

On the reconstruction of plant photosynthetic and stress physiology across the Triassic–Jurassic boundary

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Abstract: The Triassic–Jurassic boundary (TJB) coincides with major disruption to the carbon cycle and global warming as the Central Atlantic Magmatic Province developed. This resulted in both marine and terrestrial extinctions, with terrestrial plants thought to experience thermal stress as global temperatures and atmospheric CO₂ levels rose. As plant compression fossils typically only preserve external morphological features, it has not been possible to reconstruct plant paleophysiology in order to elucidate the mechanisms underlying plant stress and extinction. Here we present a new approach allowing us to infer the photosynthetic performance and stress physiology of fossil plants, applied to fossil Ginkgoales across the TJB. We use correlations between the adaxial epidermal cell density of extant *Ginkgo biloba* and photosynthetic and protective stress physiology to infer the paleophysiological condition of Late Triassic–Early Jurassic-aged plants from Astartekløft, East Greenland. The density of fossil leaf adaxial epidermal cells indicates that photosynthetic performance of Ginkgoales became increasingly impaired towards the latter stages of the Triassic, before improving into the Early Jurassic. This is consistent with δ¹³C isotope values, paleo-[CO₂] levels, and global mean temperatures, suggesting that photosynthetic performance was influenced by the prevailing environmental conditions during the TJB event. Dissipation of absorbed energy as heat would also have risen towards the boundary as plant stress increased, in order to protect the photosynthetic physiology. The increase in dissipation of energy as heat, associated with a reduction in convective heat loss due to reduced transpiration rates, would have exacerbated plant thermal stress at the TJB, thus contributing to sudden biodiversity loss and ecological change.

Key words: Triassic–Jurassic boundary, ginkgo, plant stress, thermal stress, paleophysiology, nonphotochemical quenching

1. Introduction

The Triassic–Jurassic boundary (TJB) was a major global warming event in earth history, leading to plant biodiversity loss, ecosystem collapse, and high faunal extinctions. The development of the Central Atlantic Magmatic Province (CAMP) at the boundary is widely considered to be a cause of the TJB event (e.g., Hesselbo et al., 2002; Guex et al., 2004; Marzoli et al., 2004; Kürschner et al., 2007; Ruhl et al., 2009; Van de Schootbrugge et al., 2009; Schoene et al., 2010) releasing large volumes of CO₂ (McElwain et al., 1999; Beerling and Berner, 2002; Galli et al., 2005; Huynh and Poulsen, 2005; Berner and Beerling, 2007; Cleveland et al., 2008; Van de Schootbrugge et al., 2008; Bacon et al., 2011; Schaller et al., 2011; Steinhorsdottir et al., 2011) and toxic gases such as sulfur dioxide (SO₂) into the atmosphere

(Guex et al., 2004; Berner and Beerling, 2007; Hori et al., 2007; Van de Schootbrugge et al., 2009; Bacon et al., 2013). However, a firm mechanistic explanation for how CAMP-induced environmental changes triggered Late Triassic floral biodiversity losses is still lacking (Bonis et al., 2009). In this paper we have developed a novel proxy allowing us to infer the underlying photosynthetic and protective physiological functioning of fossil leaves. We have applied this proxy to Late Triassic Ginkgoales from 6 plant beds in Astartekløft, East Greenland (Figure 1), to test the role of reduced photosynthetic performance in Late Triassic biodiversity loss under supergreenhouse conditions.

Excessive leaf temperatures are a likely cause of plant stress and extinction at the TJB. Modeling of decreased convective heat loss caused by reduced stomatal

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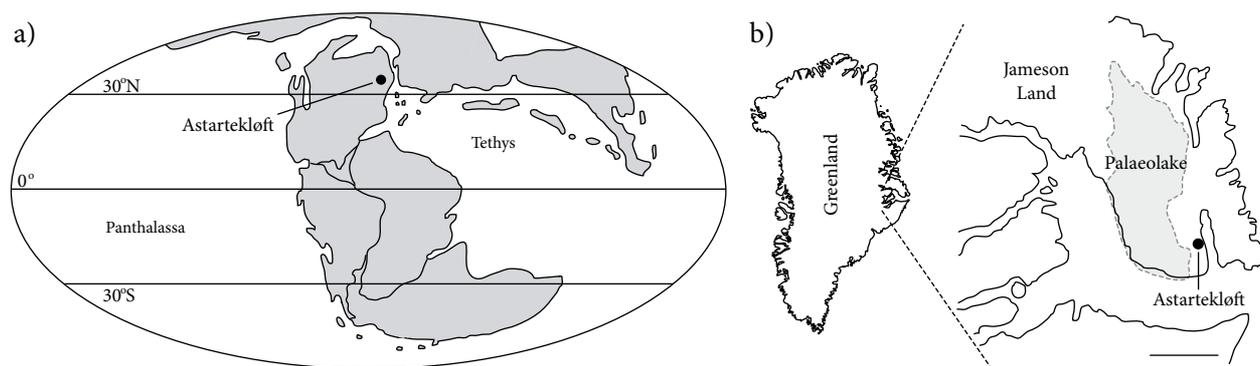


Figure 1. a) Late Triassic (Rhaetian)–Early Jurassic (Hettangian) global paleogeography showing location of Astartekløft flora (redrawn from the Scotese PaleoMap project); b) map of current location of fossil flora in East Greenland, inset shows Hurry Inlet and Jameson Land, gray shading indicates location of paleolake, scale bar indicates 50 km.

frequencies at the TJB (from approximately 50 stomata per mm^2 at the start of the Astartekløft section, reaching a low of approximately 13 per mm^2 in the Late Triassic before rising to approximately 90 stomata per mm^2 in the Early Jurassic), in conjunction with regional warming, shows that leaf temperatures would have exceeded lethal levels (McElwain et al., 1999). This is supported by fossil leaf evidence showing that leaves decrease in size and increase in dissection at the TJB, indicative of selection pressures to increase heat loss (McElwain et al., 1999; Nicotra et al., 2008). One of the most widely observed environmentally influenced features in plants is the occurrence of sun and shade leaves, whereby the amount of energy in the form of solar radiation determines specific characteristics of leaf morphology. Leaves experiencing “low” levels of photosynthetically active radiation (PAR) tend to be larger and thinner than leaves experiencing “high” levels of PAR (e.g., Kürschner, 1997; Sun et al., 2003). This relationship is evident in the micromorphology of leaves, where epidermal cell densities are lower in shade leaves and higher in sun leaves due to the effect of cell expansion (Friend and Pomeroy, 1970; Rahim and Fordham, 1991).

The level of incident radiation also affects the photosynthetic and protective physiology of plants (Kana and Vass, 2008). Once absorbed by chlorophyll, light energy can be used for photosynthesis, reemitted as chlorophyll fluorescence, or dissipated as heat (nonphotochemical quenching, NPQ). The ratio (F_v/F_m) of the variable (F_v) to fluorescence maximum (F_m) reflects the efficiency of photosystem II and is used as an indicator of plant photosynthetic performance. Values of F_v/F_m less than 0.83 indicate a plant experiencing stress (Maxwell and Johnson, 2000). The dissipation of excess energy as heat by the xanthophyll cycle (NPQ) protects the photosynthetic physiology from light-induced damage. As NPQ rises, the relative efficiency of photosystem II is reduced (Horton and Ruban, 2005; Ruban et al., 2007). As PAR increases,

both leaf temperature and the amount of energy dissipated as NPQ rise. The relationship between PAR and NPQ is not linear, with NPQ leveling off at light intensities of $>1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *Nicotiana tabacum*, reflecting the limit of effectiveness of NPQ as a tolerance mechanism to protect the photosynthetic apparatus from excess energy (Kana and Vass, 2008). Therefore, as PAR influences both leaf morphology and photosynthetic physiology in tandem, it may be theoretically possible to develop a proxy for plant stress and photosynthetic performance from fossil leaf morphological traits. In order to explore this, we investigated the effects of mean midday PAR on adaxial epidermal cell density, which is indicative of cell expansion, and plant photosynthetic and stress physiology for a range of *Ginkgo biloba* leaves from the same tree.

Secondly, in order to investigate plant photosynthesis and stress across the TJB, adaxial epidermal cell densities of ginkgoalean fossils (*Czekanowskia*, *Ginkgoites*, *Baiera*, and *Sphenobaiera*) from Late Triassic–Early Jurassic deposits at Astartekløft, East Greenland, were analyzed. The section at Astartekløft is composed of fluvial–lacustrine sediments, with the fossil plant beds occurring in crevasse splays that represent flooding events and coals deposited under swampy conditions (Figure 2) (Belcher et al., 2010). The paleoenvironmental setting of Astartekløft points to high levels of water availability during the Late Triassic to Early Jurassic (Dam and Surlyk, 1992), indicating that leaf expansion was unlikely to have been constrained by water availability. Bed 5 is considered to represent the transition from the Late Triassic to Early Jurassic, due to the last occurrence of Triassic *Lepidopteris ottonis* and the appearance of Jurassic *Thaumatopteris brauniana* (Harris, 1937; Mander et al., 2013).

An important aspect of paleobotanical research is the analysis of modern plants to understand fossil plants (Seward, 1892); in this context, when considering the

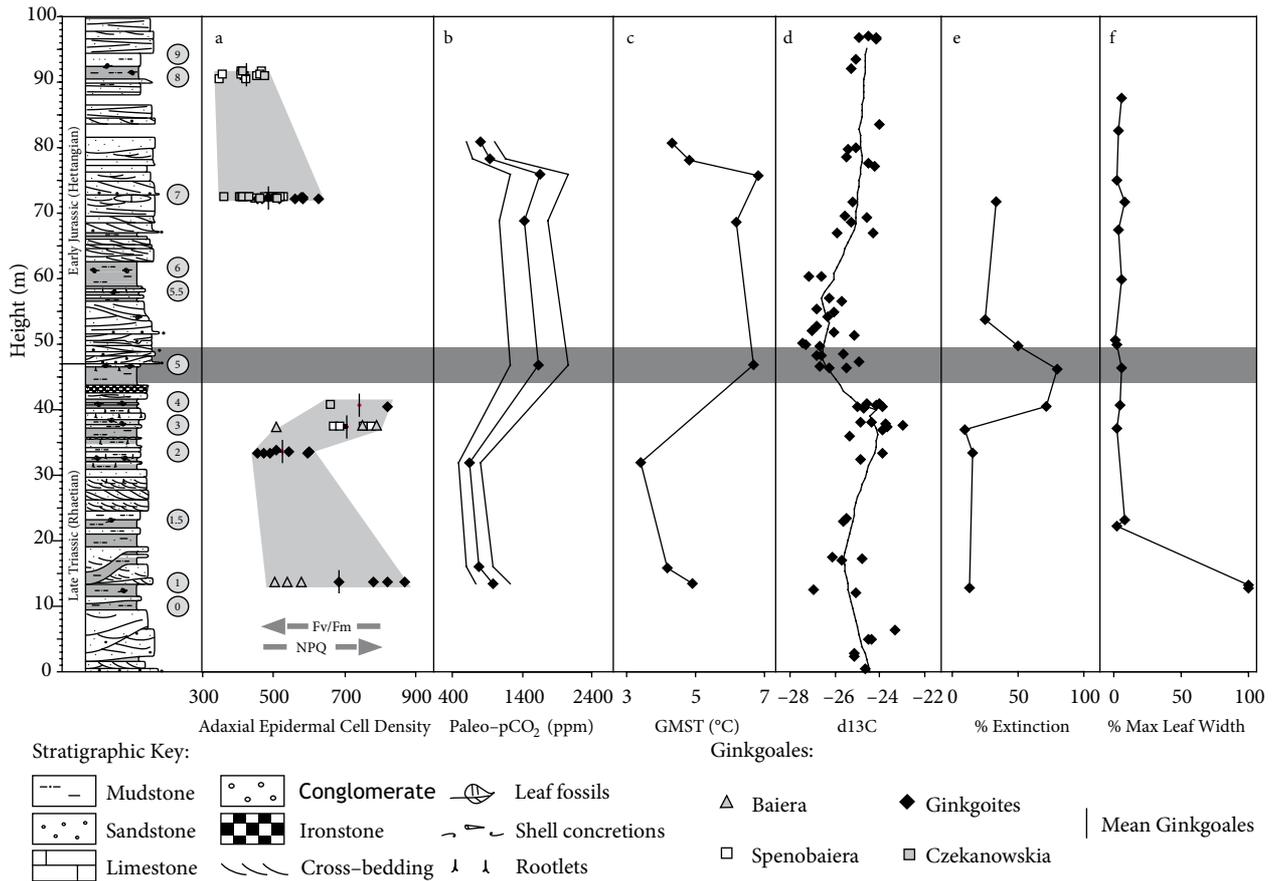


Figure 2. Stratigraphy of Late Triassic (Rhaetian)–Early Jurassic (Hettangian)-aged sediments of Astartekløft, East Greenland. Circled numbers indicate plant beds (Hesselbo et al., 2002). a) Adaxial epidermal cell densities (number of cells per mm²) of fossil Ginkgoales; b) reconstruction of paleo-[CO₂] based on stomata of fossil Ginkgoales (McElwain et al., 1999); c) difference in global mean surface temperature from present (GMST, °C) (McElwain et al., 1999); d) δ¹³C of fossil wood (Hesselbo et al., 2002), line indicates LOESS smoothed values; e) extinction as a proportion of species (McElwain et al., 2007); f) percentage maximum leaf width of fossil Ginkgoales (McElwain et al., 1999).

light environment of *G. biloba* and fossil Ginkgoales experiencing thermal stress at the TJB, we have assumed that the underlying selection pressures are the same in terms of leaf energy balance and how plants respond to these stresses. Ginkgoales in the Astartekløft flora formed the upper canopy (McElwain et al., 2007). As plants from higher in the canopy are preferentially preserved as fossils (Spicer, 1980; Kürschner, 1997), the proportion of “sun” and “shade” leaves preserved as plant fossils should be consistent throughout the section, thus giving a signal of plant performance and stress physiology related to the environment, though not an indication of the relative numbers of leaf morphotypes in the standing vegetation, nor a change in canopy structure. This study aimed to firstly examine potential correlations between leaf adaxial epidermal cell density and plant photosynthesis and the protective dissipation of excess energy as heat in modern *G. biloba*, and secondly to apply these to specimens of

fossil Ginkgoales deposited across the TJB in order to infer potential mechanisms of plant stress and extinction.

2. Materials and methods

In order to sample a gradient of leaf types, rather than subjectively classifying leaves as 2 absolutes of “sun” or “shade” (e.g., Sun et al., 2003), we randomly selected 100 *G. biloba* leaves ranging from the outermost branches to those closest to the trunk on an approximately 40-year-old tree at UCD Thornfield Agricultural Research Station, Dublin. Incident PAR and leaf temperature of fully expanded individual leaves were recorded between 1200 and 1300 hours for approximately 20 days per leaf during June–August 2008, using a Skye Instruments SpectroSense 2 and FLIR Systems ThermoCAM SC640. These values were averaged to produce a mean incident PAR level and leaf temperature for each leaf. Daily leaf temperature values were calculated using a ThermoCAM

Researcher Pro 2.9 by taking the mean temperature of a horizontal line placed across the widest part of the leaf. Chlorophyll-fluorescence measures (F_v/F_m and NPQ, where $NPQ = [F_m^o - F_m]/F_m$) were recorded between 0900 and 1000 hours using Hansatech PEA and FMS2 fluorometers (Maxwell and Johnson, 2000). *Ginkgo biloba* cuticles were macerated using standard maceration and mounted in glycerol on glass slides (Haworth et al., 2012). Cuticle images were taken under transmitted light (*G. biloba*) and epifluorescence (fossils) using a Leica DM2500 microscope attached to a Leica DFC300FX camera and Syncroscopy Auto-Montage. A 0.09-mm² grid was superimposed on the images for epidermal cell counts. As the adaxial epidermal cell densities of the fossil Ginkgoales (approximately 350–870 cells per mm²) largely lie beyond the range of values displayed by the *G. biloba* specimen studied (approximately 240–530 cells per mm²), it was not possible to quantitatively reconstruct F_v/F_m and NPQ values of fossil plants using a transfer function approach (Sokal and Rohlf, 1995). Instead, the adaxial epidermal cell densities of fossil Ginkgoales provide a qualitative indicator of plant photosynthesis and stress physiology with higher epidermal cell densities indicating higher photosynthetic stress and vice versa.

Structural engineering principles were used to reconstruct the life posture of leaves from extinct plant taxa (Pilkey, 2002). The reconstruction of Triassic *Ginkgoites minuta* was based on the nearest living equivalent species, *G. biloba*, which has a petiole of differentiated tissue with a strong structural beam shape. The dominant Early Jurassic Ginkgoales species, *Czekanowskia*, has a pseudopetiole consisting of the same tissue as the blade, with a single vein. In order to determine a modeling medium with bending properties (modulus of elasticity) similar to that of Ginkgoalean leaf tissue, weights were placed on a living *G. biloba* leaf (held in a vice) and the bending angle was measured. The same weights were then attached to a variety of papers and metal foils, cut to the size and shape of the leaf, to duplicate the angle. The appropriate modeling material (paper) was cut to the size and shape of a *Ginkgoites* and *Czekanowskia* leaf. The relationship between the cross-sectional area of an object with its bending properties is described by “the second moment of area” (Pilkey, 2002). A petiole of *G. biloba* was used to act as a petiole for *Ginkgoites*; however, as *Czekanowskia* does not have a differentiated petiole, the pseudopetiole was constructed from the same material as the leaf. This is justified because the length and width of *Czekanowskia* in comparison to the mass of the leaf blade was too large to be fully supported with a petiole constructed in a similar manner to *G. minuta*.

3. Results

In *G. biloba* the mean midday temperature of leaves is closely related to the level of incident radiation (Figure 3a). Mean

midday PAR also affects leaf micromorphology, with the density of epidermal cells on the adaxial surface (Figure 3b) increasing with PAR. The effect of increasing PAR can also be observed in the physiology of leaves, with the amount of energy dissipated as heat via NPQ increasing (Figure 3c) and the efficiency of photosystem II (expressed as F_v/F_m) decreasing (Figure 3d). These morphological and physiological characteristics also correlate, as F_v/F_m decreases with increasing adaxial epidermal cell density (Figure 3e), while NPQ increases (Figure 3f), effectively providing a qualitative proxy method of gauging F_v/F_m and NPQ in fossil plant leaves.

The adaxial epidermal cell densities of fossil Ginkgoales display relatively high values (mean of approximately 700 cells per mm²) in the earliest part of the Astartekløft section (Bed 1). Mean adaxial epidermal cell densities then decrease (mean of approximately 520 cells per mm²) before increasing towards the transition between the Late Triassic and Early Jurassic (mean of approximately 710–740 cells per mm²). Early Jurassic fossil Ginkgoales adaxial epidermal cell densities (mean of approximately 420–480 cells per mm²) are lower than those in the Late Triassic and appear to decrease later into the Early Jurassic (Figure 2a). Macrofossil Ginkgoales are not present in the Astartekløft section at depths of between 45 and 75 m (Figure 2), most likely representing local extinction and migration to suitable refugia of the Ginkgoales during this interval (Figure 1). However, dispersed *Sphenobaiera* cuticle from Bed 6 displays very high epidermal cell density values (1500–2000 per mm²) relative to the rest of the section, suggesting that epidermal cell density values of Ginkgoales continue to increase across TJB, suggestive of further physiological stress. As these Bed 6 samples are from a distinctly different taphonomic setting (swamp, as opposed to crevasse splays), this likely affected leaf development (Haworth et al., 2012) and therefore these data are not presented in Figure 2. Reconstruction of Late Triassic and Early Jurassic Ginkgoales leaf shapes using structural engineering principles suggests that Late Triassic Ginkgoales possessed more structurally rigid leaves than their Early Jurassic counterparts (Figure 4), resulting in a higher absorption of light per unit leaf area.

4. Discussion

In modern *G. biloba*, both leaf micromorphology and physiology are influenced by the amount of incident light energy (Figure 3). Photosynthetic performance (F_v/F_m) of *G. biloba* decreases with increasing mean midday PAR, while the amount of energy dissipated as heat (NPQ) increases, indicative of both photoinhibition and corresponding protection of the photosynthetic physiology from excess energy (Figures 3c and 3d) (Kana and Vass, 2008). Significant correlations are observed between

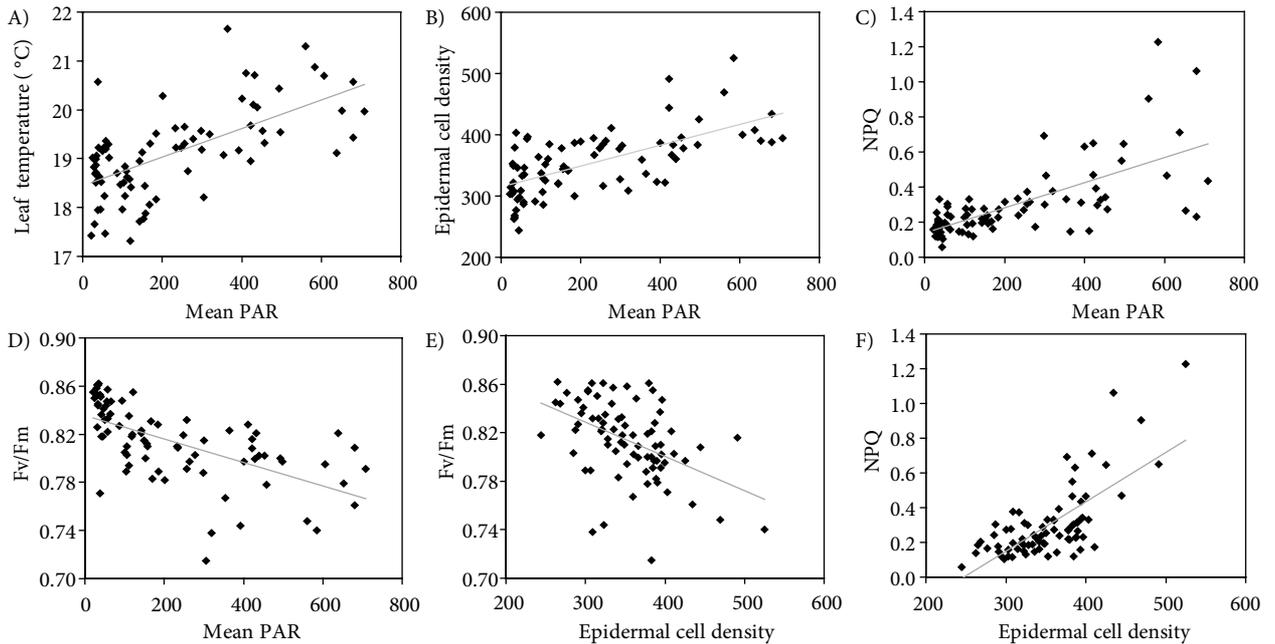


Figure 3. Effect of light intensity on the morphology and physiology of *Ginkgo biloba* leaves: a) mean midday incident PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and leaf temperature ($^{\circ}\text{C}$) ($R^2 = 0.417$; $P = 1.69 \times 10^{-10}$); b) mean midday incident PAR and adaxial epidermal cell density (number of cells per mm^2) ($R^2 = 0.404$; $P = 1.78 \times 10^{-10}$); c) mean midday incident PAR and NPQ ($R^2 = 0.468$; $P = 1.91 \times 10^{-12}$); d) mean midday incident PAR and F_v/F_m ($R^2 = 0.368$; $P = 1.89 \times 10^{-9}$); e) F_v/F_m and adaxial epidermal cell density ($R^2 = 0.212$; $P = 2.13 \times 10^{-5}$); f) NPQ and adaxial epidermal cell density ($R^2 = 0.499$; $P = 4.85 \times 10^{-13}$).

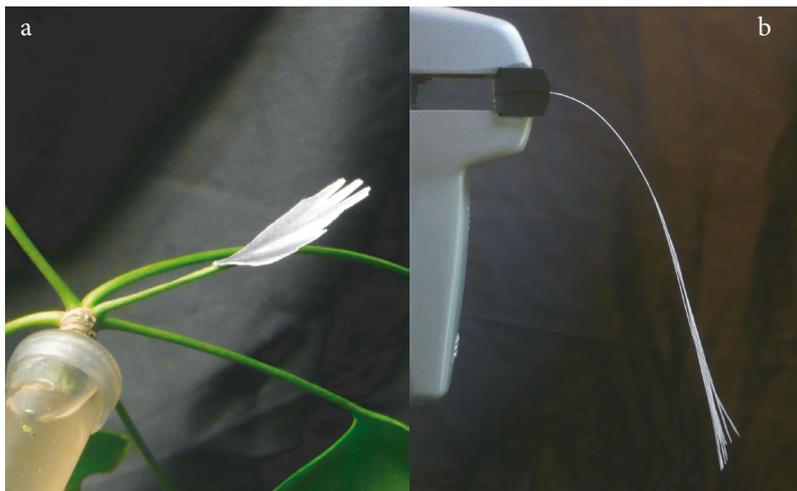


Figure 4. Leaf shape reconstructions employed using structural engineering principles: a) Late Triassic *Ginkgoites minuta* constructed using modeling paper and a petiole of *Ginkgo biloba*; b) Early Jurassic *Czekanowskia* sp. constructed using modeling paper, where the lack of structural support provided by the pseudopetiole of *Czekanowskia* results in a drooping leaf shape.

the epidermal cell density and physiological parameters of photosynthetic performance and stress physiology (Figures 3e and 3f). These correlations between physiology and morphology in extant *G. biloba* are caused by the

energy balance of the leaf (Figures 3a and 3b) (Rahim and Fordham, 1991; Kana and Vass, 2008). It should therefore be possible to apply these relationships to infer fossil plant photosynthetic performance and protective

stress physiology in a manner analogous to that employed in stomatal reconstructions of paleo-[CO₂] (McElwain et al., 1999; Kouwenberg et al., 2005; Kürschner et al., 2008) and also to inferences of carbon gain and nutrient usage based upon leaf shape economics (Poorter and Bongers, 2006). As the TJB is considered to represent an interval where plant thermal stress caused by excess leaf energy drove biodiversity loss (McElwain et al., 1999, 2007), this approach may assist in understanding the underlying physiological mechanisms that led to the plant responses evident in the fossil record.

Ginkgoales adaxial epidermal cell densities show a general trend of increased plant stress and reduced photosynthetic performance prior to the TJB, concomitant with the start of severe biodiversity loss within fossil plant assemblages from the section (Figure 1). Improved photosynthetic performance is observed in the earliest Jurassic when biodiversity levels also recovered. The responses in Ginkgoales epidermal cell density may reflect environmental fluctuations in temperature and atmospheric CO₂ levels, acclimation/adaptation of species to the changing environment, or an influx of new species more adapted to the prevailing conditions. Our qualitative record of increasing photosynthetic stress in the Late Triassic is broadly consistent with both biotic and abiotic data for the TJB (Figure 2).

Adaxial epidermal cell densities and NPQ display a highly significant correlation in *G. biloba* (Figure 3f). When applied to fossil Ginkgoales, this relationship suggests the important role of NPQ in protecting photosynthetic physiology and influencing leaf temperatures across the TJB. Fossil Ginkgoales adaxial epidermal cell density values indicate that the amount of energy dissipated via NPQ would have likely increased towards the latter stages of the Triassic, contributing to increased leaf temperature and plant thermal stress as photosynthetic performance declined. The amount of incident radiation dissipated as heat would then likely decrease into the Early Jurassic, coincident with falling atmospheric [CO₂] levels and global temperatures, indicative of an amelioration of environmental conditions and reduction in plant stress following the boundary event.

Trends in inferred plant stress and photosynthetic performance in the Late Triassic follow shifts in paleo-[CO₂] and mean global surface temperatures, displaying relatively impaired performance in Bed 1 before improving into Bed 2 as [CO₂] and global temperature falls. Plant stress increases towards the TJB in Beds 3 and 4, coincident with the initial stages of the negative $\delta^{13}\text{C}$ excursion (Hesselbo et al., 2002), suggesting that environmental conditions became less favorable to plant growth as atmospheric [CO₂] levels and global temperatures increased. In the Early Jurassic, atmospheric [CO₂] levels fall and

$\delta^{13}\text{C}$ values become less negative, possibly reflecting a reduction in degassing from the CAMP and stabilization of the carbon cycle (McElwain et al., 1999; Hesselbo et al., 2002). This amelioration of environmental conditions may have resulted in an increase in Ginkgoales photosynthetic performance relative to the Late Triassic that continued into the Jurassic.

The similarities between the stomatal reconstruction of paleo-[CO₂] and plant photosynthesis and stress physiology derived from epidermal cell density suggest that either abaxial stomatal formation and adaxial epidermal cell development are genetically and developmentally linked (Holroyd et al., 2002) and/or that reduced convective heat loss via transpiration is one of the primary hypothesized causes of plant stress across the TJB (McElwain et al., 1999). The stomatal reconstruction of paleo-[CO₂] is based on stomata of Ginkgoales and *Stenopteris* specimens collected by Thomas Harris during the 1920s from TJB sections in East Greenland compiled into a composite stratigraphy (Harris, 1937), while those specimens analyzed in this study were collected in 2002 from a single site in East Greenland (McElwain et al., 2007). In addition, the range of adaxial epidermal cell density values in extant *G. biloba* (Figure 3) was observed in leaves grown under current ambient atmospheric [CO₂] levels of approximately 390 ppm. This suggests that it is unlikely that the similarities between inferred plant photosynthesis and stress physiology and the stomatal reconstruction of paleo-[CO₂] in Figure 2 are due to any developmental link between abaxial stomata and adaxial epidermal cell formation.

The projected increase in atmospheric [CO₂] at the TJB would have resulted in warming on a global scale (McElwain et al., 1999; Steinthorsdottir et al., 2011). As part of this global warming trend, the Astartekløft region would have likely experienced a much greater increase in temperature (Huynh and Poulsen, 2005; McElwain et al., 2007), enhancing leaf thermal stress caused by reduced convective heat loss (McElwain et al., 1999). In addition to elevated atmospheric [CO₂] (McElwain et al., 1999; Berner and Beerling, 2007) and proposed emissions of methane (Palfy et al., 2001; Beerling and Berner, 2002), tropospheric SO₂ is also a powerful greenhouse gas (Grattan and Sadler, 1999). When released into the stratosphere, SO₂ causes global cooling (Zielinski et al., 1994); however, SO₂ released into the troposphere by an effusive eruption such as the CAMP may have developed into regional areas of dry fog, increasing its atmospheric residence time due to its localized heating of the lower atmosphere (Grattan and Sadler, 1999; Hantemirov et al., 2000). This may have further exacerbated leaf thermal damage in some areas. Leaf shape changes (Bacon et al., 2013) and disruption to the water-repellent properties of the leaf surface (Haworth

and McElwain, 2008; Bartiromo et al., 2012, 2013) caused by SO₂ may also have contributed to reductions in the heat dissipation capacities of leaves at the TJB.

Late Triassic *Ginkgoites* in Bed 1 display high epidermal cell densities, indicative of considerable photosynthetic and heat stress well before the peak of the δ¹³C excursion and atmospheric CO₂ levels considered to represent the nadir of the extinction event (McElwain et al., 1999; Hesselbo et al., 2002). However, this apparent contradiction of high physiological stress at a time when global temperatures and CO₂ levels were relatively low may be explained by the fact that the Ginkgoales present in Bed 1 display the highest leaf widths in the Astartekløft section. These data suggest that *Ginkgoites* may have begun to exhibit the effects of thermal stress due to larger leaf size before any significant environmental perturbation. Moving up-section from Bed 1, leaves become more dissected, indicative of selection pressures favoring enhanced heat loss (Gauslaa, 1984; McElwain et al., 1999; Nicotra et al., 2008). This is followed by a concomitant improvement in plant performance (as indicated by an increase in F_v/F_m) and reduction in heat stress (decreased NPQ) into Bed 2. These trends suggest that Ginkgoales species were initially evolving or adapting via changes in leaf shape to the deteriorating environmental conditions initiated by CAMP volcanism up until Bed 2. Between Beds 2 and 4, adaxial epidermal cell densities increase to maximum values (double the modern average) for the entire Late Triassic–Early Jurassic interval, coinciding with the last occurrence of *Ginkgoites* macrofossil leaves from this locality between Beds 5 and 6. This suggests that the *Ginkgoites* species present in Bed 1 had possibly reached the extremes of their ecophysiological tolerance, with genera such as *Baiera* not persisting into the Early Jurassic. Leaf width from Bed 1.5 throughout the remainder of the section remains fairly constant, suggesting that selection pressures favoring reduced leaf size as a mechanism of promoting efficient heat loss may have reached the limit of their effectiveness, in terms of conferred benefit and concomitant physiological cost, during the transition from Bed 1 to 2. This would suggest that reconstructed plant stress and photosynthesis in plant fossil Beds 2–7 is generally indicative of environmental fluctuations, and not a result of corresponding leaf width changes.

Ginkgoales adaxial epidermal cell densities are lower in the earliest Jurassic (Bed 7) than in the Late Triassic, while [CO₂] levels remain relatively high (Figure 2). Additionally, adaxial density values decrease at Bed 8 while atmospheric [CO₂] remains constant, suggesting possible progressive adaptation of the Ginkgoales species to the prevailing environmental conditions. This improvement in photosynthetic performance in the Early Jurassic relative to the Late Triassic may reflect selective

pressures favoring those Ginkgoales species more adapted to thermal stress. Reconstructions of the load-bearing capacity of Triassic versus Jurassic Ginkgoales leaf petioles (Figure 4) show that the most abundant Late Triassic Ginkgoales (e.g., *Ginkgoites* and *Baiera*) (McElwain et al., 2007) possessed structurally rigid leaves, where the angle of interception of light over the entire leaf surface would ensure maximum absorption of light energy per unit area for photosynthesis. However, those Ginkgoales characteristic of the Early Jurassic flora (e.g., *Czekanowskia* and *Sphenobaiera*) (McElwain et al., 2007) likely had leaves with less structural support. This results in a lower angle of interception of light energy, reducing the amount of energy absorbed per unit leaf area. The reduction in leaf structural support is consistent with selection pressures to reduce plant thermal stress as energy absorption over the leaf is decreased.

5. Conclusions

The morphology and physiology of *G. biloba* are both influenced by the energy balance of the leaf determined by incident PAR and heat loss through transpiration. In demonstrating that these correlations between leaf physiology and morphology occur in a heterogeneous seminatural habitat and can be successfully applied to plant fossils in deep time, we regard this as an important first step in the development of a new approach to reconstructing the physiology of fossil plants. This technique could equally be applied to fossil plants over periods of climate change during earth history, such as the Early Eocene Climatic Optimum (Smith et al., 2010). Developments in LED lighting technology that allow large plant growth chambers (suitable for tree species such as *G. biloba*) to achieve light intensities of approximately 2000 μmol m⁻² s⁻¹ will enable this technique to be refined in more controlled constant environments and lead to more robust and quantitative transfer functions linking plant physiology and morphology.

Our study indicates that the adaxial epidermal cell densities of Ginkgoales closely correlate with photosynthetic performance and stress physiology. This relationship suggests that plant photosynthesis became increasingly impaired towards the end of the Triassic before improving into the Jurassic. Enhancement of plant photosynthetic performance into the Early Jurassic may reflect an amelioration of environmental conditions, or the adaptation of species to the prevailing environmental conditions. As plants became increasingly stressed, the amount of incident radiation dissipated as heat would have likely risen significantly, contributing to plant thermal stress at the TJB. We propose that this thermal stress was the result of higher global temperatures, coupled with diminished convective heat loss due to reduced stomatal

densities and exacerbated by increased dissipation of absorbed energy as heat as photosynthesis became progressively impaired.

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