Forum

Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO_2 partial pressure: Comment and Reply

COMMENT

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Stomatal density (SD) has been shown to change with CO_2 concentration (at the same atmospheric pressure; Lake et al., 2001), and SD of fossilized leaf material or leaf imprints can be used to indicate past CO_2 concentrations (Beerling et al., 1998). However, the results of the analytical approach described by McElwain (2004) do not include an important parameter influencing the effect of altitude on CO_2 diffusion and uptake by a plant. Although the partial pressure of carbon dioxide does decrease in a predictable manner with decreasing atmospheric pressure, the diffusion of all gas-phase molecules increases at lower atmospheric pressure (Fig. 1). As a result, photosynthetic CO_2 uptake does not appear to become more rate-limited at greater altitudes, due primarily to the compensatory effects of increased diffusion rates (e.g., Smith and Donahue, 1991; Terashima et al., 1995). Thus, there would be no selective force for increasing SD in plant species evolving at higher altitudes, and the relationship suggested by McElwain (2004) is not expected to be generally applicable.

Analytically, diffusion is often expressed according to Fick's Law as

$$\text{Flux density of } j \ (\text{mol m}^{-2}\ \text{s}^{-1}) = D_j\,(\Delta C_j) / \Delta x, \qquad (1)$$

where D_j is the diffusion coefficient for the molecule in question, ΔC_j is the gradient in the concentration or partial pressure of molecule j, and Δx is the diffusing distance (Nobel, 1999). As seen in Figure 1, both D_j and ΔC_j influence flux density proportionally. Moreover, both terms change in similar proportions with increasing altitude, but are inversely related. For example, an increase in altitude from sea level to 4 km results in a decrease in the partial pressure of CO_2 of -38% (0.37–0.23 kPa), and an increase in D_C of 53% (1.65–2.53 m^{-2} s^{-1} x 10^{-5}) based on a relatively dry adiabatic lapse rate of 8 °C per 1000 m (Fig. 1).

A host of abiotic factors may be associated with changes in altitude, most of which can strongly influence stomatal density (e.g., Tichá, 1982; Lockheart et al., 1998; Qiang et al., 2003). Numerous studies have found increases in SD with elevation (e.g., Hovenden and Brodribb, 2000), decreases (e.g., Hultine and Marshall, 2000), or have been inconclusive (e.g., Qiang et al., 2003), suggesting that CO_2 concentration is not a primary altitudinal factor driving SD.

Although SD has been used to estimate historical CO_2 concentrations on a geological time scale, the similar proportional changes in D_{CO_2} and CO_2 partial pressure would indicate a compensating influence of the two acting in concert. As mentioned above, this compensating relationship has already been addressed in other publications dealing with the impact of altitude on the photosynthetic process. Similarly, there is no convincing evidence that greater altitude results in greater SD as a general rule. In this regard, it is actually total pore area per unit leaf area (which incorporates both stomatal size and frequency) that is the most pertinent parameter, and one which is rarely measured (e.g., Smith and Knapp, 1990). However, others have also concluded that the greatest impact of altitude is probably on plant transpiration, primarily because the increasing dryness of the air with altitude is often exacerbated by the concomitant increase in the diffusion coefficient of water vapor in air (D_{wv}) (Gale, 1972; Smith and Geller, 1979; Smith and Knapp, 1990; Terashima et al., 1995).
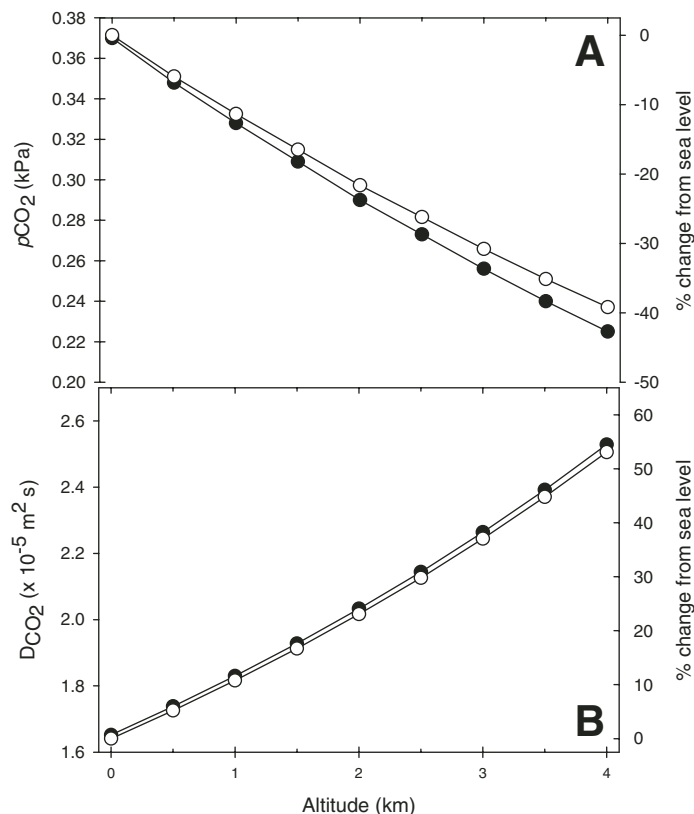

Figure 1. A: Change in CO_2 partial pressure (pCO_2). B: The diffusion coefficient for CO_2 in air (D_{CO_2}) with altitude. Curves represent absolute values (closed circles) and percent changes from sea-level values (open circles). Curve for $D_{CO_2} = 1.652 \times 10^{-5}\ (T/273)^{1.8}\ (P_0/P)$ (Nobel, 1999).

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REPLY

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The functional explanation for increased plant leaf stomatal density (SD) with elevation remains a topic of much debate among plant ecophysiologists (Friend and Woodward, 1990; Gale, 1972, 2004; Smith and Donahue, 1991; Terashima et al., 1995; Woodward and Bazzaz, 1988). Johnson et al. raise an interesting aspect of this ongoing debate. Based on the observation that gaseous diffusion increases with decreasing atmospheric pressure these authors argue that any negative impact of decreasing carbon dioxide partial pressure (pCO$_2$) with elevation on plant photosynthesis would likely be compensated for by greater diffusion rates of CO_2 into the leaf. Using these theoretical considerations Johnson et al. argue that decreasing CO_2 partial pressure is unlikely to select for increased SD in plant species evolving at high elevation, and thus, the highly significant relationship demonstrated between Californian black oak SD and elevation is unlikely to be generally applicable. In their theoretical calculations, however, Johnson et al. fail to take into account the observation that transpiration rates are often extremely elevated at high elevation due to (1) higher light intensity, (2) increased diffusion of H_2O in air at reduced atmospheric pressure, and (3) an increased density gradient of H_2O vapor out of the leaf into the ambient air (Gale, 2004). As H_2O vapor efflux through stomata has been shown to hamper CO_2 diffusion into the leaf (von Caemmerer and Farquhar, 1981), it is highly likely that increased transpirational water vapor loss at higher elevations would act to cancel out the higher diffusion coefficient of CO_2 at reduced barometric pressure (Gale, 2004), thereby selecting strongly for increased SD at high elevation to maintain adequate conductance to CO_2 diffusion.

Johnson et al. argue that many abiotic factors in addition to pCO$_2$ change with altitude and suggest that these other factors rather than pCO$_2$ may be responsible for the observed increase in SD in *Quercus kelloggii*. The potential role of other biotic and abiotic factors on SD, including temperature, light intensity, water availability, sex of the plant, etc., is well known (McElwain and Chaloner, 1996; Royer, 2001). Carbon dioxide and to a much lesser extent light intensity are the only factors which are known to control the actual development of stomata from epidermal initials. The effect of CO_2 on leaf development can be tracked by measuring stomatal index (SI); a ratio of the number of stomata to the total number of cells (stomata plus epidermal) on the leaf surface. In contrast all other biotic/abiotic variables which influence SD do so indirectly (Beerling and Kelly, 1997). In other words, although factors like temperature, water availability, and humidity do not directly influence the absolute number of stomata developing from initials, these variables can influence the size and/or spacing of epidermal cells, resulting in stomata being packed more closely together or further apart resulting in higher or lower densities but importantly the same SI.

The significant increase in both SI and SD with elevation in both sun and shade leaves of Californian black oak which I document in my paper can only therefore be explained by the effect of increasing CO_2 partial pressure on stomatal development from epidermal initials. Increasing SI rules out the effect of all other biotic and abiotic variables. In addition, to reiterate the results in the paper, a historical investigation into the effect of four climatic variables showed no significant correlation with black oak SD. However, the same historical black oak SD data set showed a highly significant inverse correlation with CO_2 concentration. Contrary to the assertions of Johnson et al. therefore, these two lines of evidence suggest that decreasing CO_2 partial pressure is indeed a primary altitudinal factor driving SD changes in Californian black oak.

This does not simply imply however, and I do not state as such in my paper, that the stomatal pCO$_2$ paleoaltimeter will be universally applicable. Certain taxa are not CO_2 sensitive—they do not show the classic inverse relationship between pCO$_2$ and SD or SI. These include many grasses and forbs (Reid et al., 2003) and plants with C4 photosynthesis (Raven and Ramden, 1989). These taxa have evolved alternative strategies for optimizing CO_2 uptake for photosynthesis against transpirational water loss, which negates the need to adjust SD. These include fine-tuned stomatal control which enable much more rapid stomatal opening and closing times within minutes rather than hours (as in grasses) and biochemical means of concentrating CO_2 internally thereby ensuring a high CO_2 gradient from the air to the leaf (as in C4 plants). It is imperative therefore that the stomatal pCO$_2$ paleoaltimeter is only applied to extant taxa, which are known to be CO_2 sensitive. Meta analysis of woody plant SD and SI responses to historical increases in pCO$_2$ over the past 200 yr and at naturally elevated CO_2 springs has shown that >70% (n = 44) of the taxa analyzed demonstrate the expected inverse relationship (Royer, 2001). This high CO_2 sensitivity among the majority of woody C3 taxa indicates that increased SD with elevation is likely to be the general rule for this group of plants. Coupled with the fact that woody C3 plants are the most well represented group in the plant fossil record, they are an ideal group for application of the stomatal pCO$_2$ paleoaltimeter.

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