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Paleoaltimetry: A Review of Thermodynamic Methods

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ABSTRACT

This review presents the use of conserved thermodynamic variables to estimate paleoaltitudes. The method based on conservation of moist static energy (the combined internal, latent heat, and gravitational potential energy of moist air) is discussed. This method exploits the physical relation between of the wind fields and the spatial and vertical distributions of both temperature and humidity. Given the climatological distributions of these three atmospheric fields, the method identifies moist enthalpy (the combined internal and latent heat energies of air) as a thermodynamic variable that varies with height in the atmosphere in a predictable fashion. To use this method, the major requirements are: (1) *a priori* knowledge of the spatial distribution of moist static energy for the paleoclimate and (2) the ability to estimate moist-enthalpy in the paleo-environment for two isochronous locations: one at sea level, the other at some unknown elevation. As presented here, the method incorporates basic physical principles of atmospheric science and inferences of paleoclimates from plant leaf physiognomy. Assuming that expected errors estimated from present-day relationships between physiognomy and enthalpy apply to ancient climates and fossil leaves, an uncertainty estimate of ± 910 m in the paleoaltitude difference between two isochronous fossil assemblage locations can be assessed.

INTRODUCTION

The fields of paleobotany, paleoclimate, and geophysics require accurate paleoaltitude estimates. Within a given field, progress requires significant advances in all fields to interpret key data. Changes in paleoflora can be interpreted as either changes in paleoclimate or paleoaltitudes. Changes in paleoclimate can be either at global or regional scales in response to multiple causes, not least of which would be a change in altitude. Likewise, temporal changes in altitudes of large regions will inform basic theory of uplift and mountain building while also providing insights for paleoclimate and paleobotanical work. The motivation for such progress is exemplified by the present volume. Furthermore, this demonstrates a renewed interest in providing robust estimates for paleo-altitudes from whatever means are available for the common goal of exploring paleo-earth. In this context, this is a review of the thermodynamic methods for estimating the paleo-elevations that have been used in the literature and it will attempt to discuss their strengths and weaknesses. The complementary chapters of this volume will provide similar discussions so that a more complete picture of paleo-altimetry research can be assessed.

At the outset, it is worthwhile to consider some simple questions:

- Why do thermodynamic methods work well for paleo-altimetry?
- Why are paleo-botanical estimates of paleoclimate well suited for this?

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- What are the requirements for estimating paleo-altitudes with such techniques?
- What are the limitations?

The introduction addresses these in short while the majority of the paper reviews the method from Forest et al. (1999).

Paleobotanical finds offer the most direct indications of paleoclimatic changes in continental regions, but clearly many ecological conditions vary similarly with latitude and altitude. (i.e., plants indicate the conditions of the local surface environment) Correspondingly, to exploit all climate information from a fossil assemblage, the component of climate relating to local elevation must be determined. Thus, the paleobotanical record on both local and global scales, climate changes of both local and global scales, and the evolution of mean elevations of large tracts of land should be closely linked to one another.

Calculating elevation from climate variables requires measuring an atmospheric quantity that varies with altitude. In other chapters, paleo-pressure are inferred by techniques such as basalt vesicularity (Sahagian and Maus 1994) or measuring cosmogenic nuclide concentrations in exposed rocks. For example, Brown et al. (1991) and Brook et al. (1995) used concentrations of ^{10}Be and ^{26}Al to place constraints on the uplift rate and duration of exposure of rocks in the Transantarctic Mountains, Antarctica. Additional methods and further discussions are available in the present volume.

Here we use paleoenthalpy (a thermodynamic variable combining the sensible and latent heat of moist air) as the quantity that varies with altitude. Paleo-temperature has been used by itself however implicit in the paleotemperature methods are the dependence of surface-temperature lapse rates on the regional moisture content. When more moisture is in the air, the surface temperature will decrease more slowly with elevation changes. In atmospheric physics, this phenomenon is explained by the conversion of latent heat energy to the sensible heat energy of air as water vapor condenses into precipitation. Given that precipitation is typically a local or regional event, one needs to understand how this relates to large-scale atmospheric circulations and remains a key question.

Estimating paleotemperatures has been used successfully for estimating paleoaltitudes. Mean temperatures show correlations with leaf morphology of living plant assemblages with uncertainties in mean annual temperature perhaps as small as 1 °C (Wolfe 1979, 1993). Hence, assuming that foliar characteristics of leaf fossil assemblages obey the same relationships, we should be able to infer correspondingly accurate paleotemperatures. Because temperature varies with latitude, longitude, and height, and because temperature has varied over geologic time, the calculation of paleoelevation from paleotemperature involves comparing the surface temperature of a high-altitude location to that of a low-altitude location at the same latitude and of the same age (Axelrod 1966). Hence, the use of paleobotanical data for paleoaltimetry includes two required steps: first, estimating a climatic parameter, like mean annual temperature, from fossil plants, and second, using differences in that parameter from separate sites to estimate elevation differences, given *a priori* knowledge of the variation of the parameter with altitude.

Two approaches to inferring paleoclimates from fossil plants have distinct philosophical bases. (Axelrod 1966; Axelrod and Bailey 1969) suggested that taxonomic similarities between floral fossil assemblages and present-day forests could be used to infer paleoclimates. Each fossil's taxon, defined at the species level when possible, is assigned a nearest living relative. Then, the climatic parameter of a present day forest containing as many nearest living relatives of the floral assemblage as possible is assigned to the paleoclimate of the fossil locality. Criticisms of this assumption are summarized in Forest et al. (1999). This assumption can be avoided if physiognomic characteristics of plants are used to infer local climates. Much work has shown that relationships exist between foliar characteristics and various climate parameters (Bailey and Sinnott 1915, 1916; Wolfe 1979, 1993; Gregory and Chase 1992; Gregory 1994) indicating that this latter approach is more useful and appropriate.

Estimating elevation from differences in climatic parameters has been accomplished via two methods. In the first method, differences in surface temperatures are used to infer paleoaltitudes. This method requires using empirical relationships between altitude and temperature derived from the present climate. Such relationships (a.k.a. surface temperature lapse rates) lack a firm theoretical basis, and variations in present-day surface temperatures with altitude in the western United States show large spatial variations (Meyer 1986, 1992; Wolfe 1992). Moreover, we have no reason to expect that such laterally varying empirical relationships should hold in the different climates that have prevailed in geologic time. We therefore seek an inferrable thermodynamic quantity whose distribution with altitude and longitude is constrained well by both theory and observation. The use of a quantity derived from fundamental thermodynamic laws is more reliable than one fit empirically to data spanning a fraction of the twentieth century—a small fraction of geologic history. The next section addresses such a quantity and develops its use as a second method for estimating paleoaltitudes. This follows the description in Forest et al. (1999).

USING MOIST STATIC ENERGY

Two conservative thermodynamic variables commonly used in atmospheric physics are moist static energy and equivalent potential temperature, each derived from the first law of thermodynamics (e.g., Wallace and Hobbs 1977; Emanuel 1994). Moist static energy (per unit mass), the sum of moist enthalpy and gravitational potential energy per unit mass, is the total specific energy content of air, excluding kinetic energy, which is very small (<<1%) compared with the other terms (Peixoto and Oort 1992). Moist static energy, h, is written

$$h = c'_p T + L_v q + gZ = H + gZ \tag{1}$$

where c'_p is the specific heat capacity at constant pressure of moist air, T is temperature (in K), L_v is the latent heat of vaporization for water, q is specific humidity, g is the gravitational acceleration, Z is altitude, and H is moist enthalpy. We use the specific heat capacity of moist air, $c'_p = c_{pd}(1 - q) + c_w q$, to account for compositional changes of the air, where c_{pd} and c_w are the specific heat capacities of dry air and liquid water respectively. For consistency, we must also account for the temperature dependence of the latent heat of vaporization, $L_v = L_{vo} + (T - 273)(c_{pv} - c_w)$, where c_{pv} is the specific heat capacity at constant pressure of water vapor and L_{vo} is the latent heat of vaporization at 0 °C. These second order effects (in both L_v and c'_p) are most important in warm and moist climates, where they contribute variations of ~5–10 kJ/kg, which, if ignored, would introduce errors in elevation of 500-1000 m.

Changed only by radiative heating and surface fluxes of latent and sensible heat, moist static energy, like equivalent potential temperature, is virtually conserved following air parcels. We consider only moist static energy because the relationship between altitude and equivalent potential temperature is less simple and direct. Considering the conservative properties of h, we note that typical variations in its components are roughly of equal magnitudes (Table 1).

Table 1. Variations in moist static energy components.

Parameter	Range	Energy Component	Range
Temperature, T	0-30 °C	Specific Heat, c_pT	0-30 kJ/kg
Specific Humidity, q	0-20 g/kg	Latent Heat, L_vq	0-50 kJ/kg
Elevation, Z	0-4000 m	Gravitational Potential, gZ	0-40 kJ/kg

Two properties of moist static energy make it a desirable candidate for inferring paleoelevations. First, as mentioned above, it is nearly conserved following air parcels and, hence, is approximately constant along trajectories. Second, the value of h in the boundary layer is usually strongly constrained by convection to be nearly equal to the value of h in the upper troposphere (see "Introduction" section). Owing to the Earth's rotation, air in the middle-latitude upper-troposphere flows nearly from west to east, so that contours of h there should also run approximately west-east. This implies that h at the surface should be nearly invariant with longitude. We will test this inference of longitudinal invariance in the "Spatial Distribution of Moist Static Energy" section.

Assuming that h is invariant with longitude along the Earth's surface, if we can estimate enthalpy at sea level ($H_{sea\ level}$) for a particular latitude, it follows from (1) that the altitude of another location at the same latitude is given by

$$Z = \frac{H_{sea\ level} - H_{high}}{g} \tag{2}$$

where H_{high} is the enthalpy at the high altitude location (see Fig. 1).

In summary, the necessary assumptions to estimate paleoaltitude are that the surface moist static energy is invariant with longitude and that the moist enthalpy is a measurable quantity for the regional paleoclimate. The remainder of this paper tests these two assumptions and quantifies each error source. Given that previous work uses paleobotanical data, the second requirement implies that moist enthalpy must be accurately estimated from extant or newly discovered paleobotanical collections.

SPATIAL DISTRIBUTION OF MOIST STATIC ENERGY

Theoretical constraints

Before testing the assumption of longitudinal invariance, we discuss several meteorological constraints on the distribution of h.[1] Particularly, we consider three processes, each affecting h differently: (1) boundary layer convection, (2) free atmosphere convection and (3) large-scale horizontal motions. The interaction of these atmospheric dynamic processes constrains moist static energy to be longitudinally invariant. First, we consider convection in an unsaturated atmospheric boundary layer, approximately the lowest 1 km of the atmosphere. Boundary layer convection maintains a dry adiabatic vertical temperature gradient (lapse rate) which is $g/c_{pd} = 9.8$ K/km. Hence, $c_{pd}T + gZ$ is essentially constant with altitude in the boundary layer. Moreover, the concentration of tracers is well mixed in such layers implying that q should be invariant with altitude in this layer (see Fig. 2). Thus h should be nearly constant with altitude, a result confirmed by observations (Stull 1989). This allows us to write

$$h_{surface} \cong h_{topBL} \tag{3}$$

where $h_{surface}$ is the value of h at the Earth's surface and h_{topBL} is the value of h at the top of the boundary layer.

[1] These concepts highlight the basic dependence of climate on latitude (not longitude) and mechanisms for supporting them. Fundamental to these are that the pole to equator temperature gradient sets up a zonal jet (a region of enhanced west-to-east winds in the upper-troposphere, see Peixoto and Oort 1992). With no topography or continents, this jet structure would be the dominant feature of the climate system (e.g., consider the banded image of Jupiter's atmosphere). For mid-latitudes on Earth (poleward of ~30°), this is approximately the appropriate framework although both continents and topographic effects alter this slightly. Were certain features of Earth to be fundamentally different (rotation rate, equator-to-pole temperature difference, radiative balance, etc.), these features would change and necessarily must be reconsidered. Assessing these fundamental constants for Earth in the past must also be considered from the paleo-record.

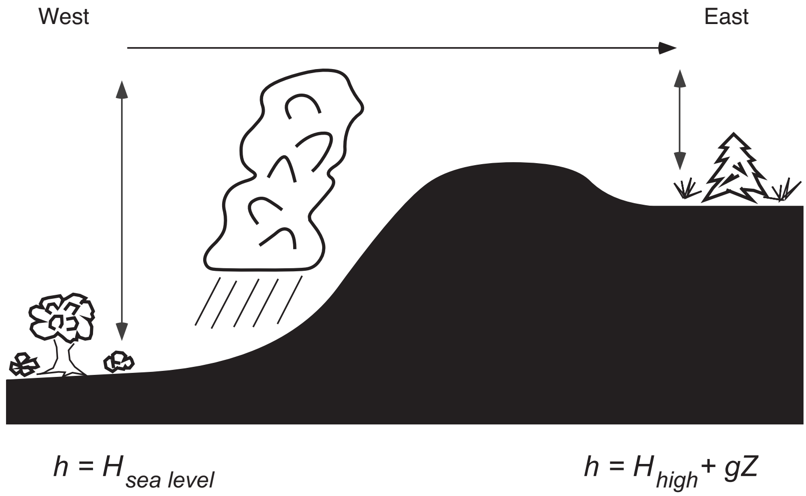
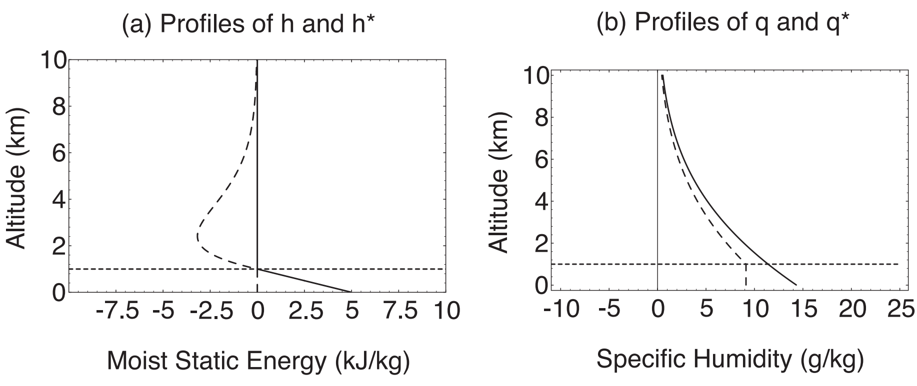


Figure 1. Surface air conserves moist static energy as it traverses a mountainous region by converting between internal heat, latent heat, and potential energy. The potential energy for the high elevation site is the difference in moist enthalpies, $H_{sea\ level} - H_{high}$, which yields the elevation estimate. The vertical arrows indicate the maintenance of the moist static energy profile by convective transports. The horizontal arrow indicates the typical west to east flow in the upper troposphere. [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 1, p. 499.]



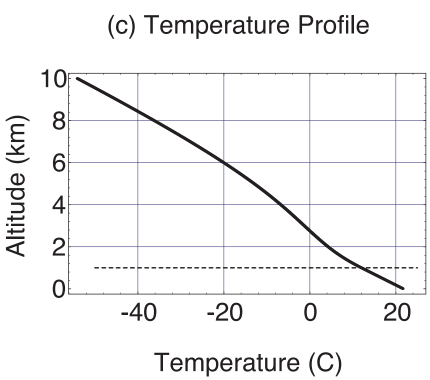


Figure 2. Schematic vertical profiles (a) h (dashed) and h^* (solid) and (b) q (dashed) and q^* (solid). (c) The temperature profile, corresponding to $c_pT = h - gZ - L_vq$, illustrates the constant lapse rate within the boundary layer and the reduced lapse rate above the boundary layer. The boundary level (1 km) is indicated by the horizontal dashed line in each panel. These profiles illustrate typical climatic values that are determined by moist convective adjustment in the free atmosphere and dry adiabatic convection in the boundary layer. [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 2, p. 500.]

Above the atmospheric boundary layer, the vertical temperature gradient is often close to its moist adiabatic value (Betts 1982; Xu and Emanuel 1989), implying the near invariance of the saturation moist static energy:

$$h^* = c'_p T + L_v q^* + gZ \tag{4}$$

where q^* is the saturation specific humidity. Unlike q, q^* is a state variable (i.e., a function of temperature and pressure alone). Now suppose a sample of air is displaced upward from the boundary layer far enough that the cooling makes it saturated; its value of h will also be its value of h^*. Comparing the air sample's value of h to the value of h^* in the immediate environment is equivalent to comparing its temperature with that of its environment. If we neglect the small dependence of density on water substance in the sample, the buoyancy of the sample is a function of T, which directly determines h^* at a given altitude. Thus, the vertical profile of h^* indicates the buoyancy of vertically displaced air parcels. The frequently observed neutral state for moist convection is thus characterized by $\partial h^*/\partial Z \approx 0$. In addition, the climatic value of h at the bottom of the free atmosphere is constrained to be the climatic value of h^*. If $h_{topBL} > h^*_{topBL}$, the atmosphere would be unstable to convection. If $h_{topBL} < h^*_{topBL}$, surface heating and boundary layer convection would raise h_{topBL} until convection occurs throughout the troposphere. For climatic time-scales, the equilibrium between free atmosphere convection and surface heating results in the statement, $h_{topBL} \approx h^*_{topBL}$. Because the vertical profiles are continuous, we can also write $h_{topBL} \approx h^*_{botFA}$ where h^*_{botFA} is the value of the saturation moist static energy at the bottom of the free atmosphere. We recognize that for mid-latitudes, this approximation holds along surfaces of constant angular momentum, rather than strictly along the vertical direction, but these surfaces are nearly vertical. Finally, in the high troposphere the absolute temperature is small and $q \approx 0$. Therefore, at these altitudes, $h \approx h^*$. These constraints allow us to write

$$h_{surface} \cong h_{top} \tag{5}$$

where h_{top} is the value in the upper troposphere (Fig. 2).

Aside from convective constraints on h, we expect h to be nearly longitudinally invariant in the upper troposphere. This results from the conservative property of h along trajectories and from the generally west-to-east winds at these high altitudes. Dynamical constraints require that basic flow properties vary only over horizontal scales greater than about 1000 km, the Rossby radius of deformation in the middle latitude troposphere. We assume that radiative cooling will not affect the distribution of h because the time-scale for radiative transfer is much longer than that associated with transport across the continent. In summary, since h should not vary rapidly with longitude in the upper troposphere and h^* is nearly equivalent to h there, and since h^* is constrained to equal h in the boundary layer by the condition of moist convective neutrality, h within the boundary layer (and thus at the surface) should be approximately invariant with longitude.

This theoretical discussion is based on a conceptual model involving the interaction of the parcel theory for convection and the large-scale circulation of the atmosphere. It is important to note that other theoretical approaches exist to explain the global-scale climatological patterns of atmospheric temperatures and wind distributions. Although their explanations may differ from the continental-scale approach here, the implications for exploring paleoclimate should be considered in the future. As an example of where one can begin, Schneider (2007) provides a recent review of the maintenance of the thermal structure in mid-latitude troposphere and provides verification for the alignment of angular momentum surfaces and moist static energy via slantwise convection (see Fig. 3.5 in Schneider 2007). In brief, this results from the combination of constraints by both baroclinic adjustment (see Stone 1978; Stone and Carlson 1979) and moist convective adjustment (Xu and Emanuel 1989) in which the large-scale mixing occurs owing to baroclinic instability but with effects of moisture included. The resulting mixing by baroclinic eddies (length-scales ~1000 km) transports heat, moisture, and momentum from high values in the low-latitude extratropics towards low values in the higher latitude regions. As discussed above and in Schneider (2007), the effects of moisture add an additional constraint on the atmosphere's thermal structure (i.e., the lapse rate is moist adiabatic along angular momentum surfaces within the baroclinic eddies) and likewise provide a constraint on the atmospheric circulations. The dynamics of these interactions is a broad field and beyond the scope of this paper although the reader is encouraged to explore these further. Two recent papers (Korty and Schneider 2007; Korty and Emanuel 2007) have explored both the assumption of zonal invariance and the implications of these constraints in more equable climates. With these discussions, they provide additional support for the assumption of the zonal invariance of h in the paleoaltimetry context.

Surface observations of moist static energy

To test the assumption of longitudinal invariance of moist static energy at least in the present climate, we use the observed distribution of h across the North American continent. Forest et al. (1999) present a thorough discussion of climatic parameters related to h and important choices regarding annual and seasonal averages. Several conclusions were drawn in Forest et al. (1999). First, the zonal invariance of h is least for autumn averages followed by annual averages. Further, given the seasonality of plant life, one does not expect the autumn climatology to influence strongly the foliar characteristics (or other botanical data.) Thus, annual averages are the best choice for estimating paleoenthalpy for use in paleoaltimetry. Second, a comparison with the equivalent method for temperature variations indicated similar errors for constant surface lapse rates but thse final error estimates are altitude dependent.

Forest et al. (1999) examined the spatial distribution of h (Fig. 3). The winter and summer means of h (not shown, see Forest et al. 1999) deviate from longitudinal invariance much more than spring, autumn, and annual means, but all show similarities to large scale circulation patterns (Oort 1983) as expected. A method to estimate the circulation patterns for paleoclimates would provide a first order correction to the assumption of zonal invariance. However, this requires predicting stationary waves for the paleoclimate setting which is a current topic of active research. One such method is based on simulations with general circulation models (GCMs) using paleoclimate boundary conditions for the relevant eras. The sensitivity to surface elevation itself must be considered in addition to geographic distributions of continents and ocean bathymetry. Further discussion on land-surface, ice-distribution, greenhouse gas concentrations, natural dust aerosols, solar constant, rotation rate, and other factors must also be considered.

Forest et al. (1999) quantified the longitudinal variability by statistically fitting h to monotonic functions of latitude, φ. Because invariance is being tested, the standard deviation from the function is more important than the actual function. The mean values of h were fit to a cubic function of φ using a standard least squares technique (Table 2) (see Fig. 3). As expected, winter and summer means show the largest deviations. Autumn exhibits the smallest deviations. We do not expect plant characteristics to correlate with mean autumn enthalpy, when photosynthesis and plant growth are minimal. Since foliar physiognomic characteristics correlate with mean annual temperature, we expect them to correlate with mean annual enthalpy. If one season revealed markedly smaller zonal variation, the correlations of climatic parameter in that season with foliar physiognomy could have been investigated, but from Table 2, we note that no seasonal deviation appears significantly better than the mean annual case. For the mean annual

Table 2. Zonal variability of moist static energy (in kJ/kg).

Period →	**winter**	**spring**	**summer**	**autumn**	**annual**
h_{mean}	6.80	5.15	5.44	3.79	4.48

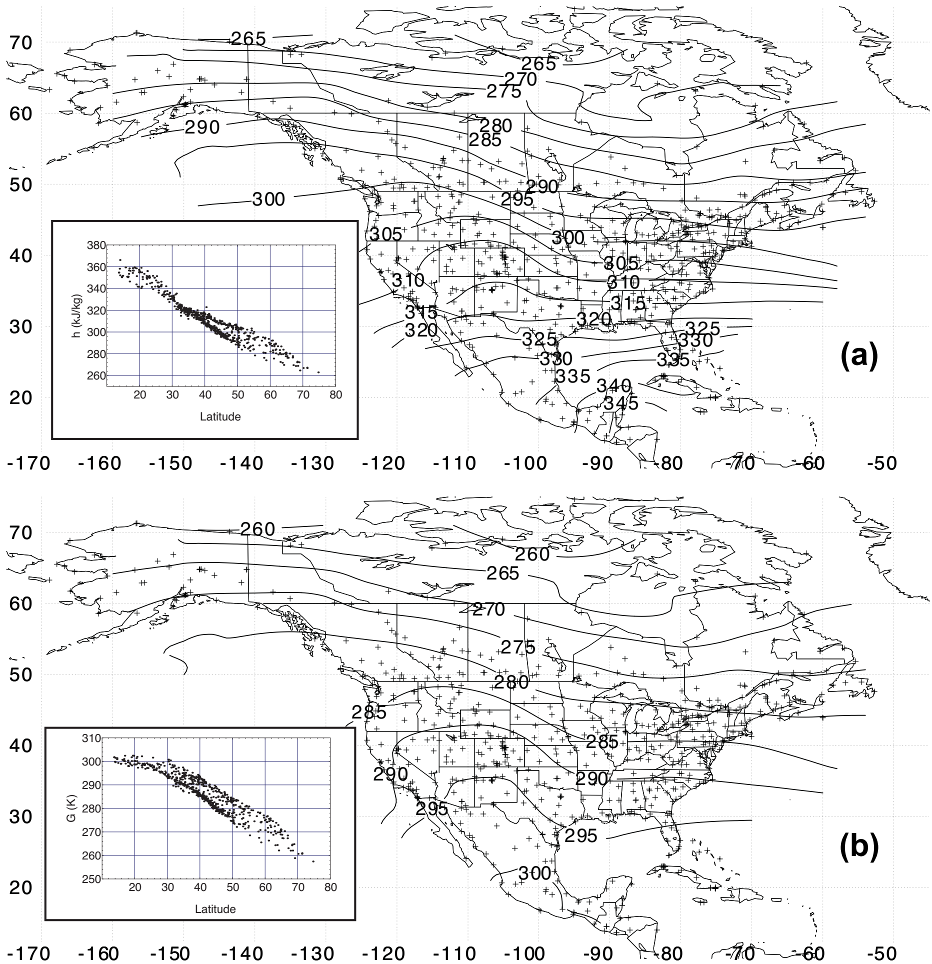


Figure 3. (a) Spatial distribution of mean annual moist static energy. The station locations (crosses) indicate the spatial coverage of the data set. (b) Spatial distribution of the function $G = T + \gamma_t Z$ where T is the mean annual temperature, Z is the station elevation, and γ_t = 5.9 K/km. The distributions of each variable as functions of latitude are shown in the insets. [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 3, p. 502.]

values, the standard deviation from zonal invariance of h is 4.5 kJ/kg (see Table 2). Dividing 4.5 kJ/kg by g yields a minimum estimate of the error in altitude of 460 m.

Moist static energy versus mean annual temperature

The focus of the previous section was to estimate the expected error from assuming the zonal invariance of mean values of moist static energy. This expected error contributes to the total expected error of a paleoaltitude estimate. Before proceeding to the next section (inferring paleoclimate from plant fossils), we examine the zonal invariance assumption as applied in the mean annual temperature approach to paleoaltimetry. Based on the initial method of Axelrod (1966), paleoaltitudes can be estimated by comparing mean annual temperature differences using the formula

$$Z = \frac{T_{sea\ level} - T_{high}}{\gamma_t} \tag{6}$$

where γ_t defines an empirical coefficient relating surface temperature linearly to elevation and is usually chosen to agree with the local climate (Axelrod 1966; Wolfe and Schorn 1989; Gregory and Chase 1992). Meyer (1992) calculated local γ_t for 39 areas of the world with surface topography greater than 750 meters and found $\gamma_t = 5.9 \pm 1.1$ K/km, but with a range from 3.64-8.11 K/km. Wolfe (1992) showed that average values of γ_t calculated from mean annual temperatures at high altitudes and at sea level at the same latitudes vary over a similar range.

In using mean annual temperatures, one implicitly assumes the longitudinal invariance of the surface distribution of a quantity $G = T + \gamma_t Z$ (bottom of Fig. 3). For $\gamma_t = 5.9$ K/km, we calculated deviations from longitudinal invariance of G to be 3.2K for the present climate. Hence, a minimum standard error, σ_Z, for estimating altitude can be computed from these results, using

$$\sigma_Z^2 = \frac{\sigma_G^2 + \sigma_T^2}{\gamma_t^2} + \frac{(\Delta T)^2 \sigma_{\gamma_t}^2}{\gamma_t^4} \tag{7}$$

where σ_G and σ_{γ_t} are the standard errors of G and γ_t respectively. With the inclusion of an uncertainty in γ_t of ± 1.1 K/km (Meyer 1992), minimum uncertainties in the estimated altitudes increase with altitude: standard errors of 540 m, 660 m, and 920 m for altitudes of 0 m, 2000 m, and 4000 m, respectively. Hence, even ignoring the unpredictable temporal changes in γ_t over geologic time, these estimates of minimum uncertainties exceed that of 460 m from assuming longitudinal invariance in h. We note that Wolfe and others typically use lower values of γ_t for the warm periods such as the Eocene. This implies that the error due simply to an uncertainty in γ_t, $[(\Delta T)\sigma_{\gamma_t}]/\gamma_t^2$, will reach 1500 m with $\gamma_t = 3$ K/km for a 4 km high mountain, and the overall altitude error, σ_Z, will increase for higher estimates of altitude.

We suspect that the variations in γ_t from 3 to 9 K/km, determined by Meyer (1986, 1992) and Wolfe (1992), are consistent with approximately longitudinal invariance of h and large variations in q. Differentiating (1) with respect to Z while holding h constant yields

$$-\frac{\partial T}{\partial Z} = (g + L_v \frac{\partial q}{\partial Z})\frac{1}{c'_p} \tag{8}$$

Because air cools adiabatically as it rises, and because q depends strongly on T (at saturation) (see Forest et al. 1999), q will not be conserved as an air mass rises over high terrain. Condensation and precipitation reduce q, but conservation of h requires that at a constant pressure, T increases when condensation occurs. Thus, in such regions like the Sierra Nevada, vertical gradients of specific humidity directly determine the vertical temperature gradients. Indeed, in that region, temperatures decrease slowly with altitude, at only 3 K/km (Wolfe 1992). Regardless of whether or not conservation of h can account for other large variations in q, clearly H, instead of temperature, should be used to estimate elevation changes, at least insofar as mean annual enthalpy can be inferred well from paleobotanical material.

RELEVANT PALEOBOTANICAL WORK

A major goal of paleobotanists is to quantitatively estimate the climatic environment of a paleoflora. To achieve this goal, paleobotanists first distinguish the various taxa represented by the fossil collection/assemblage that defines the paleoflora. The research presented here does not address problems associated with this task and assumes the taxonomy is done properly. Secondly, paleobotanists identify features of the paleoflora that are related to the local climate.

Their goal is to characterize the plant life in such a manner to distinguish ecological niches determined by climate. The method chosen here describes the average characteristics of sizes and shapes of leaves for the flora in order to make the distinctions and to estimate the mean climate. Before proceeding to quantify the relationship between leaf characteristics and climate, we recognize that from a paleoaltimetric view , one can be agnostic about the method used to determine the paleo-enthalpy of the local region provided the estimated errors have sufficiently small contribution to the total error. Were a better method available, it could complement the paleobotanical approach given here and lead to more robust paleo-altitude estimates. One recent example would be Green (2006) in which estimates of paleoenvironmental variables are done with a nearest-neighbor approach to relating foliar physiognomy to paleoclimate. As others methods are developed, they will be quite useful for obtaining robust paleoaltitude estimates.

Previous physiognomic methods for estimating paleoclimate

As summarized in Forest et al. (1999), previous work has shown (Bailey and Sinnott 1915, 1916; Wolfe 1971, 1979; Wolfe and Hopkins 1967) that foliar physiognomy correlates with climatic parameters, such as mean annual temperature or growing season precipitation, suggesting that we might expect to predict mean annual enthalpy through similar techniques. Because of other correlations between foliar shape and living environment (Givnish 1987), Wolfe (1993) expanded the list of characteristics, from the single characteristic of the fraction of species with smooth margins of leaves, to include other foliar shape parameters: size, apex and base shape, lobedness, compoundness, and overall shape. With these additions, he developed the Climate-Leaf Analysis Multivariate Program (CLAMP) utilizing correspondence analysis (Wolfe 1993) to determine the relationship between climate and leaf shapes and sizes. Others have also employed multivariate regression techniques using the CLAMP data to infer paleoclimate parameters (Wolfe 1990; Gregory and Chase 1992; Gregory 1994; Forest et al. 1995; Greenwood and Wing 1995). We note that several critiques (Wilf 1997; Royer et al. 2005; Spicer et al. 2005) of the method used here have appeared and should be considered as they relate to the robustness of estimates for paleoclimate based on foliar physiognomy. These highlight the need for careful analysis of these methods.

ESTIMATING PALEOCLIMATE

The task remains to determine the mean annual enthalpy from plant physiognomy. An analysis is presented relating foliar physiognomic characters to mean annual values of enthalpy, temperature, specific humidity, and relative humidity that exploits the method and data in the Climate-Leaf Analysis Multivariate Program (Wolfe 1993). From present-day plant data collected from North America, Puerto Rico, and Japan, the leaf parameters are searched for linear combinations of the foliar characteristics that covary with the local climates. By doing so, the foliar characteristics can be determined that covary with one another and which best correlate with climate parameters.

Data

To extract climate information (e.g., mean annual temperature, precipitation, specific humidity or moist enthalpy) from fossil flora, one must first determine which typical foliar characteristics of extant plants show relations to present-day local climate. For forests in well characterized climates, Wolfe (1993) measured average characteristics of foliar physiognomy, weighting each taxon equally (otherwise, taxa are ignored). For each taxon, he identified and recorded the characteristics of its representative leaves. The characteristics can be separated into seven categories (see Tables 3 and 4 and Fig. 4). For each vegetation site, he totaled the number of displayed characteristics for all represented species and calculated the percentage of species exhibiting a given characteristic. He called this percentage the score of the leaf

Table 3. Foliar characteristics (see Fig. 4 for examples).

Characteristic	No. of Categories	Description
lobed	1	
margin shape	6	no teeth, regular, close round, acute, compound
leaf size	9	nanophyll;leptophyll I,II; microphyll I,II,III; mesophyll I,II,III
apex shape	4	emarginate, round acute, attenuate
base shape	3	cordate, round, acute
length to width ratio	5	<1:1, 1-2:1, 2-3:1, 3-4:1, >4:1
leaf shape	3	obovate, elliptic, ovate

Table 4. Specification of foliar size categories.

Size Category	Leaf Area (mm^2)
Nanophyll	< 5
Leptophyll I	5–25
Leptophyll II	25–80
Microphyll I	80–400
Microphyll II	400–1400
Microphyll III	1400–3600
Mesophyll I	3600–9000
Mesophyll II	9000–15000
Mesophyll III	>15000

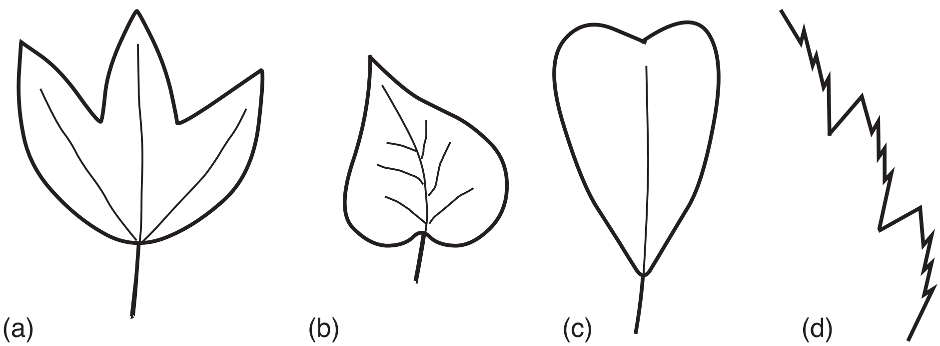


Figure 4. Sketches of representative leaves showing various leaf characteristics. (a) illustrates a lobed leaf with an acute apex, a round base, and no teeth (like (b) and (c)). (b) illustrates an ovate shaped leaf with an attenuated apex (drip-tip), and a cordate base. (c) illustrates an obovate shaped leaf with a round and emarginate apex, and an acute base. (d) illustrates a leaf margin with teeth that are compound, acute, closely spaced, and regularly spaced. (see Wolfe (1995)) [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 6, p. 505.]

characteristic for a given site. In all, Wolfe (1993) scored leaf samples for 31 leaf characteristics, using 123 vegetation sites distributed across the northern hemisphere, of which 112 are in North America, 9 are in Puerto Rico, and 2 are in Japan. Wolfe chose these sites to be near meteorological stations to obtain measurements of temperature and precipitation, but most stations did not record humidity.

To obtain an accurate score, a sufficient number of species for a given location are required. Wolfe estimated that at least 20 species are necessary to infer climate parameters reliably. This is supported by Povey et al. (1994) and by considering possible sources of error in the score data and comparing the error to some measure of information content in the data.

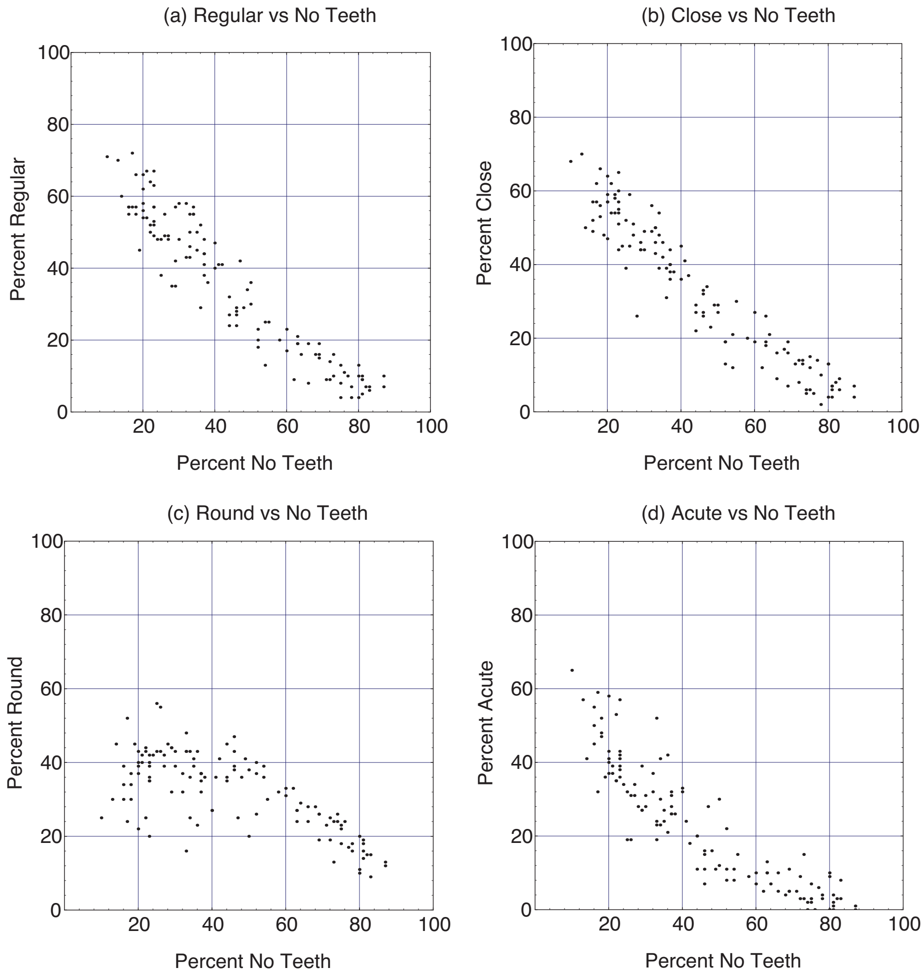
Present-day environmental data are also required for the leaf collection sites. Because humidity data are not available for each vegetation site, we could not directly calculate mean enthalpy for all sites. Instead, we used data from the meteorological stations (Fig. 3) and interpolated moist static energy to the vegetation sites. For the same reasons that we expect h to be longitudinally invariant, we expect h to be a smoothly varying field. Hence, the local variability of h should be small over dimensions of mountains and valleys. Having a non-gridded dataset, we followed meteorological methods (Barnes 1964) and interpolated from nearby stations using a distance-weighted mean,

$$h_{plantsite} = \frac{\sum_i (h_i w_i)}{\sum_i w_i} \tag{9}$$

where $w_i = exp[(r_i/d)^2]$, r_i = radial distance from plant site to the meteorological station i, and d is the average distance to the nearest station, 90.8 km. Knowledge of the elevation, Z, and mean annual temperature, T, at the vegetation sites allows the calculation of mean moist enthalpy, $H = h - gZ$, and specific humidity, $q = (H - c'_p T)/L$, from the interpolated value of h. Using data from 123 sites, we sought correlations of the 31 leaf characteristics with moist enthalpy and also, separately, with mean annual values of temperature, specific humidity, and relative humidity.

Data analysis

The relation between leaf physiognomy and climate parameters has been analyzed by Canonical Correspondence Analysis (CANOCO) (ter Braak 1986; ter Braak and Prentice 1988), a form of direct gradient analysis. Similar to ecological research regarding the relation between species and environment, predicting climate parameters from foliar physiognomic characteristics follows an analogous technique (ter Braak and Prentice 1988). Fundamentally, two problems exist in this type of research: (1) the removal of redundant information in the foliar physiognomic data and (2) estimating a robust relation between the climate parameter and physiognomic data. Traditionally, the first problem requires removing redundant information (Fig. 5) by identifying combinations of foliar data that vary together. Following the ecological community's terminology, this is the problem of ordination. The second problem has been termed gradient analysis and is a form of standard regression. Two forms of gradient analysis are common. First, indirect gradient analysis involves the use of some ordination technique before the regression relationship is found and does not make use of the climate information to constrain the linear combination of physiognomic variables. The alternative, direct gradient analysis, provides such a constraint and is implemented in CANOCO. The distinction of CANOCO from other gradient analysis techniques (e.g., canonical correlation analysis (CCA) or linear regression using principal component analysis (LR/PCA)) lies with the method of ordination. Rather than assuming a linear relation, Canonical Correspondence Analysis, like its counterpart Correspondence Analysis, assumes that the distribution of foliar characteristics along the environmental gradient has a Gaussian shape, as observed in the CLAMP data.



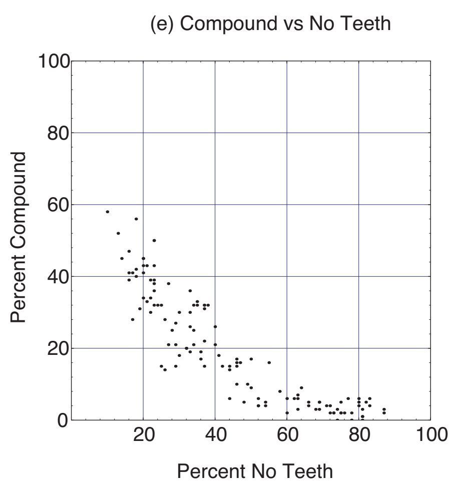


Figure 5. The correlations of the no teeth parameter with the other teeth characteristics show the interdependent nature of the untransformed plant characteristic variables. [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 7, p. 506.]

The CANOCO output includes physiognomic and environmental axes and the eigenvalues of the respective axes. Each axis represents a weighted linear combination of the physiognomic scores or environmental parameters that explains a certain amount of variance in the given data. The method chooses the first axis by determining the direction in data space that maximizes the variance explained by the first axis. Subsequent axes are chosen to maximize the variance explained in the remainder of the data. Thus, the first environmental axis represents the weighted linear combination of climate parameters that maximizes the variance explained in the physiognomic data. Similarly, the first physiognomic axis represents the weighted linear combination of physiognomic scores that explains the most variance in the environmental data. (This is only true for the first axes of each data set, however, because the subsequent axes are only constrained to be orthogonal to the previously determined axes.) Because of these relations, the environmental and physiognomic data sets are transformed onto the principal axes and the scores are combined into a single plot.

The estimate of a climate parameter is obtained by projecting the physiognomic scores of a given sample onto the vector obtained for the climate parameter. The value of the climate parameter is plotted against the value of the projection onto the climate vector in the physiognomic space. A least squares fit is obtained and provides a predictive formula for the given climate parameter. A complete discussion of this technique is given in Wolfe (1995).

Results of physiognomy/climate analysis

From the CLAMP data and associated mean annual climate data, Forest et al. (1999) obtained estimates of enthalpy, temperature, relative humidity, and specific humidity (Fig. 6). The data set has been reduced by removing the outliers as indicated by scores along the third and fourth axes (see Wolfe 1995 for a description). The axis eigenvalues from CANOCO indicate that significant information is contained in the first 6 axes and implies that the use of the axes three and four as an outlier indicator should be robust. The estimates of the climate data indicate that mean annual enthalpy can be predicted from fossil leaf physiognomy with an uncertainty of $\sigma_H = \pm$ 5.5 kJ/kg. Additionally, the standard errors for the estimates of temperature, specific humidity, and relative humidity are respectively, $\sigma_T = 1.8$ °C, $\sigma_q = 1.7$ g/kg, and $\sigma_{RH} = 13\%$.

The interpretation of the projected scores along the given axes is simplified because CANOCO transforms both the environmental and physiognomic data onto the same axes (see Fig. 7). The scores of enthalpy along the first and second axes indicate that enthalpy is related to the temperature and moisture stress axes (one and two, respectively) with about equal importance. As anticipated, the enthalpy score plots roughly equally along the first two axes. The scores of the relative humidity and specific humidity on the first and second axes indicate that relative humidity aligns more strongly with the moisture stress axis than does specific humidity. Intuitively, relative humidity should align with the moisture stress axis if we consider that relative humidity is a measure of the departure from saturation conditions and nearly independent of temperature. Alternatively, the specific humidity strongly depends on the temperature as well as on the availability of moisture which implies the specific humidity score should have a component along the temperature axis. The relative humidity vector being nearly orthogonal to the temperature vector only highlights this more clearly.

The relative lengths of the environmental parameter vectors on the first and second axes (Fig. 7) can be used a measure of importance for the various climate parameters at constraining the directions of the axes. The mean annual temperature has the longest length, followed by enthalpy, specific humidity, and relative humidity. From these scores, we can identify the first axis with mean annual temperature while the second axis aligns with the mean specific or relative humidity. These associations also allow us to infer which character states are most important for estimating the climate parameters as discussed next.

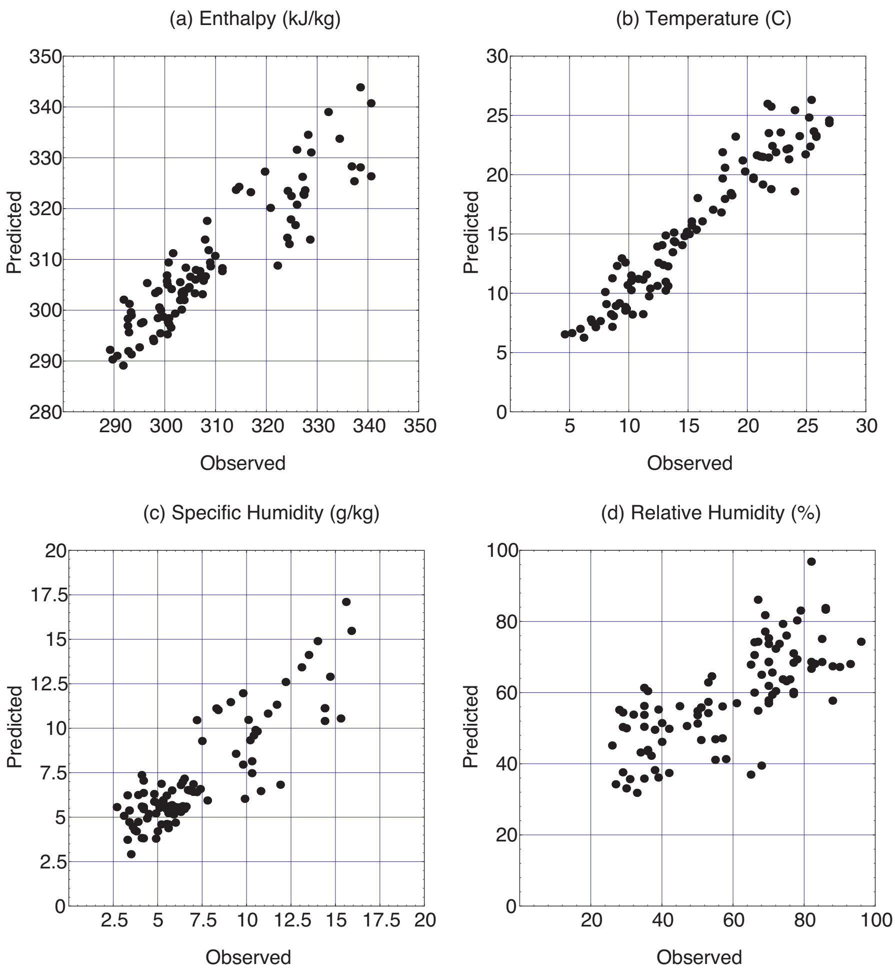


Figure 6. The predictions of the climate parameters from the plant characteristic variables as given by CANOCO are plotted versus the observations for the plant collection sites for (a) mean annual enthalpy (kJ/kg), (b) temperature (°C), (c) specific humidity (g/kg), and (d) relative humidity. [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 8, p. 507.]

The projections of the physiognomic characteristics onto a given axis represent the relative importance of the characteristics for explaining the environmental variations along that axis. The first axis (Fig. 8), which is strongly related to mean annual temperature, has significant contributions from the entire margin (i.e., no teeth), small leaf sizes, and emarginate apex character states. In contrast to this, the second axis, related to moisture stress, has contributions from the large leaf sizes, attenuate apices, and long narrow leaves. The projections onto the third through fifth axes are shown as well.

Before estimating the total expected error in paleoaltitude, we estimate the contribution, 560 m, from the uncertainty, $\sigma_H = 5.5$ kJ/kg, in predicting mean annual enthalpy. We estimate a comparable error, 390 m with $\gamma_t = 5.9$ K/km, for the mean annual temperature approach. Clearly, this latter error is an underestimate, because it is dependent on the choice of γ_t whereas the former error will remain constant.

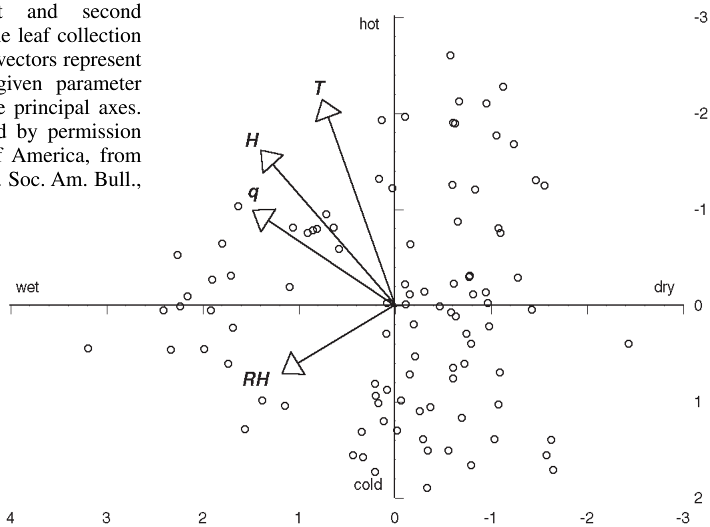


Figure 7. Projections of the physiognomic scores onto the first and second physiognomic axes for the leaf collection sites. The environmental vectors represent the correlation of the given parameter with the directions of the principal axes. (after Wolfe 1995) [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 10, p. 508.]

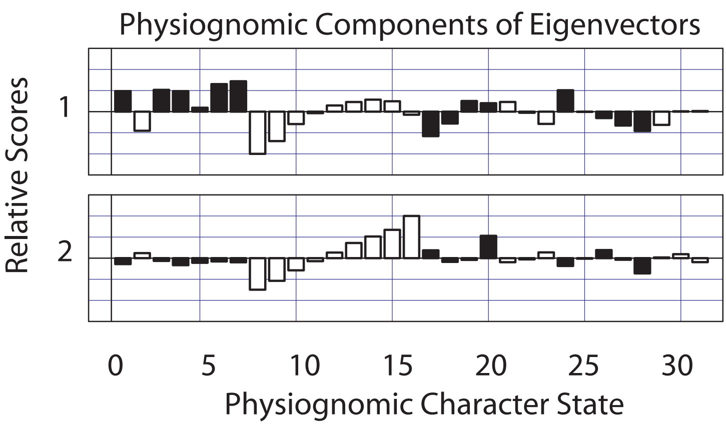


Figure 8. Normalized components of the first two eigenvectors of the Canonical Correspondence Analysis, showing the relative contributions from the 31 leaf characteristics. The order of the characteristics corresponds to that in Tables 4 and 5. Within each eigenvector, the components are normalized by the maximum value which are respectively, 1.08 and 0.88. [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 11, p. 509.]

TOTAL EXPECTED ERROR IN PALEOALTITUDE

We obtain an expected error for the paleoaltitude by combining the expected errors from the zonal asymmetry, $\sigma_h = 4.5$ kJ/kg, and from the botanical inferences of enthalpy, $\sigma_H = 5.5$ kJ/kg, at each location.

$$\sigma_Z = \sqrt{\frac{2\sigma_H^2 + \sigma_h^2}{g^2}} = 910\,\mathrm{m} \tag{10}$$

where the errors in enthalpy from sites at sea level and inland have been combined to yield the factor of two. Other quantifiable sources of error could be included in a similar manner.

We can also estimate the standard error in altitude by predicting the altitude of the present-day plant collection sites. We assume the sea level enthalpy follows a linear function of latitude based on the latitudinal distribution of moist static energy as described in the "Using Moist Static Energy" section. Restricting our data to latitudes south of 55°N, where our assumption of zonal symmetry is valid, the standard deviation of the predicted altitude is 620 m (see Fig. 9). We believe that this lower error estimate results partially from the use of altitude to estimate enthalpy at plant sites for which we have no humidity data. For such sites, we relied on meteorological estimates of h and heights of sites to infer H causing an unavoidable dependence of the value of H on altitude. The lower error estimate of 620 m implies that the error estimate of 910 m calculated from expected errors in the components is robust.

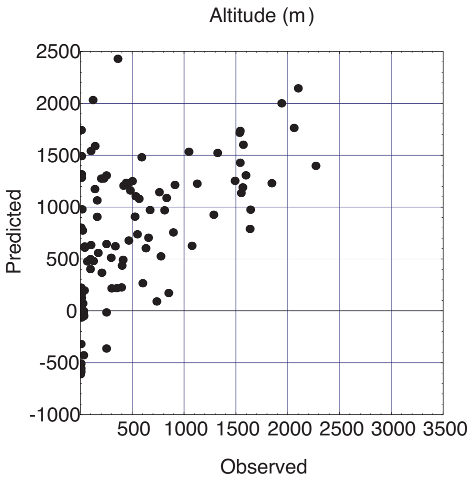


Figure 9. The predicted altitude for the plant collection sites vs. the true altitude of the sites. [Used by permission of Geological Society of America, from Forest et al. (1999), Geol. Soc. Am. Bull., Vol. 111, Fig. 12, p. 509.]

Forest et al. (1999) discussed some potential sources of error related to taphonomic, microclimatic, and fossil dating considerations, which are difficult to quantify for a paleoaltitude estimate. The reader is encouraged to review these as they represent specific issues for improving the interpretation of the fossil record. In total, only the fossil dating uncertainty can be quantified in a straightforward fashion and included as an additional source of error in Equation (10). Forest et al. (1999) estimated an additional error of 5 kJ/kg resulting from uncertainty in unforced variability in the climate system on time-scales shorter than the temporal resolution of the paleo-record. When this is included, the total expected error increases to 1080 m. In any case, the potential errors associated with transport of leaves, fossil dating, and local variations in climate are reminders that we should expect modifications and improvements in the approach taken here.

In addition to these errors, it is worth considering that the errors for the zonal invariance of h are the expected random errors and would not include any systematic biases. As discussed in the "Spatial distribution of Moist Static Energy" section, the assumptions were derived for mid-latitudes (i.e., north of ~30°N) and tested only in the northern hemisphere. There are at least two cases where the moist convective neutrality assumptions can break down and these are offered as additional caveats to those looking to apply this method or as areas to consider for theoretical improvements. The first case is in regions where moist convection is not dominating the thermal stratification of the troposphere. The descending branches of the Hadley or Walker circulations (see Peixoto and Oort 1992) are such places where the atmospheric radiative cooling is balancing the large-scale descent. When applying this in the tropical regions, the possible locations could be in one of these regions and a bias would be present. Because the thermodynamic paleoaltimetry method requires estimates of moist enthalpy from two locations, the application would require an alternative assumption for assuming the invariance of moist static energy.

A second situation is where the boundary layer may contain an additional term in its energy budget from surface fluxes as the air moves along its surface trajectory. This leads to a decoupling of the moist static energy in the boundary layer from the values in the upper troposphere and can be found in the coastal regions where colder deep-ocean waters are upwelling and affecting surface temperatures (M. Huber, pers. comm.). This would then lead to a bias in the estimated enthalpy at the sea-level location and need to be considered. In the present-day climate, this affects temperatures along the west coast of North America. The extent that this can be quantified for the present-day and incorporated into this method would be worthwhile. In both cases, the underlying assumptions of invariance of moist static energy would not be valid and so the application of this method in the appropriate paleoclimate setting would need to be considered. These issues highlight the need for estimating a complete picture of the paleoclimatic conditions that includes the oceanic and atmospheric circulations to the best extent possible. Whether theoretical conceptual models (as done here for mid-latitudes) or numerical models (e.g., Huber and Sloan 2001; Huber et al. 2003; Spicer et al. 2003) are employed, climate models of some sort are required to supply such information. Advances in these areas will be critical to improving the thermodynamic methods of paleoaltimetry.

APPLICATIONS OF THERMODYNAMIC METHODS

The following papers make reference to thermodynamic methods based on paleobotanical estimates of paleoclimate: Gregory (1994), Forest et al. (1995), Wolfe et al. (1997), Wolfe et al. (1998), Chase et al. (1998), Gregory-Wodzicki (2000), Spicer et al. (2003), and Graham et al. (2001). Though this is probably not a complete list, it indicates that the use of these methods is expanding where data are available. Three of these results are briefly discussed here with the estimated paleo-elevations and their relevance for paleoclimate or tectonics.

Wolfe et al. (1997) analyzed twelve mid-Miocene floras from western Nevada to explore the paleoaltitudes of this region and time. The analyses indicated that this part of the Basin and Range Province stood ~3 km above sea level at 15 to 16 Ma ago, which is 1 to 1.5 km higher than its present altitude. This suggests a significant collapse of this region to its present-day altitude by about 13 Ma ago.

Wolfe et al. (1998) explored the paleoclimates from Eocene and Oligocene fossil leaf assemblages from middle latitudes in western North America. These results indicated paleoaltitudes were comparable or higher than present-day altitudes. High altitudes during Eocene and Oligocene time in western North America appear to have been normal, even in areas such as the Green River basin, and therefore cast doubt on the commonly inferred late Cenozoic uplift of that region.

Spicer et al. (2003) present paleo-altitude estimates from fossil leaf assemblages from the Namling basin in southern Tibet and dated to ~15 Ma ago. One unique aspect of this work is that they use a numerical general circulation model to estimate moist static energy at the location of the fossil leaves as opposed to estimating the sea-level moist enthalpy directly from fossil leaf assemblages. Despite the uncertainties (as discussed earlier) in using general circulation models for this purpose, they estimate the elevation of the Namling basin to be about 4.7±0.9 km, which is comparable to the present-day altitude of 4.6 km. This suggests that the elevation of the southern Tibetan plateau probably has remained unchanged for the past 15 Ma. We note that this raises a question regarding the shift in monsoon climate of the region estimated to occur near 6-9 Ma ago (Molnar et al. 1993) and has given rise to a recent debate on the uplift history of Tibet (Molnar et al. 2006; Rowley and Currie 2006).

SUMMARY AND CONCLUSIONS

The methods for estimating paleoaltitudes based on thermodynamic methods have been summarized. The basic algorithm requires comparing the local paleoclimate from some elevated region to that at sea level and at approximately the same latitude. It is argued that comparing mean annual temperatures alone has inherent uncertainties for estimating paleoaltitudes and should be replaced with the method in which moist enthalpies are compared. This is equivalent to assuming the invariance of moist static energy, h, between locations. Supported by basic physics, the moist enthalpy approach incorporates the effect of moisture on the temperature distribution. To estimate a paleoaltitude, it is required that h be invariant between fossil sites and that the moist enthalpy, H, be inferrable from fossil plant leaves. These requirements were examined using the present-day climatic and foliar data to quantify the expected errors for the method.

The surface distribution for mean annual h results from two properties of atmospheric flow: conservation of h following the large-scale flow and the maintenance of the vertical profile of h by convective processes. These features of the climate system allow one to quantify the expected errors for assuming that mean annual h is invariant with longitude and altitude for the present-day distribution. Forest et al. (1999) examined the distribution and calculated the expected error from assuming zonal invariance to be 4.5 kJ/kg for the mean annual climate. This error translates to an altitude error of 460 m and is compared with an equivalent error of 540 m from the mean annual temperature approach. Moreover, the uncertainty of the terrestrial lapse rate, γ_t, increases the expected error in elevation as elevations increase, particularly when small lapse rates are assumed.

We also reviewed the method for estimating paleo-moist-enthalpy. To estimate paleoenthalpy from plant fossils, Forest et al. (1999) quantified a relationship between leaf physiognomy and enthalpy from present-day plants and their local climate. Using Canonical Correlation Analysis, mean annual moist enthalpy can be estimated with an uncertainty of 5.5 kJ/kg. The contribution to the uncertainty in altitude is 560 m and is comparable to using temperature alone. Other statistical techniques that improve the ability to estimate enthalpy could replace the current method.

To apply these methods to a paleoclimate problem, one tacitly assumes that the errors as estimated from today's climate and plants are similar to those of the past. The deposition of plant fossils appears not to affect our climate estimates. Combining the estimated uncertainties indicates an altitude error of 910 m and compares favorably with altitude errors of 1100-1400 m from differences in paleopressure (Sahagian and Maus 1994) and 800-1500 m from differences in paleotemperature.

These methods have been used effectively to explore the tectonic and paleo-climate for regions in western North America, the Andes of South America, and the Tibetan plateau. The results provide additional evidence that must be included in debates about the paleobotany, paleoclimate, and tectonic evolution of these regions. The range of these results provides additional support for the need for such evidence in interpreting Earth's history and the need for continuing research in this area.

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