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The potential of stomatal frequency analysis as a paleo-altimeter

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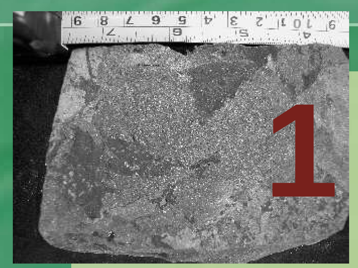


Background

The paleo-elevation of the Sierra Nevada is important to our understanding of the Cenozoic geodynamic evolution of the North America-Pacific plate boundary, but its history remains hotly debated. The long standing view on the elevational history of the Sierra Nevada has held that no significant uplift of the region occurred before 10 Ma (Axelrod 1962, Huber 1981, Winograd et al, 1985, Unrih 1991, Wakabayashi and Sawyer 2001). More recently, it has been suggested that the Sierra Nevada have been a long-standing topographic feature as early as 20 Ma and have since actually lost 1000-2000 m in elevation due to tectonic extension and crust thinning (Small and Anderson 1995, Wernicke et al 1996, Wolfe et al, 1997). Oxygen isotope evidence suggest that no uplift of the mountain range has happened after the middle Miocene at 16 Ma, and elevations might have decreased by as much as 2000m on the southern and 700 m at the northern end of the range (Chamberlain and Poage 2000; Poage and Chamberlain 2002).

U-Th ages indicate that a moderate range elevation of ± 1500 m was present at the cessation of late Cretaceous arc magmatism, followed by two events at between 32 and 3.2 Ma and since 3.5 Ma increasing the range elevation to the 4000 m observed elevation today (House et al 2001, Clark et al, 2005). Clearly, the Cenozoic elevational history of the Sierra Nevada is not well resolved, and especially data on the paleo-elevation of the central and Northern Sierra Nevada has been lacking.

Recently a new paleoaltimeter had been developed, based on the stomatal response in fossil leaves to the predictable decline in atmospheric CO_2 partial pressure with altitude. This method is now applied for the first time to obtain paleo-elevation estimates for two sites in the Northern Sierra Nevada (Gold Lake and Feather River) of early-middle Miocene age (~18-19 Ma)..

Figure 1: Location map of the Gold lake (lat. 39°41'37"N, long. 120°39'17"W and Feather River (lat. 39°45'16"N, long. 120°33'20"W) sites embedded in digital elevation map of California.

Modern *Quercus kelloggii* leaves surrounding a fossil *Quercus pseudolyrata* leaf.

Calculation of paleo-elevation: theory

CO_2 partial pressure is the product of the volume percentage of CO_2 (mole fraction) in the atmosphere, that stays constant with increasing elevation, and the barometric pressure (pp, in pascals).
The barometric pressure decreases with altitude (z) according to
(1) $pp(z) = 101325^{[-ma*g*z/R*t]}$ Jones,1992
where *ma* is the molecular weight of air (0.028964 10^{-3} kg/mol), *z* is altitude in m, *g* is acceleration due to gravity (9.806 m/s^2), R is the universal gas constant (8.3144) and *t* is mean July temperature in Kelvin.

The CO_2 partial pressure changes with elevation as follows:
(2) $cd_2(z) = [pp(z)/101325]*cd_1$ Jones, 1992
where cd_2 and cd_1 are the CO_2 partial pressure in Pa at altitude (*z*) and sea level respectively, which can both be obtained by using the stomatal proxy method on contemporaneous paleo-floras from unknown elevations and sea level.
By substituting equation 1 into 2 we can solve for altitude (z) according to equation (3) in order to estimate paleo-elevation according to equation (4)

(3) $cd_2(z) = (101325^{[-ma*g*z/R*t]}/101325)*cd_1$

(4) $Paleoaltitude(z) = \ln(cd_2/cd_1)*R*[t/(-ma*g)]$

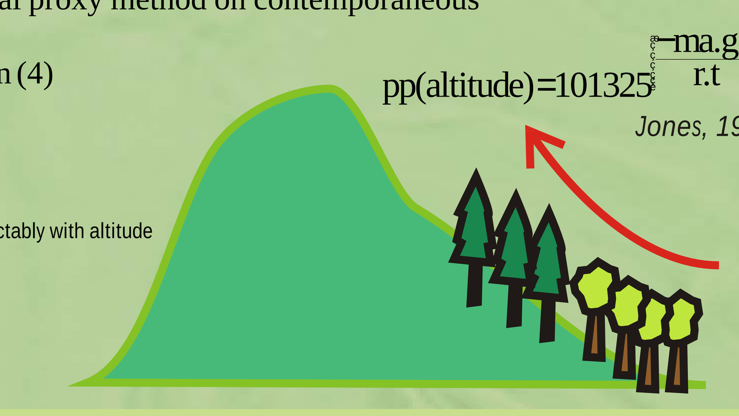
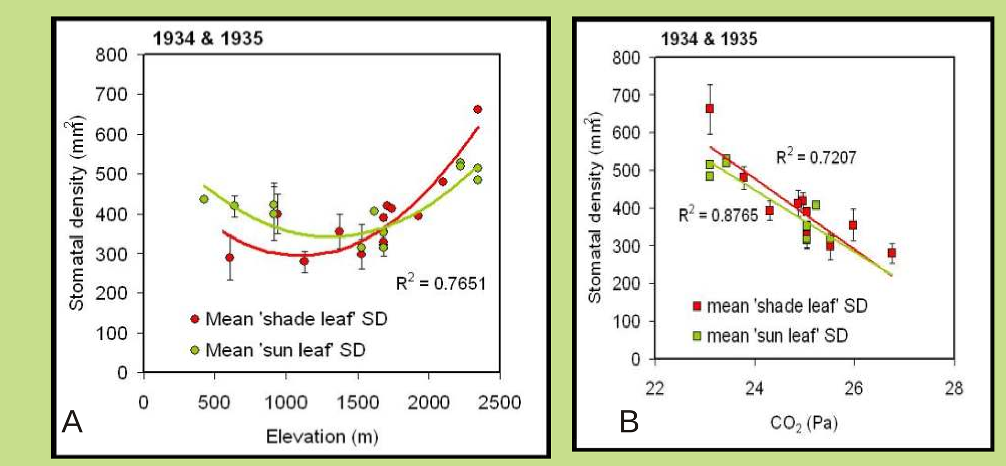


Figure 2: Barometric air pressure changes predictably with altitude

Calibration and estimation

The expected decrease in stomatal density (SD) for both sun and shade leaves of *Quercus kelloggii* over an elevational transect is shown in figure 3A, for herbarium leaves collected in 1934 and 1935 at a sea-level CO_2 partial pressure of 30.6 Pa. Figure 3B depicts the linear part of the curve (above 1000m), plotted against the CO_2 partial pressure at the altitudes. This relationship can be used to calibrate the fossil stomatal density measurements to obtain cd_2. For different sea-level CO_2 the slopes of the stomatal density response to elevation are the same, but the intercepts differ, which might introduce a potentially large error in paleo-elevation estimates (Fig 3C). Because the slopes are so similar, a simple correction factor can be applied for estimates for intervals with varying sea-level CO_2 by adding [cd1(fossil) - cd1(calibration)]. When, for example, this correction is included in the estimation of the elevation of eleven modern oaks from known altitudes, the prediction error is within ~300m (Fig 3D).

Due to its present-day low altitude habitat, no such elevational transects are available for *Platanus occidentalis*. However, the response in stomatal index to CO_2 partial pressure, as demonstrated in leaves grown over the past 150 years, should enable the calculation of paleo-CO_2 partial pressures using fossil *Platanus* leaves.



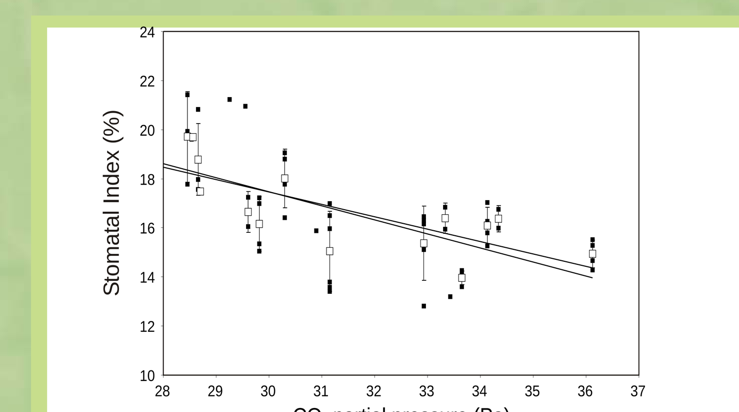
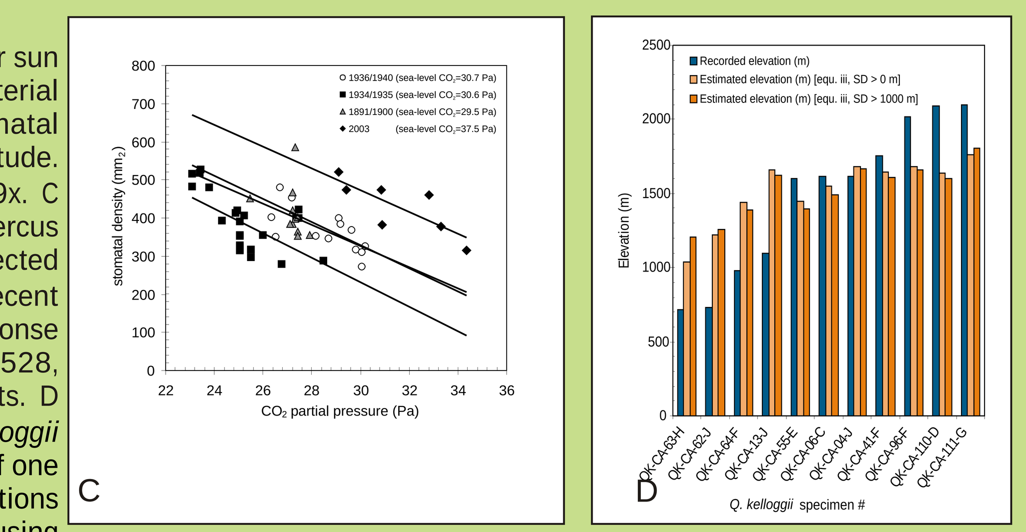
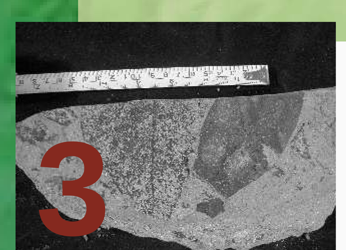


Figure 4: The relationship between stomatal index (SI: SD relative to the total number of stomatal and epidermal cells) and pCO_2 for *Platanus occidentalis* leaves from herbarium sheets collected since 1850. Black squares indicate the mean of six counts per leaf, white diamonds the average SD and standard deviation of all leaves per sheet. Linear regression of the means per sheet: y = -0.504x + 32.583; $R^2 = 0.62$.

Figure 3: A Relationship of stomatal density vs altitude for sun and shade leaves of *Quercus kelloggii* from herbarium material collected in 1934 and 1935. B Relationship between stomatal density and pCO_2 for leaves in (A) grown above 1000 m altitude. shade: y = 2719.9 - 93.449x; sun: y= 2418.5 - 82.139x. C Historical and modern stomatal density data sets of Quercus kelloggii vs. pCO_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 pCO_2 but different intercepts. D Actual (blue bars) vs. estimated elevations of *Quercus kelloggii* collected in 2003 based on mean stomatal density (SD) of one leaf sample per tree or shrub. Orange bars indicate elevations estimated by using equation 4, where cd_2 was estimated using linear transfer functions (SD vs. pCO_2 for 1934-1935 specimens from >1000 m; fig 3B) and nonlinear shade-leaf transfer functions (SD vs. pCO_2 for 1934-1935 specimens from >0 m;), respectively.





First stomata-based paleo-elevation estimates

species	sample	leaf type calibration	SD/SI (n/mm2;%)	sea-level pCO2 (Pa)	reconstructed pCO2 (Pa)	modern elevation (m)	reconstructed elevation by direct calibration (fig. 3A,D; Pa)	reconstructed elevation corrected for sea-level CO2 (m)	modern elevation - paleo elevation (m)
Q. pseudolyrata	FR-UNCAT8	shade	415	25.4*	24.66	1348		2128	-780
Q. pseudolyrata	FR-UNCAT8	sun	415	25.4*	24.39	1348		2241	-893
Q. pseudolyrata	FR-UNCAT8	shade	415	32.7**	24.66	1348		1602	-254
Q. pseudolyrata	FR-UNCAT8	sun	415	32.7**	24.39	1348		1684	-336
Q. pseudolyrata	FR-UNCAT8	shade	415	40.1***	24.66	1348		1281	67
Q. pseudolyrata	FR-UNCAT8	sun	415	40.1***	24.39	1348		1345	3
Q. pseudolyrata	FR-UNCAT8	shade	415		24.66	1348	1807		-459
Q. pseudolyrata	FR-UNCAT8	sun	415		24.39	1348	1901		-553
P. occidentalis	GL-UNCAT11P	n.a.	19.26	n.a.	26.44	1800	2734		-934
P. occidentalis	GL-UNCAT21	n.a.	18.73	n.a.	27.49	1800	2455		-655
P. occidentalis	GL-UNCAT23	n.a.	18.16	n.a.	28.62	1800	2154		-354
P. occidentalis	GL-averaged	n.a.	18.71 +/- 0.55	n.a.	27.52	1800	2448		-648

Table 1: Stomatal density and index data for fossil *Quercus pseudolyrata* and *Platanus cf. occidentalis* leaves and paleo-elevation estimates for the Gold Lake and Feather River sites. The results of several calibration methods are shown (1) calibrations using the relationship between SD and pCO_2/elevation for either sun or sahde leaves (fig. 3 A,B), (2) using the linear part of the curve in fig. 3A for direct calibration of SD to elevation, or by calculation of pCO_2 levels and solving equation 4, and (3) using different Miocene sea level pCO_2 values in equation 4. Miocene sea level pCO_2 values were obtained from the following sources (Fig 6): * = average pCO_2 from all proxies from 18 to 22 Ma (Fig. 6); ** = average maximum pCO_2 from all proxies from 18 to 22 Ma; *** pCO_2 estimate based on stomatal data at 18 Ma.

The data and paleo-elevation estimates based on *Quercus pseudolyrata* and *Platanus occidentalis* for the Feather River and Gold lake sites are presented in Table 1 and summarized in Figure 5. As the Feather River estimates are based on one oak leaf (seven counting fields), and the Gold Lake estimates on three sycamore leaves (seven counts each), the results should be considered preliminary, but they show several promising features.

- First, the difference in paleo-elevation resulting from using either the sun - or shade leaf calibration for oaks is less than 100m. The potential error created by problems distinguishing these leaf types in the fossil record is thus negligible.
- Direct calibration of the fossil stomatal data in the modern calibration curves (SD vs. elevation for oaks, calculation of the equivalent elevation to the pCO_2 for sycamore) shows higher-than-present paleo-elevations for both sites, resulting in a 450-650 m decrease in elevation over the last 18 to 19 Ma.
- Higher altitudes tend to be slightly underestimated in the oak-based elevation predictions (Fig. 3D), making higher-than-present paleo-elevation for the Feather River site even more likely.
- The correction for the difference in sea-level CO_2 between the fossil and calibration material is severely hampered by the conflicting existent sea-level CO_2 estimations for the period of 18-22 Ma (Figure 6). Therefore the paleo-elevation estimates for several sea-level CO_2 options have been calculated ([1] an average of all proxies over 18-22Ma, [2] an average of maximum CO_2 for all proxies over 18-22 Ma and [3] the stomatal based paleo-CO_2 estimate at 18 Ma). All possibilities result in a 0-900 m higher-than-present paleo-elevation for the early-middle Miocene. However, it is clear that the successful application of stomatal analysis as a paleo-altimeter hinges on reliable sea-level CO_2 estimates. To obtain such estimates, an early-middle Miocene low-altitude paleoflora containing *Q. pseudolyrata* and especially *P. occidentalis* needs to be analyzed.
- The inference of a 0- ~900 m elevation decrease in the northern Sierra Nevada since the early-middle Miocene matches very well with the existing oxygen isotope data (Poage&Chamberlain, 2002). Our preliminary data do not support any substantial uplift of the Northern Sierra Nevada over the last 20 Ma.

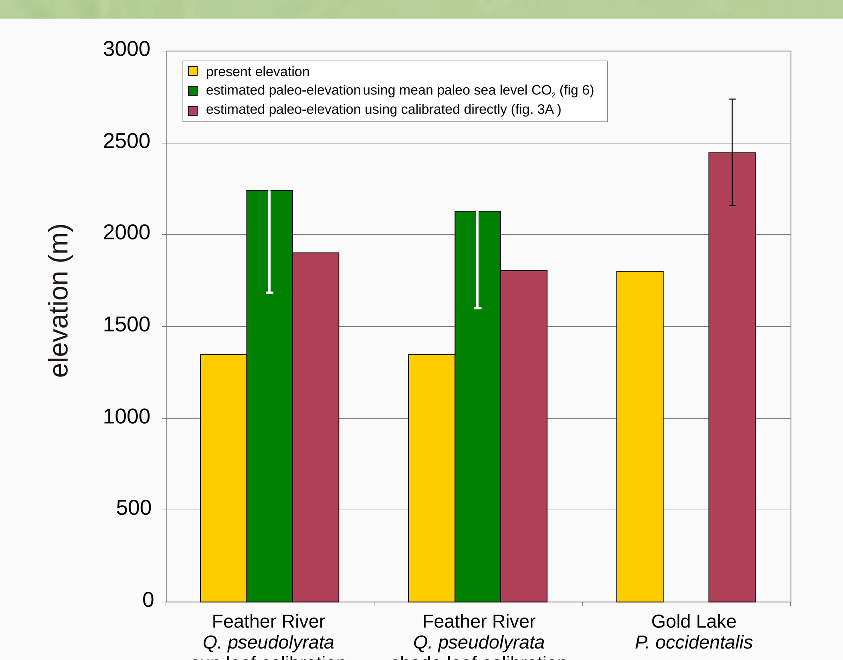


Figure 5: Modern elevation and paleo-elevation estimates using different calibration methods for the Gold Lake and Feather River sites, based on *Q. pseudolyrata* leaves (calibrated by the relationship between SD and pCO_2 for both sun and shade leaves (Fig 3 A,B) and *P. occidentalis* leaves. White error bars indicate the difference in paleo-elevation using either the mean or the maximum sea-level pCO_2 based on all proxies for 18-22 Ma (Fig. 6). Black error bar in *P. occidentalis* estimate indicates the standard deviation for the three leaves the estimate is based on.

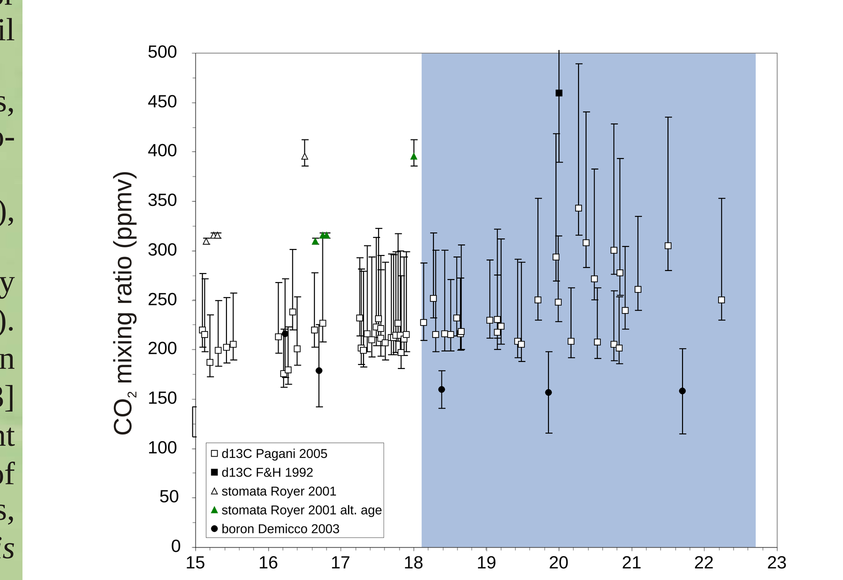
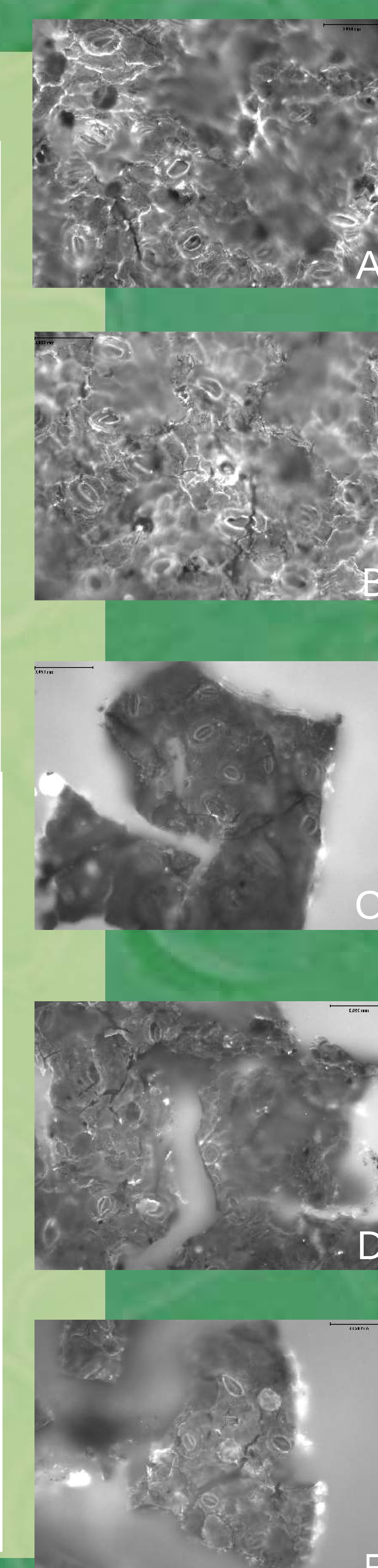


Figure 6: CO_2 mixing ratios from different proxies for the early-middle Miocene. Blue area indicates the age-envelope of the fossil flora.



Fossil cuticle of *Platanus occidentalis* from Gold Lake (A,B) and *Quercus pseudolyrata* (C,D,E) from the Feather River site.

Conclusions

The first time use of stomatal frequency analysis of fossil oak and sycamore leaves as a paleo-altimeter shows a likely 250-900 m decrease in elevation of the northern Sierra Nevada since 18-22 Ma. These preliminary data support existing oxygen isotope and paleobotanical evidence and argue against a recent uplift of the Sierra Nevada.

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