

Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO₂ partial pressure

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ABSTRACT

Existing methods for determining paleoelevation are primarily limited by (1) large errors (± 450 m), (2) a reliance on incorrect assumptions that lapse rates in terrestrial temperature decrease with altitude in a globally predictable manner, and/or (3) are inherently climate dependent. Here I present a novel paleoelevation tool, based on a predictable, globally conserved decrease in CO₂ partial pressure ($p\text{CO}_2$) with altitude, as indicated by increased stomatal frequency of plant leaves. The approach was validated using historical populations of black oak (*Quercus kelloggii*). These analyses demonstrate highly significant inverse relationships between stomatal frequency and $p\text{CO}_2$ ($r^2 > 0.73$), independent of ecological or local climatic variability. As such, this is the first paleobotanical method to be globally applicable and independent of long-term Cenozoic climate change. Further, tests on modern leaves of known elevations indicate that species-specific application to the fossil record of *Q. kelloggii* (= *Q. pseudolyrata*) will yield paleoelevation estimates within average errors of $\sim \pm 300$ m, representing a significant improvement in accuracy over the majority of existing methods.

Keywords: paleoelevation, stomatal density, California, paleoaltimeter, carbon dioxide, *Quercus*.

INTRODUCTION

Despite advances in paleoaltimetry (Forest et al., 1995; Rowley et al., 2001; Sahagian et al., 2002; Spicer et al., 2003; Mulch et al., 2004), uncertainties and limitations associated with current methods hamper our ability to test hypotheses on the links among tectonic uplift, the long-term carbon cycle, and climatic cooling through the Cenozoic (Molnar and England, 1990; Raymo and Ruddiman, 1992). Many existing paleoaltimeters are inherently climate sensitive. It remains difficult to decipher the influence of long-term global climate change from more local or regional climatic change caused by tectonic uplift (Forest et al., 1995; Meyer, 1992; Rowley et al., 2001). Among paleobotanical approaches, the CLAMP (Climate Leaf Analysis Multivariate Program)–enthalpy paleobarometer (Spicer et al., 2003) is the most accurate, as it utilizes changes in leaf physiognomy as a proxy for moist static energy, a parameter that, unlike temperature, changes predictably with elevation (Forest et al., 1995; Wolfe et al., 1997). However, the method is limited at low latitudes (Spicer et al., 2003) and is sensitive to changes in sea-surface temperature and monsoon intensity. A paleoaltimeter using bubble density and distribution in basaltic lava flows to quantify atmospheric pressure (Sahagian et al., 2002) is climate independent. However, this method, which has an error of ± 400 m, requires the lava flow to be < 1 m in height and to have a simple emplacement history (Sahagian et al., 2002).

Here I present a new climate-independent paleoaltimeter, which uses a well-established and genetically controlled inverse relationship between leaf stomatal frequency and $p\text{CO}_2$ as a proxy for paleoelevation. This relationship was first observed in plant leaves collected along elevation gradients of declining $p\text{CO}_2$ (Körner et al., 1986; Woodward, 1986) and has since been widely used as a means of estimating paleoatmospheric $p\text{CO}_2$ from fossil plants of Devonian (McElwain and Chaloner, 1995) to Quaternary age (McElwain et al., 2002). The reduction in $p\text{CO}_2$ with altitude is thought to exert a phys-

iological limitation on plant photosynthesis, which is compensated for by increasing the plant leaves' maximum conductance to gaseous diffusion, attained by increased stomatal density (SD: number of stomata per square millimeter) and stomatal index (SI: ratio of number of stomata to total number of epidermal cells plus stomata expressed as a percentage) (Woodward and Bazzaz, 1988). Although this functional explanation for increased SD and SI with elevation is still debated (Terashima et al., 1995), the potential use of this anatomical response as a paleoelevation proxy has been little realized (Beerling and Royer, 2002; McElwain, 2002) and never rigorously tested. This paper presents (1) a methodology for application of this $p\text{CO}_2$ -based paleoelevation proxy to the plant fossil record, (2) analysis of the response rate of *Quercus kelloggii* SD and SI to $p\text{CO}_2$ decline with elevation, (3) a test of the climatic sensitivity of the stomatal paleoaltimeter, and (4) an investigation of its potential accuracy.

THEORETICAL BASIS FOR A $p\text{CO}_2$ PALEOALTIMETER

The volume percentage of CO₂ (mole fraction) in the atmosphere remains almost constant with increasing elevation (Gale, 1972). The partial pressure (i.e., mass per volume) of CO₂ decreases with decreasing barometric pressure [$pp(z)$ in pascals]:

$$pp(z) = 101,325 e^{(-m_{\text{air}}gz/Rt)}, \quad (1)$$

where m_{air} is the molecular weight of air ($28,964 \times 10^{-3}$ kg·mol⁻¹), z is altitude in meters, g is acceleration due to gravity (9.806 m·s⁻²), R is the universal gas constant (8.3145 J/mol) and t is mean July temperature (in kelvin). Under the assumptions that (1) globally averaged atmospheric pressure at sea level ($101,325$ Pa) has not changed significantly over the Cenozoic, as atmospheric mass has been relatively invariant (Tajika and Matsui, 1993), and (2) available estimates of molar volume of CO₂ at sea level (from here on referred to as sea-level CO₂) from paleo-CO₂ proxies (Royer et al., 2004) are sufficiently accurate for the Cenozoic, it follows that change in $p\text{CO}_2$ with elevation is globally predictable for any time over the past 65 m.y. according to

$$cd_2(z) = \frac{pp(z)}{101,325} cd_1, \quad (2)$$

where cd_2 and cd_1 are $p\text{CO}_2$ (Pa) at altitude z (m) and sea level, respectively. The latter assumption is dependent on the proxy or indicator method employed. The stomatal proxy method (Woodward, 1987) has been used to estimate Quaternary CO₂ within ± 1 to ± 3 Pa of ice-core measurements (McElwain et al., 2002) and has an accuracy range of ± 1 to ± 4 Pa in the Tertiary (Royer et al., 2004). Therefore, a $p\text{CO}_2$ -based paleoaltimeter can be developed by using the well-established stomatal CO₂ proxy method by solving equation 2 for paleoaltitude (z) as follows (Beerling and Royer, 2002; McElwain, 2002):

$$z = \ln\left(\frac{cd_2}{cd_1}\right) R \frac{t}{-m_{\text{air}}g}, \quad (3)$$

where cd_2 and cd_1 are the estimated $p\text{CO}_2$ calculated by using the stomatal proxy CO₂ method of a high-altitude fossil plant taxon from paleoaltitude z (in meters) and an isochronous sea-level taxon, respectively.

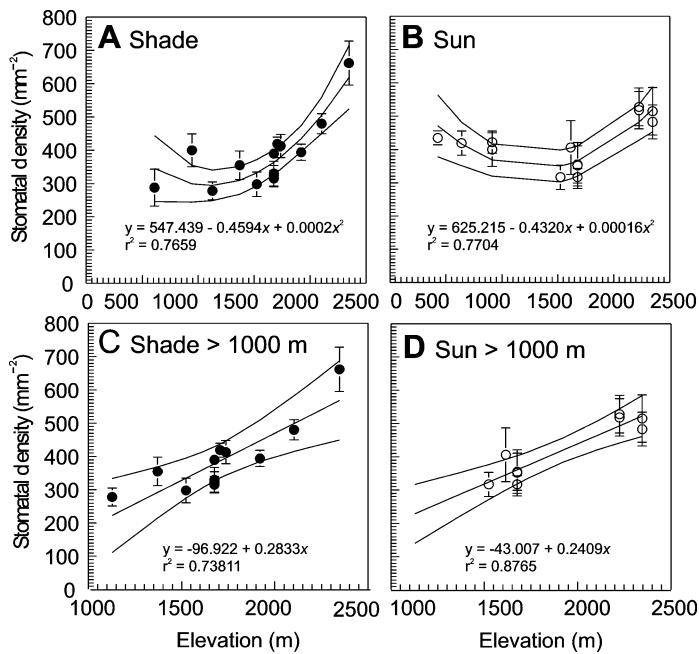


Figure 1. Relationship between stomatal density (SD) and elevation of *Quercus kelloggii* (A, C) shade and (B, D) sun leaves (collected 1934–1935). C and D show herbarium sheets collected above 1000 m only. Each point represents mean of five random SD counts per leaf. Error bars represent one standard deviation. A: F-stat. (13) = 17.996, $P \leq 0.001$. B: F-stat. (13) = 18.4544, $P \leq 0.001$. C: F-stat. (11) = 28.185, $P \leq 0.001$. D: F-stat. (9) = 56.799, $P \leq 0.001$.

MATERIALS AND METHODS

To investigate the potential sensitivity of this new paleoaltimeter approach, the rates of change in SD and SI with elevation were investigated by using georeferenced herbarium specimens of *Q. kelloggii* collected from multiple populations across California between 1934 and 1935. *Q. kelloggii* has one of the widest elevation ranges (60 to ~2440 m) of deciduous angiosperm trees in North America (Burns and Honkala, 1990) and, as *Q. pseudolyrata* (Condit, 1944), is well represented in high-elevation Miocene–Pliocene fossil floras of California and Oregon. Herbarium leaf samples were first divided into subsets of “sun” and “shade” leaves on the basis of the degree of undulation of their epidermal cell anticlinal walls, as light intensity in addition to $p\text{CO}_2$ can influence stomatal development and hence SD and SI (Lake et al., 2001), although much less so than CO_2 (Kürschner, 1997; Sun et al., 2003). SD and SI were calculated from five randomly sampled areas per leaf cuticle using a Leica DMLB epifluorescence microscope following standard protocols (McElwain et al., 2002).

LEAF STOMATAL FREQUENCY CHANGE WITH ELEVATION

Highly significant, but nonlinear, positive correlations were observed between “shade leaf” ($r^2 = 0.77$, $P \leq 0.001$) and “sun leaf” ($r^2 = 0.77$, $P \leq 0.001$) SD and elevation (Fig. 1). The analysis also indicated that the strength of the relationship was driven primarily by the SD of leaves collected at higher elevations ($\sim >1000$ m) (Fig. 1). Further analysis of SD and elevation for both sun ($r^2 = 0.88$, $P \leq 0.001$) and shade ($r^2 = 0.74$, $P \leq 0.001$) morphotypes confirmed the presence of highly significant linear correlation above ~ 1000 m (Figs. 1C, 1D). The observed SD increases with elevation in *Q. kelloggii* (Fig. 1) most likely reflect the effects of decreasing $p\text{CO}_2$ on stomatal initiation, the nonlinearity of which is expected, as numerous experimental and historical observations demonstrate diminished SD response rate with increasing CO_2 (Kürschner et al., 1997). Increased cloudiness with elevation in California diminishes the possibility that the observed

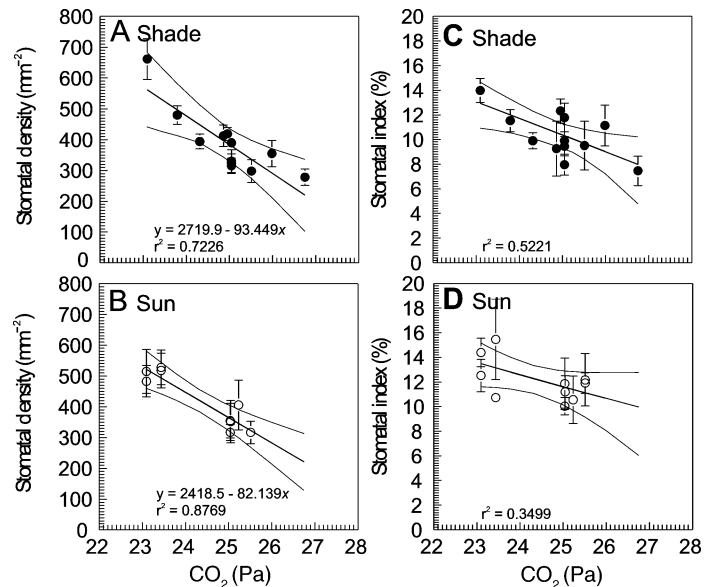


Figure 2. Relationship between measures of stomatal frequency (SD and SI; see text) with $p\text{CO}_2$ of *Quercus kelloggii* (A, C) shade and (B, D) sun leaves (collected 1934–1935 at >1000 m). A: F-stat. (12) = 26.047, $P \leq 0.001$. B: F-stat. (11) = 57.034, $P \leq 0.001$. C: F-stat. (13) = 10.926, $P \leq 0.001$. D: F-stat. (9) = 4.3068, $P \leq 0.05$.

SD increases with elevation are due to increasing light intensity in either shade or sun leaves. Significant increases in SI ($r^2 = 0.59$, $P \leq 0.001$; not shown) with elevation also preclude the alternative possibility, that decreased mean annual temperature with increasing elevation resulted in a reduction in epidermal cell area and/or number, thereby indirectly increasing SD (Kürschner, 1997; Lake et al., 2001).

Next, $p\text{CO}_2$ at the elevation of original collection of each herbarium sample was calculated by applying equation 2 to measurements of ambient sea-level CO_2 for 1934 and 1935 (30.6 Pa) from the Siple Station ice core (Nefel et al., 1994). Stomatal density (sun: $r^2 = 0.88$, $P \leq 0.0001$; shade: $r^2 = 0.72$, $P \leq 0.001$) and SI (sun: $r^2 = 0.35$, $P \leq 0.05$; shade: $r^2 = 0.52$, $P \leq 0.001$) showed strong inverse linear relationships with $p\text{CO}_2$ changes above ~ 1000 m elevation (Fig. 2) and significant, nonlinear inverse relationships when the entire SD data set for elevations >0 m were regressed (sun: $r^2 = 0.75$, $P \leq 0.0001$; shade: $r^2 = 0.88$, $P \leq 0.001$). Stable carbon isotopic analyses of the same leaves revealed consistently more negative $\delta^{13}\text{C}$ values ($<28\text{‰}$) in the three lowest elevation samples compared with those of higher elevation ($>27\text{‰}$) indicative of reduced stomatal conductances in these samples. These $\delta^{13}\text{C}$ differences suggest that physiological responses to perhaps higher temperatures or poorer water availability are likely responsible for the observed nonlinearity of the SD response below ~ 1000 m.

A weaker relationship between sun leaf SI and $p\text{CO}_2$ (Fig. 2B), in comparison to that of shade leaf SI (Fig. 2D), is consistent with expectations, if $p\text{CO}_2$ decline rather than increasing light intensity is the primary controlling factor of SD and SI. Shade leaves typically have lower maximum stomatal conductances than sun leaves because of shade leaves’ light-limited and moister microenvironments. Hence, decreasing $p\text{CO}_2$ with elevation would be expected to exert a stronger physiological pressure on shade leaves to maximize stomatal conductance (via increased SD and SI) in order to maintain a positive carbon balance and a lesser pressure on “sun leaves” owing to the negative physiological impact such anatomical responses would have on their water-use efficiencies. The marked curvilinearity of sun leaf SD responses to $p\text{CO}_2$ at lower elevations (Fig. 2B) compared with that of shade leaves also suggests that analysis of fossil shade leaf SD (not SI), in conjunction with $\delta^{13}\text{C}$ (to identify any possible low-elevation

physiological outliers indicated by more negative $\delta^{13}\text{C}$ values), will yield the most accurate paleoelevation estimates in future application of the stomatal paleoaltimeter to fossil floras.

TEST OF CLIMATE INDEPENDENCE

The climate independence of a $p\text{CO}_2$ paleoaltimeter relies on two important prerequisites: (1) decreases in $p\text{CO}_2$ with elevation are globally predictable and relatively insensitive to changes in local or global July temperatures (t ; equation 3) and (2) the relationship between SD and SI with $p\text{CO}_2$ is not influenced by regional differences in terrestrial temperature lapse rates or climate.

The first prerequisite is supported by the observation that the $p\text{CO}_2$ decrease with elevation is relatively insensitive to deviations in mean July temperature (equation 2) irrespective of differences in ambient sea-level CO_2 (data not shown). For example, a mean July paleotemperature estimate for an Eocene high-elevation fossil flora with an error of $\pm 10^\circ\text{C}$ would result in a paleoelevation error of only ± 50 m.

To test the second prerequisite, SD and SI were collected from an additional independent set of *Q. kelloggii* herbarium specimens for which historical climate records (Karl et al., 1990) were available within 0.15° latitude of the specimen for the year of leaf growth (Data Repository Table DR1¹). Stomatal densities and indices of both sun and shade leaf samples collected between 1898 and 1964 and spanning wide latitudinal temperature ($33^\circ 14' \text{W}$ to $41^\circ 21' \text{W}$) and longitudinal ($116^\circ 43' \text{N}$ to $122^\circ 17' \text{N}$) precipitation gradients showed no significant correlations with mean spring or summer temperature or mean annual or spring precipitation ($r^2 = 0.22, 0.009, 0.015, 0.011$). When regressed with sea-level CO_2 , however, SD showed the expected inverse relationship ($r^2 = 0.69$). These results support the conclusion that a new partial pressure-based paleoaltimeter, using SD as a proxy for $p\text{CO}_2$, will be independent of long-term Cenozoic climatic cooling when applied to the fossil record.

LIMITATIONS AND PROJECTED PALEOELEVATION ERRORS

Both the magnitude and rate of SD response by plants to $p\text{CO}_2$ are highly species specific (Beerling and Royer, 2002). Therefore, it is unlikely that this method of estimating paleoelevation can be applied to fossil floras not containing extant species, limiting the method to Eocene and younger fossil floras. Further, as most species occupy relatively narrower elevation ranges than *Q. kelloggii*, they are unlikely to be present in both high-elevation and coeval sea-level fossil floras. In such cases, estimation of both high-elevation (cd_2 ; equation 3) and sea-level (cd_1 ; equation 3) CO_2 will be necessary from different extant fossil species calibrated independently with their respective species-calibration data sets.

More critical is the observation that stomatal frequency responses by plants to $p\text{CO}_2$ are often nonlinear and show a tendency to saturate with increasing sea-level CO_2 (Kürschner et al., 1997). This observation has important implications for application of a stomatal $p\text{CO}_2$ paleoaltimeter to periods characterized by more elevated sea-level CO_2 than that of the present day. To explore this potential limitation further, *Q. kelloggii* SD responses to $p\text{CO}_2$ for three different historical intervals—(1) 1891–1900, (2) 1934–1935, and (3) 1936–1940, characterized by similar sea-level CO_2 (29.5, 30.6, and 30.7 Pa, respectively)—were compared with those from 2003 when sea-level CO_2 (37.5 Pa) was $>20\%$ higher because of higher fossil fuel use (Neftel et al., 1994). The data are encouraging, as no saturation in the SD response to sea-level CO_2 is apparent. However, although the slopes of the SD re-

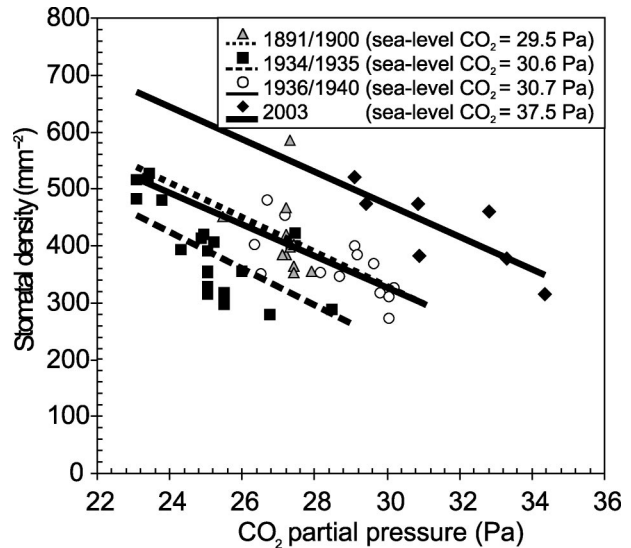


Figure 3. Historical and modern stomatal density (SD) data sets of *Quercus kelloggii* vs. $p\text{CO}_2$ from herbarium leaves (sun + shade) collected in (1) 1891–1900, (2) 1934–1935, (3) 1936–1940, and recent field collections, (4) 2003, demonstrating similar SD response rates—(1) -30.273 , (2) -32.046 , (3) -27.756 , and (4) -28.528 , respectively—to decreasing $p\text{CO}_2$ but different intercepts.

sponses are very similar, the intercepts are significantly different (Fig. 3), suggesting that differences in sea-level CO_2 between a modern SD calibration data set and that of the fossil flora for which paleoelevation is being estimated may introduce a potentially large paleoelevation error.

To estimate the magnitude of this potential error, the elevations of 11 widely geographically spaced trees of *Q. kelloggii* (Table DR2; see footnote 1), collected at precisely known elevations from California in summer 2003, were estimated by using the SD calibration data set from 1934 to 1935 to calculate cd_2 (equation 3). As expected, owing to differences in the intercepts of SD vs. $p\text{CO}_2$ between 1934–1935 and 2003 (Fig. 3), the average elevation error was large ($\sim \pm 2000$ m; data not shown). However, because the slopes of the SD response to $p\text{CO}_2$ for both 1934–1935 and 2003 are so similar (Fig. 3), application of a simple correction factor to cd_2 , taking into account differences in the intercepts (calculated as the difference in cd_1 [equation 3] between 2003 and the 1934–1935 calibration data set), reduced the average error of estimated elevation to $\sim \pm 300$ m (Fig. 4). Application of this new $p\text{CO}_2$ paleoaltimeter to high-elevation fossil floras will thus require correction of cd_2 in equation 3 by adding or subtracting [$cd_1(\text{fossil}) - cd_1(\text{calibration})$]. Use of this correction factor will ensure more accurate paleoelevation estimates from fossil-leaf SD during intervals when sea-level CO_2 was both higher as in the Eocene (~ 56 Pa) and lower as in the Miocene (~ 22.5 – 32.5 Pa) than that of the present day (~ 37 Pa).

CONCLUSIONS

Although these results are preliminary and further exploration of biological and environmental factors influencing the stomatal paleoaltimeter is required, it is projected from the analyses carried out here that application to the fossil record of *Q. pseudolyrata* will yield paleoelevation estimates within average errors of $\sim \pm 300$ m, whether linear or nonlinear transfer functions are used to estimate cd_2 from SD (Fig. 4). Such errors are lower than those associated with the majority of existing paleoaltimeters. However, as demonstrated in Figure 4, because of the nonlinearity of SD responses to $p\text{CO}_2$, results indicate that paleoelevations of $< \sim 1000$ m are likely to be underestimated, whereas those above 2000 m are more likely to be slightly overestimated. De-

¹GSA Data Repository item 2004162, Tables DR1, geographical locations and climatic data associated with herbarium specimens of *Quercus kelloggii*, and Table DR2, geographical and ecological settings of *Q. kelloggii* specimens collected in 2003, is available online at www.geosociety.org/pubs/ft2004.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

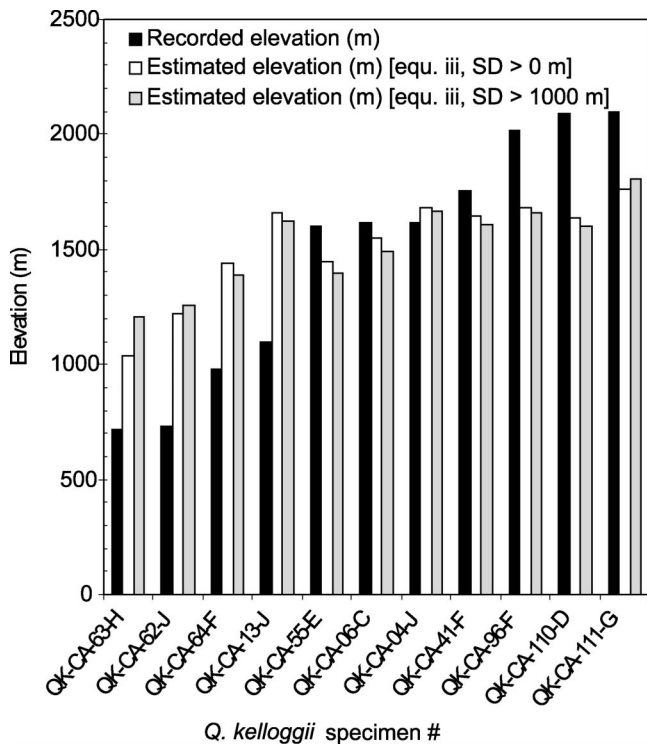


Figure 4. Actual (black bars) vs. estimated elevations of *Quercus kelloggii* collected in 2003 based on mean stomatal density (SD) of one leaf sample per tree or shrub. White and gray bars indicate elevations estimated by using equation 3, where cd_2 was estimated using linear transfer function (SD vs. pCO_2 for 1934–1935 specimens from >1000 m, Fig. 2) and nonlinear shade-leaf transfer function (SD vs. pCO_2 for 1934–1935 specimens from >0 m), respectively. Table DR2 (see footnote 1 in text) gives geographical and ecological setting of each *Q. kelloggii* specimen.

spite these limitations, this paleoaltimeter—because of its climate-independent nature and the fact that paleoatmospheric CO_2 and paleo-elevation estimates can be simultaneously generated as far back as the fossil record of extant taxa will allow—offers the potential of testing empirically for the first time whether tectonic uplift, via enhanced chemical weathering of silicates, forced Cenozoic climatic cooling.

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Notes