Leaf habit of Late Permian Glossopteris trees from high-palaeolatitude forests

ERIK L. GULBRANSON1*, PATRICIA E. RYBERG2, ANNE-LAURE DECOMBEIX3, EDITH L. TAYLOR4, THOMAS N. TAYLOR4 & JOHN L. ISBELL1
1Department of Geosciences, University of Wisconsin–Milwaukee, Milwaukee, WI 53211, USA
2Department of Physical and Natural Sciences, Park University, Parkville, MO 64152, USA
3CNRS-UMR AMAP (Botanique et Bioinformatique de l’Architecture des Plantes), Montpellier, Cedex 5, France
4Department of Ecology and Evolutionary Biology, Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence, KS 66045, USA

*Corresponding author (e-mail: gulbrans@uwm.edu)

Abstract: The leaf longevity of trees, deciduous or evergreen, plays an important role in climate feedbacks and plant ecology. In modern forests of the high latitudes, evergreen trees dominate; however, the fossil record indicates that deciduous vegetation dominated during some previous warm intervals. We show, through an integration of palaeobotanical techniques and stable isotope geochemistry of trees in one of the earliest polar forests (Late Permian, c. 260 Ma, Antarctica), that the arboreal glossopterid taxa were both deciduous and evergreen, with a greater abundance of evergreen trees occurring in the studied forests. These new findings suggest the possibility that deciduousness was a plastic trait in ancient polar plants, and that deciduous plants, migrating poleward from lower latitudes, were probably better adapted to high-disturbance areas in environments that were light-limited.

Supplementary material: Wood anatomy descriptions (supplemental file 1), stable carbon isotope data for tree rings (supplemental files 2–4), and method and parameters for modelled Δ13C (supplemental file 5) are available at www.geolsoc.org.uk/SUP18744.

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The discovery of fossil leaf mats implies that deciduous plants occupied polar landmasses in Earth history and gave rise to the hypothesis that deciduous leaf habits were favourable at high latitudes during times of global warmth (Wolfe 1980; Axelrod 1984; Spicer & Chapman 1990). This hypothesis was based on the assumption that leafless deciduous plants maintained a carbon balance edge over evergreen trees by losing less carbon through respiration during the extreme (c. 4 month) polar winter with 24h of continuous darkness. Thus, the positive carbon balance experienced by deciduous plants created a competitive edge that allowed such plants to dominate warm ancient polar ecosystems. Growth chamber experiments and numerical models, however, demonstrate that there is no carbon balance advantage for deciduous trees over evergreen trees grown under a simulated photoperiod (Osborne & Beerling 2002; Royer et al. 2003, 2005), because deciduous trees must annually regrow all leaf tissue, and the carbon source for this new growth must be derived from photosynthetic fixed during previous growing seasons (Sauter 1967; Essiamah & Eschrich 1985; Barbaroux & Breda 2002; Damesin & LeLarge 2003). Nevertheless, fossil evidence of trees such as Metasequoia, Larix, Alnus and Betula provides support that deciduous trees dominated the Northern Hemisphere polar regions during the Cenozoic (Wolfe 1980; Greenwood & Basinger 1993; Greenwood 1994; Williams et al. 2003, 2008; Ballantyne et al. 2010; Csank et al. 2011a,b) and the Cretaceous (Spicer & Parrish 1986; Spicer & Chapman 1990), and they are interpreted to have dominated the Southern Hemisphere polar regions during the Permian and Triassic (Fig. 1; Gould & Delevoryas 1977; Taylor et al. 1992; Francis et al. 1993; McLoughlin 1994; McLoughlin et al. 1997; Cúneo 1996; McLoughlin et al. 2005). Evergreen trees belonging to Araucariaceae and Podocarpaceae, on the other hand, dominated the Southern Hemisphere polar regions during the Cretaceous and Jurassic (Cantrill 1991, 1992; Pole 1999; Falcon-Lang & Cantrill 2001). These deep-time examples of polar ecosystems suggest that there may have been an adaptation of leaf longevity to high-latitude ecosystems during greenhouse intervals; however, the mechanism for determining the dominance of a particular type of leaf habit remains poorly defined.

That leaf longevity varied with latitude in the past is an important concept to understand because (1) leaf longevity affects a range of processes (e.g. photosynthetic rate, drought tolerance) that allow plants to respond to environmental stresses (Monk 1966; Mooney 1972; Reich et al. 1992), (2) leaf longevity of polar ecosystems is modelled to have a strong influence on seasonal changes in albedo and, therefore, has a strong impact on palaeoclimatic evolution (Otto-Bliesner & Upchurch 1997; Ollinger et al. 2008; Horton et al. 2010), and (3) extant forest displays latitudinal variations in leaf habit that may be dissimilar to those of the ancient forests, as evergreen trees currently dominate northern high latitudes, whereas deciduous trees dominate temperate forests (Fig. 1a; Chapin 1980; Chabot & Hicks 1982; Givnish 2002). There is parity in inferences of leaf habit from low-latitude fossil ecosystems and extant tropical ecosystems (DiMichele et al. 2010; Falcon-Lang et al. 2011; Stull et al. 2012); however, the disparity in the dominance of extant evergreen floras at modern high latitudes and interpretations of dominantly deciduous floras at high palaeolatitudes suggests that our understanding of plant migration and the ecology of plants at high latitudes is poor. Thus, to better understand plant-climate interactions in deep time it is important to understand broad-scale patterns in leaf longevity. By understanding this level of detail of plant ecology in deep time it is possible to make more meaningful connections to contemporary global change and the potential response of plants to this change.

This paper addresses the supposed dominance of deciduous vegetation in ancient forests at polar latitudes through reconstructions...
of leaf longevity from Late Permian fossil trees (Fig. 1). We infer leaf longevity from three in situ fossil forests (Fig. 2) using a multipronged approach where we (1) use traditional palaeobotanical methods to assess the wood morphology and growth characteristics by analysing the anatomy of fossil wood, determining each specimen’s morphogenus, and documenting tree ring growth patterns, and (2) use carbon stable isotope geochemistry of fossil growth rings to determine distinct patterns that we interpret as relating to the disparate carbohydrate cycling strategies of evergreen versus deciduous trees.

**Background**

**Leaf habit of Glossopteris**

Previous inferences of leaf longevity of Permian glossopterid trees were based primarily on indirect evidence from sedimentological observations that fossil Glossopteris leaves are found in dense accumulations, so-called leaf mats, which were interpreted to be the result of leaf abscission induced by seasonal light limitation (Gould & Delevoryas 1977; Retallack 1980; Cúneo et al. 1993). Direct evidence of leaf longevity can be determined by assessing whether leaf traces found in wood terminate within a single growth ring (deciduous) or transcend several annual increments of growth (evergreen) (Eames & McDaniels 1947; Falcon-Lang & Cantrill 2001). Such palaeobotanical inferences of leaf longevity, however, are limited in deep time, because of the low probability of preservation, taphonomy of the fossils and detection of such anatomy. As a consequence, our concept of the Glossopteris plant is based on indirect evidence that is interpreted to indicate that glossopterids were deciduous plants (Plumstead 1958; Retallack 1980), and this view holds for the glossopterids across Gondwana, throughout the Permian (Gould & Delevoryas 1977). We will show here that this concept is incomplete by using two independent methods to infer leaf longevity (i.e. anatomical characteristics of tree rings and carbon isotope patterns within rings) from multiple trees at three fossil forest localities, which will provide direct evidence for leaf longevity based on patterns imparted into tree rings owing to the physiological conditions of plant growth.

**Geochemical inference of leaf habit**

Stable isotope geochemistry has been applied to growth rings of modern trees for over four decades to assess the environmental controls on tree ring stable isotope composition. Such palaeobotanical inferences of leaf longevity, however, are limited in deep time, because of the low probability of preservation, taphonomy of the fossils and detection of such anatomy. As a consequence, our concept of the Glossopteris plant is based on indirect evidence that is interpreted to indicate that glossopterids were deciduous plants (Plumstead 1958; Retallack 1980), and this view holds for the glossopterids across Gondwana, throughout the Permian (Gould & Delevoryas 1977). We will show here that this concept is incomplete by using two independent methods to infer leaf longevity (i.e. anatomical characteristics of tree rings and carbon isotope patterns within rings) from multiple trees at three fossil forest localities, which will provide direct evidence for leaf longevity based on patterns imparted into tree rings owing to the physiological conditions of plant growth.
Ohashi et al. 2009; Offermann et al. 2011; Roden & Farquhar 2012), and to complement dendrochronology-based dendoecological studies (Wilson & Grinstead 1977; Schleser et al. 1999; Poussart et al. 2004; Treydte et al. 2006; Hafner et al. 2011; Au & Tardif 2012). Only in the last decade, however, have high-resolution (more than three measurements per ring) isotope analyses been completed on single growth rings in modern trees (e.g. Barbour et al. 2002; Helle & Schleser 2004; Poussart et al. 2004; Skomarkova et al. 2006; Ohashi et al. 2009; Schubert & Jahren 2011) and sub-fossil wood (Jahren & Sternberg 2003, 2008; Schubert et al. 2012). The high-resolution sampling of growth rings reveals changes in the δ 13C value of wood throughout a growing season that correspond to intra-ring patterns that are reproducible from year to year and reproducible between different species that share similar leaf longevity (Helle & Schleser 2004). Moreover, these carbon isotope patterns within growth rings are distinct between evergreen and deciduous trees (Fig. 3; Gulbranson & Ryberg 2013). Therefore, high-resolution stable carbon isotope analysis in tree rings is a new technique that can be used independent of, but in conjunction with, palaeobotanical techniques to infer the leaf habit of fossil plants.

Evergreen trees produce a nearly symmetrical pattern in δ 13C values within their growth rings (Fig. 3a), with similar δ 13C values at either end of a growth ring and a peak δ 13C value near the middle of a growth ring (Barbour et al. 2002; Schubert & Jahren 2011; fig. 1A of Gulbranson & Ryberg 2013). The symmetry is probably related to a combination of factors including the following: (1) low rates of photosynthetic CO2 assimilation early in the growing season (Francey & Farquhar 1982), resulting in relatively more negative δ 13C values in the earlywood; (2) decreasing atmospheric CO2 concentrations from bud burst to the time of peak photosynthetic rate (Keeling 1960, 1961), which can produce increasingly more positive δ 13C values, but with low magnitude near the middle of a ring; (3) increasing intercellular CO2 concentrations from the time period between peak photosynthetic capacity and dormancy (Davis & McCree 1978; Rawson & Constable 1980), which leads to successively more negative δ 13C values into the latewood. The symmetry of δ 13C patterns in a given tree ring can be complicated by the response of a plant to micrometeorological factors, which can produce slight asymmetry and multiple peaks and troughs of δ 13C pattern (Walcroft et al. 1997; Barbour et al. 2002). Therefore, the δ 13C value patterns of evergreen tree rings can be modified by variations in micrometeorological conditions that affect the balance of photosynthetic assimilation and the loss of water via stomatal conductance during the growing season (Livingston & Spittlehouse 1996; Walcroft et al. 1997; Barbour et al. 2002), which is consistent with the hypothesis developed by Francey & Farquhar (1982) to explain seasonal δ 13C variation in tree rings.
The model developed by Francey & Farquhar (1982), however, does not take into account that leaf longevity may affect the δ13C values of growth rings from deciduous trees. High-resolution sampling of tree rings of deciduous trees demonstrates a remarkably different δ13C pattern than in evergreen trees, inconsistent with the hypothesis that δ13C values of wood are controlled primarily by photosynthetic isotope discrimination (Helle & Schleser 2004). The complex trend of δ13C values in deciduous tree rings has been broken down into three phases (Fig. 3b; Helle & Schleser 2004; Oeffermann et al. 2011); (1) a δ13C peak in the earlywood corresponding to the use of stored carbohydrates prior to or concurrent with bud burst and leaf expansion; (2) a progressive lowering of δ13C values corresponding to a mixture of respiration and the use of recently fixed photosynthes and stored carbohydrate for biomass production (Lowden & Dyck 1974; Damesin & LeLargue 2003; Kuptz et al. 2011), which potentially reaches a consistent δ13C value after peak photosynthetic capacity has been reached and just prior to renewed carbohydrate storage in preparation for dormancy; (3) a slight increase in δ13C values in the latewood of a tree ring corresponding to the preparation for winter dormancy (Helle & Schleser 2004; Kagawa et al. 2006; Eglin et al. 2009). These three components produce an asymmetric, sawtooth-like, pattern in δ13C values that corresponds to storage of carbohydrates and the use of stored carbohydrates as a carbon source (latewood through a portion of earlywood), marked by an increase in δ13C values, and autotrophy, marked by a subsequent decline in δ13C values in the earlywood.

**Stratigraphic and sedimentological setting**

Fossil wood specimens studied herein were collected at Graphite Peak (accession numbers 17,771; 17,772), Wahl Glacier (17,773; 17,774; 17,775; 17,776; Knepprath 2006), and Mt. Achernar (17,169 A, B top and bottom, C; 11,617; 11,472) from the upper Buckley Formation in the central Transantarctic Mountains (Fig. 2a; Beardmore Glacier region). The Buckley Formation contains terrestrial sedimentary rocks that were deposited in a retroarc foreland basin (Dalziel & Elliot 1982; Collinson 1990; Isbell et al. 1997; Collinson et al. 2006). The Buckley Formation is informally divided into two members: a lower member consisting of quartzofeldspathic fluvial sandstones, and an upper member consisting of coal and volcanioclastic fluvial and lacustrine sandstones (Barrett et al. 1986; Isbell 1990; Collinson et al. 1994). Chronostratigraphy for the succession is based on palynomorphs, whereas chronostratigraphic results suggest potentially higher-resolution correlation of stratigraphy and the preservation of the two negative carbon isotope excursions associated with the end-Permian biotic crisis (Retallack et al. 2005, 2006). Palynological associations for the Buckley Formation include Dulhuntyispora assemblages in the lower member and Protohaploxypinus and Lunatisporites zones in the upper member (Farabee et al. 1990, 1991; Collinson et al. 2006). The microfloral zones of the upper member correlate to the Australian APP5–APT1 biozones (Price et al. 1985; Mantle et al. 2010) and indicate a Late Permian age (260–251.2 Ma) for the fossil wood analysed here.

The fossil forests are found in the upper member of the Buckley Formation in fine-grained, crudely laminated, volcanioclastic deposits. A sedimentological, stratigraphic, and palaeoecological analysis for the localities was presented by Gulbranson et al. (2012), but the salient results are summarized here to provide a palaeoenvironmental context for the studied wood specimens. The three fossil forest localities are found in channel proximal floodplain facies (Graphite Peak and Wahl Glacier), and distal floodplain or marginal lacustrine facies (Mt. Achernar) (Taylor et al. 1992). Despite the absence of higher-precision chronostratigraphic resolution, Gulbranson et al. (2012) interpreted these three localities as approximately time equivalent based on the stratigraphic position of the fossil forests relative to the stratigraphically younger contact between the Upper Permian Buckley and Triassic Fremouw formations. The fossil forests display variation in tree density, tree height, and wood basal area that may correspond to variations in palaeoenvironments (Fig. 2b–d; Gulbranson et al. 2012), as well as differences in forest age (Taylor et al. 1992). High-density juvenile forests (Mt. Achernar) occur on distal floodplains or lake margins, whereas low–density mature forests occur at Wahl Glacier and Graphite Peak, which contain large-diameter trunks (30–60 cm) that correspond to tree heights of 20–30 m (Knepprath 2006; Gulbranson et al. 2012).

We compare the documented plant macrofossils from the three fossil forests with the well-preserved macrofossils from permineralized peat collected at Skaar Ridge (84.77°S, 163.28°E), which is located on the Beardmore Glacier c. 42 km east and north of Graphite Peak. Plants identified in the Skaar Ridge peat that could probably be representatives of understorey vegetation include a fern (Galtier & Taylor 1994), moss (Smoot & Taylor 1986), and a lycopsid (Ryberg et al. 2012). One of the few anatomical attachments of Glossopertis leaves to wood, G. skaerensis, has been recovered from the Skaar Ridge peat (Pigg & Taylor 1993). Given the proximity of Skaar Ridge to the studied fossil forests, the abundance of macroflora and the specific plants preserved at Skaar Ridge have significant implications for our palaeoecological reconstruction. To date, understorey vegetation is known from Mt. Achernar, where a herbaceous lycopsid is preserved in siltstone of the upper Buckley Formation (Schwendemann et al. 2010), but understorey vegetation has not been recovered at Graphite Peak or Wahl Glacier. It is unclear if the difference in plant communities recovered from Skaar Ridge, Mt. Achernar, Wahl Glacier, and Graphite Peak reflects a taphonomic bias (e.g. DiMichele & Falcon-Lang 2011) in the stratigraphic record or a variation in palaeoecology such as the occurrence of ferns in permineralized peat at the Skaar Ridge locality (Galtier & Taylor 1994) and absence of ferns and permineralized peat at the nearby Mt. Achernar locality.

**Methods**

Thin sections were prepared from transverse, radial, and tangential sections of fossil wood for wood taxonomic identification. Observation and photography were conducted using Sony XCD-U100CR digital cameras attached to an Olympus SZX12 stereomicroscope and an Olympus BX51 compound microscope. Images were captured using Archimded software (Microvision Instruments) and Figure 4 was composed using Adobe Photoshop CS5 version 12.0 (Adobe Systems Inc.). Transformations made to the images in Photoshop include cropping, rotation, and adjustment of contrast. Figure 4g is a composite of several photographs in different focus planes created with the Multifocus option of Archimed. Measurements for taxonomic identification were made using ImageJ (Rasband 2013).

Leaf longevity was reconstructed using two independent methods, measurement of tracheid cells within growth rings known as the cumulative sum of deviations from the mean (CSDM) (Creber & Chaloner 1984) and stable carbon isotope patterns in tree rings. For the CSDM approach, we used the method developed by Falcon-Lang (2000) to determine leaf longevity in the fossil wood specimens. Transverse thin sections were prepared from the matching face of the specimen that was used for wood taxonomy. Five adjacent rows of tracheid radial diameters were measured in a single ring to determine the average change in cell formation.

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across a single season’s growth. Leaf longevity was determined by graphing the CSDM curve.

Prior to stable carbon isotope analysis ring width measurements were made with calipers (±0.001 mm), or via optical microscopy for poorly preserved rings, to document growth characteristics of wood specimens. To assess the acceptability of the data, duplicate measurements of ring widths were made and differences between the original and duplicate measurements were squared and summed, where acceptable data have a summed square difference value <0.2 (Fritts 1976). We measured all preserved rings in the specimens and the data are used to calculate two metrics used to assess growth characteristics, annual sensitivity and mean sensitivity. Annual sensitivity (AS) values, \( AS = \frac{Rw_1 - Rw_2}{Rw_1 + Rw_2} \), where \( Rw_1 \) and \( Rw_2 \) denote ring widths for two successive tree rings, range from zero to two, and are an indicator of the relative change in ring widths, where AS values <0.3 indicate fluctuating growing conditions and low AS values indicate complacent growth. Mean sensitivity (MS), \( MS = \frac{1}{n-1} \sum_{i=1}^{n} AS_i \), is a measure of whether a plant is stressed (MS >0.3) or maintained all of the essential conditions for growth (MS <0.3) (Fritts 1976). For leaf longevity analysis we hypothesize, based on the principle of limiting factors, that microsampling increments of fluctuating growth may be more informative owing to the potential to isolate a dominant climate control on plant growth, whereas growth intervals with little variation in ring width reflect equitable growth and could be less sensitive to climate owing to the competing effects of physiological and/or genetic factors.

Stable isotope ratios of carbon (\(^{13}\)C/\(^{12}\)C) in fossil wood specimens were measured in the Stable Isotope Facility at the University of California–Davis. Samples of permineralized wood were ground away from a pre-cut billet (small portion of rock trimmed with a rock saw) by hand with a rotary tool equipped with a diamond bit at the University of Wisconsin–Milwaukee. The sampled length (in the growth direction) was measured with calipers, and the homogenized powders were transferred to tin capsules for analysis via elemental analyser–continuous flow isotope ratio mass spectrometry (EA-CFiRMS). Sample sizes ranged from 23 to 56 mg and a billet with a cross-sectional area of 6 cm\(^2\) was appropriate for sampling at <0.1 mm resolution. Billets were cut such that ring boundaries were approximately parallel, straight, and had minimal distortion, to avoid mixing of different components of a growth ring during grinding. The outermost growth rings were preferentially sampled to avoid physiological differences that can occur during tree maturation (Francey & Farquhar 1982; Falcon-Lang 2005). X-ray diffraction analysis and petrography did not indicate
the presence of carbonate minerals, thus contamination from inorganic carbon sources is unlikely in these specimens. Results of isotope analysis are reported in the conventional delta notation (parts per thousand) relative to the Vienna Pee Dee Belemnite (VPDB) international reference.

Samples analysed at the UC Davis Stable Isotope Facility were run with secondary reference materials (nylon, $\delta^{13}C = -27.81‰$; bovine liver, $\delta^{13}C = 21.69‰$; peach leaves, $\delta^{13}C = -26.12‰$), each calibrated against primary reference materials, to correct and normalize the data. These secondary reference materials have standard deviations better than 0.1‰ (analysis period July 2011–June 2013); however, the nylon reference material had a standard deviation of 0.2‰ for April 2012. A quality assurance standard was included in the batches to assess the performance of the instrument in the long term. This standard (USGS-41 Glutamic Acid, $\delta^{13}C = +37.62‰$) had a standard deviation better than 0.3‰ over the course of the experiment and a mean $\delta^{13}C$ value of $+37.62‰$.

Specimens and slides are curated in the Paleobotanical Collections (KUPB) of the Natural History Museum and Biodiversity Institute, University of Kansas.

### Results

#### Wood affinities

All specimens lack preserved primary vascular structures; therefore they are classified only to wood morphogenera. They show distinct growth rings (Fig. 4a–c). When compared with woods previously reported from Antarctica, the new specimens can be distinguished from *Megaporoxylon*, *Protophyllocladoxylon*, and *Dadoxylon* (Maheshwari 1972). Both *Megaporoxylon* and *Protophyllocladoxylon* can be recognized by the presence of a single, large pit in most cross-fields, and none of the specimens show this characteristic (Fig. 4d and e). *Dadoxylon* is easily recognized by the presence of biseriate rays and none of the specimens show this characteristic either (Fig. 4f and g). The observed characters indicate that the specimens from the three localities all have affinities with *Australoxylon*, a genus close to *Araucarioxylon* (Philippie 2011). *Australoxylon* was created by Marguerier (1973) for wood specimens from the Permian of Gondwana and has the following characteristics: distinct growth rings, square to rectangular tracheids in transverse section, three types of radial pitting (araucarian, abietinean, and conspicuous arrangements of independent and spaced radial files of circular pits), and groups of 2–3–4–5 pits distant from each other. Pits are small (<15 µm). *Australoxylon* is recognized as a well-circumscribed group of wood closely related to *Araucarioxylon* and is associated with *Glossopteris* flora across Gondwana (Merlotti & Kurzawe 2006; Philippie 2011). The main character distinguishing *Australoxylon* from typical *Araucarioxylon* is the presence of mixed-type pitting on the tracheid radials, whereas *Araucarioxylon* has only araucarian radial pitting (contiguous when uniseriate, crowded and alternate when multisericate). *Vertebraria* axes in the Permian of Brazil, Skaar Ridge in Antarctica, and Prince Charles Mountains in Antarctica have an *Australoxylon* wood type (Mussa 1978; Neish et al. 1993; Decombeix et al. 2009). *Glossopteris skarrensis*, one of three known taxa that has anatomical attachment of *Glossopteris* leaves to wood (Pigg & Taylor 1993), has wood with uni- to biseriate pits that are crowded to widely spaced and can be compared with *Australoxylon*. All of the specimens in this study show a mixed type of pitting, with both araucarioid and abietinean pitting; in addition, pits arranged in radial groups are present in at least four specimens (Fig. 4h–j). On this basis, all of the wood specimens studied herein can be classified as *Australoxylon* with a probable affinity to the glossopterids.

#### Anatomical ring analysis

Mean sensitivity for Mt. Achernar specimens ranges from 0.39 to 0.78 and average ring widths are between 1.1 and 1.4 mm (Table 1). Annual sensitivity (AS) is highly variable within each specimen, but in general, intervals of 2–4 rings have AS lower than 0.3, the cutoff for tree rings that are considered ‘complacent’; that is, they provide little record of climate variation (Fig. 5). These intervals are punctuated by 3–6 ring intervals where AS is >0.3. Tree ring intervals with high AS were preferentially selected for microsampling for carbon isotope analysis (Fig. 5), with the exception of specimen 11,617B, which has better preservation of tree rings on the outer portion of the specimen that facilitate microsampling. The sampled interval of 11,617B, however, has AS values below 0.3. Mean sensitivity for Wahl Glacier specimens ranges from 0.25 to 0.42 and average ring widths are between 0.93 and 1.5 mm (Table 1). In contrast to Mt. Achernar, the Wahl Glacier specimens display longer continuous intervals where AS is <0.3 (intervals of c. 14 rings), and shorter intervals, 2–5 rings, where AS is >0.3 (Fig. 5). The two specimens from Graphite Peak have a mean sensitivity of 0.43 for specimen 17,771 and 0.31 for 17,772. Specimen 17,771 has an average ring width of 1.9 mm, and 17,772 has an average ring width of 2.3 mm. Both specimens display highly varied AS values with intervals of 2–3 rings with AS >0.3, and intervals of 3–5 rings with AS >0.3 (Fig. 5).

Leaf longevity reconstructions based on the CSDM method depend upon the position of the earlywood-latewood boundary (EW–LW) relative to the median point of a ring. If the EW–LW point on the graph is to the left (<10%) of the median point, then the tree can be classified as deciduous. If the EW–LW point is to the right (>10%) of the median point, then the tree can be classified as evergreen. If the percentage skew is between −10% and +10% of the median point, then the leaf habit is inconclusive, but may

<table>
<thead>
<tr>
<th>Specimen number</th>
<th>Total rings</th>
<th>Maximum width (mm)</th>
<th>Minimum width (mm)</th>
<th>Mean width and SD (mm)</th>
<th>Mean sensitivity (MS)</th>
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<tr>
<td>17,169</td>
<td>26</td>
<td>2.1</td>
<td>0.36</td>
<td>1.1±0.4</td>
<td>0.46</td>
</tr>
<tr>
<td>11,472A</td>
<td>20</td>
<td>3.4</td>
<td>0.33</td>
<td>1.1±0.8</td>
<td>0.78</td>
</tr>
<tr>
<td>11,617D</td>
<td>39</td>
<td>2.8</td>
<td>0.61</td>
<td>1.4±0.6</td>
<td>0.40</td>
</tr>
<tr>
<td>11,617B</td>
<td>39</td>
<td>3.3</td>
<td>0.49</td>
<td>1.4±0.7</td>
<td>0.39</td>
</tr>
<tr>
<td>17,773</td>
<td>36</td>
<td>2.3</td>
<td>0.66</td>
<td>1.4±0.4</td>
<td>0.35</td>
</tr>
<tr>
<td>17,774</td>
<td>32</td>
<td>2.9</td>
<td>0.65</td>
<td>1.4±0.5</td>
<td>0.42</td>
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<tr>
<td>17,775</td>
<td>24</td>
<td>2.2</td>
<td>0.53</td>
<td>1.5±0.4</td>
<td>0.25</td>
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<tr>
<td>17,776</td>
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<td>2.0</td>
<td>0.24</td>
<td>0.93±0.4</td>
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<td>1.9±0.9</td>
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<td>3.3</td>
<td>1.4</td>
<td>2.3±0.6</td>
<td>0.31</td>
</tr>
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indicate relatively short-lived leaves. Measurement of tracheid cell diameter was possible for seven specimens; poor preservation of tracheid cells owing to compression and distortion did not permit such measurements in all specimens. Two samples from Mt. Achernar (17,169; 11,617) were measured (Fig. 6). Tangential tracheid diameters for sample 17,169 range from 11 to 31 µm (n = 19) and radial tracheid diameters range from 11 to 50 µm (n = 22). The per cent skew of 17,169 is 24.5%. In sample 11,617 the radial tracheid diameters range from 7 to 39 µm. The per cent skew of 11,617 is 15.1%. We interpret these CSDM results as indicating an evergreen habit for all of the studied specimens.

Four specimens were analysed from Wahl Glacier. Specimen 17,776 has tracheid diameters in tangential section that range from 7 to 31 µm (n = 18) and tracheid diameters in radial section that range from 6 to 25 µm (n = 15). Per cent skew of 17,776 is 31.2%. Specimen 17,773 has tracheid diameters in tangential section that range from 12 to 40 µm (n = 25) and tracheid diameters in radial section that range from 12 to 42 µm (n = 23). Per cent skew for 17,773 is 23% (Fig. 6). Specimen 17,774 has tracheid diameters in tangential section that range from 8 to 44 µm (n = 23) and tracheid diameters in radial section that range from 12 to 38 µm (n = 23). Per cent skew for 17,774 is 33.7%. Specimen 17,775 has tracheid
Stable isotope geochemistry

Palaeoecology and leaf longevity in this study are partly based on stable carbon isotope ratios measured from 339 microsamples of 39 growth rings from eight wood specimens. Microsamples were taken from intervals of tree rings that display AS values higher than 0.3 (Fig. 5), fluctuating AS values or, in the case of specimen 11,617B, low AS values owing to the practical necessity of sampling rings with well-defined ring boundaries. Average δ13C values for the wood specimens range from −25.5‰ to −22.1‰ (Table 2), 5–10 microsamples were collected per tree ring, and 3–8 growth rings were sampled per specimen. Differences in δ13C values among the study localities are marked, and δ13C value patterns expressed within tree rings vary between some specimens. Our geochemical inferences of leaf habit are based on recognition of δ13C value patterns within tree rings (Fig. 3). The criteria for the recognition of these patterns are listed in Table 2.

Mt. Achernar. Sample 17,169 has an average δ13C value of −22.2‰ (±0.1‰) and a mean δ13C value difference of 0.3‰ (±0.1‰, n = 4), measured from the most negative and most positive δ13C value within a tree ring averaged over n rings (Fig. 7). Sample 11,472A has an average δ13C value of −22.1‰ (±0.3‰) and a mean δ13C value difference of 0.7‰ (±0.3‰, n = 3). Sample 11,617B has an average δ13C value of −23.2‰ (±0.3‰) and a mean δ13C value difference of 0.6‰ (±0.1‰, n = 4). The studied specimens from Mt. Achernar display a predominantly symmetrical δ13C value pattern with peak values near the middle of most tree rings (Table 2; Fig. 7). This symmetrical pattern with well-defined δ13C peak occurs for nine out of 12 tree rings studied from the Mt Achernar specimens. In contrast, one ring in specimen 17,169 displays a relatively uniform δ13C value with a single prominent negative excursion. The third ring in 11,472A displays a progressive increase in δ13C value throughout the ring in the direction of growth and a sharp decrease in δ13C value at the ring boundary (Fig. 7b). The fourth ring in 11,617B displays no clear pattern.

Interpretation. The prominent peak in δ13C patterns near the middle of the rings in specimens 17,169 and 11,472A and roughly equivalent δ13C values at the ring boundaries lead us to interpret these specimens as representing trees with an evergreen leaf habit (Fig. 7). Specimen 11,617B displays highly varied δ13C values within each of the studied growth rings, leading to a difficult interpretation of leaf habit from this specimen (Fig. 7). This δ13C variation may be related to the fact that the studied specimens have AS values <0.3 for the sampled tree-ring interval, and therefore may represent a complacent growth interval (Fig. 5), resulting in low sensitivity to the limiting factors for growth (Fritts 1976; Phipps 1982; Orwig & Abrams 1997; Abrams et al. 1998; Carrer & Urbiniati 2006). In contrast, growth rings from specimens 17,169 and 11,472A were sampled from intervals where growth was probably stressed, as interpreted by annual sensitivity values >0.3 and large variations in annual sensitivity (Fig. 5). For rings with annual sensitivity >0.3 it is likely that the limiting factors for growth exceeded the capacity for wood growth, resulting in greater sensitivity to a given limiting factor (Fritts 1976), and in such cases leaf habit and environmental effects on the δ13C values of wood may be better expressed.

Wahl Glacier. Sample 17,773 has an average δ13C value of −22.7‰ (±0.2‰) and a mean δ13C value difference of 0.6‰ (±0.3‰, n = 5). Sample 17,774 has an average δ13C value of −22.9‰ (±0.2‰) and a mean δ13C value difference of 0.5‰ (±0.2‰, n = 4). Sample 17,775 has an average δ13C value of −23.2‰ (±0.3‰) and a mean δ13C value difference of 0.6‰ (±0.4‰, n = 5). Specimen 17,776 is not represented by stable carbon isotope data owing to weight per cent carbon values <1%, which do not permit accurate and precise isotope ratio measurements. Two of three specimens from Wahl Glacier (17,773; 17,774) display a predominantly symmetrical intra-ring δ13C pattern (Table 2; Fig. 8). In contrast, ring 1 from 17,773 displays a sharp decrease in δ13C value at the beginning of the ring, a sharp increase in δ13C value that remains uniform for 30% of the ring thickness and a sharp decrease in δ13C value near the earlywood–latewood boundary (Fig. 8a). Rings 3 and 4 from specimen 17,774 display a secondary peak that is 30–40% of the magnitude of the prominent peak (Fig. 8b). The δ13C value pattern for growth rings
in specimen 17,775 displays three distinct components (Table 2): (1) a sharp increase in δ13C value across a ring boundary; (2) a maximum δ13C value in the earlywood; (3) a gradual decline in δ13C values into the latewood.

**Interpretation.** We interpret specimens 17,773 and 17,774 as having an evergreen habit, because of the nearly symmetrical variations in δ13C within the tree rings (Fig. 8). Specimen 17,775 displays a three-component δ13C pattern in each of the four studied rings, which we interpret as being consistent with a deciduous habit (Table 2).

**Graphite Peak.** Specimen 17,771 has an average δ13C value of −25.5‰ (±0.6‰) and a mean δ13C value difference of 1.7‰ (±1.2‰, n = 6). Sample 17,772 has an average δ13C value of −24.5‰ (±0.7‰) and a mean δ13C value difference of 2.0‰ (±0.9‰, n = 5). Intra-ring patterns for Graphite Peak specimens are summarized in Table 2. Ring 3 of 17,771 displays a pronounced decrease in δ13C values at the beginning of the ring followed by a sharp increase in δ13C value; the δ13C value pattern continues for the remainder of this ring in a similar fashion to the other rings (Fig. 9a). Patterns in δ13C values for growth rings in specimen 17,772 display three components: (1) an increase in δ13C value across ring boundaries; (2) a peak δ13C value in the earlywood; (3) a decline in δ13C value into the latewood (Fig. 9b).

**Interpretation.** Specimen 17,771 displays a nearly symmetrical δ13C pattern within the growth rings that we interpret as reflecting an evergreen leaf habit. Ring 3 in 17,771 may have been affected by enhanced precipitation early in the growing season (Fig. 9a), because similar isotope excursions are observed in extant evergreen gymnosperms in conjunction with high rainfall events (Livingston & Spittlehouse 1996; Walcroft et al. 1997). In contrast, we interpret a deciduous leaf habit for specimen 17,772 because of the well-expressed asymmetric δ13C pattern in each of the three rings, and the increase in δ13C values across each of the four ring boundaries.

### Discussion

We use a multipronged approach to determine the leaf habit of glossopterids and to assess the ecological significance of leaf longevity in polar environments during the Late Permian. We infered leaf longevity from (1) skewedness of the EW–LW boundary on the CSDM of cell widths within tree rings (Fig. 6; Falcon-Lang 2000; Falcon-Lang & Cantrill 2001) and (2) the stable carbon isotope signature within multiple tree rings from a given specimen (Figs 7–9; Table 2). Growth characteristics of the wood are inferred from ring width measurements (Fig. 5; Table 1) and compared with the results of the stable isotope data to assess whether the principle of limiting factors can affect geochemical interpretations of leaf longevity. To understand the ecological significance of these results we examine the distribution of the leaf habit in the context of the forest structure on a Late Permian palaeolandscape, and in the broader context of Late Permian *Glossopteris* floras in Antarctica.

### Interpretation of leaf habit

The results of CSDM analysis and δ13C pattern recognition agree for six of the seven fossil wood specimens that had both methods applied (Table 2), with an evergreen habit interpreted for all of the Mt. Achernar specimens, two of the Wahl Glacier specimens, and one Graphite Peak specimen. Stable isotope data suggest a deciduous habit for two specimens, one at Wahl Glacier and another at Graphite Peak. Rings with relatively uniform δ13C trends, highly varied δ13C values, and progressive increases in δ13C values are uninformative for leaf habit determinations, and these patterns occur in seven out of the 35 rings studied (Figs 7–9).

CSDM results and δ13C patterns suggest an evergreen habit for two specimens from Wahl Glacier, 17,774 and 17,775 (Figs 6b and 8). In contrast, δ13C patterns for 17,776 suggest a deciduous habit, whereas CSDM analysis for 17,776 resulted in a positive per cent skew, which indicates an evergreen habit. The discrepancy between the isotopic inference of leaf longevity and the CSDM approach could be based on the following reasons: (1) inaccuracy of the CSDM method based on overestimation of latewood and thus erroneous conclusions on leaf longevity; (2) microsampling of distorted or deformed growth increment; or (3) diagenetic alteration of the sample material. The CSDM proxy relies heavily on assuming a consistent growth pattern within studied tree rings,

### Table 2. Criteria for inferring leaf habit from tree ring δ13C values

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Peak shape</th>
<th>δ13C increase through ring boundary?</th>
<th>δ13C peak following ring boundary?</th>
<th>δ13C decrease, or plateau into latewood?</th>
<th>δ13C Peak near middle of ring?</th>
<th>Similar δ13C value at ring boundaries?</th>
<th>Interpretation</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>17,169</td>
<td>Symmetrical</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Evergreen</td>
<td>Ring 4 displays sharp 0.3‰ decrease in earlywood</td>
<td></td>
</tr>
<tr>
<td>11,472A</td>
<td>Symmetrical</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Evergreen</td>
<td>Ring 3 displays progressive δ13C increase, but 0.3‰ decrease into latewood</td>
<td></td>
</tr>
<tr>
<td>11,617B</td>
<td>Symmetrical</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Evergreen</td>
<td>Highly variable δ13C values within each ring, but peak δ13C values occur near middle of rings</td>
<td></td>
</tr>
<tr>
<td>17,774</td>
<td>Symmetrical</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Evergreen</td>
<td>Progressive δ13C increase from ring 1 to ring 5</td>
<td></td>
</tr>
<tr>
<td>17,775</td>
<td>Symmetrical</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Evergreen</td>
<td>Rings 3 and 4 display secondary δ13C increase c. 30–40% of the initial δ13C increase</td>
<td></td>
</tr>
<tr>
<td>17,776</td>
<td>Asymmetrical</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Deciduous</td>
<td></td>
</tr>
<tr>
<td>17,777</td>
<td>Asymmetrical</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Evergreen</td>
<td>Prominent negative δ13C excursion in earlywood of ring 3 δ13C plateau into latewood of ring 2</td>
<td></td>
</tr>
<tr>
<td>17,771</td>
<td>Asymmetrical</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Deciduous</td>
<td></td>
</tr>
</tbody>
</table>
thus only those rings that do not exhibit features such as ‘false rings’ can be used. Wood growth, however, is non-linear and intra-annual variations in environmental conditions and auxin synthesis (e.g. drought, day length) can affect terminal elongation, which will affect the diameters and wall thicknesses of tracheid cells (Larson 1960). The day length effect is especially pronounced in the experiments of Larson (1960), and this would be expected to be a dominant signal in the studied specimens as rapid changes in day length occur in the weeks-long transition from summer to winter at polar latitudes (Llorens et al. 2009). As an example, tracheid cell diameter gradually decreases throughout growth rings in similar Late Permian wood specimens from Skaar Ridge as a result of decreasing cell lumen diameter, as opposed to increasing cell wall thickness (Taylor & Ryberg 2007). Thus, the nuances of the growth characteristics of these fossil wood specimens are masked by the CSDM approach, which considers only cell diameter, which would estimate more latewood (by a factor of about four) than is evident from petrographic analysis and the formulae of Denne (1989). Because CSDM was initially created to determine earlywood–late-wood boundaries (Creber & Chaloner 1984), the potential for inaccuracy of this method in establishing fundamental plant physiological traits would be expected to carry over in the use of CSDM to provide leaf longevity determinations. Accurate results of CSDM analysis applied to extant wood (Falcon-Lang & Cantrill 2001), however, suggest that there is probably a signal of leaf longevity expressed by this proxy, but the application of this proxy to fossil specimens should be aided by the use of independent determinations of leaf longevity until more refinements are made to the

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Fig. 7. Stable carbon isotope results for Mt. Achernar wood specimens: (a) specimen 17,169; (b) specimen 11,617B; (c) specimen 11,472A (MA-3). Data points reflect single microsamples collected along the direction of growth; ring boundaries are indicated by vertical dotted lines.

Fig. 8. Stable carbon isotope results for Wahl Glacier wood specimens: (a) specimen 17,774; (b) specimen 17,775; (c) specimen 17,776. Data points reflect single microsamples collected along the direction of growth; ring boundaries are indicated by vertical dotted lines.
CSDM approach that provide accurate determinations of early-wood–latewood boundaries. The microsamples used for stable isotope analysis reflect an average over c. 100–500 µm sample thicknesses, which correspond to c. 10–50 tracheid cells, thus wood distortion might be less well expressed in the isotopic data. Therefore, with wood distortion it is likely that each microsample contains a wood component from the previous microsampled interval in addition to a second component from the following microsampled interval. This interpretation is consistent with the intra-ring δ13C pattern, which shows little scatter in δ13C values and a well-defined trend that is consistent with δ13C trends observed in extant wood. Diagenetic alteration of the sample is not suspected for this discrepancy because of (1) the lack of carbon-bearing secondary minerals that are known to be produced through decarboxylation of wood in a burial environment (e.g. calcite, goethite), (2) the repeating δ13C pattern that displays little scatter, and (3) δ13C values that fall within the range of C3 vegetation.

Taylor & Ryberg (2007) applied the CSDM proxy to Late Permian glossopterid fossil wood specimens from Antarctica and found a predominance of positive per cent skew values for the studied samples, indicating that the majority of the specimens studied were evergreen. This conclusion, however, was rejected on the basis that the sedimentological evidence for deciduousness provided by leaf mats (Plumstead 1958; Retallack 1980) was stronger than the inferences from the CSDM proxy. The new carbon isotope technique for interpreting leaf habit of fossil plants presented here suggests that the general result of the CSDM analysis presented by Taylor & Ryberg (2007), that evergreen trees dominated Late Permian polar forests in Antarctica, was probably accurate to some degree. Moreover, the specimens studied by Taylor & Ryberg (2007) were collected from the Skaar Ridge locality, which has a similar lacustrine or distal floodplain facies association to the fossil forest site at Mt. Achernar (Fig. 2). Therefore, the application of two independent leaf habit proxies to fossil wood associated with the Glossopteris flora indicates that this flora was composed of both deciduous and evergreen varieties, as opposed to the long-held assumption of a deciduous habit for this flora. Additionally, both evergreen and deciduous trees occupied the same forests on some landscapes in the palaeo-polar environment.

The potential for both leaf habit end-members to have existed within glossopterids is valid for two reasons: (1) congeneric deciduous and evergreen habits occur in extant floras (e.g. Quercus); (2) the Glossopteris plant is notoriously complex, covering a wide geographical and latitudinal range (Rigby 1972; Meyen 1987; Cúneo

Fig. 9. Stable carbon isotope results for Graphite Peak wood specimens: (a) specimen 17,771; (b) specimen 17,772. Data points reflect single microsamples collected along the direction of growth; ring boundaries are indicated by vertical dotted lines.

Fig. 10. Mean δ13C values for wood samples versus reconstruction of the fossil forests. (a) Means and standard deviations for δ13C values for wood specimens from Graphite Peak, Wahl Glacier, and Mt. Achernar versus the log10 of tree density estimated for each fossil forest; n, number of data points used. Despite the overlap, Mt. Achernar and Wahl Glacier mean δ13C values are significantly different based on an F-statistic of 29.836 (F < 0.0001) with a DF of 218. (b) Basal area of wood (solid line) and tree height (dotted line) versus log10 tree density for each fossil forest.
We observe that δ13C values of the whole wood at each of the study localities display important differences: (1) the mean δ13C values of fossil wood are significantly different for each fossil forest site (Fig. 10; one-way ANOVA, P < 0.0001); (2) differences in the magnitudes of intra-ring δ13C variation are significant between the distal floodplain and channel-proximal facies (Mt. Achernar, Graphite Peak, P < 0.00066). In contrast, differences in the magnitude of intra-ring change in δ13C are not significant between Mt. Achernar and Wahl Glacier specimens, P < 0.672. Moreover, there is a trend towards increasingly positive δ13C values in the fossil wood from Graphite Peak to Wahl Glacier and from Wahl Glacier to Mt. Achernar (Fig. 10a). These isotopic differences possibly reflect different ecological habitats of glossopterids on this Late Permian palaeolandscape or they may reflect different ages of the studied forests (Taylor et al. 1992). Carbon isotope variations on modern landscapes exhibit trends towards increasingly smaller Δ13C values (the difference between δ13C values of atmospheric CO2 and plant tissue) as plant water-use efficiency (WUE) increases (Ehleringer & Cooper 1988), where plants with high WUE tend to occur in drier sites (Ehleringer 1993a; Stewart et al. 1995). Low Δ13C values occur in evergreen plants relative to low WUE deciduous plants (Kloeppe1 et al. 1998), or in sites where competition is high (Ehleringer 1993b). For the following discussion we model Δ13C for these Late Permian fossil forests using the method of Lloyd & Farquhar (1994). Where the δ13C value of atmospheric CO2 is estimated from equilibrium calculations against marine carbonate from the surface ocean, temperature is inferred from palaeoclimate models of intra-ring δ13C variation are significant between the distal floodplain and channel-proximal facies (Mt. Achernar, Graphite Peak, P < 0.00066). If the fossil...
be related to intraspecific competition on a stable landscape, whereas mortality and exploitation of forest gaps produced through disturbance allowed mixed stands to develop at Graphite Peak and Wahl Glacier. The adaptation of leaf longevity as a function of climate change during the Late Permian, however, is not known and may provide crucial insights into the dynamics of plant–climate interactions.

Conclusions

We applied two independent proxies to infer leaf longevity from multiple fossil wood specimens collected from three Late Permian fossil forests in Antarctica. Our results show that all of the fossil wood specimens belong to the same morphogenus of wood, Glossopteris, which has an affinity to the Glossopteris flora. The leaf longevity proxies converge on similar results for 83% of the specimens and suggest mixed evergreen and deciduous Glossopteris trees in the forests of the palaeo polar latitudes during the Late Permian. This conclusion is in contrast to the long-held assumption that the Glossopteris plant was strictly deciduous, an assumption primarily based on the occurrence of leaf mats containing Glossopteris leaf fossils. The congeneric occurrence of deciduous and evergreen trees in forests of the palaeo polar latitudes further demonstrates that deciduous trees may not have had a general competitive advantage at polar latitudes, rather we infer the dominance of particular leaf habits in Late Permian polar forests to be a function of plant responses to environmental stress and disturbance. Competition might give rise to evergreen-dominated forests in relatively stable Late Permian environments and mixed stands may occur in areas of high disturbance, where mortality may have provided more avenues for the migration of deciduous trees.

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References


