IAWA Journal, Vol. 16 (4), 1995: 353–359

THE DEFINITION OF SEASONAL GROWTH ZONES IN SOME AFRICAN ACACIA SPECIES – A REVIEW

by

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SUMMARY

This paper reviews and summarizes the results of investigations at the Oxford Forestry Institute on the occurrence of seasonal growth rings in the wood of one of Africa's most widely distributed genera in the arid areas, *Acacia*. The ring boundaries are marked by fine marginal parenchyma containing small crystals of Ca-oxalate. Rings are usually annual and produced in the rainy season. Ring width is related to precipitation and / or minimum temperature. Rooting characteristics of the various species studied influence the type of relationship found.

Key words: African *Acacia* species, arid woodland, crystalliferous chains, growth rates, marginal parenchyma, wood anatomy.

INTRODUCTION

Forests in the arid and semi-arid regions of Africa fulfil many roles: they are of vital importance in preserving the soil and limiting desertification; they provide between 60% to 90% of the energy requirements for cooking in the form of both wood and charcoal; they provide fodder for domestic and wild animals. The woodland areas that have survived to the present have reached an ecological balance between climate, soil, human and livestock activities, and firewood yields in these areas are often underestimated, due to traditional forestry methods that measure only stem wood. Knowledge of age and growth rates of trees is necessary for an understanding of forest dynamics and, therefore, ecologically sound woodland management (Jackson et al. 1983; Jacoby 1989).

Brenan suggested (foreword to Ross 1979) that "there is probably no group of trees and shrubs in Africa that can rival the *Acacia* spp. in the combined importance of their ecology and extent of their geographical range." As with many other genera in the Leguminosae, *Acacia* spp. have the ability to fix nitrogen and, therefore, many are important in agro-forestry systems. There are many other benefits from *Acacia* spp., including the provision of fuel in the form of wood and charcoal, medicines, tannins, gums, building materials, rope and fibres, honey, and shade. In addition to these uses, for many nomadic and pastoralist people in the arid areas of Africa *Acacia* spp. represent the major source of food for their livestock at certain periods in the year.

There have been a few other studies that have sought to identify growth rings in African *Acacia* spp. and they had conflicting results, see Gourlay (1995). Trees growing in the tropics and sub-tropics seldom reveal their growth periodicity (and subsequent age) as clearly as do most temperate trees by concentric changes in their wood anatomy. Anatomical features that clearly denote annual growth rings in temperate trees, such as ring-porosity of some angiosperms and the pronounced changes in cell wall thickness and cell dimensions of earlywood and latewood in conifers, are uncommon in tropical species. In the wet tropics, the absence of seasons and of extremes in rainfall and temperature is largely responsible for poorly defined rings in wood. It is often assumed that in many tropical areas the cambium is active throughout the year. This may well be true for perpetually wet regions of the tropics but is certainly not so for much of the arid tropics, where the growth is closely related to short rainy seasons. In the more arid areas of the tropics, the abrupt transition from wet to dry season can produce the necessary dormancy that will result in a detectable anatomical change (Worbes 1990).

OBJECTIVES

Following exploratory work using *Acacia bussei* from Somalia by Gammadid (1989) at the Oxford Forestry Institute, the number of species to be examined for the possibility of age determination in African *Acacia* species was extended to include over 40 trees from 15 species, sampled from six African countries, covering over 14 degrees of latitude (Gourlay & Kanowski 1991; Gourlay & Barnes 1994; Gourlay, 1995).

The majority of the trees sampled for this study were actively sought from material of known age, particularly those for which the history of management was known. The advantage of this approach is that if a discernible annual growth pattern in the wood anatomy of material of known age is found, the techniques employed can be transferred to material of unknown age. As a check on the validity of the results in this research a proportion of samples had their maximum age estimates withheld from the author by the collectors.

RESEARCH METHODS AND RESULTS

The preferred sample was a whole disc or log taken at 1.3 m height from the main stem of the tree. As this necessitated felling the tree, such sampling was not always possible. In the cases where trees could not be felled but the material appeared to be suitable and was well-documented, samples were collected as increment cores. Increment core sampling in species with such dense wood as *Acacia* (commonly more than 1.0 g/cm^3) is extremely difficult. It is not unusual for the tempered steel borer to break due to excessive torque. The operator may, therefore, miss or fail to reach the pith in some cases. Reliable meteorological data consisting of monthly or annual rainfall records and, in a few sites, monthly evaporation and temperature values, were collected for all sites where trees were sampled.

The sample discs or cores were prepared for examination of growth zones and microtome sections cut for microscope studies (Gourlay & Kanowski 1991). In the case of discs, two or more radii were examined. Due to the practical difficulties experienced in coring *Acacia* spp. (as mentioned earlier), only one radius was sampled, prepared and examined as above. Examination of the microtome sections revealed a concentration of small crystals in continuous single or double vertical chains, in the marginal parenchyma or its periphery.

X-ray densitometry

A range of *Acacia* spp. samples were also selected for X-ray densitometry analysis as described by Hughes and Sardinha (1975) and Kanowski (1985). Although the X-ray densitometry assisted in the delineation of the growth rings, it did not produce sufficiently clear images to enable reliable age determination of *Acacia* spp. without comparisons with previous detailed microscope examination. This is largely due to *Acacia* spp. possessing relatively high density wood and the presence of gum. Both of these features contribute to the lack of growth ring definition by densitometric analyses.

Scanning Proton Microprobe (SPM)

Further sections (20–30 µm approximately) were also prepared from samples of *Faidherbia albida* (previously *Acacia albida*), *Acacia karroo*, and *Acacia nilotica*, for analyses by the SPM facility of Oxford University's Department of Nuclear Physics. The technology and methodology have been described by Grime and Watt (1990) and Watt and Grime (1987). The SPM confirmed the crystals present as calcium oxalate (CaC_2O_4). Results also indicated concentrations of several other elements in and around the marginal parenchyma band (Gourlay & Grime 1994).

Periodic tree wounding

Two stands of *Acacia karroo* near Bulawayo, Zimbabwe, were used as a basis for this work. The aim of this study was to wound the cambium of selected trees at documented time intervals in order to produce a callus which could be located and examined when the tree was felled at a later date. Following felling of the wounded trees, the marginal/crystalliferous bands were marked and the band formed just before the felling of the tree closely examined in relation to the position of the callus areas, produced by wounding the cambium at monthly intervals. Examination revealed that this band first became visible between the wounds made in March and April. The production of new xylem commenced between mid-September and mid-October; this implies that the tree did not produce wood during the dry winter period from late March to early September (Gourlay & Barnes 1994).

DISCUSSION

The marginal parenchyma bands can usually be distinguished from the frequent intraseasonal banded parenchyma by their fineness, by more irregular spacing between the broader bands, and by evenness of appearance in contrast to the more irregular, wavy, confluent bands. The results of this investigation suggest that the marginal parenchyma

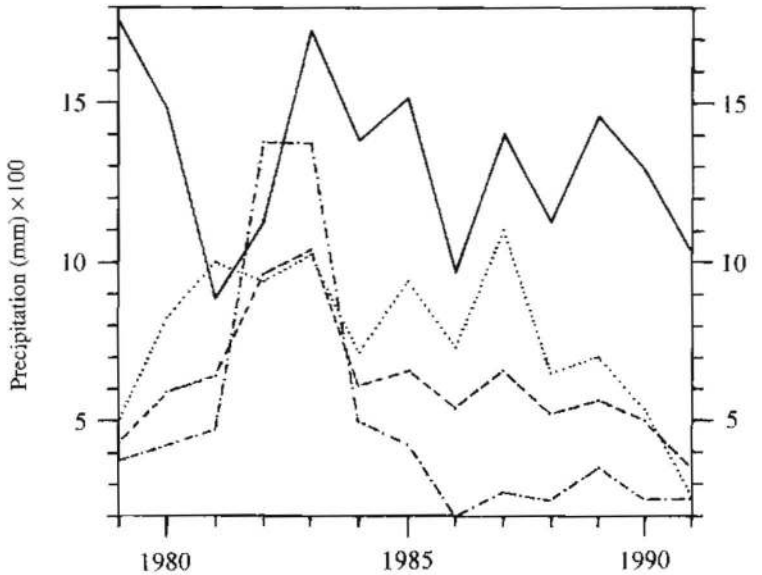

Fig. 1. Changes in annual ring width and precipitation with time. Seven trees from three species on the same site (Bamburi, Kenya coast), bimodal rainfall; measured for a 12-month period, ending in February of the year indicated. ——— = precipitation; – – – – = *Faidherbia albida* (3 trees); – · – · – · = *Acacia tortilis* (1 tree); ········ = *A. nilotica* (3 trees).

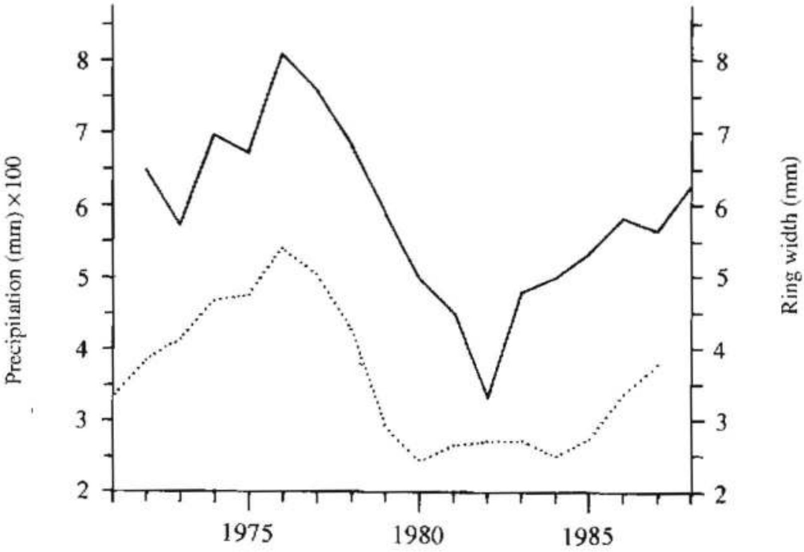

Fig. 2. Changes in annual ring width and precipitation with time. Ring width (········) against annual precipitation (——) for *Acacia karroo* at the Matopos site, Zimbabwe (2 trees), unimodal rainfall; this plot incorporates smoothing (three-year moving average) and a one-year lag (ring width = year + 1); measured for a 12-month period, July–June of the year indicated.

bands and crystalliferous chains associated with them do indicate seasonal growth patterns in the *Acacia* species examined.

At most sites with reliable rainfall data, a good relationship was evident in the graphs between annual rainfall and mean ring width (Fig. 1). Simple smoothing of the data was also applied to some samples using a running mean of three years; in general this improved the correlation results. With more data and older trees, together with such statistical methods as 'standardization' and other more appropriate analyses, the 'noise' associated with individual tree data should be filtered out. However, the nature of this particular research project did not warrant the development of more sophisticated mathematical analyses, particularly as the majority of sample trees examined were less than 20 years old. As mentioned by Pilcher (1990) and others, it is the experience of most dendrochronology laboratories that reliable tree-ring analyses should not be expected for sequences of less than about 40 years.

It was also found desirable to introduce a 'lag' of one year into the models of rainfall and growth data (Fritts 1962). Growth in any given year may respond more to preceding than to current precipitation, the closeness of the relationship between the two parameters improved markedly in many cases (Fig. 2). In a few cases the correlations between mean minimum temperature and ring width were greater than those between precipitation or evaporation and ring width.

The mean annual ring width across all *Acacia* spp. and sites examined in this work would appear to be very similar, i.e. between 6–7 mm radial growth per year, corresponding to an annual diameter increment of 12–14 mm (Gourlay & Barnes 1994; Gourlay 1995).

In all samples of known age in this study, the number of rings defined by marginal parenchyma bands with crystalliferous chains could be related to the age of the tree. The annual frequency of these bands corresponded to the number of peaks in the rainfall distribution at the geographic origin of the sample. Elucidation of this pattern in areas of bimodal rainfall distribution requires more precise information describing the origin of a particular sample and closer examination of the growth zones, than with trees from unimodal areas (Gourlay 1995). Minor discrepancies, of the order of two or three years, which were found in some cases could be accounted for by uncertainty as to the precise time of establishment, variation in the age of transplanting of some individuals sampled, and sample collection at a height approximately of 1.3 m rather than at ground level.

The important influence of aridity on the occurrence of crystals in wood has been observed by several authors (e.g. Kingsbury 1964; Carlquist 1988: John 1990). Fahn et al. (1986), for example, found crystals to be more numerous in wood from the tropics than temperate regions and in wood from desert areas rather than those with more water availability.

In addition, the results from the SPM show a concentration of many important elements asssociated with the crystalliferous bands, suggesting that the tree concentrates various salts and metals as well as calcium oxalate in woody tissues at this time of the year (Gourlay & Grime 1994). Probably the most comprehensive overview of calcium oxalate crystals in plants is that presented by Franceschi and Horner (1980).

The influence of the form of rooting profile and the interaction between climate and the geology of the sites are probably the most likely explanations for the considerable variation in correlations between species at different sites and the various meteorological parameters. In arid environments, it is important for the survival and development of the tree that its roots reach the water table as quickly as possible. Genetic variation in root development appears to be considerable, as was illustrated for African *Acacia* spp. by Vandenbeldt (1991). He found that, in a trial planted in Niger with *Faidherbia albida* from 32 African provenances, seedlings of west African origin survived in the regularly drought-stressed region of the trials, whereas provenances of southern and eastern African origin did not. On this basis he proposed two ecotypes. a riparian/lowland type of the south and east, requiring a high water table to survive droughts, and a west African plateau type adapted to seasonal droughts and deep water tables. He also found differences between these ecotypes in the emerging root system, particularly in the degree of natural aggressiveness of the tap root.

Several of the correlations calculated in this study indicate that tree growth is strongly influenced by rooting characteristics in combination with water availability. In the case of *Acacia fleckii* Schinz. from southern Zimbabwe, for example, a species known to be a shallow rooting tree, the results indicated a good visual fit when ring width was plotted against current annual rainfall. Similarly for *Faidherbia albida* from central Malawi the introduction of a one-year lag in rainfall produced an improved visual match for a species commonly found in riverine situations in east Africa. The latter two cases, therefore, suggest that shallow rooting trees are more sensitive to current rainfall, whilst deeper rooted trees are able to reach a more permanent water table.

The reservations expressed earlier in this paper regarding the suitability of the type of correlation used and the influence of outlying points in relatively young sample trees could limit the confidence that can be placed in these results. With more data and more sophisticated analyses, the cross matching of tree ring sequences for areas in Africa might be possible and studies with climate and archaeology contemplated. The difficulties of sampling and examining hard, dark, and often gum-filled tropical species will, of course, remain. However, through the process of identifying seasonal growth changes in the wood anatomy it has been the conclusion of this work that in fact many *Acacia* spp. are probably far younger and of considerably faster annual increment than people commonly believe.

ACKNOWLEDGEMENTS

The author would like to express his appreciation to many people for their help in this work. First, to some of the people who helped with the locating and provision of samples and information in the field: Jennifer Bickle, Paul Camp, Chris Fagg, Dr. René Haller, Gary Olver, Tom Muller and in particular Dr. Richard Barnes. My thanks, too, to several members of the Oxford Forestry Institute, in particular John Baker, Margaret Evans. Peter Frauklin, Bernard Lobo, Julie Smith and Chris Walker. Thanks also to the members of the staff at the Oxford Scanning Proton Microprobe and to the Overseas Development Administration for financially supporting this research.

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