Letters

Photosynthetic responses to altitude: an explanation based on optimality principles

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, 2007; Shi *et al.*, 2006). 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 ratio of leaf-internal to ambient CO_2 partial pressures ($c_i : c_a$; hereafter, χ), 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 (N) 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 χ (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.*, 2015). 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.*, 2015).

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, for example, 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 *coordination*

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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. Eqns 1, 2, 4)

Quantity	Formula[a]	Absolute change	Relative change (%)	Partial effect on photosynthesis (%)
(Assuming constant leaf temperature = 293 K)				
Atmospheric pressure	$P = P_0 (1 - Lz/T_b)^{gM/RL}$	−11.5 kPa	−11.3	+1.8
Ambient partial pressure of CO_2	$c_a = c_{a0} P/P_0$	−4.5 Pa	−11.3	−3.8
Ambient partial pressure of O_2	$O = O_0 P/P_0$	−2.4 kPa	−11.3	+3.3
Clear-sky transmittivity	$\tau = \tau_0 (1 + 0.027\, z)$	+0.020	+2.7	+2.7
Vapour pressure deficit	$VPD = e_s - e_{a0} (P/P_0)$	+0.15 kPa	+15.1	−0.6
Photorespiratory compensation point	$\Gamma^* = 0.5\, O/\tau^*$	−0.37 Pa	−11.3	+3.6
Effective Michaelis–Menten coefficient of Rubisco	$K = K_c (1 + O/K_o)$	−2.6 Pa	−5.5	−0.2
Psychrometric constant	$\gamma = Pc_p/\varepsilon\lambda$	−7.5 Pa K^{-1}	−11.3	
Diffusion coefficient for CO_2	$D_c = D_{c0} (P_0/P)$	+1.9 $mm^2\ s^{-1}$	+12.9	
Diffusion coefficient for water vapour	$D_w = D_{w0} (P_0/P)$	+3.1 $mm^2\ s^{-1}$	+12.9	
(Assuming leaf temperature declines with altitude)				
Air temperature	$T = T_0 - Lz$	−6.5 K	−2.2	
Leaf temperature	$Tl = Tl_0 - dLz$	−4.33 K	−1.5	+6.9
Vapour pressure deficit	$VPD = e_s - e_{a0} (P/P_0)$	−0.41 kPa	−40.7	+2.0
Photorespiratory compensation point	$\Gamma^* = 0.5\, O/\tau^*$	−0.97 Pa	−29.7	+9.7
Michaelis–Menten coefficient for carboxylation	$K_c = K_{cref}\, e^{\Delta Hc(1/Tref - 1/Tl)/R}$	−15 Pa	−63.9	−5.5
Michaelis–Menten coefficient for oxygenation	$K_o = K_{oref}\, e^{\Delta Ho(1/Tref - 1/Tl)/R}$	−8.1 kPa	−37.3	+1.0
Effective Michaelis–Menten coefficient of Rubisco	$K = K_c (1 + O/K_o)$	−26 Pa	−56.5	−4.3

[a]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, in kilometres; 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); c_{a0}, ambient partial pressure of CO_2 at sea level, 40 Pa (www.esrl.noaa.gov/gmd/ccgg/trends/); O_0, ambient partial pressure of oxygen at sea level, 21 kPa (NOAA *et al.*, 1976); τ_0, clear-sky transmittivity at sea level, 0.75 (Allen, 1996). e_s, temperature-dependent saturated vapour pressure, 2.338 at 273 K (Murray, 1967); e_{a0}, vapour pressure of water at sea level, 1.338 kPa, corresponding to the reference condition VPD = 1 kPa; τ^*, 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, respectively (Bernacchi *et al.*, 2001); c_p, specific heat of air at constant pressure, 1.004 kJ kg^{-1} K^{-1} (Fritschen & Gay, 1979); ε, molecular mass of water relative to air, 0.622 (Fritschen & Gay, 1979); λ, latent heat of vaporization of water at 298 K, 2.465 MJ kg^{-1} (Fritschen & Gay, 1979); 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 $mm^2\ s^{-1}$, respectively (Jones, 2013); T_0 and Tl_0, reference air and leaf temperature at sea level, 293 K; d, scaling factor correcting lapse rate for leaf temperature, 0.667 (Michaletz *et al.*, 2015); K_{cref} and K_{oref}, parameters K_c and K_o at a reference temperature of 298 K (T_{ref}), 40.49 Pa and 27.84 kPa; ΔH_c and ΔH_o, the activation energies for K_c and K_o, 79.43 kJ mol^{-1} and 36.38 kJ mol^{-1} (Bernacchi *et al.*, 2001).

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). Equation 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 approximately 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 χ, which is a decreasing function of the leaf-to-air vapour pressure deficit (VPD) (D, in pascals) as predicted by the following equations (Prentice *et al.*, 2014):

$$\chi = \frac{\xi}{\xi + \sqrt{D}} \qquad \text{Eqn 1}$$

$$\text{where} = \sqrt{\frac{bK}{1.6a}},\ K = K_c\left(1 + \frac{O}{K_o}\right) \qquad \text{Eqn 2}$$

The composite parameter ξ represents the sensitivity of χ 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 (λ) in that expression is not clearly defined. In the least-cost hypothesis, by contrast, the parameter ξ can be expressed explicitly as a function of the cost factors and the effective Michaelis–Menten coefficient of Rubisco (K), which is

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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 ξ (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 χ.

The *coordination 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:

$$A_C = V_{cmax} \cdot \frac{c_i - \Gamma^*}{c_i + K} \quad \text{Eqn 3}$$

$$A_J = \varphi_0 \cdot \text{PPFD} \cdot \frac{c_i - \Gamma^*}{c_i + 2\Gamma^*} \quad \text{Eqn 4}$$

where φ_0 is the intrinsic quantum efficiency of photosynthesis, PPFD is the photosynthetic photon flux density and Γ^* is the CO_2 compensation point, influenced by both pressure and temperature (Table 1). Equation 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 coordination hypothesis the two rates are equal under typical daytime conditions. Therefore,

$$V_{cmax} = \varphi_0 \cdot \text{PPFD} \cdot \frac{c_i + K}{c_i + 2\Gamma^*} \quad \text{Eqn 5}$$

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 elevation

By introducing the known altitudinal responses of various key biophysical quantities, we show here how the partial responses of χ, V_{cmax} and A to atmospheric pressure and leaf temperature along the altitude gradient can be predicted from the equations mentioned earlier. Moreover, these predictions appear to be consistent with the field observed altitudinal trends in χ, V_{cmax} and A (Table 2; Fig. 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 10 potential influences of atmospheric pressure on plant physiological processes under constant leaf temperature, which may be a reasonable approximation for herbaceous plants as discussed earlier. 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.*, 2015). 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 χ (Eqns 1, 2), whereas Γ^*, c_a, and PPFD impose further effects on V_{cmax} and A (Eqns 4, 5).

Table 2 Comparison between observations (Körner & Diemer, 1987) and theoretical predictions of changes in χ (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)

Variable	Observed (mean ± SE)	Predicted	Prediction formula
$\chi_h - \chi_l$	−0.1 ± 0.02	−0.098	$\frac{\partial\chi}{\partial z} = -\frac{0.114}{2}\left(\frac{\text{RH}}{1-\text{RH}} + \frac{P_o}{P_o + K_o}\right)\chi(1-\chi)$
$(\text{PPFD}_h - \text{PPFD}_l)/\text{PPFD}_l$	0.054[a]	0.054	$\frac{1}{\text{PPFD}}\frac{\partial\text{PPFD}}{\partial z} = 0.027$
$(V_{cmaxh} - V_{cmaxl})/V_{cmaxl}$	0.41 ± 0.13	0.28	$\frac{1}{V_{cmax}} \cdot \frac{\partial V_{cmax}}{\partial z} = 0.027 + \left(\frac{1}{\chi+\kappa} - \frac{1}{\chi+2\gamma^*}\right)\frac{\partial\chi}{\partial z} + \frac{0.114\kappa}{\chi+\kappa}$
$(A_h - A_l)/A_l$	ns	−0.004	$\frac{1}{A} \cdot \frac{\partial A}{\partial z} = 0.027 + \left(\frac{1}{\chi-\gamma^*} - \frac{1}{\chi+2\gamma^*}\right)\frac{\partial\chi}{\partial z}$

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. κ, the ratio of K to ambient CO_2 partial pressure; γ^*, the ratio of Γ^* to ambient CO_2 partial pressure. Mathematical derivations of the theoretical predictions are provided in the Supporting Information Notes S1. ns, not significant.
[a]Average from continuous monitoring by Körner & Diemer (1987).

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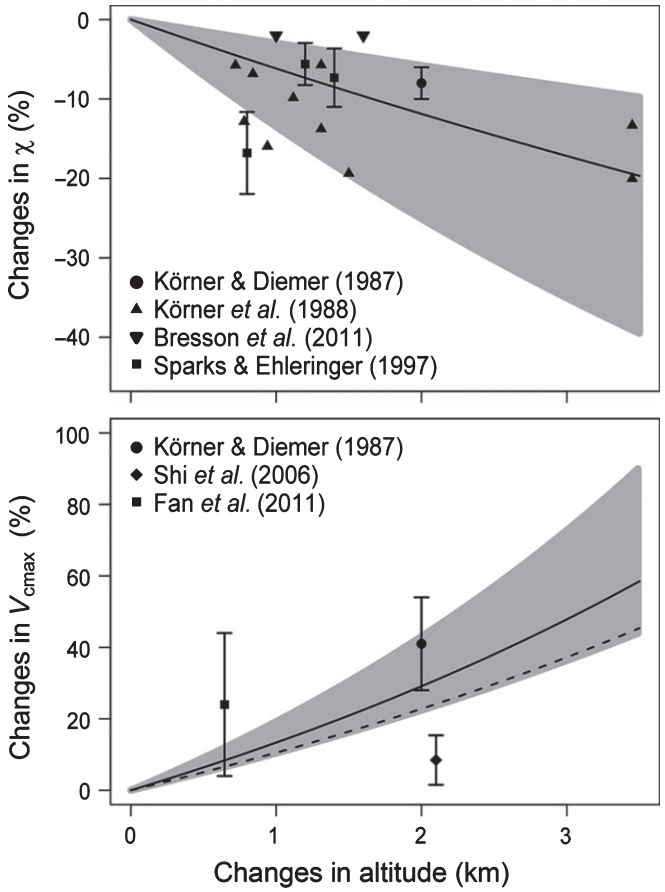

Fig. 1 Theoretically predicted responses of leaf internal to ambient CO_2 partial pressure (χ) and the photosynthetic capacity for carboxylation (V_{cmax}) to air pressure along an altitude gradient. The prediction formula presented in Table 2 is evaluated under global mean conditions defined as leaf temperature = 293 K, z = 0 km, relative humidity (RH) = 0.8, χ = 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 CO_2 partial pressure, is shown by the dashed line. Various observations with standard errors (Bresson *et al.*, 2011; Fan *et al.*, 2011; Körner & Diemer, 1987; Körner *et al.*, 1988; Shi *et al.*, 2006) are superimposed for comparison.

Lower χ 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 χ 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). However, 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 χ with atmospheric pressure can be shown mathematically by differentiation of the expression for optimal χ, which shows that the partial response of χ to decreasing atmospheric pressure is always negative (Supporting Information Notes S1). Our predicted response of χ 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 χ (Table 1). By separating altitudinal and latitudinal trends, Körner *et al.* (1991) showed that aside from the effect of pressure, lower temperature reduces χ, potentially reinforcing the decline of χ with altitude.

The leaf-internal partial pressure of CO_2, c_i, is the product of χ and c_a. Although c_i declines with altitude due to declines in both c_a and χ, 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 (Γ^*), as shown by Eqn 4. If a constant leaf temperature is assumed, Γ^* 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 χ (not due to c_a or Γ^*) is expected for alpine plants. After imposing a temperature effect, the decline in Γ^*, following an Arrhenius relationship (Bernacchi *et al.*, 2001), is much faster than that of χ (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, 1991; Terashima *et al.*, 1995). 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_{cmax} 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_{cmax}, as required (by the coordination hypothesis) to achieve an optimal assimilation rate that is set by PPFD. Mathematically, the sensitivity of V_{cmax} 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_{cmax} 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 negative

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effect on V_{cmax}, which is opposite to 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 Γ^*) to temperature and is supported by field observations (Dong *et al.*, 2016).

Our predictions are supported by previous observations (Table 2; Fig. 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 χ and V_{cmax} (Table 2). Our literature search revealed a number of other studies of altitude effects (Fig. 1) but it was not generally possible to exclude other effects, for example, 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 (Fig. 1).

The coordination 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 χ, but should not influence its value, nor the value of A. As discussed earlier, 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 χ and the positive effects of enhanced PPFD, due to a shorter path length (enhanced clear-sky transmittivity), and reduced Γ^* 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 χ and increasing V_{cmax} can be predicted by air pressure change alone, while superimposed temperature effects typically modify the magnitude of the responses – accounting for why these trends in χ and V_{cmax} have been so widely observed.

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Author contributions

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.

Han Wang[1,2]*, I. Colin Prentice[1,2,3], Tyler W. Davis[3,4], Trevor F. Keenan[2,5], Ian J. Wright[2] and Changhui Peng[1,6]*

[1]State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, College of Forestry, Northwest A&F University, Yangling 712100, China;
[2]Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia;
[3]AXA Chair Programme in Biosphere and Climate Impacts, Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, SL5 7PY, UK;
[4]United States Department of Agriculture – Agricultural Research Service, Robert W. Holley Centre for Agriculture and Health, Ithaca, NY 14853, USA;
[5]Earth Sciences Division, Lawrence Berkeley National Laboratory, 1 Cyclotron Road, Berkeley, CA 94720, USA;
[6]Department of Biological Sciences, Institute of Environmental Sciences, University of Quebec at Montreal, C.P. 8888, Succ. Centre-Ville, Montréal H3C 3P8, QC, Canada
(*Authors for correspondence: tel +86 (29) 87080608; email wanghan_sci@yahoo.com (H.W.); tel +86 (29) 87080608; email peng.changhui@uqam.ca (C.P.))

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Notes S1 Mathematical derivation of the effects of air pressure on plant photosynthetic traits.

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Key words: atmospheric pressure, attitude, leaf temperature, leaf-internal to ambient CO_2 partial pressures ratio ($c_i : c_a$), optimality, photosynthetic capacity, theory.

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