

# Wood growth indices as climate indicators from the Upper Cretaceous (Cenomanian–Turonian) portion of the Winton Formation, Australia

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## ABSTRACT

Although the mid- to Late Cretaceous is regarded as a global warm period, increasingly a more complex picture of warming and cooling is emerging. New techniques allow more precise dating of terrestrial localities, opening opportunities for using climate proxy approaches on terrestrial fauna and flora to better capture the complexity of Cretaceous climate. Here an attempt is made to understand the seasonality and inter-annual variability of two newly dated localities from the upper preserved portion (Cenomanian–Turonian) of the Winton Formation, Australia. Primarily quantitative approaches to palaeodendrology are used. The results suggest both seasonality and high variability in climate conditions that affect growth between years, including evidence for floods. The longest series (QM F44338) suggests oscillatory patterns of good and poor growth in a 15 year alternating cycle similar to the contemporary Pacific Decadal Oscillation, although other potential explanations should be considered and tested.

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## 1. Introduction

The mid-Cretaceous is often regarded as the warmest period in Earth's history, reaching the Cretaceous Thermal Maximum in the Turonian (89.8–93.9 million years ago; [Wilson et al., 2002](#)), although increasingly evidence suggests a much more complex picture with cool events throughout the mid to Late Cretaceous ([Veizer et al., 2000](#); [Weissert and Erba, 2004](#); [Haworth et al., 2005](#)). The climatic changes at this time are also associated with the Cenomanian–Turonian Boundary Event or Bonarelli Event (91.5 ± 8.6 million years ago; [Selby et al., 2009](#)), which caused significant marine extinctions ([Cetean et al., 2008](#)). Although some quantitative studies of the palaeoclimate from terrestrial localities of this period have been conducted ([Parrish et al., 1998](#); [Tarduno et al., 1998](#); [Falcon-Lang and Cantrill, 2001](#); [Haworth et al., 2005](#); [Miller et al., 2006](#)), and other qualitative observations of mid to Late Cretaceous greenhouse conditions have been made ([Cantrill, 1995](#)), terrestrial localities that fall in this Cretaceous 'quiet zone' are often poorly dated as magnetostratigraphy cannot be used ([Tucker et al., 2013](#)), and thus unsuitable for uncovering the finer temporal scale needed to understand the climate of the mid to Late Cretaceous.

The Winton Formation is a terrestrial deposit, which has recently been the subject of improved dating techniques using U–Pb isotope dating of detrital zircons by laser ablation ([Tucker et al., 2013](#)). This

study has been able to constrain the ages of the fossiliferous sediments of the upper-most exposed portions of the Winton Formation to close to the Cenomanian–Turonian boundary. Foliar physiognomic methods and bioclimatic analysis on both museum collections and new collections from within the Lark Quarry Conservation Area (approximately –23° 01'S, 142° 40'E, 95 km south-west of Winton, central-western Queensland, Australia), suggest mean annual temperatures (MAT) of ~15 °C from climate leaf-analysis multivariate programme (CLAMP), and ~16 °C from bioclimatic analysis and leaf margin analysis, whilst annual rainfall was likely between 1300 and 1600 mm as estimated from CLAMP, bioclimatic analysis and leaf area analysis ([Fletcher et al., 2013, 2014b](#)).

The described fauna of the Winton Formation are consistent with the climate estimates derived from the flora. The basal eusuchian crocodyliform, *Isisfordia duncani* ([Salisbury et al., 2006](#)), suggests a MAT over 16 °C if eusuchians are accepted as palaeothermometers (as proposed by [Markwick, 1994, 1998](#)). In addition, even cold-adapted modern freshwater turtles require warmest mean monthly temperatures over 17.5 °C ([Tarduno et al., 1998](#)), thus the presence of fresh water turtles in the Winton Formation ([Molnar, 1991](#); [Salisbury et al., 2006](#)) supports the flora-derived climate estimates above, in that they confirm that the palaeoenvironment of the upper portion of the Winton Formation was warm. Finally, the presence of traces from probable oribatid mites ([Fletcher and Salisbury, 2014](#)) may suggest a moist environment ([Kellogg and Taylor, 2004](#)) consistent with the rainfall estimates above, although only moist microhabitats are required and the absence of more 'dry-loving' species so far recorded is not evidence of their absence in the fauna. However, the geology of the upper portion of

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the Winton Formation has been interpreted as a freshwater, broad fluvial–lacustrine environment (Exon and Senior, 1976; Tucker et al., 2013) and thus a xeric environment is highly unlikely, even if precipitation was not considered to be local. Although these proxies are able to estimate the averages and minima of the temperature and likely precipitation, they do not indicate how much variability there was in climate between years.

Fossilized wood is commonly preserved from the Devonian onwards, and under the right preservational conditions, allows for detailed examination on the cellular scale (Creber and Chaloner, 1984). In addition, growth rings provide information on intra-annual seasonality and inter-annual variability, and lend themselves to quantitative analysis and comparison to modern flora (Creber and Chaloner, 1984; Francis, 1984; Chaloner and Creber, 1988; Falcon-Lang, 2000a,b).

Silicified wood is rarely found in situ across the Eromanga Basin, but does occur on the surface where the Winton Formation is exposed or partly overlain unconformably by Cenozoic alluvia. Because the wood is indurated compared with the surrounding sediment, even where that sediment has been lithified (pers. obs), and because the Winton Formation is the youngest Cretaceous strata of the Eromanga Basin (Gray et al., 2002), much of this wood is considered to be derived from portions of the Winton Formation that have previously eroded.

The wood sampled for this study is largely comprised of this surface material and has been identified as *Protophyllocladoxylon owensii* Fletcher et al., with likely affinities to modern Podocarpaceae (Fletcher et al., 2014a). In addition to the reasoning above, the material for this study is considered to be autochthonous or para-autochthonous, because the sediments they are associated with are fine clays, dolostones and siltstones (Dettmann et al., 2009) suggesting a low energy depositional environment which is unlikely to have uprooted and transported root and stump material. The low diversity of wood species matches the low diversity of pollen species at site QM L311, whereas other plant macrofossil sites in the upper portion of the Winton Formation are more diverse (e.g. McLoughlin et al., 1995, 2010) and the pollen type and wood type found at QM L311 are both considered associated with the Podocarpaceae (Dettmann et al., 2009; Fletcher et al., 2014a). The pollen and three dimensionally-preserved macrofossils at this site are very complete, thus it is suggested that they were not transported any great distance. Finally, because the wood is silicified similarly to the preservation of the other macrofossil materials found at QM L311, it is likely that the material was at least buried at approximately the same time as the other plant material, which Dettmann et al. (2009) suggest was replaced with silica early in preservation, during or soon after burial.

To determine the intra-annual seasonality, and inter-annual variability of the climate of the Winton Formation, this paper focuses on quantitative methods analysing aspects of the growth rings of *P. owensii*.

### 1.1. Geological setting

The Winton Formation is the sediment infilling of the Eromanga Basin and contains rich fossil assemblages in the upper, Cenomanian–Turonian portion. At the time the upper portion of the Winton Formation was deposited, central-western Queensland would have been at approximately 50°S (Li and Powell, 2001). The formation consists of complex and repetitive sediments, including fine- to medium-grained feldspatholithic or lithofeldspathic arenites, siltstones, mudstones and claystones (Fielding, 1992; Romilio and Salisbury, 2011; Romilio et al., 2013; Tucker et al., 2013), with very minor coal seams (Senior et al., 1978), which has been interpreted as a freshwater, broad fluvial–lacustrine environment deposited on an extensive coastal plain as the epicontinental Eromanga Sea withdrew (Exon and Senior, 1976; Tucker et al., 2013).

The Winton Formation crops out over an area from north-western New South Wales, to north-eastern South Australia and throughout central-western Queensland (Fig. 1; Gray et al., 2002). Outcrops of this

formation are scattered due to deep weathering and overlaying alluvium. Trenches excavated at the fossiliferous sites from this study, namely Queensland Museum (QM) Locality QM L311 and University of Queensland localities within Bladensburg National Park, suggest that the facies below the surface are a good match (Tucker et al., 2013).

## 2. Materials and methods

### 2.1. Preparation

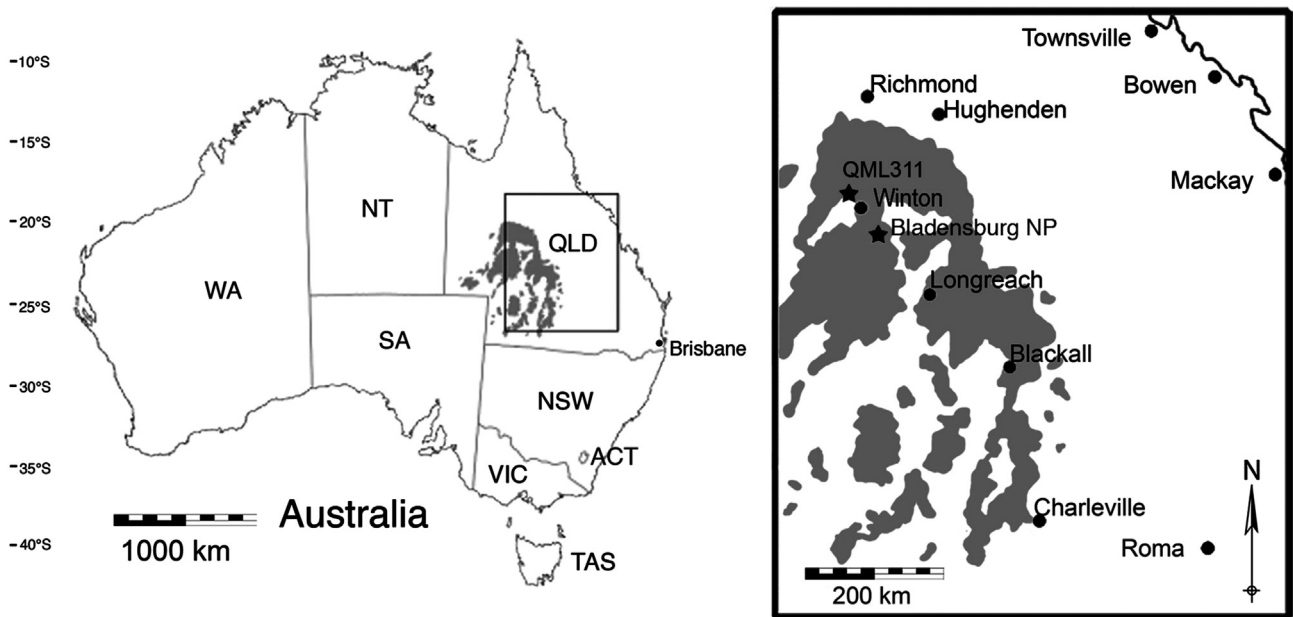
Preparation of the specimens was by conventional rock thin section, ground to varying thicknesses to account for the unique preservational characteristics of each specimen, averaging ~70 µm. The sections were oriented in transverse, radial longitudinal and tangential longitudinal planes. These sections were examined under a Nikon eclipse 50ipol and captured using a Nikon DS-Fi1. Overlapping images of the transverse sections were then stitched together manually using Adobe Photoshop, and measured using ImageJ (Rasband, 1997–2008, version 1.48i). The material described here is accessioned to the Queensland Museum collections (QM), Queensland, Australia.

### 2.2. Analysis

It is usually considered that only wood from some parts of the tree (trunk and stump but not branch and root) is useful for palaeoclimatic analysis due to the properties of the wood in different parts of the tree (Chapman, 1994; Falcon-Lang, 2005; Schweingruber, 2007), and as it is the stem or trunk that is generally sampled and studied in dendrology (Fritts, 1976; Vincent et al., 2007; Fowler, 2008; Heinrich et al., 2009; Mundo et al., 2012), identification of the likely origin of the wood from within the tree was completed using the characteristics described in Chapman (1994), however, in part because identification of the origin of the wood from Chapman's (1994) characteristics is not certain, we conducted the analysis on all materials and took the likely position of the wood into consideration when interpreting the results, rather than discarding the other materials.

None of the samples were able to meet the ideal prerequisites suggested by Poole and van Bergen (2006) for pre-Quaternary material, such as having a complete cross-section of the organ or having a taxonomically diverse assemblage. However we were able to identify the taxon of all materials used and can thus estimate leaf longevity/retention times from the nearest living relatives, as per Falcon-Lang (1999). We also consider that none of the trunk or stump material is likely to be from juvenile trees primarily due to the shape of the rings in the portions preserved, which lack the curvature that would indicate its position near the core of the tree, but also because there is not a particularly high proportion of early wood and because of the narrow average widths (Creber and Chaloner, 1984).

The quantitative methods and observations of characters used here have all been used previously in palaeodendrology. The presence or absence of rings was recorded as a broad indicator of seasonality (Creber, 1977; Brison et al., 2001). The number of rings indicates the sample size of usable rings for our study, and the relative magnitude or number of tracheids per ring may indicate generally favourable or unfavourable conditions. Average ring width is also regarded as a general indicator of favorability (Fritts, 1976), but is dependent on position in the tree and age (Chapman, 1994), as well as tree architecture (Briffa et al., 1996), and thus must be interpreted with these characteristics in mind. We recorded the absence (scored as 0), presence (1), or high frequency (2) of crush zones in early wood. These sections showed no evidence of fungal hyphae or other evidence of attack, but the few cells within these sections preserved such that they could be measured were unusually large. As such we have interpreted the crush zones as sections of very large, thin-walled early wood cells indicative of very fast growth, without which may skew interpretation towards rings from poorer growth years (Fig. 2). Frost rings, which are usually found



**Fig. 1.** A map of Australia. Area marked in grey indicates the extent of the outcropping Winton Formation in Queensland. Stars mark the fossil localities QML311 and Bladensburg National Park, from which these samples were taken. State abbreviations: NT – Northern Territory, QLD – Queensland, NSW – New South Wales, ACT – Australian Capital Territory, VIC – Victoria, TAS – Tasmania, SA – South Australia, WA – Western Australia.

in branches or juvenile wood (Creber and Chaloner, 1984; Francis, 1984), and false rings, which were distinguished by the more gradual return to large size tracheids, and checked against cell wall thickness due to the absence of full cross sections of the organs (Creber and Chaloner, 1984; Francis, 1984), were recorded using the same scoring as crush zones.

We recorded the percentage of the ring that was comprised of late-wood because a high percentage late-wood may suggest that good growing conditions occur late into the growth season (Creber, 1977; Creber and Chaloner, 1984; Koizumi et al., 2003; Savva et al., 2003); although note that this is relative for particular taxa as percentage late wood is highly conserved within groups (Falcon-Lang, 2000a). The percentage latewood was used in conjunction with percentage diminution, which measures the percentage reduction in cell diameter across a ring (Falcon-Lang, 2000a), to calculate the ring markedness index (RMI). The RMI quantitatively measures the distinctness of the ring boundary, where a high RMI suggests high seasonality (Creber and Chaloner, 1984; Francis, 1986; Ash and Creber, 1992; Yao et al., 1994; Keller and Hendrix, 1997; Francis and Poole, 2002). However, we note that RMI is also strongly correlated with leaf retention time (Falcon-Lang, 2000a) and must be interpreted accordingly. The percentage skew was calculated from the cumulative algebraic sum of the difference between each tracheid's width and the mean for that ring, plotted as a zero trending curve (CDSM curve), where a positive, right shifted curve suggests an evergreen leaf habit, and conversely a negative, left shifted curve suggests a deciduous habit (Falcon-Lang, 2000b). Finally, we calculated the mean sensitivity, which is a measure of the variability in growth ring width between years, where a score  $>0.3$  has been taken to suggest irregularity in climatic conditions that limit growth (Fritts, 1976; Creber, 1977; Creber and Francis, 1999).

### 3. Results

Four trunk pieces with measurable rings, and one trunk piece with severe early-wood crush zones in every ring rendering it unusable, were identified, as well as four pieces of stump and two of root (Table 1). From these 170 rings, 13 ring sequences were measured. The statistical tree ring analyses are summarised in Table 2. High variability is characteristic of nearly all of the measures taken, with the exception of percentage diminution.

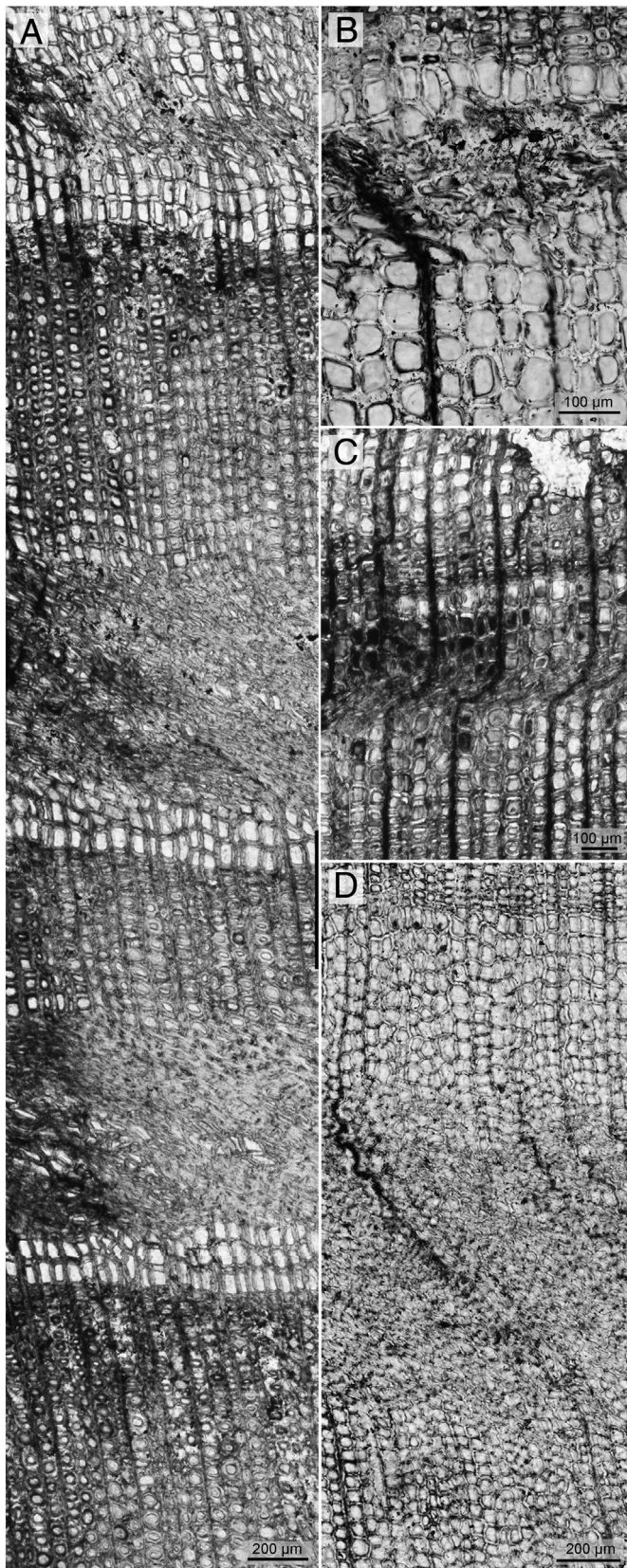
The mean ring width varied in different parts of the tree with the trunk having the smallest mean of 1.294 mm, and stump and root over 2 mm, but both with great variation around these means. All mean sensitivity values, for each part of the tree were over 0.3, and had high standard deviations indicative of the change in ring width between adjacent years sometimes being great (from small rings to large or vice versa) and sometimes being very small (a series of years with small rings or a series of years with large rings adjacent to each other). Crush zones were almost always present and common in more than half of the samples, with QM F44336 unable to be quantitatively studied due to the frequency and level of crushing. Frost damage was absent in all specimens studied and false rings were present. Percentage latewood was between ~10% and 30%. Percentage diminution was low and showed little variability. Ring markedness index averaged around 15.5 in the stump and trunk sections, and higher, approximately 20, in the roots. The very large standard deviations around percentage skew render it uninformative.

### 4. Discussion

Ring width was variable between parts of the tree and within each tree. The variability in ring width is reflected in the mean sensitivity values, with the trunk and stump values  $>0.3$  considered indicative of sensitive trees in a variable environment. Mean sensitivity values higher than that of the trunk or stump are expected for root wood, and thus the very high mean sensitivity recorded in the root wood (0.67) is not exceptional. The high standard deviation on mean sensitivity may reflect multi-year cycles of favourable and unfavourable conditions for growth similar to conditions caused by the Pacific Decadal Oscillation (PDO), or the El Niño Southern Oscillation (ENSO) phenomena.

Favourable and unfavourable conditions for growth may also be caused by the cyclical population dynamics in forest insects, such as *Zeiraphera diniana* Guenée in which outbreaks occur every 7–10 years causing defoliation (Schweingruber, 2007). Outbreaks of herbivorous insects tend to result in an abrupt reduction in growth in the event year, followed by a period of recovery in which radial growth is still reduced (Vejpustková and Holuša, 2006). The role of climate in influencing or exacerbating the effect of these outbreaks on radial growth is still not clear (Esper et al., 2007). However, insect attacks





**Fig. 2.** Examples of crush zones in rings showing their position in the ring (early wood), thin tracheid walls, large size and lack of disordered growth of tracheids in the following section. A – QM F44336, showing repeated annual crushing; B – QMF44330; C – QM F44339; D – QM F44334.

affect wood structure in more ways than just narrowed growth rings. For example, in the well studied arthropod–plant interaction of the larch, *Larix decidua* Mill., and larch budmoths, *Z. diniana*, ring width is dramatically reduced during the event year, but additionally cell wall thickness is greatly reduced and latewood forms fewer cells, resulting in very low latewood density (Vejpustková and Holuša, 2006; Esper et al., 2007; Schweingruber, 2007), a pattern also observed in the Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, and little spruce budworm, *Choristoneura occidentalis* Walsingham (Schweingruber, 2007). This reduction in cell wall thickness and latewood density is not observed in our specimens. Arthropods that attack the bark or wood of the tree leave even more conspicuous evidence in addition to narrow rings, such as bore holes and crescent shaped resin patches (Rolland and Lempérière, 2004), pithflecks, galls or calluses (Schweingruber, 2007). Although the tunnels and fossilised faeces of oribatid mites have been identified in two of these fossil wood specimens (Fletcher and Salisbury, 2014), this is most likely to be the result of detritivory, and is very unlikely to be the cause of the apparent ring size oscillations, as oribatids rarely bore into living plants (Wallwork, 1967). No other evidence of bark or wood boring arthropods has been discovered in wood from the upper portion of the Winton Formation to date.

Alternatively, the pattern of growth in *P. owensii* may be a result of the architectural history of the tree. This is difficult to test as there are limited rings in continuous sequences of sufficient length to illustrate such an oscillation (Fig. 3), and there are no pieces of size sufficient to test tree architecture as per Philippe et al. (2009). If accepted as climate induced, the longest sequence (from QM F44338) suggests an approximately 15 year period of better than average conditions for growth followed by an approximately 15 year period of below average conditions for growth. More ring sequences of over 30 years need to be analysed before these oscillations can be confirmed because of the low sample size available for this study, and the length of the cycle, however similar oscillations, with climatic links, have been detected in modern dendrology (e.g. Fowler, 2008; Heinrich et al., 2009; Mundo et al., 2012). For example, Heinrich et al. (2009) found that the growth index for *Toona ciliata* M. Roem. from near Brisbane, Australia, shows a multi-decadal oscillation of around 30–40 years with its most recent peak in the 1970s suggesting that ring width in this species is correlated to the PDO and showing a similar periodicity to that in our study. Heinrich et al. (2009) found that there was some correlation with temperature, light index, and relative humidity but the primary explanator of ring width was rainfall. Fowler (2008) found that *Agathis robusta* (C. Moore ex F. Muell.) F. Muell. ring widths correlate strongly with regional-scale climate in New Zealand, which is dominated by ENSO. The correlation was such that *A. robusta* ring widths may be used as part of a multi-proxy approach for the reconstruction of past SOI, but are not sufficiently correlated for use alone, partly because ENSO cycles do not always align with the growth season in the southern hemisphere. Where *Agathis* is found in the warm temperate climate of New Zealand ring width is correlated with both temperature and rainfall (Ogden and Ahmed, 1989; Buckley et al., 2000), but in tropical northern Queensland, Australia (Ash, 1983) and tropical New Caledonia (Vincent et al., 2007), only a relationship with rainfall was found to be significant. Mundo et al. (2012), found that ring width in *Araucaria araucana* (Molina) K. Koch in Argentina, is highly correlated with both ENSO and SAM/AO mediated by the effect on both temperature and rainfall, however temperature was more important in high altitude than at low altitude. Together these studies suggest that in temperate areas, particularly at higher altitudes, temperature can limit growth, whereas in sub-tropical and tropical environments rainfall is the most important variable. In addition, we know that in modern systems, in any given region, rainfall is not only dependent on climate cycles but also the interaction of climate oscillations (as above, Crimp and Day, 2003; Fogt and Bromwich, 2006).

**Table 1**

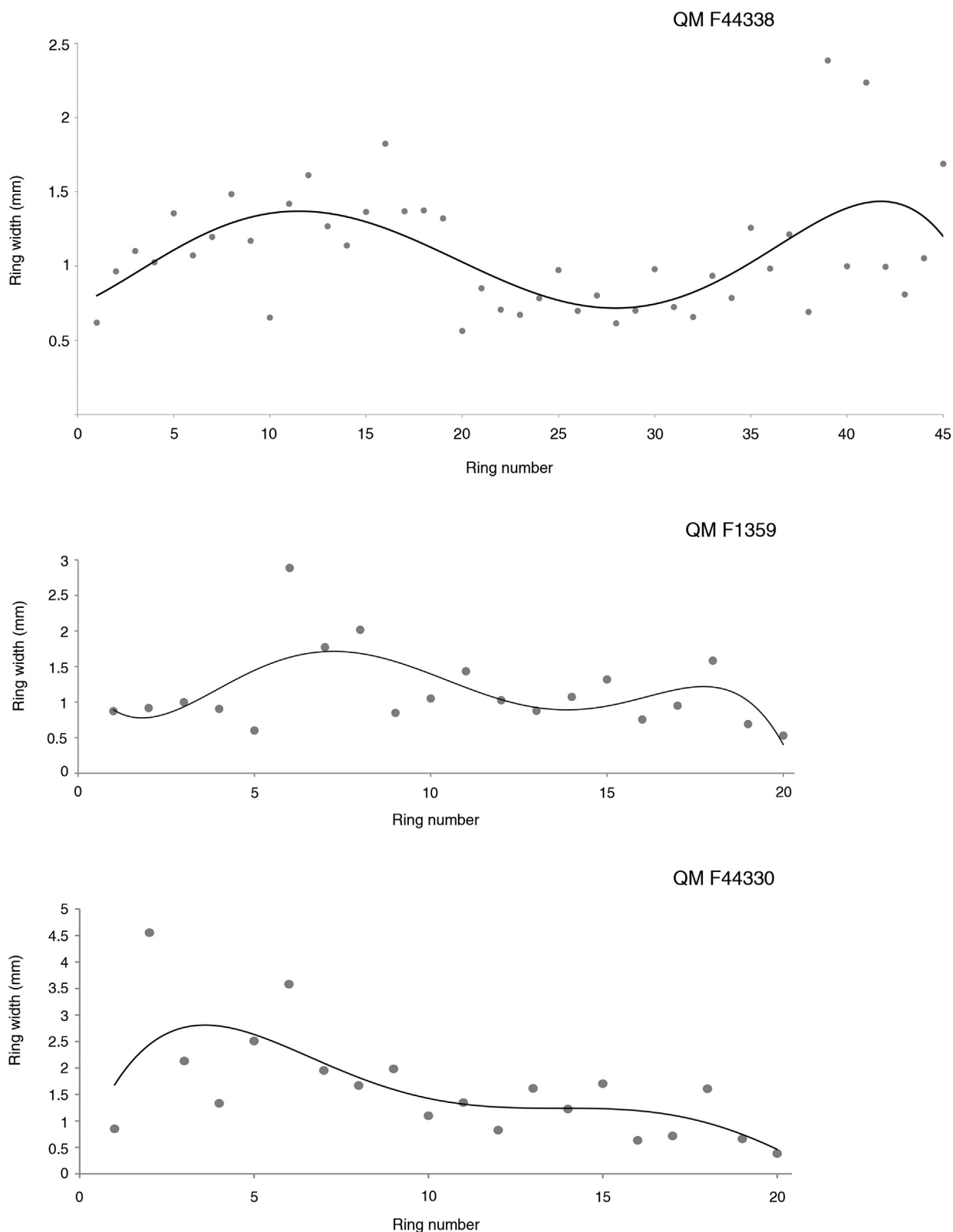
The characteristics, based on Chapman (1994) used to determine likely original position in the tree for each specimen used.

Accession number	Length (cm)	Width (cm)	Breadth (cm)	Ring profile	Rings narrow	Rings wide	Rings very wide	Intra-ring spacing regular	Intra-ring spacing irregular	Few LW cells	LW walls thin	Rounded cell walls	Crushing in EW	Spiral thickening	Pith present	Likely position
QM F44330	10.5	10.5	4	Undulate	–	–	+	–	+	+	?	–	+	–	–	Root
QM F44331	6	3.5	3	Straight to slightly undulating	+	–	–	+	–	–	–	–	+	–	–	Trunk
QM F44332	4	6	8	Undulating	+	+	–	–	+	–	–	–	+	–	–	Stump
QM F44333	9	6	3.5	Slightly curved	+	–	–	+	–	–	–	–	+	–	–	Trunk
QM F44334	2.5	6	3	Very curved, likely missing only 2 cm to centre.	–	–	+	+	–	+	–	–	+	–	–	Root
QM F44335	5.5	5.5	6.5	Curved in parts straight towards outside	–	+	+	–	+	–	–	?	+	–	–	Stump
QM F44336	8	5	4	Straight to slightly undulate	+	–	–	+	–	–	–	–	+	–	–	Trunk
QM F44337	16.5	5.5	3	Undulate wide to narrow across the section	+	+	–	–	+	–	–	–	+	–	–	Stump
QM F44338	6	4	5.5	Straight and even	+	–	–	+	–	–	–	–	–	–	–	Trunk
QM F44339	18	10	3	Straight to slightly undulating	+	–	–	+	–	–	–	–	+	–	–	Trunk
QM F1359	8	11	2	Very variable with some sections of straight even and narrow rings, followed by wide irregular spaced rings	+	+	+	+	+	–	–	–	+	–	–	Stump

**Table 2**

A summary of the measurements and results of the statistical analysis for each of the specimens used in this study.

Specimen	Likely position	Average WIDTH (mm)	# rings	Crush zones	Frost rings	False rings	Relative magnitude	% late wood	% diminution	RMI	% skew	Mean sensitivity
QMF1359	Stump	1.113 ± 0.489	32	1	0	1	15 ± 6.3	21.32 ± 11.65	62.13 ± 10.99	12.94 ± 6.5	–36.21 ± 28.43	0.37 ± 0.28
QMF44330	Root	1.619 ± 1.020	20	1	0	1	30 ± 14	29.22 ± 13.91	66.94 ± 11.55	19.27 ± 8.8	–4.89 ± 32.52	0.53 ± 0.31
QMF44331	Trunk	1.475 ± 0.651	19	2	0	0	24.1 ± 11.86	19.2 ± 9.43	73.05 ± 9.5	13.72 ± 6.0	–33.33 ± 26.8	0.46 ± 0.43
QMF44332	Stump	0.974 ± 0.123	5	2	0	0	17.8 ± 2.59	18.77 ± 6.25	67.07 ± 3.31	12.67 ± 4.46	7.77 ± 38.77	0.16 ± 0.1
QMF44333	Trunk	1.582 ± 0.415	5	2	0	0	27.4 ± 7.77	26.52 ± 8.81	69.23 ± 5.2	18.13 ± 5.41	4.21 ± 35.7	0.27 ± 0.14
QMF44334	Root	2.317 ± 1.242	11	2	0	1	57.1 ± 31.5	30.59 ± 16.21	68.82 ± 5.92	21.05 ± 10.98	13.59 ± 44.14	0.6 ± 0.37
QMF44335	Stump	3.312 ± 1.895	8	1	0	0	50.38 ± 30.79	22.89 ± 13.59	72.22 ± 3.05	16.19 ± 8.92	–21.38 ± 27.16	0.76 ± 0.49
QMF44336	Trunk	–	–	2	–	–	–	–	–	–	–	–
QMF44337	Stump	2.877 ± 0.571	4	2	0	0	56 ± 8.98	25.89 ± 3.7	77.34 ± 4.59	20.1 ± 3.75	–10.01 ± 8.74	0.24 ± 0.11
QMF44338	Trunk	1.091 ± 0.410	45	0	0	1	13 ± 4.15	21.19 ± 9.8	65.33 ± 8.88	13.63 ± 6.05	–38.5 ± 19.37	0.32 ± 0.25
QMF44339	Trunk	1.209 ± 0.428	21	1	0	1	21.67 ± 7.64	24.15 ± 12.21	67.54 ± 9.3	16.34 ± 8.12	–15.41 ± 32.86	0.31 ± 0.24
QMF44338	Trunk	1.091 ± 0.410	45	0	0	1	13 ± 4.15	21.19 ± 9.8	65.33 ± 8.88	13.63 ± 6.05	–38.5 ± 19.37	0.32 ± 0.25
Trunk mean		1.294 ± 0.487	22.5				21.54 ± 8.32	22.77 ± 10.14	68.79 ± 8.41	15.46 ± 6.48	–20.76 ± 29.36	0.34 ± 0.28
Stump mean		2.069 ± 1.021	12.25				34.8 ± 16.39	22.22 ± 9.66	69.69 ± 6.37	15.48 ± 6.24	–14.96 ± 27.95	0.38 ± 0.29
Root mean		2.169 ± 1.163	15.5				43.55 ± 24.37	29.91 ± 15.1	67.88 ± 9.18	20.16 ± 9.95	4.35 ± 38.77	0.67 ± 0.34
Mean		1.797 ± 0.876	17				31.25 ± 15.94	23.97 ± 11.14	68.97 ± 7.83	16.4 ± 7.22	–13.42 ± 30.95	0.4 ± 0.33



**Fig. 3.** Three scatter plots of the ring widths of QM F44338, QM F1359 and QM F44330 through time, where the ring number is counted from what was considered to be the internal side of the wood sample, outwards. In our interpretation we consider the rings to be roughly annual, as few rings were considered to be potentially false rings. The polynomial trendline, which was the trend line with the best-fit to the data, shows the possible oscillations in growth in QM F44338, which may be attributable to favourable and unfavourable climatic conditions or other oscillatory causes. QM F1359 and QM F44330 both record a shorter continuous time-span and any pattern is less clear.

The number of rings measured for each sample varies greatly as it is dependent on the size of the wood, the preservation of the wood cells and the degree of crushing of early wood cells, limiting series of adjacent

rings that could be measured. Seven of the 11 pieces of wood that were adequately preserved to allow identification of the taxon had frequent crush zones in the early wood. Crush zones that produce



characteristic *zigzags* such as is found in our specimens, suggest very favourable conditions for growth, as they are more likely to occur where tracheids are very large and thin walled or have failed to sufficiently lignify (Taylor et al., 1992; Bera and Banerjee, 2001). Some of the smaller sections of crush zones were able to be included, but others, including all of QM F44336, were too crushed and the crush zones were too wide for inclusion. This results in systematic underrepresentation of large growth rings from very favourable years, which may affect relative magnitude, mean sensitivity, percentage latewood, percentage diminution, ring markedness index, and percentage skew as well as the total ring width measures.

Our sample did include false rings. False rings may be indicative of frost (Glock et al., 1960), fire (Dechamps, 1984), flooding (Young et al., 1993), herbivorous attack particularly from insect outbreaks (Schweingruber, 1996, 2007) and drought (Ash, 1983). As noted above, there is no evidence of frost in the sample. Although charcoal has been recorded in some parts of the Winton Formation (Pole and Douglas, 1999) there was no evidence of charcoal or the traumatic tissue damage associated with canopy fire damage (Falcon-Lang et al., 2001), in the specimens examined from this locality.

The detection of flooding is made complex by the different reactions of wood depending on the level of inundation, the amount of protection of the tree, the physical damage to the tree, the timing of the flood (during early wood formation or late wood formation) and the level of adaptation of the plant to flooding (Yanosky, 1983; Martens, 1992). There was no relationship between ring width and minimum tracheid width, a poor but positive relationship between ring width and latewood tracheid number, and no evidence of rounded cross sections and intercellular spaces that would indicate that the narrow rings are 'flood rings' (as per Falcon-Lang et al., 2001) in QM F44338. However, flooding in the early wood portion of the ring may produce subtle changes that are difficult to detect amongst normal variation, and are less pronounced in wood at the base of the tree than in the wood near the stem apex (Yanosky, 1983), the first of which comprises our sample. If inundation falls below the first branch height, it is unlikely to produce the kind of damage (e.g. defoliation) that results in small rings in the years following the flood as a tree recovers, and indeed non-damaging inundation may cause a burst of rapid growth with large tracheids due to increased water availability (Martens, 1992), which may explain the frequent crush zones in the early wood (see previous comments). If this is the case, our flood rings are not the small rings, but the largest. Alternatively, if *P. owensii* was adapted to swampy or frequently inundated environments, such as the modern podocarp species *Dacrycarpus dacrydioides* (A. Rich.) de Laub., a dominant tree on poorly drained soils (Smale, 1984; Duncan, 1993), it may produce little evidence of flooding in the wood structure. Finally flood rings may not be evident in the wood if the portions of wood preserved were not inundated as they were formed, as may be the case if floods were infrequent, but scouring when they occurred. This type of flooding, suggested by the geology and sedimentology of the region, (Tucker et al., 2013; R. Tucker pers. comm., 2013), is in keeping with the taphonomy of the fauna (pers. obs.). These three lines of evidence suggest that flooding may have been part of the palaeoenvironment of the upper Winton Formation.

Although herbivorous insect outbreaks may cause false rings and oscillations in ring growth, both features of our wood indices, we have not found other indicators to suggest that ring width and formation are being driven by insect outbreaks, as discussed in detail above. Experimental defoliation has produced similar wood characters as from insect outbreak (Schweingruber, 2007), and thus other herbivorous agents are also unlikely to be the cause of the false rings in *P. owensii* from this locality.

The final potential cause, drought, may have affected growth despite the high (1300–1600 mm) average rainfall estimated by previous studies, especially if climatic conditions were being affected by climate oscillations. A modern analogue for this is modern North-East Queensland. Rainfall records from the Atherton Post Office from 1895–1972, record

an average rainfall of 1414 mm, but the year with the lowest rain fall recorded less than 500 mm and the highest is over 2400 mm (BOM – Australian Bureau of Meteorology, 2014; accessed 15-1-14).

The relative magnitude of rings was both variable and relatively low. The low magnitude may be in part due to the inability to measure very large rings due to crushing, as mentioned above, may be because podocarps are universally slow growing (Coomes and Bellingham, 2011), or may be indicative of another factor stunting growth such as inundation (Martens, 1992). The variability is in keeping with an environment with large changes in conditions for growth between years.

Unlike Creber and Chaloner (1984) we did not find anomalously high percentages of latewood in rings with low relative magnitude (<30 cells). Falcon-Lang (2000a) found a strong relationship between percentage latewood, percentage diminution and ring markedness index with median leaf longevity. The percentage latewood values herein (~10–30%) are similar to those of *A. araucana*, which has a leaf retention time of 3–15 years, whilst the percentage diminution (~70%) is more similar to *Cedrus libani* A. Rich., which has a leaf retention time of 3–6 years, and the RMI (~15.5) falls between the range of the two species (Falcon-Lang, 2000a), similar *Podocarpoxyylon mazonii* Petriella from the Danian of Central Patagonia (Brea et al., 2011). This suggests a leaf retention time of ~3–10 years and thus an evergreen habit.

That the percentage latewood, percentage diminution and ring markedness index, are consistent with the evergreen habit of modern podocarps, the likely nearest living relatives, is useful as the variability around the percentage skew is high such as to be uninformative, in contrast to Falcon-Lang and Cantrill (2001), in which both *Podocarpoxyylon* showed a clear skew to the right.

## 5. Conclusion

The climate of the upper portion (Cenomanian–Turonian) of the Winton Formation was seasonal, and variable between years. This variability may have been cyclical, and had regional climatic effects similar to PDO and ENSO. The wood potentially records flooding and/or drought, which is associated with ENSO and PDO in modern Queensland, Australia, and is in keeping with the geology of the upper Winton Formation.

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