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SENSITIVITY OF XYLEM VESSEL SIZE AND FREQUENCY TO RAINFALL AND TEMPERATURE: IMPLICATIONS FOR PALAEONTOLOGY

by

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ABSTRACT

Based on the xylem vessel size and frequency in fossil wood, a number of studies have developed theories on climate change through time. The basic premise of these studies is that xylem vessel size decreases while vessel frequency increases with intensifying aridity. In this paper the relationship between rainfall and xylem vessel size and frequency is examined in two extant tree species. The results indicate that rainfall is related positively to vessel diameter and negatively to vessel frequency in *Combretum apiculatum* and *Protea caffra*. Xylem vessel size of both species is between 50 and 100μm. However, the two species exhibit different responses to rainfall in that *P. caffra* has much smaller diameter vessels than *C. apiculatum* in high rainfall areas. These differences indicate that the potential for using xylem anatomy as a palaeoclimatic indicator has not been fully utilised. A more precise picture of climate change through time is possible with a more refined statistical analysis of reliably identified fossil wood.

KEY WORDS: Wood anatomy, fossil wood.

INTRODUCTION

Palaeontologists are constantly debating the consequences of climate change at specific periods in time. A number of investigators have attempted to use Carlquist's (1966, 1975 , 1977) vulnerability (calculated by dividing mean vessel diameter by number of vessels) and mesomorphy values (calculated by multiplying the V value by the mean vessel length) in an analysis of growth conditions in Late Cretaceous and Early Tertiary wood (Wolf and Upchurch 1987, Landon 1988). However, an analysis of vessel diameter and vessel frequency of fossil wood should be sufficient to indicate changes in plant conductivity across a rainfall/temperature gradient. The potential of this line of investigation is illustrated here by an analysis of an extant wood sample of *Combretum apiculatum* and *Protea caffra* from some 20 locations within the summer rainfall region of South Africa.

In determining the effects of climate and environment on the settlement patterns of prehistoric hunter gatherer societies, I have utilised a number of methods of climate reconstruction. One of these methods, xylem analysis, is based on the premise that measurements of xylem vessel size and frequency in archaeological wood samples may be related to climate when compared to the same measurements on an extant sample from areas of known temperature and rainfall (Scholtz 1986; February 1990, 1992). In assessing this technique of climate reconstruction it was necessary to determine the exact relationship between rainfall and xylem vessel size and frequency in a number of woody species. It is this relationship that can be useful in determining climate change from fossil wood.

At present the only method for obtaining any reasonable climatic data from certain wood anatomical features is in a comparison of the anatomy of all woody species from one epoch with another. Creber and Chaloner (1984, 1985) have developed hypotheses on the climate of the Mesozoic and early Tertiary based on trunk diameter and ring width of fossil wood. Wolfe and Upchurch (1987) concluded, through an analysis of fossil wood, that the Late Cretaceous climates were characterised by low but largely aseasonal rainfall with a change to high precipitation at the Cretaceous - Tertiary boundary. Wheeler & Baas (1991), on the other hand, suggested that the changes in wood anatomy from the Cretaceous to the Tertiary were probably associated with the emergence of angiosperms as dominants in multistratal forests. They did, however, claim that wood anatomical changes in Laurasia at the Palaeocene – Eocene boundary could probably be related to climate change. Their research was directly based on the work of Carlquist (1966, 1975, 1977), Baas (1982) and others, which shows that xylem vessel size decreases while vessel frequency increases with intensifying aridity.

ECOLOGICAL INFERENCES FROM XYLEM ANATOMY

It makes no sense to argue that xylem vessel size and frequency are the only wood anatomical characteristics which are habitat controlled. The conduction of water through a plant depends on too many factors (porosity, transpiration rates, intervessel pitting, leaf surface area, type of perforation plate etc.) for such a simplistic assumption (Zimmerman 1983). Baas (1982) pointed out that, as early as 1889, Vesque was of the opinion that taxonomic identification using wood anatomy was not possible because of the intraspecific diversity brought about by ecological factors. In their study of the *Styracaceae* Dickison and Phend (1985) found correlations between latitude and multiseriate ray frequency, ray height, fibre tracheid diameter, vessel frequency and both vessel and tracheid wall thickness. Fidel and Roig (1986) in their observations on *Adesmia horrida* found that trees growing on well watered slopes were diffuse porous, while those growing under water restriction were ring porous. Den Outer and Van Venendaal (1976) found a significant correlation between increased ray tissue and environmental conditions in savannah and rain forest trees of the same species.

There are thus a number of ecological inferences which can be drawn from xylem anatomy, but in this paper I will only focus on the relationship between vessel diameter, vessel frequency and rainfall and temperature.

Vessel diameter and vessel frequency are probably the most significant parameters for water transportation in angiosperm wood. According to Poiseuille's law for ideal capillaries, hydraulic conductivity is proportional to the sum of the vessels radius each raised to the power of four. This r^4 relationship means that a slight increase in vessel radius is equivalent to an enormous increase in ability to transport sap. For example the proportional percentage of sap transported by three vessels with relative diameters of 1, 2 and 4 will be 0.4, 5.9 and 93.7 (Zimmerman 1978, 1983).

Based on his observations of the *Asteraceae*, Carlquist (1966) may have been the first to point out that the diameter of xylem vessels decreases whilst vessel frequency increases with intensifying drought. His observations have been upheld by further studies such as those of Baas (1982), Baas and Schweingruber (1987), Wilkins & Papassotiriou (1989) and others.

None of these studies addresses the relationship between specific vessel characteristics and mean annual rainfall and temperature. Carlquist (1966, 1977) compared the wood anatomy of the *Asteraceae* and *Penaeaceae* across a wide range of ecological habitats. In this study, however, it was not possible to obtain actual rainfall figures. Baas and Schweingruber (1987) also did not determine mean annual rainfall figures, but instead determined ecological trends for occurrence of certain vessel characteristics along a macroclimatic gradient from boreal via temperate to Mediterranean. Wilkins & Papassotiriou (1989) compared wood samples of *Acacia melanoxylon* from Queensland and Tasmania. All of these studies refer to macroclimate. In order to determine the relationship between vessel diameter, vessel frequency, mean annual rainfall, and mean annual temperature, I analysed a sample of *Combretum apiculatum* and *Protea caffra* along a climate gradient within the summer rainfall region of South Africa (Figure 1).

For the purposes of this study, the area termed the summer rainfall region of South Africa has been defined as that area stretching from Messina on the Zimbabwean border in the north, to Umtamvuma Nature Reserve on the Transkei border in the south and from the Indian ocean and Moçambique border in the east to Johannesburg in the West.

The ecological zonation of the research area runs roughly north/south parallel to the Drakensberg escarpment. There are four broad ecoclimatic zones within this area. These zones can be defined as coastal and interior lowlands, uplands region, interior plateau and high mountains. Of the many woody species growing within these ecoclimatic zones two *Protea* species *P. caffra* and *P. roupelliae* and *C. apiculatum* have an extremely wide distribution range, and are also very easily identifiable. *P. caffra* and *C. apiculatum* were chosen for this study on the basis of ease of identification and wide distribution.

METHODS

In my analysis I relate the cross sectional xylem anatomy of *C. apiculatum* and *P. caffra* to mean annual rainfall and mean annual temperature. I test the hypothesis

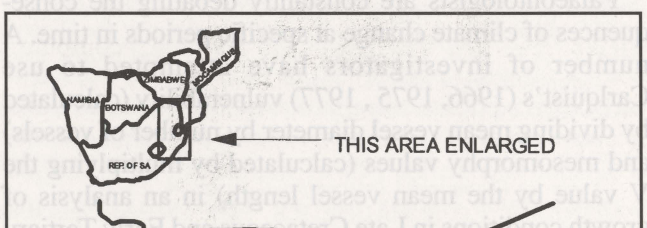

Figure 1: Localities from which an extant sample of *P. caffra* and *C. apiculatum* were collected.

that with the seasonal nature of the rainfall corresponding with the high transpiration rates in the hot summers, vessel diameter and vessel frequency are directly related to rainfall. More specifically, vessel diameter increases while vessel frequency decreases with increases in transpiration rates due to high temperatures and increases in plant available water. This adaptation to available water had been stressed by Carlquist (1980) who concluded that xylem vessel size and frequency is a quantitative feature in trees which represents an adaptation to the environmental conditions under which the wood is formed.

To relate the anatomy of wood to climate, samples were collected from undisturbed sites as close to weather stations as possible. Roads, buildings and other constructions were avoided as increased runoff as well as watering of domestic plants may affect vessel size and frequency. In order to fulfil these requirements most of the samples were collected in either private nature reserves or reserves administered by the various National or Provincial authorities. Where possible, rainfall records were obtained from the reserves where samples were collected, supplied by the Weather Bureau or the Computer Centre for Water Research. For the purposes of this study rainfall was averaged over four years to December 1990 when the samples were collected. Temperature data for the reserves were very difficult to obtain as very few of the weather stations close to the reserves record both rainfall and temperature. As a result, temperature data were obtained from the computer generated minute by minute data available from the Department of Agricultural engineering at the University of Natal (Schultze and Maharaj 1993).

Within a tree, vessel diameters tend to be greater in roots than in stems, and greater in the stem than in the branches (Zimmerman 1978, 1983). As a control for this variation only branch samples were collected. Measurements of vessel size and number were taken on that section of wood immediately related to the previous four years of growth.

In the laboratory a 2 cm thick disc was cut off the end of each piece of wood and then split into sections about 5-8 mm wide, incorporating both the pith and the cambium. Prior to photography, the wood was softened by boiling before samples were cut in transverse section at thicknesses of between 25 and 30 µm using a base sledge microtome. The thin sections were stained, mounted on glass microscope slides, and photographed at a magnification of 40X. Measurements of vessel size and number were then made using a custom written computer programme linked to a Summagraphics digitising tablet. Diameters were measured for a maximum of 50 vessels per section of wood with approximately 10 individual specimens per collecting site. Number of vessels was obtained by placing a plastic sheet marked out in a 10 mm square grid over the photographic image to be digitised. Total vessel area was then calculated by dividing the sum of the areas of the measured vessels by the number of vessels measured. This value (i.e. mean vessel area) was then divided into the total vessel area to obtain a figure for the number of vessels per square mm. In accordance with the recommended procedure by the International Association of Wood Anatomists, vessel diameters were measured in the tangential direction at the widest part of the opening and excluding the cell wall (I.A.W.A. Committee 1989).

TABLE 1

Mean (Meanv) and maximum values (Maxv) for tangential vessel diameter, number of vessels (Numv) and standard error (Std) for *C. apiculatum* across a climate gradient within the research area; *, **, * and **** denote significant differences between means at P< 0.05, 0.01, 0.001 and 0.0001 respectively. N= number of samples from each locality.**

Locality	N	Rain in mm	Temp in°C	Maxv in µm	Std error	Meanv in µm	Std error mm²	Numv per	Std error
Letaba	10	385	23	80	3	59	2	33	3
Serala	9	400	19	86	3	61	2	23	1
Bourke's Luck	10	401	16	84	4	61	3	27	2
Dzata	6	412	19	86	1	60	2	27	3
Phalaborwa	10	420	22	86	3	62	2	27	2
Pafuri	10	434	23	89	4	64	3	33	3
Timbavati	14	439	22	89	3	62	2	26	2
Punda Maria	13	493	22	96	3	69	2	22	1
Hans Merensky N. R.	15	538	22	92	3	65	2	24	1
Rust de Winter dam	10	600	19	94	3	69	2	28	2
Ben Lavin	10	631	20	95	3	65	2	24	1
Nylsvlei	4	663	19	97	10	70	6	17	1
Barberton	9	815	20	95	6	61	3	22	2
Itala N. R.	10	940	21	105	4	72	3	18	1
Correlation coefficient (R)				0.88		0.63		-0.67	
(R^2)				0.77		0.40		0.45	
Probability				****		**		***	
Multiple regression (Rain & Temp)				0.78		0.40		0.51	
Probability				****		*		**	

TABLE 2

Mean (Meanv) and maximum values (Maxv) for tangential vessel diameter, number of vessels (Numv) and standard error (Std) for *P. caffra* across a climate gradient within the research area NS, *, **, and * denote significant differences between means at P< 0.05, P<0.01, and P<0.001 respectively. N= number of samples from each locality.**

Locality		N	Rain in mm	Temp in°C	Maxv in µm	Std error	Meanv in µm	Std error mm²	Numv per	Std error
Oog van Malemane		4	546	17	54	3	40	2	53	8
Suikerbosrand		10	765	16	58	3	36	2	89	5
Kamberg		10	1100	14	66	2	45	1	55	6
Cathedral Peak		9	1153	15	60	3	40	2	54	4
Hluhluwe N. R.		10	1170	21	65	2	47	2	44	3
Umtamvuma N.R.		10	1164	18	72	2	51	2	54	3
Correlation coefficient	(R)				0.94		0.82		-0.36	
	(R^2)				0.88		0.67		0.13	
Probability					**		*		NS	
Multiple regression (Rain & Temp)					0.88		0.73		0.20	
Probabilty					*		NS		NS	

Maximum and minimum vessel diameters were obtained from the means of the five largest and five smallest vessels measured. Mean vessel diameters are the mean value of the number of individual vessels measured. Mean annual rainfall and temperature were correlated on the means per sample area.

RESULTS

In both *C. apiculatum* and *P. caffra* the relationship between xylem morphology and rainfall agrees with the findings of previous studies (Carlquist 1966, 1977, Baas *et al.*, 1983, Zhang *et al.*, 1988, Wilkins and Papassotiriou 1989). Those plants growing in wet environments have larger and fewer vessels than conspecifics growing in a more xeric environment (Table 1). The results of a correlation coefficient analysis show very strong correlations on the means between maximum vessel diameter and rainfall for *C. apiculatum* (N = 14, R = 0.88, P <0.0001, Table 1) and for *P.caffra* (N = 6, R = 0.94, P<0.01, Table 2). There are no statistically significant results for a correlation coefficient analysis between xylem anatomy and temperature. A multiple regression analysis using both temperature and rainfall data also does not show any statistically significant results (Table 1 & 2).

DISCUSSION AND CONCLUSIONS

There was no significant correlation between temperature and xylem vessel size and numbers. I will therefore discuss the relationship between vessel morphology and rainfall. Wheeler and Baas (1991) suggested following the IAWA convention for descriptions of fossil and archaeological wood. The vessel diameters in this study would therefore fall into four classes (in µm < 50, 50-100, 100-200 and > 200). The sample of *P. caffra* in the present study follows a rainfall gradient of more that 1000 mm, yet average vessel diameters do not range over more than 30 µm with a maximum vessel diameter at the Umtamvuma Nature Reserve near Port Edward (rainfall 1664 mm) of 84 µm, which is comparable to the lowest value 81 µm obtained from the *Combretum* sample at Letaba (see Table 1). On the basis of IAWA (1989) listing, all but one of the results obtained for the extant sample (*Combretum* and *Protea*) would be placed in the category 50-100µm thereby masking a considerable variability.

If placed into a specific category these results would be useful in a number of ways. In developing hypotheses on the xylem characteristics of woody flora across an ecological gradient, as in studies such as those of Carlquist (1966, 1977), these results may be representative of the xylem vessel size and frequency for the woody flora of subtropical southern Africa. In fossil wood studies such as those of Wheeler & Baas (1991), the results would also prove to be useful, as an ecological determinant, representing the woody flora of a subtropical savannah region. In an environmental reconstruction, fossil wood with a comparable xylem anatomy would be synonymous with an African plains land (grassland studded with flat topped acacias and carrying a number of ungulates).

It is, however, possible to extract more information from the fossil record. The savannah biome in southern Africa ranges from tall woodlands receiving 1800 mm of rain per annum to sparse grasslands on the edge of the Namib where rainfall is not much over 50 mm (Rutherford & Westfall 1986). This biome can be divided into two distinctive zones, "arid" and "moist" both of which differ substantially in terms of flora, fauna and physiognomy. Within these distinctive zones, flora and fauna are again different depending on mean annual rainfall.

The results in the present study show that values for tangential vessel diameter of *C. apiculatum* range from 80 to 105 µm following a rainfall gradient from 385 mm to 940 mm. This represents a range in rainfall of 555 mm with a difference in vessel diameter of 25 µm. A difference of 25 µm may not seem to be very much but a correlation coefficient analysis does reveal a strong correlation between tangential vessel diameter and rainfall (N = 14, R = 0.88, P < 0.0001). Within the subtropical savannah region of southern Africa a difference of 555 mm in rainfall constitutes a considerable difference in environment. The *Combretum* sample from Itala was growing close to a forest margin with *Protea* shrubs less than 1 km away. The sample from Letaba on the other hand was confined to a *Combretum/Mopane* scrubland. The results for the *Protea* sample are even more striking in that the range in rainfall is more than 1000 mm from arid savannah at Suikerbosrand to forest margin in moist grassland at the Umtamvuma Nature Reserve.

These results indicate that a better understanding of climate change through time is possible through an analysis of fossil wood. Further refinement lies in a more rigorous analysis which would include the identification of fossil wood to genus or species level as well as the precise measurement of a statistically significant sample. Rather than categories of vessel frequency and size classes, actual values for specific genera should be computed and related to the ecological characteristics of the taxon in question. Based on an analysis of fossil wood it is possible to develop more precise analogies with contemporary environments. These methods are especially possible for the Pliocene, Pleistocene and Holocene where the fossil wood species can be identified and compared with extant species.

The implications for palaeontology are, however, limited to pieces of fossil wood of the same size and species. How available are such pieces of wood and how reliably can these be identified?

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