Photosynthetic responses to altitude: an explanation based on optimality principles

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Summary

Increasing altitude is commonly accompanied by a declining ratio of leaf-internal to ambient CO\textsubscript{2} partial pressures ($c_\text{i}:c_\text{a}$; hereafter, $\chi$) and an increase in carboxylation capacity ($V_{c\text{max}}$), while carbon assimilation ($A$) shows little to no change. Here we provide a consistent, quantitative explanation for these responses based on the ‘least-cost hypothesis’ for the regulation of $\chi$ and the ‘co-ordination hypothesis’ for the regulation of $V_{c\text{max}}$. With leaf temperature held constant, our analysis predicts that the cost of maintaining water transport capacity increases with altitude (due to declining atmospheric pressure and increasing vapour pressure deficit, VPD) while the cost of maintaining carboxylation capacity decreases (due to the enhanced affinity of Rubisco for CO\textsubscript{2} at low O\textsubscript{2} partial pressures). Both effects favour investment in carboxylation capacity rather than water transport capacity. The response of $A$ then reflects the competing effects of stronger CO\textsubscript{2} limitation at low $c_\text{i}$ versus increased radiation penetration through a thinner atmosphere. These effects of atmospheric pressure are expected to be most strongly expressed in herbaceous plants that can maintain leaf temperatures in a narrow range. In leaves closely coupled to the atmosphere additional effects of declining temperature on photosynthesis are expected to modify but not obliterate those of pressure.

Key words: Attitude; atmospheric pressure; leaf temperature; photosynthetic capacity; $c_\text{i}:c_\text{a}$ ratio; optimality; theory
Introduction

Ecophysiologists have long been fascinated by the photosynthetic behaviour of alpine plants, which often have to withstand extreme environmental pressures (Gale, 1972; Friend & Woodward, 1990; Körner, 2003; Shi et al., 2006; Körner, 2007). About 8% of the world’s land surface is above 1500 m altitude (Körner, 2007). High altitudes can be climatically unusual, often with (for example) low temperatures, strong winds, and now high rates of warming (Körner, 2003; Pepin & Lundquist, 2008; Rangwala & Miller, 2012). Moreover, the low atmospheric pressure provides a set of environmental conditions unique on Earth (Table 1). There has been extensive speculation about altitudinal effects on photosynthesis and, in particular, how to account for the puzzling – but consistently observed – tendencies towards higher carbon dioxide (CO$_2$) drawdown (low $\chi$, resulting in low carbon isotope discrimination) and higher carboxylation capacity ($V_{cmax}$) with increasing altitude (Gale, 1972; Körner & Diemer, 1987; Friend et al., 1989; Terashima et al., 1995; Bresson et al., 2009; Zhu et al., 2010). At first glance, it might be expected that CO$_2$ assimilation rates would be reduced at high altitudes due to the low partial pressure of CO$_2$ (Friend & Woodward, 1990). However, actual measured photosynthetic rates are usually as high as, or even higher than, those at low altitudes (Mächler & Nösberger, 1977; Körner & Diemer, 1987; Cordell et al., 1999; Shi et al., 2006).

One group of hypotheses that attempt to explain the effects of altitude on photosynthetic physiology focuses on the effects of low temperature. It has been argued that alpine plants possess thick leaves as an adaptation to low temperatures, and thus higher leaf nitrogen on an area basis ($N_{area}$). Higher $N_{area}$ is taken to imply higher $V_{cmax}$, in turn leading to higher CO$_2$ drawdown due to higher photosynthetic
rates (Woodward, 1979; Körner & Diemer, 1987; Friend et al., 1989; Sparks & Ehleringer, 1997). This reasoning assumes that higher $N_{area}$ in thicker leaves would be associated with higher $V_{cmax}$, but this is not necessarily so, as a substantial fraction of leaf N in thick leaves (with low specific leaf area) is located in cell walls rather than in chloroplasts (Onoda et al., 2004). An alternative argument, from the perspective of carbon isotope discrimination, suggests that increased leaf thickness could lengthen the diffusional pathway for CO$_2$ from the atmosphere to the site of carboxylation, and therefore potentially decrease $\chi$ (Vitousek et al., 1990). However, low air pressure would be expected to counteract this effect, by allowing CO$_2$ to diffuse more readily through the stomata (Table 1).

In any case, no hypothesis based on temperature effects can account for the difference in plant responses to altitudinal and latitudinal gradients, i.e. why the same adaptations in photosynthetic capacity observed on high mountains are not observed in polar regions where growing-season temperatures are also low (Billings et al., 1961; Mooney & Billings, 1961; Billings & Mooney, 1968; Chabot et al., 1972; Zhu et al., 2010). It is moreover worth noting that although low temperatures can depress photosynthesis, measured growing-season leaf temperatures and optimal temperatures for photosynthesis in both alpine and arctic plants are typically only reduced by a few degrees, in contrast with a much larger decline in air temperature with altitude or latitude (Körner & Diemer, 1987; Körner, 2007). The dense canopy structure and crowded leaf arrangement on stems of cushion and prostrate alpine plants create a low boundary-layer conductance and thus allow the maintenance of large differences between the temperatures of leaves and air (Gauslaa 1984; Körner 2003; Michaletz et al., 2016). The effect of such morphological adaptations is superimposed on the universal tendency, rooted in the fundamentals of leaf energy balance, for leaf
temperatures to be maintained in a narrower range than air temperatures (Campbell & Norman 1998; Michaletz et al., 2016).

A further group of hypotheses suggests that low atmospheric pressure might influence photosynthesis through more direct physiological influences, independently of temperature (Decker, 1959; Billings et al., 1961; Mooney & Billings, 1961). However, despite much previous speculation, and the fact that many biophysical quantities relevant to gas exchange are known to change with air pressure and leaf temperature in a predictable manner (Table 1), effects of those biophysical quantities on plant physiology have not been fully explored. Misconceptions abound in the literature. For example, alpine plants were predicted to be more sensitive to the decreased CO$_2$ concentration (molar mixing ratio) in the Quaternary glacial periods simply because the CO$_2$ partial pressure at high altitudes is low (Street-Perrott et al., 1997). This is incorrect, however, because the partial pressure of O$_2$ is also reduced at high altitudes – implying a reduced photorespiratory burden which counteracts the effect of CO$_2$ concentration on photosynthesis, as previously noted e.g. by Körner et al. (1991) and Terashima et al. (1995).

‘First-principles’ hypotheses on photosynthetic behaviour

Natural selection implies that plants optimize ecophysiological traits by regulating the allocation of resources to different functions. This principle leads to the least-cost hypothesis and the co-ordination hypothesis for the optimal photosynthetic behaviour of C$_3$ plants. These hypotheses can be incorporated into the standard (Farquhar et al., 1980) model, thereby potentially generating a unifying explanation and prediction of photosynthetic trait responses to environmental factors (Wang et al., 2016).
The least-cost hypothesis considers maintenance respiration costs associated with transpiration ($E$) and carboxylation ($V_{cmax}$) that are required in order to achieve a given photosynthetic carbon gain ($A$). The hypothesis states that the total (combined) cost per unit assimilation is minimized (tissue construction costs and other costs, such as those of nutrient uptake, may be relevant but have been neglected for simplicity.)

Denoting $a$ and $b$ as dimensionless cost factors for $E$ and $V_{cmax}$ respectively, the formal optimality criterion is to minimize $aE/A + bV_{cmax}/A$ (Wright et al., 2003; Prentice et al., 2014). Eqn 11 in Prentice et al. (2014) indicates that the cost factor, $a$, depends on water viscosity, plant properties and the maximum water potential difference between soil and leaf, while $b$ is generally taken to be constant (Farquhar et al. 1980). Analysis of a global carbon isotope dataset indicates the ratio of $b$ to $a$ is about 240 under standard conditions (Wang et al., 2016). According to this hypothesis, plants weigh the two costs under different environments. For example, if increasing aridity increases the unit cost of transpiration while the unit cost of carboxylation remains constant, the optimal plant strategy is to shift investment towards $V_{cmax}$. Formally this criterion can be represented by an optimal value of $\chi$, which is a decreasing function of the leaf-to-air VPD ($D$, in Pa) as predicted by the following equations (Prentice et al. 2014):

$$\chi = \frac{\xi}{\xi + \sqrt{D}}$$  \hspace{1cm} (1)

where $\xi = \frac{bK_{c}}{1.6a}$, $K = K_{c}\left(1 + \frac{\theta}{K_{w}}\right)$  \hspace{1cm} (2)

The composite parameter $\xi$ represents the sensitivity of $\chi$ to $D$ and is influenced by both the cost terms. The mathematical form of Eqn 1 is the same as that proposed by Medlyn et al. (2011), which is based on a widely-cited stomatal optimality hypothesis.
stating that plants minimize $E - \lambda A$ (Cowan & Farquhar, 1977). However, the marginal cost of transpiration ($\lambda$) in that expression is not clearly defined. In the least-cost hypothesis, by contrast, the parameter $\xi$ can be expressed explicitly as a function of the cost factors and the effective Michaelis-Menten coefficient of Rubisco ($K$), which is related to the partial pressure of $O_2$ ($O$) and the Michaelis-Menten coefficients of Rubisco for $CO_2$ and $O_2$ ($K_C$ and $K_O$). The temperature dependencies of $K_C$ and $K_O$ follow an Arrhenius relationship as described by Bernacchi et al. (2001) and this also gives rise to a temperature dependency of $\xi$ (Prentice et al., 2014).

The leaf-to-air VPD ($D$) is the difference between the vapour pressure in the intercellular spaces and the vapour pressure in the free air beyond the leaf boundary layer. The intercellular vapour pressure is usually assumed to be saturated and is determined by the leaf temperature. The free-air vapour pressure is the actual vapour pressure, which depends on the molar mixing ratio of water vapour in the air and on the atmospheric pressure. The conductance for gas exchange between leaves and air that corresponds to this vapour pressure gradient is composed of stomatal conductance and boundary-layer conductance in series. The boundary-layer conductance is generally many times larger than the stomatal conductance, so differences among leaves in boundary-layer conductance can be compensated by changes in stomatal conductance, allowing the maintenance of optimal $\chi$.

The co-ordination hypothesis states that investment in Rubisco is matched to average light conditions, so that the Rubisco-limited and electron transport-limited rates of photosynthesis are approximately equal (Chen et al., 1993; Haxeltine & Prentice, 1996; Maire et al., 2012; Xu et al., 2012). The Farquhar et al. (1980) model
describing Rubisco-limited ($A_C$) and electron transport-limited ($A_J$) photosynthesis rates can be expressed in a simplified way as follows:

$$A_C = V_{cmax} \cdot \frac{c_i-I^*}{c_i+K}$$  \hspace{1cm} (3)

$$A_J = \varphi_0 \cdot PPFD \cdot \frac{c_i-I^*}{c_i+2I^*}$$  \hspace{1cm} (4)

where $\varphi_0$ is the intrinsic quantum efficiency of photosynthesis, $PPFD$ is the photosynthetic photon flux density and $I^*$ is the CO$_2$ compensation point, influenced by both pressure and temperature (Table 1). Eqn 4 makes the simplifying assumption that the response of assimilation to $PPFD$ is linear up to the point where Rubisco becomes limiting. According to the co-ordination hypothesis the two rates are equal under typical daytime conditions. Therefore,

$$V_{cmax} = \varphi_0 \cdot PPFD \cdot \frac{c_i+K}{c_i+2I^*}$$  \hspace{1cm} (5)

where $PPFD$ is now an average daytime value over a period of about a week to a month, i.e. long enough to allow the acclimation of $V_{cmax}$.

**Predicting responses of photosynthetic traits to atmospheric pressure**

By introducing the known altitudinal responses of various key biophysical quantities, we show here how the partial responses of $\chi$, $V_{cmax}$ and $A$ to atmospheric pressure and leaf temperature along the altitude gradient can be predicted from the equations above. Moreover, these predictions appear to be consistent with the field observed altitudinal trends in $\chi$, $V_{cmax}$ and $A$ (Table 2, Figure 1). To separate the effects of pressure and temperature, and also to cover a realistic leaf temperature variation along altitude gradients, we start by listing ten potential influences of atmospheric pressure on plant
physiological processes under constant leaf temperature, which may be a reasonable approximation for herbaceous plants as discussed above. Then we impose the additional effects of temperature, assuming that leaf temperature declines with altitude but follows a lapse rate shallower than air temperature due to the general homoeostatic tendency of leaf temperatures (Campbell & Norman 1998; Michaletz et al., 2016). This approach may be realistic for tree species, whose leaves are situated well above the ground and subject to a potentially high wind speed, and therefore cannot be expected to maintain leaf temperatures near-constant with altitude (Table 1).

Among the listed biophysical quantities, $VPD$ and $K$ are key variables predicting an altitudinal response of $\chi$ (Eqns 1-2), whereas $I^*$, $c_s$, and $PPFD$ impose further effects on $V_{\text{max}}$ and $A$ (Eqns 4-5).

**Lower $\chi$ minimizes the costs of carbon assimilation at high altitudes**

With a constant leaf temperature, the pressure-induced decrease in $K$ and enhancement of $D$ both lead to a lower $\chi$ for alpine plants (Eqns 1-2). As indicated in Table 1, $K$ declines with altitude, due to the reduced partial pressure of $O_2$, thereby increasing the affinity of Rubisco for $CO_2$ and reducing the carboxylation capacity required per mole of carbon fixed (Bresson et al., 2009). On the other hand, for a given molar mixing ratio of water vapour to air, lowered atmospheric pressure leads to reduced actual vapour pressure. As the saturated leaf-internal vapour pressure is invariant with atmospheric pressure, this reduction tends to increase leaf-to-air $VPD$, thereby increasing the water transport required per mole of carbon fixed. According to the least-cost hypothesis, both effects support a shift in the investment of resources towards increased Rubisco capacity and against water transport capacity (Wang et al., 2016). The predicted outcome of a lowered $\chi$ with atmospheric pressure can be shown...
mathematically by differentiation of the expression for optimal $\chi$, which shows that the partial response of $\chi$ to decreasing atmospheric pressure is always negative (Notes S1). Our predicted response of $\chi$ to pressure is consistent with observations by Körner & Diemer (1987) where leaf temperature was shown to vary only a few degrees (Table 2).

After superimposing temperature effects, declining leaf temperature reduces the saturated vapour pressure, and thus decreases the leaf-to-air VPD – leading to a lower cost of water transport, opposite to the effect of air pressure. However, the declining leaf temperature still reduces $K$ and this has the stronger influence, favouring a decline in $\chi$ (Table 1). By separating altitudinal and latitudinal trends, Körner et al. (1991) showed that aside from the effect of pressure, lower temperature reduces $\chi$, potentially reinforcing the decline of $\chi$ with altitude.

The leaf-internal partial pressure of CO$_2$, $c_i$, is the product of $\chi$ and $c_a$. Although $c_i$ declines with altitude due to the declines in both $c_a$ and $\chi$, this does not automatically imply an increased limitation of CO$_2$ on photosynthesis. This is because CO$_2$ limitation is also determined by the CO$_2$ compensation point ($I^*$), as shown by Eqn 4. If a constant leaf temperature is assumed, $I^*$ is proportional to the O$_2$ partial pressure and thus changes in proportion to $c_a$ (Farquhar et al., 1980) (Table 1). Consequently, a stronger CO$_2$ limitation due to the reduction in $\chi$ (not due to $c_a$ or $I^*$) is expected for alpine plants. After imposing a temperature effect, the decline in $I^*$, following an Arrhenius relationship (Bernacchi et al., 2001), is much faster than that of $\chi$ (Table 1) and this leads to a weaker CO$_2$ limitation on photosynthesis.

It has been suggested that photosynthesis might be influenced by the more rapid diffusion of gases in air at lower pressure (Table 1) (Gale, 1972; Smith & Donahue, 1987).
We might therefore predict that the consequence of more rapid gaseous diffusion at high altitudes would be a reduction in stomatal density and/or diameter. In reality, both positive (Wagner, 1892; Bonnier, 1895; Paridari et al., 2013) and negative (Körner et al., 1983) responses of stomatal density to altitude increase have been reported, suggesting that some other environmental factors or morphological adaptations might also be involved in determining stomatal density (Körner et al., 1986; Friend & Woodward, 1990).

**Higher $V_{c_{\text{max}}}$ is required to maximize carbon assimilation**

According to the least-cost hypothesis, a relatively lower cost of maintaining carboxylation due to increased affinity to CO$_2$ (lower $K$) in turn implies an increased $V_{c_{\text{max}}}$, as required (by the co-ordination hypothesis) to achieve an optimal assimilation rate that is set by PPFD. Mathematically, the sensitivity of $V_{c_{\text{max}}}$ to air pressure based on Eqn 5 (Notes S1) shows that the response is always positive provided $K \gg \Gamma^*$. In this response, either enhanced PPFD on clear days or reduced $c_i$ is a secondary contributor to the positive response of $V_{c_{\text{max}}}$ to altitude, whereas the decline in $K$ is the main contributor – being about three times larger than the other contributions. Reduced leaf temperature superimposes a small negative effect on $V_{c_{\text{max}}}$, which is only about one fifth of the positive effect of pressure decline. This can also be theoretically predicted by the ‘kinetic’ response of biochemical rate parameters ($K_c$, $K_o$ and $\Gamma^*$) to temperature and is supported by field observations (Dong et al., 2016; Togashi et al., in revision).

Our predictions are supported by previous observations (Table 2, Figure 1). Quantitative comparison with Körner & Diemer (1987) is possible because this study reported all of the relevant environmental variables (in addition to altitude) that would
be expected theoretically to influence $\chi$ and $V_{cmax}$ (Table 2). Our literature search revealed a number of other studies of altitude effects (Figure 1) but it was not generally possible to exclude other effects, e.g. of changes in leaf temperature or cloudiness (it is worth noting that Körner & Diemer (1987) reported negligible changes in leaf temperature). Therefore, the observed changes in $V_{cmax}$ are variable (Shi et al., 2006; Fan et al., 2011), but nonetheless consistent with our predicted range (Figure 1).

The co-ordination hypothesis also allows prediction of the sensitivity of the assimilation rate $A$ to air pressure through Eqn 4 (Notes S1). Table 1 shows how much each pressure-dependent quantity contributes to changes in $A$ under defined reference conditions. The increased diffusion coefficients for water vapour and CO$_2$ may physically affect how stomatal regulation achieves the optimal $\chi$, but should not influence its value, nor the value of $A$. As discussed above, the opposite effects of the declining O$_2$ and CO$_2$ partial pressures approximately cancel each other. Therefore, the sensitivity of $A$ to altitude depends on the competition between the negative effect of reduced $\chi$ and the positive effects of enhanced PPFD, due to a shorter path length (enhanced clear-sky transmittivity), and reduced $I^*$ if leaf temperature declines. Therefore, either a negative or a positive response of $A$ can be expected, depending on the conditions. Referring again to the study by Körner & Diemer (1987), as altitude increases from 600 m to 2600 m, PPFD is predicted to increase by 5.4%, as observed (Table 2). Our predicted change in $A$ is only 0.4%, and Körner & Diemer (1987) reported no significant change (Table 2). Bresson et al. (2009) also found no significant change in $A$ with altitude, while measurements made at constant (low-elevation) CO$_2$ partial pressure showed a consistent increase; this is in line with our
prediction of increasing $V_{cmax}$ with altitude. Bresson et al. (2009) also found increasing $N_{area}$ with altitude, which is to be expected, given increasing $V_{cmax}$.

In principle, photosynthesis could be enhanced at high altitudes, if the benefit from increased radiation and reduced photorespiration were to overcome the effect of the reduction of $c_i$. However, reduced photorespiration relies on a reduction in leaf temperature, whereas radiation is also influenced by cloud cover, which in reality can decrease or increase with altitude, depending on latitude and continentality (Barry, 1992). Thus a diversity of trends might be found in a wider sampling of altitudinal gradients in different plant types and climatic regions. Nevertheless, the theoretical analysis presented here provides a first-order explanation for some commonly observed trends in photosynthetic traits along altitudinal gradients. The explanation is derived from a proposed general model to predict photosynthetic rates via eco-evolutionary optimization of photosynthetic traits (Wang et al., 2016). By disentangling the effects of pressure and temperature on a number of variables influencing leaf-level gas exchange, we show that both declining $\chi$ and increasing $V_{cmax}$ can be predicted by air pressure change alone, while superimposed temperature effects modify the magnitude rather than the sign of the responses – accounting for why these trends in $\chi$ and $V_{cmax}$ have been so widely observed.

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Author contribution

H.W. and I.C.P. derived the predictions. H.W. carried out all the analyses, constructed
the figures and tables, and wrote the first draft. H.W., I.C.P., T.F.K., I.J.W., T.W.D.
and C.P contributed to subsequent drafts. H.W., T.W.D. and I.C.P. summarized
altitudinal dependences of gas exchange and various relevant biophysical quantities.
I.C.P. and T.F.K contributed to the data analysis. I.J.W. first proposed the least-cost
theory, and I.C.P further developed the theory.

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**Notes S1** Mathematical derivation of the effects of air pressure on plant photosynthetic traits
Table 1. Partial effects of a 1 km increase in altitude above sea level on key biophysical quantities relevant to gas exchange, and the consequent effects on electron transport-limited photosynthetic rate based on the least-cost hypothesis and the coordination hypothesis (i.e. Eqn 1, 2 and 4).

<table>
<thead>
<tr>
<th>Quantity</th>
<th>Formula</th>
<th>Absolute change</th>
<th>Relative change</th>
<th>Partial effect on photosynthesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atmospheric pressure</td>
<td>$P = P_0(1 - Lz/T_b)^{\gamma M/RL}$</td>
<td>$-11.5$ kPa</td>
<td>-11.3%</td>
<td>+1.8%</td>
</tr>
<tr>
<td>Ambient partial pressure of CO₂</td>
<td>$c_a = c_{a0} P/P_0$</td>
<td>$-4.5$ Pa</td>
<td>-11.3%</td>
<td>-3.8%</td>
</tr>
<tr>
<td>Ambient partial pressure of O₂</td>
<td>$O = O_0 P/P_0$</td>
<td>$-2.4$ kPa</td>
<td>-11.3%</td>
<td>+3.3%</td>
</tr>
<tr>
<td>Clear-sky transmittivity</td>
<td>$\tau = \tau_0 (1 + 0.027 z)$</td>
<td>+0.020</td>
<td>+2.7%</td>
<td>+2.7%</td>
</tr>
<tr>
<td>Vapour pressure deficit</td>
<td>$VPD = e_s - e_{a0}(P/P_0)$</td>
<td>+0.15 kPa</td>
<td>+15.1%</td>
<td>-0.6%</td>
</tr>
<tr>
<td>Photorespiratory compensation point</td>
<td>$\Gamma^* = 0.5 O/\tau^*$</td>
<td>$-0.37$ Pa</td>
<td>-11.3%</td>
<td>+3.6%</td>
</tr>
<tr>
<td>Effective Michaelis-Menten coefficient of Rubisco</td>
<td>$K = K_c (1 + O/K_o)$</td>
<td>$-2.6$ Pa</td>
<td>-5.5%</td>
<td>-0.2%</td>
</tr>
<tr>
<td>Psychrometric constant</td>
<td>$\gamma = P c_p/\tilde{\varepsilon}_\lambda$</td>
<td>$-7.5$ Pa K$^{-1}$</td>
<td>-11.3%</td>
<td></td>
</tr>
<tr>
<td>Diffusion coefficient for CO₂</td>
<td>$D_c = D_{c0} (P_0/P)$</td>
<td>+1.9 mm$^2$ s$^{-1}$</td>
<td>+12.9%</td>
<td></td>
</tr>
<tr>
<td>Diffusion coefficient for water vapour</td>
<td>$D_w = D_{w0} (P_0/P)$</td>
<td>+3.1 mm$^2$ s$^{-1}$</td>
<td>+12.9%</td>
<td></td>
</tr>
</tbody>
</table>

(Assuming constant leaf temperature = 293 K)

(Assuming leaf temperature declines with altitude)
<table>
<thead>
<tr>
<th>Property</th>
<th>Formula</th>
<th>Value</th>
<th>Relative Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature</td>
<td>$T = T_0 - Lz$</td>
<td>$-6.5$ K</td>
<td>$-2.2%$</td>
</tr>
<tr>
<td>Leaf temperature</td>
<td>$T_l = Tl_0 - dLz$</td>
<td>$-4.33$ K</td>
<td>$-1.5%$</td>
</tr>
<tr>
<td>Vapour pressure deficit</td>
<td>$VPD = e_s - e_{a0} (P/P_0)$</td>
<td>$-0.41$ kPa</td>
<td>$-40.7%$</td>
</tr>
<tr>
<td>Photorespiratory compensation point</td>
<td>$\Gamma^* = 0.5 O/\tau^*$</td>
<td>$-0.97$ Pa</td>
<td>$-29.7%$</td>
</tr>
<tr>
<td>Michaelis-Menten coefficient for carboxylation</td>
<td>$K_c = K_{c ref} e^{\Delta Hc/(1/T_{ref}-1/T_l)/R}$</td>
<td>$-15$ Pa</td>
<td>$-63.9%$</td>
</tr>
<tr>
<td>Michaelis-Menten coefficient for oxygenation</td>
<td>$K_o = K_{o ref} e^{\Delta Ho/(1/T_{ref}-1/T_l)/R}$</td>
<td>$-8.1$ kPa</td>
<td>$-37.3%$</td>
</tr>
<tr>
<td>Effective Michaelis-Menten coefficient of Rubisco</td>
<td>$K = K_c (1 + O/K_o)$</td>
<td>$-26$ Pa</td>
<td>$-56.5%$</td>
</tr>
</tbody>
</table>

Symbols and reference values:
- $P_0$, atmospheric pressure at sea level, 101.325 kPa (Allen 1973).
- $L$, mean temperature lapse rate, 0.0065 K m$^{-1}$ (Allen 1973).
- $z$, elevation above sea level, km.
- $T_b$, base temperature for the barometric formula, 288.15 K (Berberan-Santos et al., 1997).
- $g$, acceleration due to gravity, 9.8066 m s$^{-2}$.
- $M$, molecular mass of dry air, 0.028 963 kg mol$^{-1}$ (Tsilingiris 2008).
- $R$, universal gas constant, 8.314 J mol$^{-1}$ K$^{-1}$ (Moldover et al., 1988).
- $e_{a0}$, vapour pressure of water at sea level, 1.338 kPa, corresponding to the reference condition $VPD = 1$ kPa.
- $\tau^*$, temperature-dependant Rubisco specificity factor at 293 K, 3228 (Bernacchi et al., 2001).
- $K_c$ and $K_o$, temperature-dependant Michaelis-Menten coefficients for carboxylation and oxygenation at 293 K, 23.82 Pa and 21.84 kPa (Bernacchi et al., 2001).
- $c_p$, specific heat of air at constant pressure, 1.004 kJ kg$^{-1}$ K$^{-1}$ (Fritschen & Gay, 1979).
- $\varepsilon$, molecular mass of water relative to air, 0.622 (Fritschen & Gay, 1979).
- $\lambda$, latent heat of vaporization of water, 2260 J kg$^{-1}$ (Fritschen & Gay, 1979).
water at 298 K, 2.465 MJ kg$^{-1}$ (Fritschen & Gay, 1979). $\tau_0$, clear-sky transmittivity at sea level, 0.75 (Allen, 1996). $D_{c0}$ and $D_{w0}$, diffusion coefficients for CO$_2$ and water vapour in air at sea level and 293 K, 14.7 mm$^2$ s$^{-1}$ and 24.2 mm$^2$ s$^{-1}$ (Jones, 2013). $T_0$ and $T_{l0}$, reference air and leaf temperature at sea level, 293 K. $d$, scaling factor correcting lapse rate for leaf temperature, 0.667 (Michaletz et al., 2016). $K_{c_{\text{ref}}}$ and $K_{o_{\text{ref}}}$, parameters $K_c$ and $K_o$ at a reference temperature of 298 K ($T_{\text{ref}}$), 40.49 Pa and 27.84 kPa. $\Delta H_c$ and $\Delta H_o$, the activation energies for $K_c$ and $K_o$, 79.43 kJ mol$^{-1}$ and 36.38 kJ mol$^{-1}$. 
Table 2: Comparison between observations (Körner & Diemer, 1987) and theoretical predictions of changes in $\chi$ (the ratio of leaf-internal to ambient CO$_2$ partial pressure), and fractional changes in PPFD (photosynthetic photon flux density), $V_{cmax}$ (maximum carboxylation capacity) and $A$ (photosynthetic assimilation rate) corresponding to altitude changes of 2 km (from 0.6 to 2.6 km, denoted with subscripts $l$ and $h$ respectively). Theoretical predictions are estimated by evaluating the prediction formula under the mean conditions reported by Körner & Diemer (1987): $\chi = 0.75$, $z = 1.6$ km and $c_a = 33.5$ pa with a constant leaf temperature = 22.55 °C, and climatological RH (relative humidity at sea level) = 80.6% extracted from Climate Research Unit data. $\kappa$: the ratio of $K$ to ambient CO$_2$ partial pressure, $\gamma^*$: the ratio of $\Gamma^*$ to ambient CO$_2$ partial pressure. Mathematical derivations of the theoretical predictions are provided in the supporting information Notes S1.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Observed (mean±SE)</th>
<th>Predicted</th>
<th>Prediction formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\chi_h - \chi_l$</td>
<td>$-0.08 \pm 0.02$</td>
<td>$-0.098$</td>
<td>$\frac{\partial \chi}{\partial z} = 0.114 \left( \frac{RH}{1-RH} \frac{P}{P_a + K_a} \right) (1 - \chi)$</td>
</tr>
<tr>
<td>$(PPFD_h - PPFD_l) / PPFD_l$</td>
<td>$0.054^a$</td>
<td>$0.054$</td>
<td>$\frac{1}{PPFD} \frac{\partial PPFD}{\partial z} = 0.027$</td>
</tr>
<tr>
<td>$(V_{cmax_h} - V_{cmax_l}) / V_{cmax_l}$</td>
<td>$0.41 \pm 0.13$</td>
<td>$0.28$</td>
<td>$\frac{1}{V_{cmax}} \frac{\partial V_{cmax}}{\partial z} = 0.027 + \left( \frac{1}{X + \gamma} - \frac{1}{X + 2\gamma} \right) \frac{\partial \chi}{\partial z}$</td>
</tr>
<tr>
<td>$(A_h - A_l) / A_l$</td>
<td>n.s.</td>
<td>$-0.004$</td>
<td>$\frac{1}{A} \frac{\partial A}{\partial z} = 0.027 + \left( \frac{1}{X + \gamma} - \frac{1}{X + 2\gamma} \right) \frac{\partial \chi}{\partial z}$</td>
</tr>
</tbody>
</table>

$^a$Average from continuous monitoring by Körner & Diemer (1987).
Figure 1: Theoretically predicted responses of leaf internal to ambient CO₂ partial pressure ($\chi$) and the photosynthetic capacity for carboxylation ($V_{cmax}$) to air pressure along an altitude gradient. The prediction formula presented in Table 2 is evaluated under global mean conditions defined as leaf temperature = 293 K, $z = 0$ km, $RH = 0.8$, $\chi = 0.75$, and $c_a = 40$ pa, illustrated by the solid line. Grey areas represent uncertainties related to a 10% variation in environmental factors around the standard conditions. The predicted response of $V_{cmax}$ under standard conditions, but with doubled CO₂ partial pressure, is shown by the dashed line. Various observations with standard errors (Körner & Diemer, 1987; Körner et al., 1988; Shi et al., 2006; Bresson et al., 2011; Fan et al., 2011) are superimposed for comparison.