A novel palaeoaltimetry proxy based on spore and pollen wall chemistry

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Highlights

A novel palaeoaltimetry proxy based on spore and pollen wall chemistry

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► Existing palaeoaltimetry proxies have poor resolution and are climate dependent. ► There is a highly significant positive relationship between altitude and UV-B. ► Pollen and spore wall chemistry tracks changes in UV-B radiation. ► We propose that these advances offer a novel palaeoaltimetry proxy.

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ABSTRACT

Understanding the uplift history and the evolution of high altitude plateaux is of major interest to a wide range of geoscientists and has implications for many disparate fields. Currently the majority of palaeoaltimetry proxies are based on detecting a physical change in climate in response to uplift, making the relationship between uplift and climate difficult to decipher. Furthermore, current palaeoaltimetry proxies have a low degree of precision with errors typically greater than 1 km. This makes the calculation of uplift histories and the identification of the mechanisms responsible for uplift difficult to determine. Here we report on advances in both instrumentation and our understanding of the biogeochemical structure of sporopollenin that are leading to the establishment of a new proxy to track changes in the flux of UV-B radiation over geological time. The UV-B proxy is based on quantifying changes in the concentration of UV-B absorbing compounds (UACs) found in the spores and pollen grains of land plants, with the relative abundances of UACs increasing on exposure to elevated UV-B radiation. Given the physical relationship between altitude and UV-B radiation, we suggest that the analysis of sporopollenin chemistry, specifically changes in the concentration of UACs, may offer the basis for the first climate independent palaeoaltimetry proxy. Owing to the ubiquity of spores and pollen in the fossil record, our proposed proxy has the potential to enable the reconstruction of the uplift history of high altitude plateaux at unprecedented levels of fidelity, both spatially and temporally.

1. Introduction

Knowledge of the uplift history of high altitude plateaux underpins our understanding of (i) the interactions between climate and tectonics, (ii) the first-order controls on the evolution of the monsoon systems and (iii) the mechanical behaviour of the lithosphere during, and following thickening. For example, Tibetan Plateau uplift impacted on global atmospheric circulation patterns and resulted in a shift in monsoonal seasons compared with the period prior to Tibetan uplift (Molnar et al., 1993). On a global scale, plateau uplift may have enhanced siliciclastic rock weathering (Raymo et al., 1988, DeConto et al., 2003) and a drawdown of atmospheric CO_2 that may be linked to cooling across the Eocene/Oligocene and the onset of glacial conditions (Raymo and Ruddiman, 1992), although the linkage between global erosion rates and Cenozoic cooling has been challenged more recently (Willenbring and Blanckenburg, 2010).

From a continental geophysics perspective, deformation leading to uplift and plateaux formation can be variously described by a number of models. The first of these is the “thin viscous sheet” model, whereby deformation occurs in a vertically coherent manner, and vertical planes deform by pure shear (England and Houseman, 1986, England and Molnar, 1997). Alternatively, the “channel flow model” predicts deformation focused in a thin lower-mid crustal channel, so that the brittle upper crust is decoupled from the upper mantle (Royden, 1996; Clark and Royden, 2000). Finally, the “block model” describes elevation of the plateau as determined by time-dependent localised shear between coherent lithospheric blocks (Tapponnier et al., 2001). These competing models make differing predictions regarding surface uplift patterns that could be rigorously assessed if uplift histories of plateaux were tightly constrained. Consequently, there is an urgent need to develop quantitative palaeoproxies to determine the palaeoaltimetry of high altitude plateaux such as the Tibetan Plateau is of interest to a wide spectrum of scientists working within the geoscience community.

Here we set out to briefly summarise existing quantitative palaeoaltimetry proxies. We then follow this with a discussion on UV-B change with altitude and the newly identified UV-B proxy

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based on detecting changes in pollen and spore wall chemistry. This analysis is presented with the overall aim of suggesting that changes in pollen and spore wall chemistry may form the basis for developing a new climate independent palaeoaltimetry proxy.

2. Existing palaeoaltimetry proxies

Reconstructing palaeoaltimetries requires the exploitation of a physical variable that is directly dependent on the elevation of the surface on which it is measured. One such property is the change in oxygen isotope composition ($\delta^{18}O$) of precipitation. This approach has been calibrated by assuming that equilibrium isotope fractionation during Rayleigh distillation is linked to the thermodynamics of atmospheric ascent and water vapour condensation (Rowley et al., 2001). The technique has been criticised because Rayleigh distillation provides an idealised model that assumes the immediate removal of precipitation (Shuguia et al., 2003) and it oversimplifies the treatment of isotopic ratios in stratified atmospheric flows (Galewsky, 2009). Convective conditions are more appropriate for monsoon systems; these yield weaker isotope fractionation responses to elevation gradients that would lower the predicted altitude. More recently, the measurement of *D*/*H* ratios of *n*-alkanes from plant material in Tibetan lake sediments has been invoked as a potential isotopic proxy (Polissar et al., 2009). The results of this study proved inconclusive because of the uncertainties in moisture palaeosources and in the isotopic gradient across the northern plateau.

A different approach to palaeoaltimetry reconstruction rests on palaeobotanical data. The Climate Leaf Analysis Multivariate Program (CLAMP) has been applied to the Namling locality from South Tibet (Spicer et al., 2003) to reconstruct elevations at ~15 MyBP, with data suggesting that present-day elevations (*ca.* 5 km) were achieved by the Miocene. This technique is dependent on global climate models and assumptions regarding atmospheric lapse rates. The propagated uncertainties on the estimated altitudes are calculated as ±900 m. A series of model experiments have demonstrated that changes in climate associated with uplift have a greater control on the oxygen isotopic composition of the precipitation than the attitudinally induced changes in the atmospheric lapse rates which are used to underpin the proxy (Ehlers and Poulsen, 2009). Furthermore, in a recent publication Peppe et al. (2010) indicate that palaeoaltimetry proxies based on CLAMP, e.g. Spicer et al. (2003), may have significantly underestimated errors associated with leaf-sized bias in the fossil record leading to uncertainties in palaeoaltitude estimates that might exceed ±2 km. A subsequent rebuttal (Spicer and Yang, 2010) of this assertion demonstrated that removal of all size information from the dataset increased uncertainties by only ±50 m. However, although the CLAMP technique provides a potential palaeoaltimeter with overall uncertainties less than ±1 km, its applicability is strictly limited by stringent field requirements; fossil leaves need to be abundant, exceptionally well preserved and diverse (the Namling section included 35 well-preserved morphotypes). In addition the section needs to be precisely dated by radiometric techniques (which generally require the leaf beds to be interlayered with volcanic horizons). Despite several expeditions across the Tibetan Plateau to identify suitable locations for further study no second locality has yet been identified making the Namling dataset unique.

Another approach, also based on fossil leaves, rests on the correlation between stomatal density and the decrease in CO_2 partial pressure with altitude (McElwain, 2004). This is based on the well characterised negative relationship between stomata (either measured as the number of stomata per unit area (stomatal density, SD) or the ratio of the number of stomata to the number of stomata and epidermal cells expressed as a percentage (stomatal index, SI, Salisbury, 1928)) and CO_2 (Woodward, 1987). Correlation between CO_2 and SD/SI is strongly species-specific and so can only be applied to fossil floras that include extant species (making it of limited use for pre-Quaternary assemblages) and is further limited by the requirement for validation by comparisons with coexisting floras that grew at or near to sea-level. The requirement for co-occurring floras is needed to isolate the altitudinal effects of CO_2 decline from the background atmospheric CO_2 concentration. Moreover uplift and mountain building are predicted to result in the drawdown of atmospheric CO_2 potentially diminishing the predictive power of the relationship.

Recent work using pollen distribution and abundance linked to modern day temperature-dependent altitude ranges (Dupont-Nivet, 2008) suggests that the presence of high-altitude floras in northern Tibet preceded the Eocene/Oligocene boundary. The dataset is also used to predict elevation but the range in predicted palaeoelevation is large (1.5–2.8 km) and there are confounding effects imposed by plant ecophysiology. Indeed the use of modern temperature-dependent altitude ranges as an indicator of past altitudes may be over simplistic because elevated atmospheric CO_2 increases ice nucleation temperatures within leaves resulting in plants becoming more susceptible to frosts (Beerling et al., 2001) potentially altering their altitudinal range.

This summary of quantitative palaeoaltimetry illustrates that existing palaeoaltimetry proxies are subject to substantial uncertainty and are limited in their application owing to the requirements of highly specific depositional environments. Furthermore the resolution provided by published studies does not allow the testing of different uplift and deformation models. Therefore, what is required is a novel technique for measuring palaeoaltimetry that is (1) independent of climate; (2) widespread in applicability; (3) has a precision better than ±1 km, and (4) is independent of global climate models (GCMs) and assumptions relating to atmospheric lapse rates.

3. UV-B flux

Variation in globally incident UV-B radiation flux is controlled by changes in the overhead thickness of the stratospheric ozone (O_3) layer. Stratospheric O_3 is produced in the tropics by the photolysis of O_2; O_3 is then transported to high latitudes via the Brewer–Dobson cell resulting in a thickening of the stratospheric ozone layer with increasing latitude, and a corresponding decrease in the incident flux of UV-B at the Earth's surface. On a regional scale UV-B radiation flux increases with altitude (Fig. 1) due to the physical properties of the atmosphere, coupled with the changes in albedo with the rate of increase in the incident flux of UV-B per km of altitude being dependent on the latitude of the mountain range/plateau (Blumthaler et al., 1997, Pfeifer et al., 2006). It is this physical relationship between altitude and UV-B radiation that provides the basis for our proposed novel palaeoaltimetry proxy. This relationship was recently highlighted by modelling changes in the flux of UV-B radiation as a result of the uplift of the Tibetan Plateau (Willis et al., 2009). This study suggests that uplift and plateau formation would have resulted in a 100% increase in the total UV-B radiation flux at 5000 m above sea level (m.a.s.l.) when compared to pre-uplift sea level values (Willis et al., 2009).

A key aspect of the relationship between altitude and UV-B is that it is independent of climate in contrast to existing palaeoaltimetry proxies that are derived from detecting climate change triggered by uplift. UV-B changes are however also associated with changes in the solar cycle but the influence of sun spot cycles are limited because these short-term oscillations only result in a small (≤1%) change in UV-B flux to the land surface which is of minor

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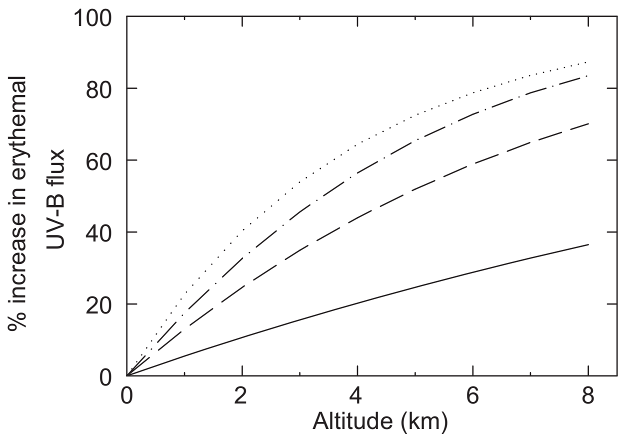

Fig. 1. Linear modelled regional percentage increase in erythemal UV-B radiation flux with altitude. Calculations based on clear sky sea-level erythemal UV-B flux estimates for each region (data from the WMO, 2007 report). Dotted line North America; dot/dash line South America; dash line Europe and solid line Pacific region. UV-B percent increase data was calculated from the following: Blumthaler et al. (1992, 1994, 1997), Dubrovský (2000), Gonzalez et al. (2007), Kudish et al. (1997), McKenzie et al. (2001), Pachart et al. (1999), Piazena (1996), Rigel et al. (1999) and Sullivan et al. (1992).

significance when compared to changes associated with increases in elevation (~5–20% increase per 1 km, Blumthaler et al., 1992, 1994, 1997; Dubrovský, 2000; Gonzalez et al., 2007; Kudish et al., 1997; McKenzie et al., 2001; Pachart et al., 1999; Piazena, 1996; Rigel et al., 1999; Sullivan et al., 1992; Fig. 1).

Model simulations of changes in UV in response to orbital cycles have suggested large scale changes in UV radiation (Shaffer and Cerveny, 2004). However, these simulations report radiative insolation values in non-systematic contiguous wavebands (225–285, 300–325, 325–690 nm), and in a split (175–225/285–300 nm) waveband. None of these wavebands adequately incorporates UV-B radiation alone (280–315 nm). The only waveband that includes wavelengths within the UV-B spectral range is the 'splitband'. However, this combines both UV-C and UV-B; UV-C radiation is not experienced at the Earth's surface due to absorption within the stratosphere. Thus ~75% of the wavelengths of the calculated influx of the 'UV splitband' cannot have reached the Earth's surface in an oxygenated atmosphere. Mass independent fractionation of sulphur isotopes suggest this occurred after the "Great Oxidation Event" ca. 2.45 Ga when O_2 concentrations increased to >1% of present atmospheric levels resulting in the development of a effective stratospheric ozone layer (Farquhar et al., 2000). Thus the percentage change in UV previously reported (Shaffer and Cerveny, 2004) is an over-estimate, and is referred to as "first approximations" by the authors (Shaffer and Cerveny, 2004). Therefore, orbital cyclicity is unlikely to adversely affect long-term fossil samples of pollen/spores due to the difference of time-scales and the fairly minor change in biologically active radiation at relevant wavelengths. Indeed over the last 550 million years long-term 2D modelling (Harfoot et al., 2007) of the response of the stratospheric ozone layer to changes in atmospheric O_2 indicates that this gradient has remained more or less stable, except for periods of intense and profound climate change associated with the end-Permian mass extinction event (Beerling et al., 2007).

4. Plant responses to UV-B radiation

The vast majority of terrestrial land plants require sunlight to drive photosynthesis leading to exposure to high-energy short wavelength UV-B radiation, resulting in damage to plant proteins, membrane lipids and DNA. One mechanism by which plants can mitigate these effects is via the up-regulation of UV-B absorbing compounds (UACs). UACs are found in a wide variety of plant tissue types including wood, leaf cuticle, seeds, pollen and spores (Cockell, 1999). Leaf cuticle, seeds, pollen and spores all contain ferulic acid (FA) and *para*-coumaric acid (*p*CA) that absorb UV-B radiation due to the physical nature of their chemical structure with an aromatic ring (common to both compounds) absorbing and dissipating incident UV-B radiation (Rozema et al., 2009). FA and *p*CA are products of the phenyl propanoid pathway (PPP) which is stimulated by UV-B radiation (Meijkamp. et al., 1999). Thus the stimulation of the PPP by UV radiation results in the greater production of UACs. Meta-analysis on whole plant responses to UV-B confirms that, in response to increased UV-B radiation flux, the up-regulation of UACs is one of the most consistent responses across a wide a variety of species (Searles et al., 2001; Newsham et al., 2009), with a 10% increase in UACs in response to growth at elevated UV-B (Searles et al., 2001). Meta-analysis also shows that plants can rapidly acclimate to UV-B exposure through the production of UACs (Newsham et al., 2009). Additionally, recent work has identified the protein (UVR8) responsible for the perception and subsequent upstream regulation of plant responses to UV-B radiation (Rizzini et al., 2011). The mechanism behind this response has been identified at the genetic level in *Arabidopsis thaliana* with orthologous genes being reported in algae and mosses suggesting evolutionary conservatism in UV-B perception (Christie et al., 2012).

Sporopollenin, the biopolymer that makes up the exine (outer wall) of spores and pollen, can be broadly grouped as fatty acids (containing unbranched aliphatic chains) and phenolic components, FA and *p*CA (containing aromatic rings) which provide protection against UV-B (van Bergen, 2004; Watson et al., 2007; Lomax et al., 2008; Fraser et al., 2011). Fourier transform infrared (FTIR) microspectroscopy can be used to detect and identify the type of bond/functional group present based on wavenumber of the band, whilst variations in band height and area represent changes in the relative abundance of such bonds/groups. To determine the relative abundance of individual functional groups of interest, FTIR spectra analyses are normalised to an internal stable absorption band, thus enabling inter-comparison of spectra by investigating relative changes in abundance of bonds/functional groups (Watson et al., 2007; Lomax et al., 2008; Fraser et al., 2011). The absorbance band due to the hydroxyl (OH) groups is chosen for normalisation both because of its stability and because the absolute IR-absorption is proportional to the quantity of sample analysed for each spectrum.

Based on previous work (Watson et al., 2007; Lomax et al., 2008; Fraser et al., 2012), any changes in absorption band peak height due to aromatic rings (at 1520 cm^{-1}) measured using FTIR can be regarded as a change in abundance of UACs within sporopollenin. Nitrogen-containing compounds are widely documented to have the potential to contribute towards the absorption band at ~1520 cm^{-1} (Williams and Fleming, 1980; Coates, 2000); however, work using pyrolysis–GC-MS shows no evidence of such compounds in spore walls (Watson et al., 2007; Lomax et al., 2008).

Previous work has shown that the biochemical composition of Lycopodiaceae (club mosses) sporopollenin can adapt to variations in the local UV-B radiation environment. For example, the analysis of herbarium samples of *Lycopodium magellanicum* and *Lycopodium annotinum* shows a strong correlation between UAC concentration and overhead stratospheric O_3 column depth obtained from satellite data (Lomax et al., 2008). *L. annotinum* UAC concentration can also be influenced by the flux of UV-B with plants decreasing their UAC concentration in response to a drop in UV-B (Fraser et al., 2011). Experimental evidence, in support of

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these findings, confirms that changes in the flux of UV-B radiation can induce an increase in the capacity of sporopollenin to absorb UV-B radiation. For example, in a field setting UACs increase by 95% in *Vicia faba* (broad bean) when compared to plants grown without UV-B (Rozema et al., 2001). Given that absorption of UV-B radiation in the spore/pollen wall is based on the physical properties of the aromatic ring and the need for plants to protect themselves from the harmful effects of UV-B we hypothesise that the UAC/UV-B relationship holds across a wide range of plant species. Experimental evidence to support this assumption is documented in the literature. For example, Blokker et al. (2005) report finding both *p*CA and FA within the sporopollenin of bryophytes and from widely divergent angiosperms. Furthermore, changes in UAC concentrations are not significantly related to other key environmental parameters including relative humidity, temperature and precipitation (Lomax et al., 2008) (Fig. 2).

Spore UACs of *Lycopodium cernuum* collected in tropical SE Asia (Watson et al., 2007) show a positive relationship with

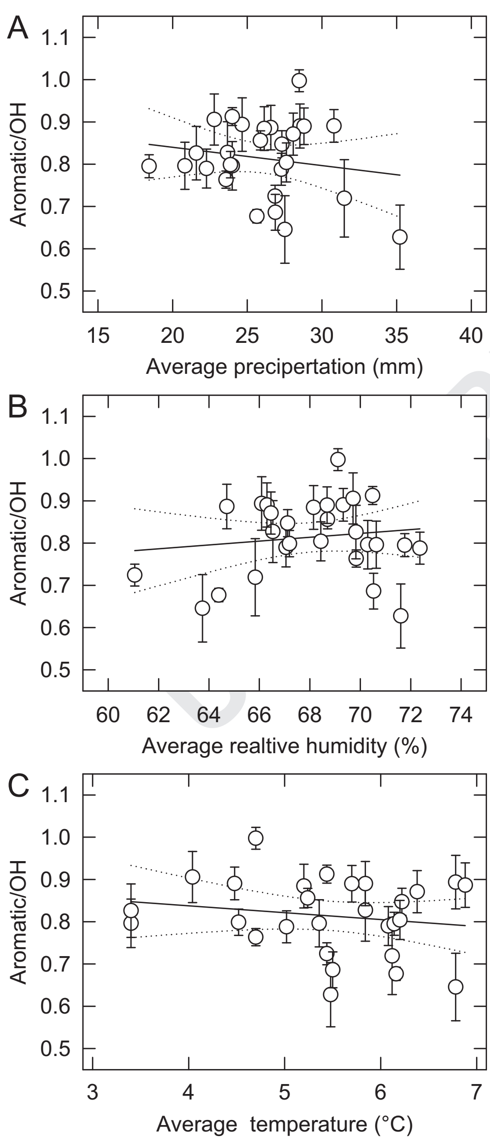

Fig. 2. Greenland *Lycopodium annotinum* spore wall UV-B absorbing compounds (UACs) concentrations against environmental variables averaged over the growing season. (A) precipitation; (B) relative humidity; and (C) temperature. Data show no statistical relationship between these key environmental variables and UAC concentration. Climate data are from the UEA CRU TS 2.1 dataset (Mitchell and Jones, 2005).

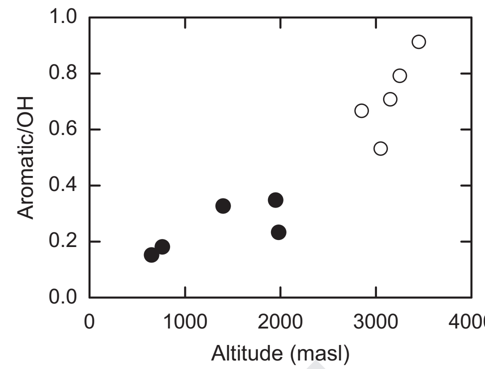

Fig. 3. Spore and pollen wall UV-B absorbing compounds (UACs) plotted against altitude. Closed circles are *Lycopodium cernuum* spores collected from SE Asia (data from Watson et al., 2007) and open circles are *Polygonum* sp. pollen from the Hengduan Mountains (27°00′29.8″N, 100°10′40.1″E). Data used to plot this figure are available as the supplementary content.

altitude and analysis of *Polygonum* sp. pollen collected in the Hengduan Mountains (27°00′29.8″N, 100°10′40.1″E) again demonstrates the same positive relationship (Fig. 3). Spearman's rank correlation coefficient analysis of the combined dataset reveals a strong correlation coefficient (altitude vs. UACs $r_s = 0.95$, $p < 0.0001$). The pilot data (Fig. 3) also suggest increasing sensitivity at higher altitudes due to the increase in UV-B radiation flux. This implies that the relationship between UACs, UV-B and altitude is non-linear and that transfer functions used to predict altitude from UACs would be derived from either a power law or some other non-linear function. The prospect of increasing sensitivity at high altitude is intriguing as this is currently an area of uncertainty in existing palaeoaltimetry proxies. However, caution is warranted when interpreting our combined dataset due to different geographic locations and thus varying overhead stratospheric O_3 and UV-B fluxes, the data clearly indicate a strong relationship between UACs present in spore and pollen walls with altitude.

The chemical analysis of leaf tissue indicates that there is a significant positive relationship between altitude, UV-B radiation flux and leaf tissue UACs. For example in the Blue Mountains, Jamaica, at altitudes from 800 to 1600 m.a.s.l. the calculated UV-B flux increases from 9.45 kJ m^{-2} day^{-1} to 9.75 kJ m^{-2} day^{-1} and total UV-B absorbance by leaf tissue UACs increase by 67% in leaves of *Bocconia frutescens* (Tree poppy); a further three species yield similar results, although the pattern is less clear in an introduced species *Trifolium repens* (white clover) (Rozema et al., 1997). An additional study, looked at the response of *Fagus sylvatica* (European Beech) over an altitudinal transect of 685 m, from 131 to 816 m.a.s.l. to altitudinal UV-B fluxes in the Hunsrück mountain range (Germany), showed a highly significant (r^2 0.68, $P < 0.001$) linear relationship between leaf UACs and altitude; the relationship between leaf UACs and the sum of the daily maximum UV index (UV-I) during the growth season is also highly significant (r^2 0.54, $P < 0.005$) (Fig. 4A and B) (Neitzke and Therburg, 2003). Furthermore, analysis of 14 plant species collected in Hawaii spanning a 3000 m elevation transect resulting in a 15% increase in UV-B radiation reveals a statistically significant positive relationship between UV-B tolerance and elevation with tolerance increasing with altitude (Sullivan et al., 1992). A companion paper (Ziska et al., 1992) reported that plants from high elevations consistently produced more leaf tissue UACs than lowland species even when grown without exposure to UV-B, suggesting both adaptation and acclimation to high incident levels of UV-B (Ziska et al., 1992). The analysis of leaf UAC found in the high altitude specialist *Polylepis tarapacana* (high altitude quenoa) from two sites (4300 and 5000 m.a.s.l.) again reveals a

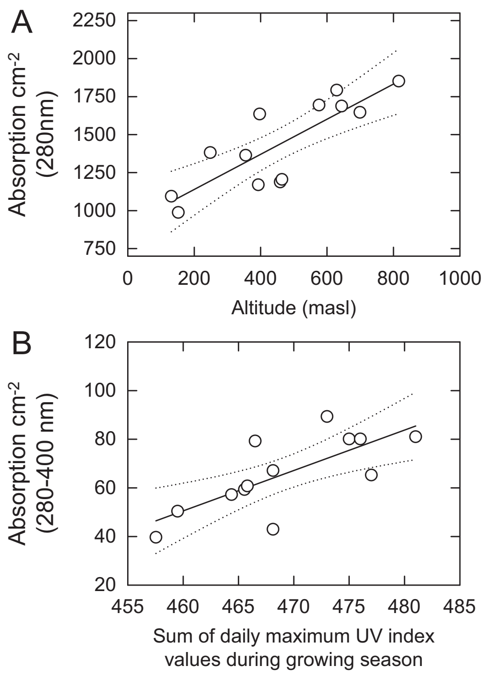

Fig. 4. Leaf UV-B absorbing compounds (UACs) responses to altitude and UV-B radiation flux (measured as UV absorption of methanolic extracts per cm^2). (A) Absorption at 280 nm by *Fagus sylvatica* leaf UACs in response to changes in altitude; (B) Absorption over 280–400 nm in response to changes in UV-B as measured using the UV index weighted to erythemal UV-B (305 nm). Redrawn from Neitzke and Therburg (2003).

strong positive relationship between UACs and altitude with a 35% (winter) and 32% (summer) increase in UACs between the sites in response to a 15% increase in winter UV-B flux and a 12% increase in summer UV-B flux between the two sites (Gonzalez et al., 2007), demonstrating that the UAC/altitude relationship is sensitive to changes in UV-B over a very wide altitudinal range.

This consistent series of results – from widely spaced geographic locations and across several phylogenetic species exposed to different total UV-B fluxes, rates of change in UV-B flux with altitude and overhead stratospheric ozone concentrations – suggests that the plant responses to changes in altitudinal UV-B fluxes are highly consistent and mechanisms underpinning this response are evolutionarily conserved. Therefore, the positive relationship between altitude and UV-B radiation, as reflected by changes in plant chemistry, and as corroborated by our recent findings open up the exciting possibility of developing a novel palaeoaltimetry proxy that is truly climate independent, which is applicable over a wide range of altitudes.

Although the relationship between altitude and UV-B flux is independent of climate, the flux of UV-B to the surface can be influenced by overhead conditions. For example, cloud cover frequently increases with altitude in mountainous terrain. Eco-physiological, morphological and biochemical investigations have demonstrated that plants are adapted to the high flux of UV-B radiation associated with high altitude (Sullivan et al., 1992; Ziska et al., 1992; Rozerma et al., 1997; Neitzke and Therburg, 2003; Gonzalez et al., 2007). Meta-analysis also suggests that UACs response to changes in UV-B radiation flux are rapid (Searles et al., 2001) implying that plants are responding to maximum UV-B flux characteristic of clear skies. Consequently, even though cloud cover may increase with altitude, we hypothesise that this factor will not directly impinge on the predictive power of the relationship, however this clearly requires testing in the field. Nonetheless, our pilot data (Fig. 3) show a clear relationship between spore and pollen UACs supporting our hypothesis that cloud cover does not limit the predictive capability of the relationship.

5. Taphonomic factors

There are several factors that could impact the effective assessment of UV-B based on fossilised dispersed pollen and spores. These fall under the categories of taphonomy that acts as a powerful filter for any palaeobotanical investigation. Some of these factors are specific to dispersed terrestrial palynomorphs. They centre on two questions: where do the pollen and spores come from, and how are they altered by diagenesis? Pollen produced by some wind-pollinated plants, particularly temperate trees and herbs, such as pines, oaks, alders, hazels and grasses, can be dispersed long distances from the parent plants and in huge quantities (Bush and Rivera, 1998, 2001; Culley et al., 2002; Poska et al., 2010; Hjelle and Sugita, 2012). Pollen taken from sediments and surface samples are therefore regarded as distance-weighted assemblages with predominantly local pollen represented alongside some long-distance transported grains (Prentice, 1988; Odgaard, 1999, 2001; Jackson and Williams, 2004; Bunting and Hjelle, 2010). Such long-range dispersal can subtly change the composition of pollen assemblages from sites that do not contain the parent plants, especially those where there is little surrounding vegetation of significant stature such as tundra and alpine regions (Gajewski, 1995; Sugita et al., 2010). While this exotic pollen is detectable with altitudinal changes as well (Willis, 1994) it does not obscure the dominant local vegetation signal: Even at altitudes in excess of 2500 m the pollen record can preserve local vegetation type information without a loss of fidelity (Willis, 1994; Hooghiemstra and van der Hammen, 2004). Studies from moss polsters (surface samples representing no influx of water borne grains) indicate that the majority of pollen are contributed from a 10 m radius with a significantly smaller [illegible]ortion of grains from up to 1000 m (Bunting and Hjelle, 2[illegible]). Even lakes of up to 19 ha in size from western Norway indicate that most pollen is received from within a 1 km radius (Hjelle and Sugita, 2012).

The proxy is based on extracting geochemical information from fossil spores and pollen grains. It is essential, therefore, to understand the stability of sporopollenin in response to diagenesis before undertaking extensive analysis. Fossil *Pinus* pollen UACs have recently been recovered from Holocene sediments (Willis et al., 2011). Steemans et al. (2010) demonstrated that the chemical composition of sporopollenin is stable at lower grades of diagenesis with samples dating to the Late Silurian (~419 MyBP) showing excellent biogeochemical preservation.

The geochemical stability of sporopollenin has also been confirmed in an experimental setting (Watson et al., 2012). Artificially simulated diagenesis of spore material was generated by pyrolysis at varying temperatures for 48 h, representing different degrees of subsurface maturation of sporopollenin. Results specifically demonstrated that the phenolic content of sporopollenin (i.e. the UACs which are the basis of this proxy) remains unaffected at lower grades of diagenesis and is stable up to an experimental temperature of 200–250 °C. This level of experimental heating represents thermal alteration equivalent to the lignite rank.

For application of the proxy to establish the palaeoelevation and the uplift history of the Tibetan Plateau, we note that average maximum exhumation rates obtained by fission track studies from across the plateau lie in the range 0.1 km/Ma, from zircon ages in northern Tibet (Jolivet et al., 2001), to 0.5 km/Ma, from apatite ages in deeply incised gorges from SE Tibet (Clark et al., 2005). These results indicate that, even in the most rapidly

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exhuming regions, the rocks exposed on the Tibetan Plateau have not been heated above 200–250 °C (the approximate zircon annealing temperature) since the Paleogene or earlier, implying that pollen recovered from basins of Neogene age are most likely to have retained their primary biogeochemical signature.

6. Conclusions

Understanding the relationship between orogensis, high-altitude plateau evolution and climate change requires the development of palaeoproxies that can both constrain uplift rate and palaeoaltitude with a high degree of fidelity. Current palaeoaltimetry proxies are underpinned by a large degree uncertainty leading to poorly constrained estimates of uplift rate and predicted palaeoaltitude. To fully deconvolve the relationship between climate and orogenesis a climate-independent proxy is required; currently published proxies all rely on uplift-derived climate change to provide the mechanistic underpinning of the proxy.

We propose that the physical relationship that exists between altitude and UV-B radiation and newly developed techniques/instrumentation to quantify spore and pollen UACs now offer the potential to deliver a palaeoaltimetry proxy that can be widely applied. This proxy also has the potential to satisfy all of the necessary requirements i.e. (1) is independent of climate; (2) is widespread in applicability; (3) has a precision better than ± 1 km, and (4) is independent of global climate models (GCMs) and assumptions relating to atmospheric lapse rates. To fully test these assertions the challenge is to test this newly identified potential proxy to determine: (i) the sensitivity of spore and pollen wall UACs to altitudinal fluxes in UV-B radiation and (ii) construct a series of UAC/altitude transfer functions to predict present day altitudes as a mechanisms for proxy validation. Pilot data (Fig. 3) combined with the examination of the literature presented here lead us to hypothesise that these conditions will be met resulting in the first widely applicable climate independent palaeoaltimetry proxy.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.epsl.2012.07.039.

References

Beerling, D.J., Terry, A.C., Mitchell, P.L., Callaghan, T.V., Gwynn-Jones, D., Lee, J.A., 2001. Time to chill: effects of simulated global change on leaf ice nucleation temperatures of subarctic vegetation. Am. J. Bot. 88, 628–633.

Beerling, D.J., Harfoot, M.B.J., Lomax, B.H., Pyle, J.A., 2007. The stability of the stratospheric ozone layer during the end-Permian eruption of the Siberian Traps. Phil. Trans. R. Soc. A 365, 1843–1866.

van Bergen, P.F., Blokker, P., Collinson, M.E., Damsté, J.S.S., deLeewu J.W., 2004. Structural biomacromolecules in plants: what can be learnt from the fossil record. Linnaean Society Symposium Series, vol. 21, pp. 133–154.

Blokker, P., Yeloff, D., Boelen, P., Broekman, R.A., Rozema, J., 2005. Anal. Chem. 77, 6026–6031.

Blumthaler, M., Ambach, W., Rehwald, W., 1992. Solar UV-A and UV-B radiation fluxes at 2 alpine stations at different altitudes. Theor. Appl. Climatol. 46, 39–44.

Blumthaler, M., Webb, A.R., Seckmeyer, G., Bais, A.F., Huber, M., Mayer, B., 1994. Simultaneous spectroradiometry—a study of solar UV irradiance at 2 altitudes. Geophys. Res. Lett. 21, 2805–2808.

Blumthaler, M., Ambach, W., Ellinger, R., 1997. Increase in solar UV radiation with altitude. J. Photochem. Photobiol. B 39, 130–134.

Bunting, M.J., Hjelle, K.L., 2010. Effect of vegetation data collection strategies on estimates of relevant source area of pollen (RSAP) and relative pollen productivity estimates (relative PPE) for non-arboreal taxa. Veg. Hist. Archaeobot. 19, 365–374.

Bush, M.B., Rivera, R., 1998. Pollen dispersal and representation in a neotropical rainforest. Global Ecol. Biogeogr. Lett. 7, 379–392.

Bush, M.B., Rivera, R., 2001. Reproductive ecology and pollen representation among neotropical trees. Global Ecol. Biogeogr. 10, 359–367.

Coates, J., 2000. Interpretation of infrared spectra: a practical approach. In: Meyers, R.A. (Ed.), Encyclopaedia of Analytical Chemistry. John Wiley and Sons, Chichester, pp. 10815–10837.

Clark, M.K., Royden, L.H., 2000. Topographic ooze: building the eastern margin of Tibet by lower crustal flow. Geology 28, 703–706.

Clark, M.K., House, M.A., Royden, L.H., Whipple, K.X., Burchfiel, B.C., Zhang, X., Tang, W., 2005. Late Cenozoic uplift of southeastern Tibet. Geology 33, 525–528.

Cockell, C.S., Knowland, J., 1999. Ultraviolet radiation screening compounds. Biol. Rev. Camb. Philos. Soc. 74, 311–345.

Christie, J.M., Arvai, A.S., Baxter, K.J., Heilmann, M., Pratt, A.J., O'Hara, A., Kelly, S.M., Hothorn, M., Smith, B.O., Hitomi, K., Jenkins, G.I., Getzoff, E.D., 2012. Plant UVR8 photoreceptor senses UV-B by tryptophan-mediated disruption of cross-dimer salt bridges. Science 335, 1492–1496.

Culley, T.M., Weller, S.G., Sakai, A.K., 2002. The evolution of wind pollination in angiosperms. Trends Ecol. Syst. 17, 361–369.

DeConto, R.M., Pollard, D., 2003. Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO_2. Nature 421, 245–249.

Dubrovský, M., 2000. Analysis of UV-B irradiances measured simultaneously at two stations in the Czech Republic. J. Geophys. Res. 105 (D4), 4907–4913.

Dupont-Nivet, G., Hoorn, C., Konert, M., 2008. Tibetan uplift prior to the Eocene–Oligocene climate transition: evidence from pollen analysis of the Xining Basin. Geology 36, 987–990.

Ehlers, T.A., Poulsen, C.J., 2009. Influence of Andean uplift on climate and paleoaltimetry estimates. Earth Planet. Sci. Lett. 281, 238–248.

England, P., Houseman, G., 1986. Finite strain calculations of continental deformation.2. comparison with the India-Asia collision zone. J. Geophys. Res. 91, 3664–3676.

England., P., Molnar, P., 1997. Active deformation of Asia: from kinematics to dynamics. Science 278, 647–650.

Fraser, W.T., Sephton, M.A., Watson, J.S., Self, S., Lomax, B.H., James, D.I., Wellman, C.H., Callaghan, T.V., Beerling, D.J. 2011. UV-B absorbing pigments in spores: biochemical responses to shade in a high-latitude birch forest and implications for sporopollenin-based proxies of past environmental change. Polar Res. 30, Article Number: 8312.

Farquhar, J., Bao, H.M., Thiemens, M., 2000. Atmospheric influence of Earth's earliest sulfur cycle. Science 289, 756–758.

Gajewski, K., 1995. Modern and Holocene pollen assemblages from some small Arctic Lakes on Somerset Island, NWT, Canada. Quat. Res. 44, 228–236.

Galewsky, J., 2009. Orographic precipitation isotopic ratios in stratified atmospheric flows: implications for paleoelevation studies. Geology 37, 791–794.

Gonzalez, J.A., Gallardo, M.G., Boero, C., Cruz, M.L., Prado, F.E., 2007. Altitudinal and seasonal variation of protective and photosynthetic pigments in leaves of the world's highest elevation trees *Polylepis tarapacana* (Rosaceae). Acta Oecol. 32, 36–41.

Harfoot, M.B.J., Beerling, D.J., Lomax, B.H., Pyle, J.A., 2007. A two-dimensional atmospheric chemistry modeling investigation of Earth's Phanerozoic O-3 and near-surface ultraviolet radiation history. J. Geophys. Res. 112 (D7) Article Number: D07308.

Hjelle, K.L., Sugita, S., 2012. Estimating pollen productivity and relevant source area of pollen using lake sediments in Norway: how does lake size variation affect the estimates? Holocene 22, 313–324.

Hooghiemstra, H., van der Hammen, T., 2004. Quaternary ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. Philos. Trans. R. Soc. B 359, 173–181.

Jackson, S.T., Williams, J.W., 2004. Modern analogs in Quaternary palaeoecology: here today, gone yesterday, gone tomorrow? Annu. Rev. Earth Planet. Sci. 32, 495–537.

Jolivet, M., Brunel, M., Seward, D., Xu, Z., Yang, J., Roger, F., Tapponnier, P., Malavieille, J., Arnaud, N., Wu, C., 2001. Mesozoic and Cenozoic tectonics of the northern edge of the Tibetan plateau: fission-track constraints. Tectonophysics 343, 111–134.

Kudish, A.I., Evseev, E., Kushelevsky, A.P., 1997. The analysis of ultraviolet radiation in the Dead Sea basin, Israel. Int. J. Climatol. 17, 1697–1704.

Lomax, B.H., Fraser, W.T., Sephton, M.A., Callaghan, T.V., Self, S., Harfoot, M., Pyle, J.A., Wellman, C.H., Beerling, D.J., 2008. Plant spore walls as a record of long-term changes in ultraviolet-B radiation. Nat. Geosci. 1, 592–596.

McElwain, J.C., 2004. Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO_2 partial pressure. Geology 32, 1017–1020.

Please cite this article as: Lomax, B.H., et al., A novel palaeoaltimetry proxy based on spore and pollen wall chemistry. Earth and Planetary Science Letters (2012), http://dx.doi.org/10.1016/j.epsl.2012.07.039

McKenzie, R.L., Johnston, P.V., Smale, D., Bodhaine, B.A., Madronich, S., 2001. Altitude effects on UV spectral irradiance deduced from measurements at Lauder, New Zealand, and at Mauna Loa Observatory, Hawaii. J. Geophys. Res. 106 (D19), 22845–22860.

Meijkamp, B.B., Aerts, R., van de Staaij, J.W.M., Tosserams, M., Ernst, W.H.O., Rozema, J., 1999. Effects of UV-B on secondary metabolites in plants. In: Rozema, J. (Ed.), Stratospheric Ozone Depletion; the Effects of UV-B Radiation on Terrestrial Ecosystems, 1999. Backhuys, Leiden, pp. 70–99.

Mitchell, T.D., Jones, P.D., 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int. J. Climatol. 25, 693–712.

Molnar, P., England, P., Martinod, J., 1993. Mantle dynamics, uplift of the Tibetan Plateau, and the Indian monsoon. Rev. Geophys. 31, 357–396.

Neitzke, M., Therburg, A., 2003. Seasonal changes in UV-B absorption in beech leaves (*Fagus sylvatica* L.) along an elevation gradient. Forstwiss. Centralbl. 122, 1–21.

Newsham, K.K., Robinson, S.A., 2009. Responses of plants in polar regions to UVB exposure: a meta-analysis. Global Change Biol. 15, 2574–2589.

Odgaard, B.V., 1999. Fossil pollen as a record of past biodiversity. J. Biogeogr. 26, 7–17.

Odgaard, B.V., 2001. Palaeoecological perspectives on pattern and process in plant diversity and distribution adjustments: a comment on recent developments. Divers. Distrib. 7, 197–201.

Pachart, E., Lenoble, J., Brogniez, C., Masserot, D., Bocquet, J.L., 1999. Ultraviolet spectral irradiance in the French Alps: results of two campaigns. J. Geophys. Res. 104 (D14), 16777–16784.

Peppe, D.J., Royer, D.L., Wilf, P., Kowalski, E. A., 2010. Quantification of large uncertainties in fossil leaf paleoaltimetry. Tectonics 29, Article Number: TC3015.

Pfeifer, M.T., Koepke, P., Reuder, J., 2006. Effects of altitude and aerosol on UV radiation. J. Geophys. Res. 111 (D1), D01203.

Piazena, H., 1996. The effect of altitude upon the solar UV-B and UV-A irradiance in the tropical Chilean Andes. Solar Energy 54 (2), 133–140.

Polissar, P.J., Freeman, K.H., Rowley, D.B., McInerney, F.A., Currie, B.S., 2009. Paleoaltimetry of the Tibetan Plateau from *D/H* ratios of lipid biomarkers. Earth Planet. Sci. Lett. 287, 64–76.

Poska, A, Meltsov, V., Sugita, S, Vassiljev, J., 2010. Relative pollen productivity estimates of major anemophilous taxa and relevant source area of pollen in a cultural landscape of the hemi-boreal forest zone (Estonia). Rev. Palaeobot. Palynol. 167, 30–39.

Prentice, I.C., 1988. Records of vegetation in time and space: the principles of pollen analysis. In: Huntley, B., Webb III, T. (Eds.), Vegetation History. Kluwer Academic Publishers, pp. 17–42.

Raymo, M.E., Ruddiman, W.F., Froelich, P.N., 1988. Influence of late Cenozoic mountain building on ocean geochemical cycles. Geology 16, 649–653.

Raymo, M.E., Ruddiman, W.F., 1992. Tectonic forcing of Late Cenozoic climate. Nature 359, 117–121.

Rigel, D.S., Rigel, E.G., Rigel, A.C., 1999. Effects of altitude and latitude on ambient UVB radiation. J. Am. Acad. Dermatol. 40, 114–116.

Rizzini, L., Favory, J.J., Cloix, C., Faggionato, D., O'Hara, A., Kaiserli, E., Baumeister, R., Schafer, E., Nagy, F., Jenkins, G.I., Ulm, R., 2011. Perception of UV-B by the Arabidopsis UVR8 Protein. Science 332, 103–106.

Rowley, D.B., Pierrehumbert, R.T., Currie, B.S., 2001. A new approach to stable isotope-based paleoaltimetry: implications for paleoaltimetry and paleohypsometry of the High Himalaya since the Late Miocene. Earth Planet. Sci. Lett. 188, 253–268.

Royden, L.H., 1996. Coupling and decoupling of crust and mantle in convergent orogens: implications for strain partitioning in the crust. J. Geophys. Res. 101, 17679–17705.

Rozema, J., Chardonnens, A., Tosserams, M., Hafkenscheid, R., Bruijnzeel, S., 1997. Leaf thickness and UV-B absorbing pigments of plants in relation to an elevational gradient along the Blue Mountains, Jamaica. Plant Ecol. 128, 150–159.

Rozema, J., Broekman, R.A., Blokker, P., Meijkamp, B.B., de Bakker, N., van de Staaij, J., van Beem, A., Ariese, F., Kars, S.M., 2001. UV-B absorbance and UV-B absorbing compounds (*para*-coumaric acid) in pollen and sporopollenin: the perspective to track historic UV-B levels. J. Photochem. Photobiol. B 62, 108–117.

Rozema, J., Blokker, P., Fuertes, M.A.M., Broekman, R., 2009. UV-B absorbing compounds in present-day and fossil pollen, spores, cuticles, seed coats and wood: evaluation of a proxy for solar UV radiation. Photochem. Photobiol. Sci. 8, 1233–1243.

Salisbury, E.J., 1928. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. Philos. Trans. R. Soc. Lond. Ser. B 216, 1–65.

Searles, P.S., Flint, S.D., Caldwell, M.M., 2001. A meta analysis of plant field studies simulating stratospheric ozone depletion. Oecologia 127, 1–10.

Shaffer, J.A., Cerveny, R.S., 2004. Long-term (250,000 BP to 50,000 AP) variations in ultraviolet and visible radiation (0.175–0.690 μm). Global Planet. Change 41, 111–120.

Shugui, H., Masson-Delmotte, V., Qin, D.H., Jouzel, J., 2003. Modern precipitation stable isotope vs. elevation gradients in the High Himalaya. Comment on "A new approach to stable isotope-based paleoaltimetry: implications for paleoaltimetry and paleohypsometry of the High Himalaya since the Late Miocene" by David B. Rowley et al.,. [Earth Planet. Sci. Lett. 188 (2001) 253–268]. Earth and Planetary Science Letters 209, 395–399.

Spicer, R.A., Harris, N.B.W., Widdowson, M., Herman, A.B., Guo, S.X., Valdes, P.J., Wolfe, JA., Kelley, S.P., 2003. Constant elevation of southern Tibet over the past 15 million years. Nature 421, 622–624.

Steemans, P., Lepot, K., Marshall, C.P., Le Herisse, A., Javaux, E.J., 2010. FTIR characterisation of the chemical composition of Silurian miospores (cryptospores and trilete spores) from Gotland, Sweden. Rev. Palaeobot. Palynol. 162, 577–590.

Sugita, S., Hicks, S., Sormunen, H., 2010. Absolute pollen productivity and pollen–vegetation relationships in northern Finland. J. Quat. Sci. 25, 724–736.

Sullivan, J.H., Teramura, A.H., Ziska, LH., 1992. Variation in UV-B sensitivity in plants from a 3000 m elevational gradient in Hawaii. Am. J. Bot. 79, 37–743.

Tapponnier, P., Xu, Z.Q., Roger, F., Meyer, B., Arnaud, N., Wittlinger, G., Yang, J.S., 2001. Geology – oblique stepwise rise and growth of the Tibet plateau. Science 294, 1671–1677.

Watson, J.S., Sephton, M.A., Sephton, S.V., Self, S., Fraser, W.T., Gilmour, I., Wellman, C.H., Beerling, D.J., 2007. Rapid determination of spore chemistry using thermochemolysis gas chromatography-mass spectrometry and micro-Fourier transform infrared spectroscopy. Photochem. Photobiol. Sci. 6, 689–694.

Watson, J.S., Fraser, W.T., Sephton, M.A., 2012. Formation of a polyalkyl macromolecule from the hydrolysable component within sporopollenin during heating/pyrolysis experiments with Lycopodium spores. J. Anal. Appl. Pyrol. 95, 138–144.

WMO (World Meteorological Organisation), 2007. Scientific assessment of Ozone depletion: 2006. World Meteorological Organisation Global Ozone Research and Monitoring Project, Report No. 50, Geneva, Switzerland.

Willenbring, J.K., von Blanckenburg, F., 2010. Long-term stability of global erosion rates and weathering during late-Cenozoic cooling. Nature 465, 211–214.

Williams, D.H., Fleming, I., 1980. Spectroscopic Methods in Organic Chemistry. McGraw-Hill, London.

Willis, K.J., 1994. Altitudinal variation in the late Quaternary vegetational history of Northwest Greece. Hist. Biol. 9, 103–116.

Willis, K.J., Bennett, K.D, Birks, H.J.B., 2009. Variability in thermal and UV-B energy fluxes through time and their influence on plant diversity and speciation. J. Biogeogr. 36 (9), 1630–1644.

Willis, K.J., Feurdean, A., Birks, H.J.B., Bjune, A.E., Breman, E., Broekman, R., Grytnes, J.-A., New, M., Singarayer, J.S., Rozema, J., 2011. Quantification of UV-B flux through time using UV-B-absorbing compounds contained in fossil Pinus sporopollenin. New Phytol. 192, 553–560.

Woodward, F.I., 1987. Stomatal numbers are sensitive to increases in CO_2 from preindustrial levels. Nature 327, 617–618.

Ziska, LH., Teramura, A.H., Sullivan, J.H., 1992. Physiological sensitivity of plants along an elevational gradient to UV-B radiation. Am. J. Bot. 79, 863–871.

Please cite this article as: Lomax, B.H., et al., A novel palaeoaltimetry proxy based on spore and pollen wall chemistry. Earth and Planetary Science Letters (2012), http://dx.doi.org/10.1016/j.epsl.2012.07.039