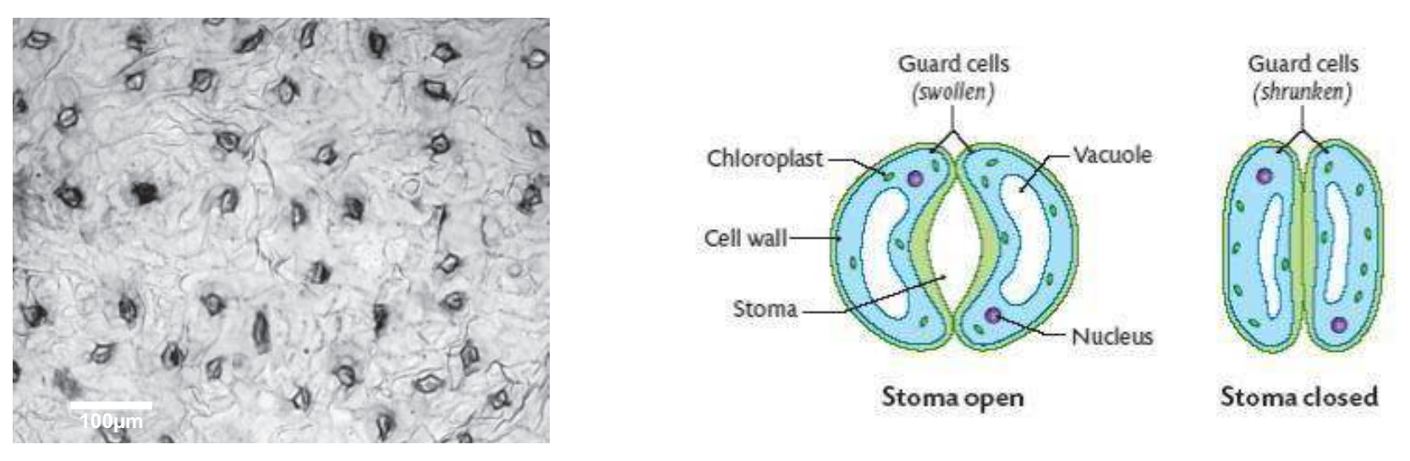

FIGURE 3: Leaf openings (stomata) on lower leaf surface of *Ginkgo biloba* (left) and stomatal anatomy (right).

Plants cope with this conflict by varying stomatal conductance g by
(i) opening and closing stomata actively, reacting on the diurnal cycles of incident solar radiation Q, temperature T, atmospheric humidity w_a and soil water supply,
(ii) varying the stomatal density ν by creating or removing whole stomata, reflecting long-term changes in C_a.
2. An optimisation principle ([1],[3],[4]) — the core of our model — predicts a fictitious stomatal conductance g_{opt} solely from information about the environmental variables of Q, T and w_a and from the "strength" of photosynthesis.
3. Since plants seem to act as predicted ([5]), the equality $g = g_{opt}$ implies the sought for relation $\nu(C_a)$.
4. Because the model is analytic, sensitivity studies can be easily performed (e.g. to assess which input parameters have the highest impact on the results).

References

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The model

Plant regulation of gas exchange

Fick's Law allows to express stomatal conductance in terms of leaf anatomy (see Fig. 1):

$$g = \frac{D_{CO_2}}{\left[\left(d_{bl} + d_{as}\frac{\tau_{as}^2}{n_{as}}\right) + \frac{d_{st}}{\nu a_{st}}\right]} \tag{1}$$

Plants adjust g to g_{opt} by varying the stomatal cross section a_{st} (short-term regulation) or the stomatal density ν (long-term regulation).

Submodel diffusion

Leaves and atmosphere exchange CO_2 and H_2O by diffusion. Fick's Law connects transpiration rate E with stomatal conductance g and the H_2O concentrations within leaves (w_i) and atmosphere (w_a) and similarly for the assimilation rate A and the CO_2 concentrations C_i and C_a ($a := D_{H_2O}/D_{CO_2}$).

$$E = g\,a\,(w_i - w_a) \qquad A = g\,(C_a - C_i) \tag{2}$$

Submodel photosynthesis

Assimilation of C_3 plants consumes CO_2 molecules according to the Farquhar model ([2]) of photosynthesis (q, Γ, K, R_d depend on T):

$$A = q\,\frac{C_i - \Gamma}{C_i + K} - R_d \tag{3}$$

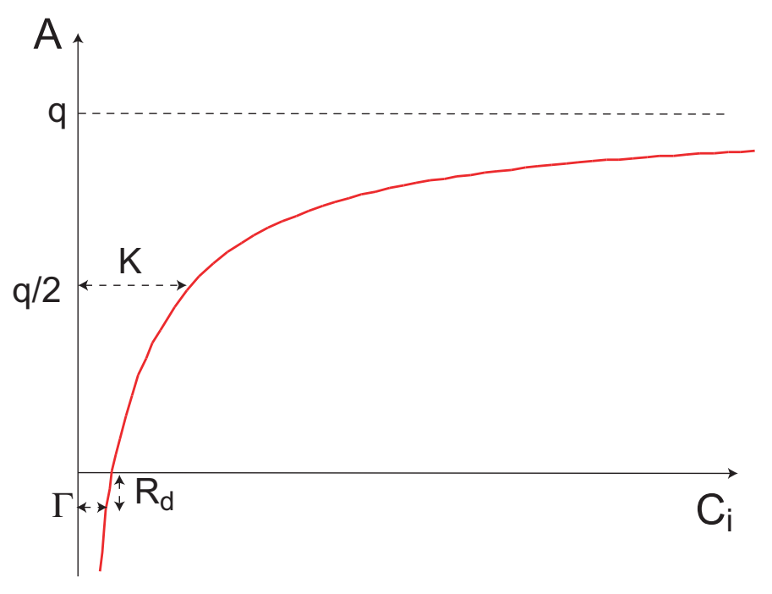


FIGURE 4: The more CO_2 molecules (C_i) are around the chloroplasts the more assimilates (A) they produce.

Submodel optimisation

Combining (2) and (3), A and E can be expressed in terms of the stomatal conductance g:

$$A[g] = \frac{1}{2g}\left\{g\,(C_a + K) + (q - R_d) - \sqrt{[g\,(C_a - K) - (q - R_d)]^2 + 4g\,(gKC_a + q\Gamma + KR_d)}\right\} \qquad E[g] = (w_{sat} - w_a)\;ag \tag{4}$$

Optimisation according to "Variation subject to constraints" (weighing carbon gain $\int_{\Delta t} A[g]\,dt =$ max. by assimilation versus water loss $\int_{\Delta t} E[g]\,dt = W_0$ by transpiration) produces the (fictitious) optimum stomatal conductivity

$$g_{opt} = \frac{1}{(C_a + K)^2}\left\{\sqrt{\frac{q\,(K + \Gamma)\,[C_a\,(q - R_d) - (q\Gamma + KR_d)]}{[C_a + K - \lambda\,(w_{sat} - w_a)]\,\lambda\,(w_{sat} - w_a)}}\,[C_a + K - 2\lambda\,(w_{sat} - w_a)] + (q - R_d)\;C_a - (q\Gamma + KR_d) - q\,(K + \Gamma)\right\} \tag{5}$$

Once g_{opt} is known, insertion into (4) produces A and E. The relation $\nu(C_a)$ is obtained from equating (5) and (1), replacing stomatal area a_{st} by maximum stomatal area a_{st}^{max} and solving for ν.

Results for *Ginkgo biloba*

Input values

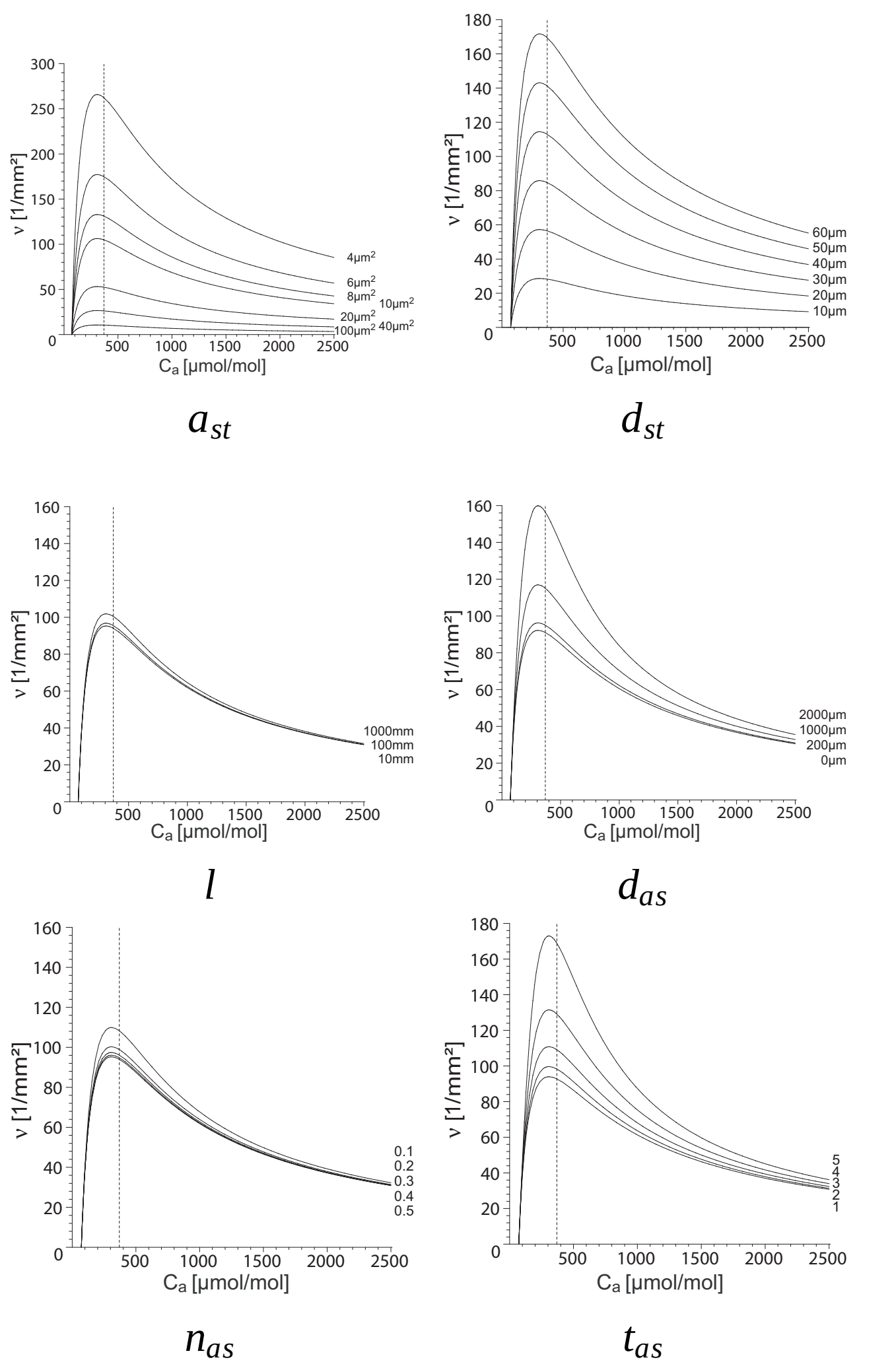
TABLE 1: Photosynthetic, environmental and anatomical parameters used to calculate $\nu(C_a)$ related to *Ginkgo biloba*.

Symbol	Value	Quantity/Source/Remarks
Leaf anatomical parameters		
l	84 ± 11 mm	Average leaf length
d_{st}^{geom}	31.9 ± 3.7 µm	Depth
w_{st}^{max}	1.2 ± 0.4 µm	Maximum width
h_{st}	13.1 ± 1.7 µm	Length of stomatal opening
d_{as}	218 ± 32 µm	Thickness
τ_{as}	1.571	Tortuosity
n_{as}	0.35	Porosity of assimilation tissue
Environmental parameters		
u_{wind}	3 m/s	Wind speed
w_{rel}	60 %	Relative atmospheric humidity
T	19.07 °C	Temperature
λ	1.57×10^{-3}	"Cost of water"
Photosynthetic parameters		
q	4.28 µmol/m²/s	Maximum rate of carboxylation
R_d	0.11 µmol/m²/s	Mitochondrial respiration rate in the light
K	205 µmol/mol	A Michaelis-Menten constant
Γ	43 µmol/mol	CO_2-compensation point in the absence of dark respiration

Output: $\nu(C_a)$-curves

Each family of $\nu(C_a)$-curves has been generated by varying just one of the parameters of the input parameter set of Table 1.

Leaf anatomical parameters:

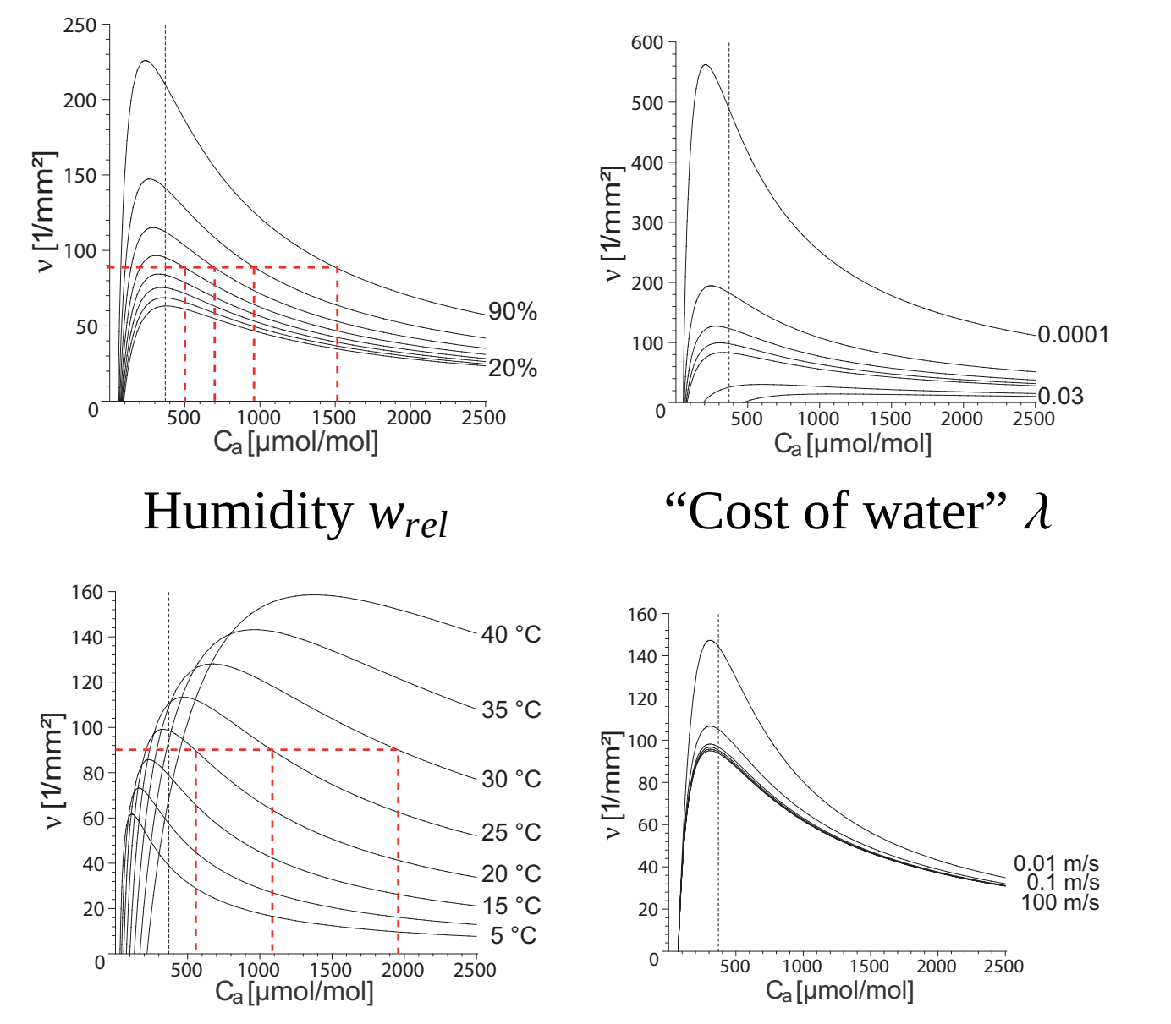


a_{st} d_{st}

l d_{as}

n_{as} t_{as}

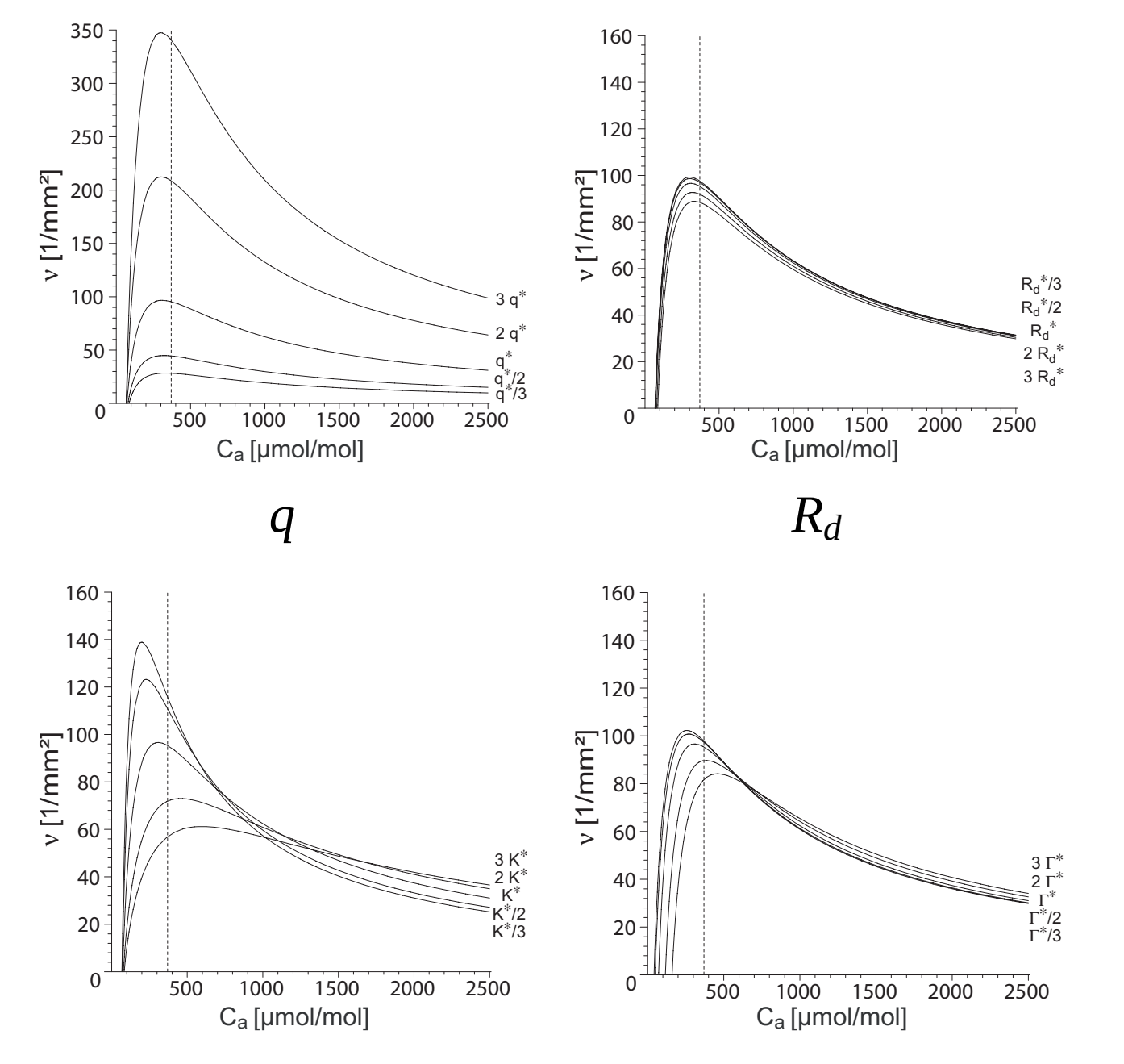
Environmental Parameters:



Humidity w_{rel} "Cost of water" λ

Temperature T Wind speed u_{wind}

Photosynthesis Parameters:



q R_d

K Γ

Conclusions

1. Stomatal density ν depends strongly on atmospheric CO_2 concentration C_a, leaf temperature T, atmospheric humidity w_a, soil water content (hidden in λ), stomatal area a_{st}, stomatal depth d_{st} and the photosynthetic parameter q.
Compared to these, the influence of the other parameters in Table 1 (for example, wind speed) is negligible.

2. The model ties the (fossil) stomatal density not only to (palaeo-)atmospheric CO_2-concentration, but also to stomatal anatomy and the three (palaeo-)environmental quantities temperature, atmospheric humidity and soil water content.

3. Attempts to obtain the atmospheric CO_2 concentration from stomatal density (or stomatal index) should therefore be accompanied by additional palaeoclimate studies of the considered sites.