

FRONTIERS IN PALAEOONTOLOGY

3 PALAEOPROXIES: BOTANICAL MONITORS AND
RECORDERS OF ATMOSPHERIC CHANGE

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Abstract

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The integration of plant and Earth sciences offers the opportunity to develop and test

palaeobotanical monitors and recorders (palaeoproxies) of past atmospheric change that are

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understood from a mechanistic perspective, with the underpinning responses being identified and understood at the genetic level. This review highlights how this approach has been used

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to deliver two distinct palaeoproxies. The first is based on the negative relationship between stomata (breathing pores found on the leaf surface) and atmospheric CO₂ concentration; the

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second is based on tracking chemical changes seen in the composition of pollen and spores to reconstruct changes in the flux of UV-B radiation on the Earth's surface and from this infer

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changes in stratospheric processes linked to the eruption and emplacement of Large Igneous Provinces. Here we highlight the potential of integrating a new rapid, inexpensive chemical

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analysis technique with existing, robust palynological methods, opening the door to a deeper understanding of past environments via the palaeo-biological record. A look to the future

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suggests a combined solar radiation-CO₂ concentration approach could be readily applied across the geological record.

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Key words

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atmospheric change, Fourier transform infrared (FTIR) spectroscopy, palaeoproxies, stomata, sporopollenin, CO₂ and UV-B.

42 The fifth International Panel on Climate Change (IPCC) assessment AR5 (IPCC 2013), states
“Warming of the climate system is unequivocal” and that “It is extremely likely that human
influence has been the dominant cause of the observed warming since the mid-20th century”.
45 Being able to place anthropogenic warming into context and establish how the Earth system
responds to climate perturbation is becoming an ever more important area of study; one to
which the paleontological community is in a unique position to contribute to, providing
48 impact that is both relevant to policy maker and wider society.

Throughout the majority of the Phanerozoic the Earth’s climate state has been that of a
greenhouse world, with equitable temperatures, a low tropic to pole heat gradient and little
51 polar ice (Frakes et al, 1992). The unlocking of this record will enhance our understanding of
and capacity to predict future climate change scenarios and importantly help to reduce
uncertainty around these predictions. To achieve this it is necessary to develop well
54 constrained and robustly tested paleo-proxies (Lomax et al. 2012a). Plants are innately
coupled to the atmosphere requiring both sunlight and CO₂ to drive photosynthesis and
carbon assimilation. When combined with their resilience and persistence (discussed below),
57 the study of plant responses to climate change in concert with the analysis of fossil plants
offer the opportunity to monitor past atmospheric conditions and infer palaeoclimate change.
Here we highlight how this approach has led to the development of mechanistic
60 palaeoproxies tested on palaeobotanically relevant extant species showing that plant fossils
can be used as both monitors and geochemical recorders of atmospheric changes.

The evolutionary pressures on plants and animal are intrinsically different; effectively
63 plants dance to an “evolutionarily different beat” (Traverse 1988). This was recognised in
the late 1950’s with Gothan and Remy (1957) proposing the division of the Phanerozoic into
three eras (Palaeophytic, Mesophytic and Cenophytic) based on major plant transitions that
66 are clearly distinct from faunal extinctions (Traverse 1988). Viewing the stratigraphic column

through the lens of plant evolution fundamentally alters the timing of these major transitions and demonstrates the innate resilience of plants to abiotic forcing. The Palaeophytic/ Mesophytic transition is defined as a switch in dominance from Rhyniophytic (Eotrachyophytic) (Gray, 1993; Cleal et al. 2014) to cycadophytes, ginkgophytes and conifers, and occurs in the Early upper Permian. The Mesophytic/ Cenophytic transition is identified by the occurrence of Angiosperms in the Early Cretaceous. Consequently Traverse (1988) suggested that a land plant division of the Phanerozoic is based on originations and/ or changes to the dominance of ecological groups rather than extinctions. This fundamental mismatch has recently been highlighted by Cascales-Miñana and Cleal (2013), who in their family level investigation showed just – two major extinction events – in the plant fossil record; as opposed to the big five recognised in the marine realm (Raup and Sepkoski 1982). Furthermore others have argued that only one of these, the end Permian, was common to both databases (Cascales-Miñana and Cleal 2013). Plant responses to mass extinction typically take the form of ecological reorganisation, floral turnover and species level extinction e.g. Wolfe and Upchurch (1986) reviewed in McElwain and Punyasena (2007) and/or migrations (e.g Wing and Harrington 2001). These data indicate that plants have inherent resilience; achieved via a combination of factors related to reproduction (sexual and asexual) and dormancy, reviewed in Traverse (1988).

As sessile organisms, plants must be able to adapt to their local environment and retain a certain amount of capacity for acclimation. Often these responses can take the form of physiological adjustment(s) and/or changes in biochemistry. This gives plants further flexibility in the face of environmental pressure and offers a suite of mechanisms to safeguard against extinction. This in built resilience when coupled with our increased understanding of extant plant adaptation to a changing climate, often understood at the genetic level which is enabling the development of well constrained palaeoproxies which are understood in a

mechanistic manner. In this review we discuss how this bottom up mechanistic approach is
93 leading to the enhanced understanding of two key environmental parameters of the
palaeoatmosphere: atmospheric CO₂ and UV-B flux

96 PALAEOATMOSPHERE

The study of past atmospheric composition has gained traction since the 1980's, via a
combination of geochemical modelling approaches e.g. the BLAG model of Berner et al.
99 (1983) and the development of palaeoproxies both to test and validate model outputs, and
further our understanding of the atmosphere e.g. (McElwain and Chaloner 1995). This
integrated, interdisciplinary approach has been at the focus of research in this area since
102 initiation. For example a joint meeting of the Paleontological Association and Linnaean
Society held at the Geological Society produced a thematic set of papers on Biota and
Palaeoatmospheres (Chaloner and Cocks 1989). Given the concurrent discovery of the
105 stratospheric 'ozone hole' above Antarctica (Farman et al. 1985) and the dawning realization
of the consequences of fossil fuel combustion, a major aim of aforementioned meeting
(Chaloner and Cocks 1989) and subsequent research has been to place anthropogenic
108 perturbations of the stratosphere and atmosphere into geological context. Hudson (1989)
considered atmospheric change over a wide range of time scales and discussed the use of
fossils as monitors and geochemical recorders of atmospheric changes. Since initial studies
111 these complementary fields have developed in concert with model refinement (e.g. Bergman
et al. 2004, Berner 2006) and palaeoproxy development (e.g. Fletcher et al 2008; Franks et al.
2014). The importance of developing an understanding on climate change over geological
114 time has been recognised by the wider scientific community with palaeoclimate work being
included in assessment report four and five of the IPCC (IPCC 2007, 2013).

117 PALAEOBOTANICAL MONITORS: CO₂

Stomata are small pores on the leaf surface which regulate gas exchange between the plant and the atmosphere. In his ground breaking paper Woodward (1987) demonstrated a significant negative relationship between that stomatal density (SD, the number of stomata per unit area) and stomatal index (SI, the number of stomata as a ratio of the number of stomata to epidermal cells expressed as a percentage) and atmospheric CO₂. Through the analysis of herbarium samples spanning 200 years this paper provided the first direct evidence for human acceleration (via the combustion of fossil fuels) of the carbon cycle, based on evidence that is was driving plant adaptation /acclimation. Since this publication, pCO₂ has continued its rapid rise and today the mean annual CO₂ concentration is close to exceeding 400ppm. The paper linked observations from herbaria with experimental work to demonstrate causation as well as correlation; Woodward (1987) indicates that the negative relationship between CO₂ and SD/ SI is a function of plants adaptation to maximise carbon gain whilst minimising water loss, providing a mechanistic basis for the relationship (Fig. 1). The genes responsible for the stomatal CO₂ responses have since been identified (Grey et al. 2000) and the systemic nature of the signal has been established (Lake et al. 2001), demonstrating a causal link between CO₂ and stomata, which in turn provides underpinning confidence in the ability to use the distribution of stomata on fossil leaf surfaces to reconstruct palaeoatmospheric CO₂ concentration.

Both SD and SI are known to vary in response to a number of abiotic stimuli (see for example Tichá 1982). Because SD is linked to leaf expansion, it is inherently more variable than SI which is a measure of stomatal initiation. As a result of this much work has tended to focus on SI. However, Lake and Woodward (2008) reason that a SI can change when either

SD or epidermal cell density (ED) remain constant and either ED or SD change, also because
141 guard cell length (GCL) is relatively stable (Lomax et al. 2009, 2014) and ED is highly
dynamic SI does not reflect stomatal initiation which is lost as leaf development continues
(Lake and Woodward 2008). Furthermore ED detail is often obscured as a function of fossil
144 preservation making it difficult to calculate SI. This issue was highlighted in the recent study
of Smith et al (2010) working on Ginkgo cuticle who observed that the anticlinal wall is often
obscured by papillae again making the calculation of SI problematic. Therefore, although
147 palaeo-CO₂ reconstructions based on SI may have theoretical advantages practical
considerations combined with our new understanding of SI (Lake and Woodward 2008) may
negate this advantage and estimates based on SD could be more robust (Smith et al 2010).

150 Changes in SD and SI have been used both in a semi-quantitative and quantitative way to
predict changes in atmospheric CO₂ (Lomax et al 2012a). Semi-quantitative reconstructions
are based on comparing fossil data with that of their nearest living relative (NLR) and/ or
153 their nearest living ecological equivalent (NLE) (McElwain and Chaloner 1995, Chaloner and
McElwain 1997, McElwain et al 1999) and CO₂ estimates are calculated based on the ratio of
stomata in NLR and/ or NLE to their fossil counterpart. Quantitative use of SD and SI to
156 estimate palaeo-CO₂ is based on the development of species specific (NLR/ NLE) training
sets which describe the mathematical relationships between SD and SI to known changes in
atmospheric CO₂. This relationship is then used to predict palaeo-CO₂ from counts SD and
159 SI made from fossil cuticle. palaeo-CO₂ fossil cuticle. These studies are increasingly linking
experimental work on plants grown in high and low CO₂ growth chambers to information
recovered from plants held in herbaria. This combined approach captures stomatal responses
162 to a wide range of atmospheric CO₂ concentrations from sub-ambient through to elevated
greenhouse conditions representative of Phanerozoic. For example calibration curves using
this approach have been constructed for *Ginkgo biloba* and *Metasequoia glyptostroboides*

165 with an upper experimental CO₂ concentration of 790ppm to constrain Paleogene CO₂
(Royer et al 2001a) and using *Stenochlaena palustris* grown at 2300ppm, Beerling et al
(2002) estimated changes in CO₂ across the Cretaceous/ Paleogene boundary. Stomatal
168 analysis of the Cretaceous Paleogene indicates super greenhouse conditions in the earliest
Paleogene, with CO₂ concentrations in excess of 2000ppm (Beerling et al., 2002). These
findings support the lower range of modelled CO₂ perturbations as a function of the
171 degassing of limestone from the Chicxulub limestone platform (O'Keefe and Ahrens 1989)
but these stomatal estimates are lower than palaeo-CO₂ estimates derived from palaeosols
(Nordt, Atchley and Dworkin 2002, Huang et al., 2013). The apparent discrepancy between
174 stomatal and paleosol reconstructions could be related to stratigraphic position above the
Cretaceous Paleogene boundary with stomata data been recovered from within the fern spike,
which has an estimated duration of a few hundred to a few thousand years (Vajda and
177 McLoughlin 2007).

The major rate limiting step in developing CO₂ estimates based on stomatal analysis is
the recognition that the response appears to be species specific, with plants showing an
180 increase, a decrease or no change in stomatal numbers in response to elevated CO₂ (Royer
2001b). Furthermore, the pattern of response seems to be independent of phylogeny with
closely related species behaving in differently (reviewed in Jordan 2011). These data
183 suggests that quantitative CO₂ reconstructions based on stomatal analysis of NLR could be
hindered by the need to work within characterised and constrained phylogenetic groups.
Consequently the power of the technique to explore variations in CO₂ over geological time
186 may become more limited (an increase in uncertainty around the predicted CO₂) when it is
applied further back in geological time when the relationship between NLRs and the fossil
target species becomes obscured. This maybe further compromised if fossil values of SD
189 and/or SI are outside of the range of training set. This results in statistical uncertainty around

predicted palaeo-CO₂ concentration resulting in large error bars around the predicted value. However, how much of the stomatal variation identified by Royer (2001) and Jordan (2011) represents actual biological variation in response to changing atmospheric CO₂ concentration has been questioned recently (Lake and Woodward 2008). Experimental data indicates that changes in humidity can suppress stomatal responses to an increase in atmospheric CO₂ concentration. Data from *Arabidopsis thaliana* shows that in response to a doubling of CO₂ SD decreased by 13% in low relative humidity (RH 45%) conditions, whereas when RH was increased to 65% SD declined by 32% (Lake and Woodward 2008). Therefore the lack of RH control in experimental settings might contribute to some variations recorded in response to changes in CO₂; it may also explain why there is variation in SD with changes in altitude (Lake and Woodward 2008). These findings suggest that if hydrology can be controlled for, SD may effectively monitor changes in atmospheric CO₂. Given the longstanding acknowledgment of wetland bias in the plant fossil record (e.g. Spicer 1981, Channing and Edwards 2013) from a palaeobotanical standpoint this may indeed be achievable.

Franks et al (2014) have developed an alternative approach to address the need for phylogenetically well constrained training sets via the development of a mechanistic model. The model was developed by linking the universal gas exchange equation (Farquhar, Caemmerer and Berry 1980) to anatomical and geochemical information that can be readily recovered from the plant fossil record (Franks et al. 2014). Applying this model (at a low resolution) over the Phanerozoic suggests that large scale, first order fluctuations in the atmospheric carbon cycle may not have occurred. Specifically their model suggests that atmospheric CO₂ has remained relatively stable and below 1000ppm (Franks et al. 2014) since the evolution and radiation of forests in the Middle Devonian (Stein et al. 2012). These data and modelled solutions for CO₂ concentrations are low when compared to other CO₂ proxy records (Ekart et al. 1999) but compare favourability to recent modelled solutions of

the long-term carbon cycle (Berner et al. 2006) and the proxy record generated from the
216 carbon isotope analysis of fossil liverworts (Fletcher et al. 20008). If correct these, data
suggest that the Earth system, specifically temperature, is much more sensitive to changes in
the carbon cycle than previously thought (Franks et al 2014). However, what is required to
219 fully evaluate this controversial finding is full testing of the model boundary conditions and
the ecophysiological responses that underpin the model over a wider range of atmospheric
CO₂ concentrations using a broader phylogenetic spectrum of plants, with the with analysis
222 being conducted at a finer temporal resolution. However these preliminary findings
demonstrate the importance of developing proxies to understanding past climatic conditions
which can be robustly tested. Furthermore, they demonstrate how palaeoclimate work can be
225 used to understand how the Earth system may respond to future, anthropogenic climate
forcing.

228 PALAEOBOTANICAL GEOCHEMICAL RECORDERS: UV-B

The sporomorph (pollen and spore) fossil record is one of the most complete records
available to palaeontologist both in terms of temporal and spatial range. This richness is a
231 function of the amount produced (for example Traverse 2008 “guestimates” that an average
hectare of woodland in eastern North America would produce at least 3000 litres of
sporomorphs) and their recalcitrant chemistry. The biopolymer sporopollenin is a major
234 component of the outer walls (exine) of terrestrial plant-derived pollen and spores (Brooks
and Shaw 1968, 1978; Hemsley et al. 1996) and it is this biopolymer which is responsible for
their high preservation potential of sporomorphs. Recent work (e.g. Lomax et al 2008, Fraser
237 et al. 2011, 2012) has focused on using Fourier transform infrared (FTIR) spectroscopy to
further the understanding of the structure of sporopollenin via the detection and quantification

of functional groups. The topic of spectroscopy and its application to fossils was the subject
240 of a recent *Frontiers in Palaeontology* review (Marshall and Marshall 2015). Sporopollenin is
constructed of two groups of chemicals, phenolic derivatives (*para*-coumaric and ferulic
acids) and straight chain aliphatic moieties in the range C8-C22. The aromatic ring common
243 to the phenolic compounds within sporopollenin absorbs and dissipates the energy associated
with ultraviolet radiation (Rozema et al. 2001; Rozema et al. 2002), while the straight chain
aliphatic moieties do not absorb UV-B radiation (Fraser et al. 2011). Recent work further
246 suggests that the chemical composition of sporopollenin is a function of the local
environment with plants responding to an increase or decrease in ambient UV-B by up or
down regulating the phenolic component of sporopollenin (Figure 2; Fraser et al. 2011).

249 Geochemical analysis demonstrates that sporopollenin was present in essentially the
same chemical form in sporomorphs dating to the Early-Middle Pennsylvanian (~310 Ma)
(Fraser et al. 2012), and that it is very similar to Silurian cryptospores with recognised
252 embryophytic affinity (Steemans et al. 2010). Furthermore sporopollenin chemistry is
structurally similar to the zygote wall of the closely related charophycean alga *Coleochaete*
(Delwiche et al. 1989). Fraser et al. (2012) indicate that these findings suggest that the
255 chemical structure of sporopollenin has remained highly conserved since the embryophytes
invaded land in the Middle Ordovician (Rubinstein et al. 2010). Biomolecular work has
identified the protein (UVR8) responsible for the perception and subsequent upstream
258 regulation of plant responses to UV-B radiation (Rizzini et al. 2011) and the mechanism
behind this response has been identified at the genetic level in *Arabidopsis thaliana* with
orthologous genes being reported in algae and mosses, strongly suggesting evolutionary
261 conservatism in UV-B perception (Christie et al. 2012). Most recently, evolutionary
development work has presented evidence that the genetic basis of sporopollenin production,

and subsequent generation of a spore wall, was recruited early on in land plants and has been
264 highly conserved since (Wallace et al. 2015).

When seeking to establish if biogeochemical information extracted from fossil spores
and pollen grains can be used in either a quantitative or semi- quantitative manner it is
267 important to consider the fate of sporomorphs as they undergo diagenesis and the transitions
from the biosphere to the geosphere. Analysis of geological material from sites recognised as
having being subjected to low grade diagenetic alteration indicated that the primary
270 biogeochemical signature can be recovered (Steemans et al. 2010; Fraser et al. 2012).
Experimental analysis using lycopodium spores further supports these findings (Fraser et al.
2014) in these experiments fresh lycopods spores were heated in a hydrous bomb over a
273 range of temperatures (0, 100, 150, 200, 250, 300, and 350 °C) to simulate varying intensities
of diagenetic alteration from immature to thermally mature. Results specifically
demonstrated that the phenolic content of sporopollenin remains unaffected at lower grades
276 of diagenesis and are stable up to an experimental temperature of 200-250°C. Similarly,
oxidative processes, whether geologically driven, or preparative in the laboratory, are proving
to have minimal impact upon sporopollenin chemistry demonstrating a relatively broad
279 window of opportunity in terms of viability of samples for successful analysis (Jardine et al.
2015).

Taken collectively these findings show that sporopollenin chemistry and the perception
282 of UV-B radiation within plants is from an evolutionary perspective highly conserved. It is
possible to recover primary biogeochemical information from the fossil record, and that
within extant plants the functional chemistry of sporopollenin is influenced by the local
285 environment; plants respond to an increase in the ambient UV-B flux by producing more
phenolic compounds (Figure 2; Lomax et al. 2008; Fraser et al. 2011). These findings
indicate that quantification of the phenolic component within sporopollenin may provide the

288 ability to track changes in ambient UV-B through geological time, effectively using the
sporomorph record as a geochemical recorder of stratospheric change.

The development of a new proxy to track UV-B flux, and from this infer changes in
291 stratospheric process over geological time, allows for the testing and development of new
investigative pathways. For example, a growing body of work has linked the end Permian
mass extinction event to a global collapse of the stratospheric ozone layer as a consequence
294 of the eruption and emplacement of the Siberian Traps Large Igneous Province (Beerling et
al. 2007; Black et al. 2014). The occurrence of abnormal lycopsid spores (Visscher et al.
2004) and gymnosperm pollen (Foster and Affoni 2005) has been interpreted as evidence for
297 UV-B driven mutagenesis, with recent experimental evidence confirming pollen mutation in
A. thaliana in response to elevated UV-B flux (Murphy and Mitchell 2013). Therefore
chemical analysis of the end Permian sporomorph record may provide an opportunity to test
300 this hypothesis and determine stratospheric and atmospheric perturbations through this likely
tumultuous period in Earth history.

Looking beyond direct stratospheric processes, in the modern world the UV-B flux is
303 positively correlated to altitude, with the magnitude of the UV-B flux being controlled by
latitude (Lomax et al. 2012b). This altitudinal relationship is governed by the physical
properties of the atmosphere, surface albedo, and pathlength of incoming solar radiation.
306 Geochemical analysis of extant sporomorphs has demonstrated a statistically significant
relationship between altitude and the phenolic component of sporopollenin (Lomax et al.
2012b). This pattern is also repeated in other plant tissues (Rozema et al. 1997) and the
309 relationship is found to hold across phylogenetically disparate groups (Sullivan et al. 1992).
These data indicate that the chemical record of pollen and spore assemblages may have the
potential to be exploited as a novel palaeoaltimetry proxy (Lomax et al. 2012b) and record
312 elevation history.

CONCLUSIONS AND FUTURE DIRECTIONS:

315 The research reviewed in this paper demonstrates that the plant fossil record has the
capacity to be used in a mechanistically understood framework to record and monitor
changes in environmental conditions over geological time. These data could therefore allow
318 for historical and current anthropogenic climate change to be placed within a broader
geological context as originally proposed by Chaloner and Cocks (1989), demonstrating the
broader impact and utility of paleontologically based research.

321 Specifically the development of a mechanistic model to estimate palaeo-CO₂
independent of the need for phylogenetically constrained training sets would enable CO₂
reconstructions of the lower Palaeozoic atmosphere, allowing for the development of
324 Phanerozoic CO₂ curves. These could then be used to test/ validate long term carbon cycle
models. This mechanistic approach may lead an increase in certainty of the predicted
atmospheric CO₂ concentration and importantly minimise the uncertainty underpinning these
327 prediction.

The chemistry of sporopollenin is regulated by UV-B exposure and that these signals can
be recovered from the fossil record. Prior to this work differences in the chemical signature
330 of sporopollenin (and fossil macromolecules in general) were generally attributed to either
evolution or diagenetic alteration, or a combination of both. The realisation that the
environment alters the primary configuration of plant macromolecules and that this
333 information can be recovered from the fossil record has the potential to transform how we
see/use these data. The future for chemical palynological investigations should look to
address global challenges that are underpinned by changes in energy input to the Earth
336 system from the Sun, such as: global hydrology on geological timescales (increased

atmospheric moisture is likely to impair transmittance of ultraviolet radiation); verification of orbital cyclicity within the sedimentary record, and from this chemical palynology could potentially act as a tuning device for correlation work. Looking outside of palaeoclimate reconstruction the nature of sporopollenin itself spanning geological/evolutionary time - the exact nature of sporopollenin remains enigmatic, but recent had made some headway; if such work continues a much deeper understanding of the role of sporopollenin in plants survival and adaptation since invading the terrestrial realm is a realistic possibility.

A key advantage of the using FTIR to interrogate sporopollenin is low cost and relative ease of analysis, this provides the opportunity to integrate such a technique within the course of "standard" palynological investigations, thus developing a greater understanding of the ancient ecosystems being studied. A key aspect that provides the greatest potential for a chemical palynology proxy for solar radiation is the long-term preservation that is possible; the pervasive nature of sporomorphs throughout the sedimentary record suggests a globally abundant information resource is waiting to be analysed. Combining biogeochemical analysis of the sporomorph record to track changes in incoming total solar irradiance with stomatal estimates of CO₂ could provide key information on long term climate forcing mechanisms.

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681 **Figure Legends**

684 **FIG. 1.** Schematic representation of changes in stomatal density and index as a function of declining atmospheric CO₂ over geological time. A, CO₂. B, Water availability is indicated

by the solid blue line, dotted blue line indicates changes in plant water use efficiency (*WUE*) as a function of changing stomatal numbers in response to atmospheric CO₂. A shift to the right relative to the solid blue line indicates a reduction in *WUE* whereas a shift to the left indicates an increase in *WUE*. C, schematic representation of a 1mm⁻² of leaf cuticle SD, stomatal density and SI stomatal index.

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FIG. 2. Schematic representation demonstrating the mechanistic process driving chemical changes within sporopollenin composition. Specific regions (ultraviolet-B) within the electromagnetic spectrum of incoming solar radiation (insolation) trigger genetically controlled chemical responses in plants. UV-B radiation stimulation leads to the up-regulation of two specific phenolic-based components of sporopollenin, which are then incorporated into the exine of pollen/spores, providing a passive protective mechanism against damage to internal structures, proteins and DNA by UV-B radiation. Once released from the plant, pollen/spores retain this phenolic-based chemical signature, which can be later recovered if these pollen/spores are conserved within the geological record. The image of the Sun is courtesy NASA/JPL-Caltech.

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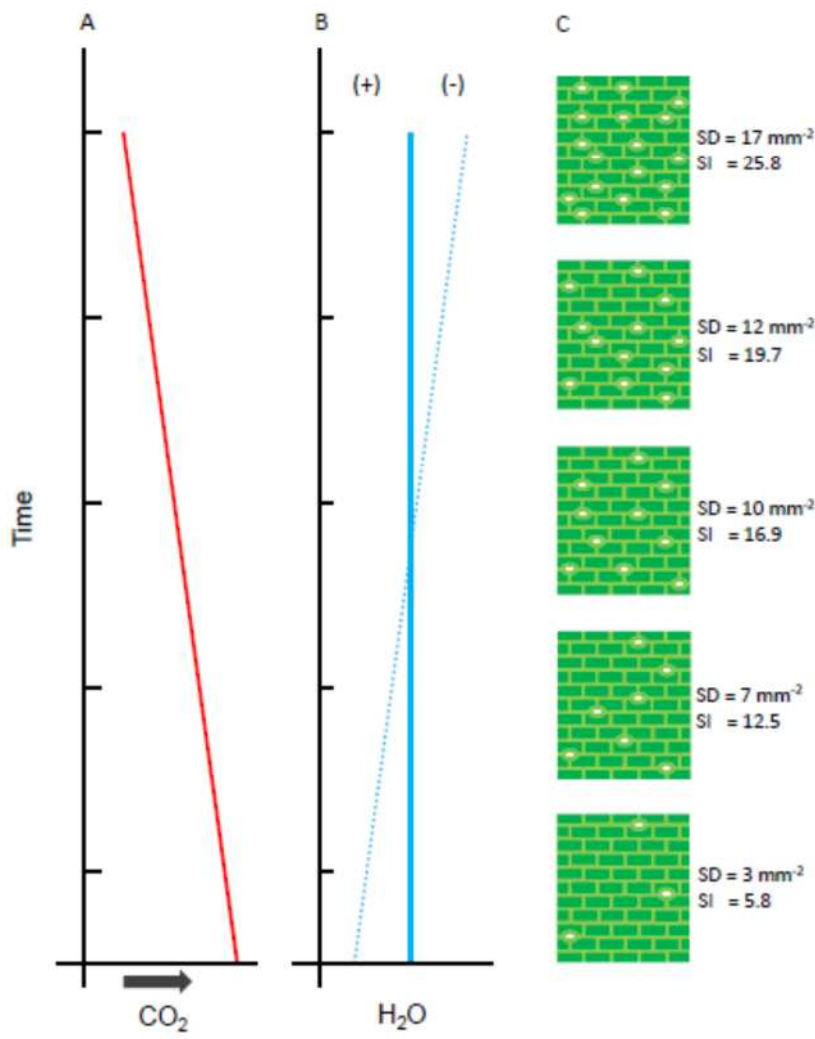


Fig.1.
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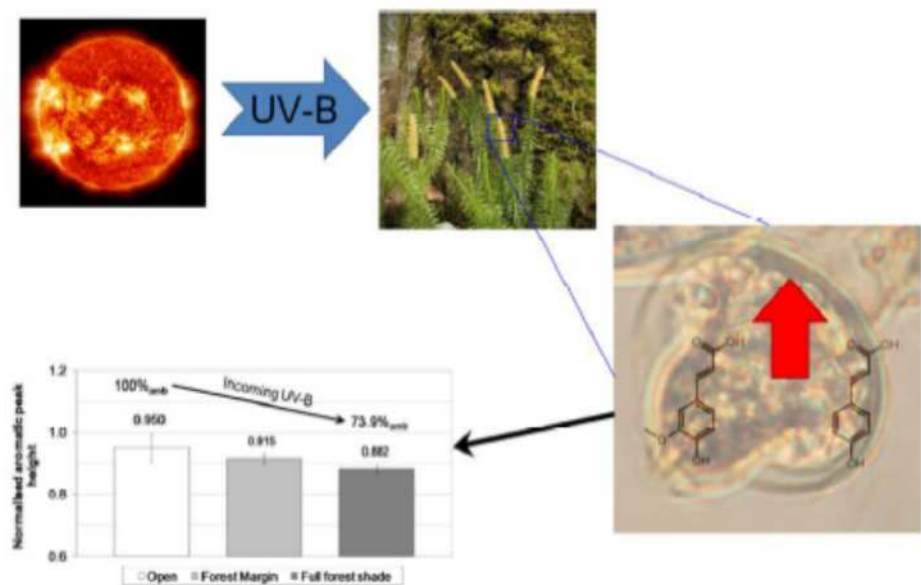


Fig. 2.
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