University of Pretoria etd – Steenkamp, C J (2000)

CHAPTER 4

LITERATURE REVIEW ON DENDROCHRONOLOGY

4.1 DENDROCHRONOLOGY AND ITS APPLICATION TO TROPICAL TREES

Dendrochronology can be defined as the science of dating annual growth layers (rings) in woody plants and the use of the information they contain to manage the plants and the environment (Fritts 1971).

Dendrochronology is based on the biological principle that a tree grows both apically and radially each growing season; the radial increase being visible as a distinct ring on a transverse section of certain trees (Curtis *et al.* 1979). It is well known that the age of a tree which produces annual growth-rings can be estimated by counting the rings present in a portion of the stem as close to the ground as possible (Fritts 1976).

The science of dendrochronology has centred around the strong tendency of coniferous trees in temperate areas to produce an identifiable layer of wood each year (Jacoby & Wagner 1993). However, in the tropics, sub-tropics and semi-arid regions, only an annual period of cambium dormancy, such as would be incurred by an extended dry season, would result in a similar growth pattern (Jacoby & Wagner 1993). The major difficulty in applying dendrochronological techniques to tropical areas has been in ascertaining if growth-rings are formed annually (Ogden 1981).

The ability to develop growth layers is determined by the genetic constitution of the particular species and is found in trees of both temperate and tropical zones. A growth layer is usually a product of one season's growth, but various environmental conditions may induce the formation of more than one growth layer in one season (Esau 1977).

Dendrochronologists are concerned with patterns of variability in tree ring width measurements, their correlation from tree to tree, site to site or their relationships to environmental influences, particularly climate (Ogden 1981). Moreover, a correlation of patterns of wide and narrow rings between trees can be used to establish the year in which the rings were formed. Such dating of rings is possible due to the fact that tree growth, in terms of changes in ring widths, is often affected by variations in climate (Fritts 1976; Curtis *et al.* 1979).

Stokes and Smiley (1968), as quoted in Curtis *et al.* (1979), pointed out that four conditions are imperative for a dendrochronological study:

- It is essential that only one ring be laid down per growing season.
- There must be one environmental factor which is dominant in limiting growth.
- The limiting factor must vary in intensity from year to year.
- The limiting factor must be uniformly effective over a large geographical area so that samples from different areas may be cross-dated.

The most suitable trees for dendrochronological studies are those growing in somewhat stressed environments or environments with significant seasonal variations, for example high altitude or semi-desert conditions. In these environments narrow rings occur as a result of slow growth. Any variation in moisture or temperature is reflected in the tree ring sequences, producing alternating wide and narrow ring-width patterns. In contrast, particularly in the tropics, the absence of seasons and of extremes in rainfall and temperature are largely responsible for poorly defined tree rings.

According to Wyant and Reid (1992), even though rings might be missing or poorly demarcated, dendrochronological techniques provide an improvement over size measurements for determining tree ages.

4.2 DENDROCHRONOLOGICAL POTENTIAL OF ANGIOSPERMS

The secondary vascular tissues in a tree are produced during the second major stage of plant development, in which an increase in thickness results from lateral additions of new tissues to the axial parts of the plant. This results from the activity of the vascular cambium (Figure 4.1). Successive growth layers are formed. Each growth layer may be a product of one season's growth, but various environmental conditions may induce the formation of more than one growth layer in one season (Esau 1977, Fahn 1982).

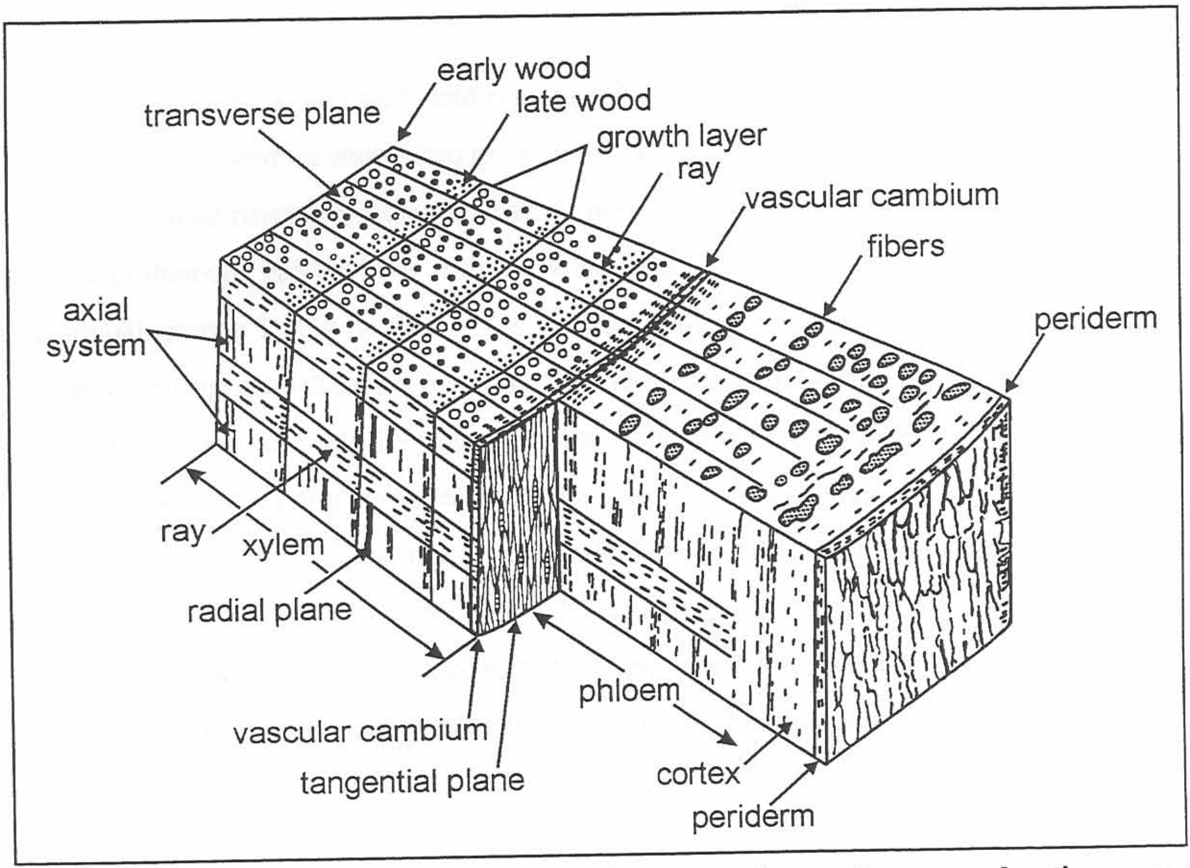

Figure 4.1 Block diagram illustrating basic features of secondary vascular tissues and their spatial relation to one another and to vascular cambium and periderm (after Esau 1977).

When conspicuous layering is present each growth layer is divisible into early and late wood (Figure 4.1). Early wood is the distinct inner component of a growth-ring, formed during the first part of the growing season whereas late wood constitutes the distinct outer component of the growth-ring. The early wood is less dense than the late wood because wider cells with thinner walls predominate in the early wood and narrower cells with thicker walls in the late wood (Esau 1977; Fahn 1982). The late wood forms a distinct boundary in a growth-ring because of its sharp contrast to the early wood of the following season, but the change from early wood to late wood of the same growth layer is more or less gradual. The earlier increments of secondary xylem

University of Pretoria etd – Steenkamp, C J (2000)

become nonfunctional in conduction and storage. The relative amounts of the non-functioning wood, the heartwood, vary in different species and are also affected by environmental conditions. The heartwood is the non-living and commonly darker-coloured wood at the centre of the tree, which can be distinguished from the outer living part of the trunk, the light-coloured sapwood (Esau 1977; Fahn 1982).

In tropical, sub-tropical and semi-arid regions the majority of trees are angiosperms. Angiosperms frequently produce anomalous growth patterns and rings which, for the most part, are not necessarily annual rings. For example, a stress period may occur during a growing season and cause more than one growth layer to form within that year. These growth features are termed intra-annual growth bands or false rings (Fritts 1976). Alternatively, when conditions are extremely limiting, growth cannot occur and no ring is produced. Locally absent or missing rings may occur during excessively dry years with little or no growth. Certain regions of the cambium may not divide at all giving the appearance of a missing ring (Fritts 1976; Lilly 1977; Curtis *et al*. 1979; Gourlay 1995). False rings are dark late wood- type bands in light early wood which give the appearance of an extra ring. The exact cause of false rings is not known, but may be related to sudden abnormal weather conditions, insect infestations, disease or some other factor temporarily halting growth (Curtis *et al*. 1979). Dating may be complicated due to the occurrence of missing and/or false rings.

Lilly (1977) noted that, unlike gymnosperms where a ring margin is clearly demarcated by a change in density, angiosperm ring margins can be delimited in various ways which are not equally distinct. In gymnosperms we find only two unfavourable growth features (false and missing rings), whereas in angiosperms there are five features which reduce the clarity of ring margins. Angiosperm wood is composed of a large variety of cell elements arranged in different ways and a standard angiosperm ring structure does not exist. Instead numerous combinations of cell types give rise to an infinite number of ring-structures.

Angiosperm ring-structures

The following five ring features can occur in any number of combinations (Lilly 1977):

- **Boundary/marginal parenchyma**

Certain species produce longitudinal parenchyma strands either at the end or the beginning of a growth season and are referred to as boundary or marginal parenchyma. The fineness of marginal parenchyma can be a disadvantage when it is blurred or hidden by dense paratracheal parenchyma. It is advantageous if marginal parenchyma is the only form of parenchyma present.

- **Ring porosity**

Ring porosity is the only form of angiosperm growth structure in which early wood and late wood are as well defined as in the gymnosperm growth-ring and where there is a similar marked change in density. It is due to this similarity that dendrochronologists have used ring-porous woods in preference to any other dicotyledonous wood structure. Lilly's (1977) survey of 115 species indigenous to South Africa indicated only one indigenous ring-porous tree i.e. *Celtis africana*.

- **Dense late wood lines**

Angiosperm growth-rings mostly consist of early wood with a fine late wood margin; unlike gymnosperm rings which are made up of two distinct sections. As the change in density is minimal, a sharp contrast is not produced between rings.

- **Semi-ring-porous structures**

It is generally agreed that a ring-porous structure consists of early wood pores which are both larger and more numerous than late wood pores and consequently form a well defined ring. Various gradations of ring-porous structure exist, four of which are specific enough to indicate a ring-structure:

  - tangential pore alignment;
  - diminution in pore size;
  - reduction in pore numbers; and
  - concentric zone devoid of pores.

- **Growth-related variations in parenchyma patterns**

Certain woods display variations in their distribution of longitudinal parenchyma. Only metatracheal and confluent parenchyma tend to be strongly modified as the growing season advances.

The marked changes in parenchyma distribution which indicate the positions of ring margins are:

- concentrations of metatracheal parenchyma;
- coalescence of confluent bands; and
- concentric zones free of parenchyma.

Generally, the clarity of ring margins outlined by variations in parenchyma distribution is highly variable. Frequently, only the approximate positions of ring boundaries are indicated. For this reason changes in parenchyma arrangement cannot be relied on as sole indicators of ring margins, although it is valuable as an additional feature which aids in highlighting and delimiting rings (Lilly 1977).

Only two of the five basic types of angiosperm growth-rings mentioned above are commonly recognised as ring-structures; these are ring porosity and an increase in wood fibre density. Of these only the former has been used in American and European dendrochronological studies. It can therefore not be taken for granted that the remaining four types of ring margins reliably delimit seasonal growth increments. The seasonality of these different forms of ring-structure within particular trees must first be determined before correlation between ring width and various environmental controls can be made (Lilly 1977).

The appearance of a particular type of angiosperm ring-structure does not automatically ensure that the wood is suitable for dendrochronological purposes. The manner in which the favourable and unfavourable anatomical features of angiosperm xylem interact must be taken into account when assessing the dendrochronological potential of a particular hardwood species (Lilly 1977).

Lilly (1977) devised a rating system taking into account all favourable and unfavourable characteristics in order to evaluate the ring-structures of indigenous woods. The criteria chosen for the rating system are listed in descending order of dendrochronological suitability (Table 4.1). These features contribute either positively or negatively to the clarity of the ring margins and have been rated accordingly. The summation of these positive and negative values equals the final dendrochronological rating (DR) (Table 4.1). The system ultimately determines which trees have a structural combination suitable for dendrochronological purposes.

Table 4.1 Criteria used in rating dendrochronological potential of indigenous South African plant species (after Lilly 1977)

Criterion Rating	Criteria
7	Slow growth rate (6-14 rings per cm)
6	Boundary parenchyma
5	Ring porosity
4	Denser late wood fibres
3	Semi-ring-porous structures
2	Growth-related variations in parenchyma patterns
1	Evidence of a ring-structure
0	Diffuse porosity
-1	Sapwood/heartwood differentiation
-2	Banded parenchyma
-3	False or disjointed rings
-4	Missing or discontinuous rings
-5	Indistinct boundaries
-6	Fast growth rate (3 rings per cm)
-7	Macroscopically deceptive ring pattern

Depending on the dendrochronological rating (DR) of a species it can then be divided into the following three categories:

(a) promising species: $DR > 5$;

(b) possible species: $0 \leq DR \leq 5$;

(c) rejected species: $DR < 0$.

Most indigenous angiosperms are hardwood species that impede coring (the standard method of collecting wood samples). They also have extremely complicated ring structures and many have no discernable structures at all. Lilly (1977) suggests that among South African angiosperms only *Albizia forbesii, Burkea africana, Clutia abyssinica, Ekebergia capensis, Fagara davyi, Rhus pyroides* and *Vepris undulata* show a sufficiently high dendrochronological potential to warrant further study.

University of Pretoria etd – Steenkamp, C J (2000)

Evaluating the dendrochronological potential of ring structures

According to Lilly (1977), wood anatomists do not always recognise boundary parenchyma as a ring-structure. Boundary parenchyma is frequently blurred or hidden by dense paratracheal parenchyma, especially if it is confluent or banded. Obviously it is advantageous if marginal parenchyma is the only form of parenchyma present. The fineness of marginal parenchyma can however be a disadvantage as the bands are not easily recognised when the ring structure is complex.

While a single layer of radially compressed fibres does create a definite boundary between rings, thicker-walled cells tend to produce a gradual transition between increments, which becomes increasingly apparent with higher magnification.

The following difficulties are faced in dendrochronological studies where identification and counting of marginal parenchyma bands (growth-rings) are used:

- confusion with other wood parenchyma (Détienne 1989; Gourlay & Kanowski 1991; Gourlay & Barnes 1994; Martin & Moss 1997);
- inability to be certain of the presence of a growth-ring where it can not be traced around the circumference (Jacoby 1989; Worbes 1989; Gourlay & Kanowski 1991; Gourlay & Barnes 1994);
- detecting rings where they are very narrow (Mariaux 1981; Détienne 1989);
- identifying rings near the cambium (Mariaux 1981);
- identifying rings near the pith (Fahn *et al.* 1981; Gourlay 1995);
- merging or dividing rings (Gourlay & Kanowski 1991; Martin & Moss 1997);
- different numbers on different radii (Mariaux 1981);
- false rings (Curtis *et al.* 1979; Fahn *et al.* 1981; Détienne 1989; Gourlay 1995);
- incomplete, discontinuous rings (Fahn *et al.* 1981; Ogden 1981; Gourlay & Kanowski 1991);
- dark heartwood and other changes in wood colouration (Gourlay & Kanowski 1991; Martin & Moss 1997);
- missing rings (Curtis *et al.* 1979; Détienne 1989; Wyant & Reid 1992; Gourlay 1995);

University of Pretoria etd – Steenkamp, C J (2000)

- variation in ring width (Worbes 1989); and
- rings with ill-defined boundaries (Ogden 1981).

4.3 DENDROCHRONOLOGICAL POTENTIAL OF INDIGENOUS AFRICAN TREES

The estimation of tree ages in southern Africa and in tropical, sub-tropical and semi-arid areas in general, has been problematic due to the lack of distinct growing seasons and corresponding climatic extremes. The lack of distinct ring boundaries and the frequency of anomalous growth patterns have hindered the science of dendrochronology in southern Africa. Little information is therefore available on growth-ring characteristics in indigenous trees.

Although dendrochronology is not a common practise in South Africa, attempts to introduce tree ring analysis have been made in neighbouring countries (Curtis *et al*. 1979). The earliest dendroclimatic investigations were carried out in Namibia by Walter (1940) who analysed the ring widths of *Acacia erioloba*. Although Walter could not identify growth-rings with certainty, he found that ring-width correlated positively with rainfall (Walter 1940).

In the wood of *Acacia erioloba*, ring margins are demarcated by strands of disjointed boundary parenchyma which are poorly defined. The distinctness of ring boundaries is further reduced by wide aliform-confluent parenchyma (Figure 4.2). This probably explains why Walter (1940) could not identify the growth-rings with certainty.

In investigations carried out by Guy (1969) in Zimbabwe on *Adansonia digitata*, no correlation was found between ring width and rainfall, although it was suggested that *Adansonia digitata* does offer some evidence that annual rings are produced.

In a preliminary dendrochronological study of seven indigenous species in Zimbabwe, Storry (1975) found five of the species i.e., *Rapanea melanophloeos, Macaranga capensis, Maesa lanceolata, Hypericum revolutum* and *Acacia abyssinica* unsuitable for normal dating techniques because no recognisable growth patterns could be distinguished in the sample cores. Storry (1975) also recorded the difficulty of obtaining suitable cores.

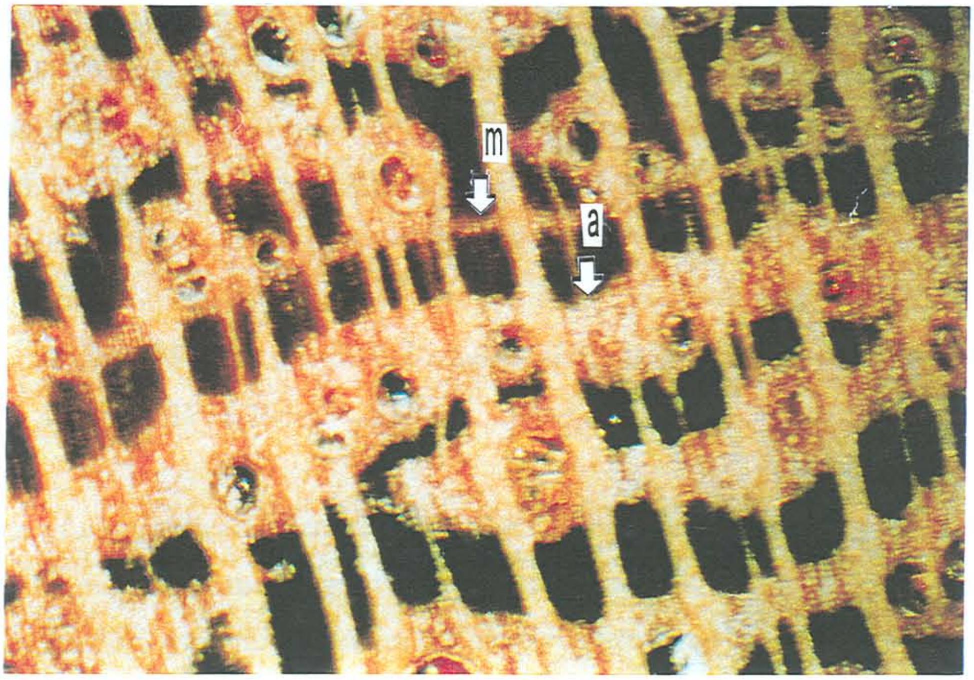

Figure 4.2 **Wide aliform-confluent (a) parenchyma and thin marginal (m) parenchyma visible in a transverse section of a sanded disc of *Acacia erioloba* from the Kalahari Gemsbok National Park (4x magnification).**

According to Lilly (1977) macroscopic and microscopic characteristics of the wood anatomy of a very limited number of southern African trees were described in early publications. However a comprehensive microscopic identification key which describes transverse, radial and tangential surfaces of 136 of South Africa's most important indigenous trees was subsequently compiled by Kromhout (1975). Unfortunately, although the occurrence of distinctive rings is mentioned, Kromhout gives no definite information on the appearance of ring-structures. A survey by Lilly (1977) to determine the dendrochronological potential of 108 South African tree species, is probably the most extensive on African tree species. Lilly (1977) concluded that indigenous tree species in South Africa are not as well suited to dendrochronological studies as their European and North American counterparts. Lilly's work was followed by a study of the wood anatomy of 37 *Acacia* spp. by Robbertse *et al.* (1980).

Tree ring research in southern Africa appears to have been hampered by a lack of suitable species (Lilly 1977; Curtis *et al.* 1979). Problems encountered include indistinct ring boundaries, severe ring wedging and short life spans (Norton 1990). The occurrence of clearly defined boundary parenchyma in a few hardwood species however does indicate their possible successful application in dendrochronological work.

4.4 ANATOMICAL FEATURES USEFUL IN DEFINING GROWTH ZONES IN *ACACIA* SPECIES

The specific anatomical characters responsible for delineating growth-rings vary greatly between different tree species, and the growth zone is often incomplete when traced around the circumference of a disc. Anatomical features that clearly denote annual growth-rings in temperate trees, such as ring-porous wood and pronounced cell-wall thickness and dimensional changes, are uncommon in tropical species. Tropical woods are typically diffuse in their anatomical structure and exhibit predominantly parenchyma (Gourlay 1992).

4.4.1 MARGINAL PARENCHYMA

Several forms of parenchyma occur in *Acacia* species. The two main forms of banded parenchyma are apotracheal bands, which are independent of the vessels, and paratracheal bands which are associated with the vessels. Both forms can complicate the determination of growth-rings by producing light coloured concentric bands that give the appearance, to the inexperienced observer, of regular growth-rings. Irregular convoluted paratracheal bands, much broader than the marginal parenchyma, often obscure the much finer marginal parenchyma bands (Figure 4.3) (Gourlay 1995).

It is generally accepted by botanists that marginal parenchyma is either initial or terminal; that is, it occurs at the beginning or the end of a growth-ring (Lilly 1977). Parenchyma formation and reduced vessel size appear to correspond with slow growth, which can arise through a variety of environmental stresses (Ogden 1981).

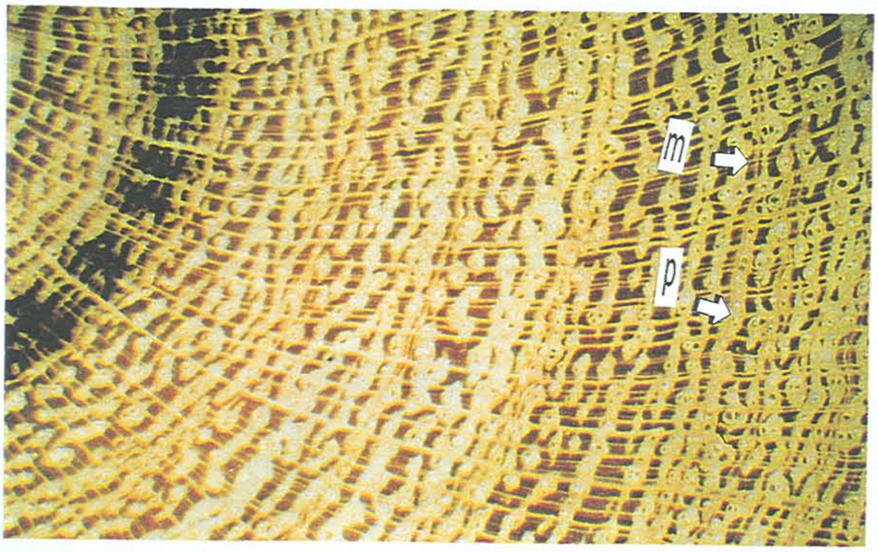

Figure 4.3 **Transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park showing marginal (m) parenchyma bands obscured by broader, convoluted paratracheal (p) bands.**

According to Mariaux (1975), as quoted in Gourlay (1995), the paratracheal bands produce patterns of decreasing and increasing frequencies at a growth-ring boundary where the feature positively assists in identifying the growth-ring zone (Figure 4.4).

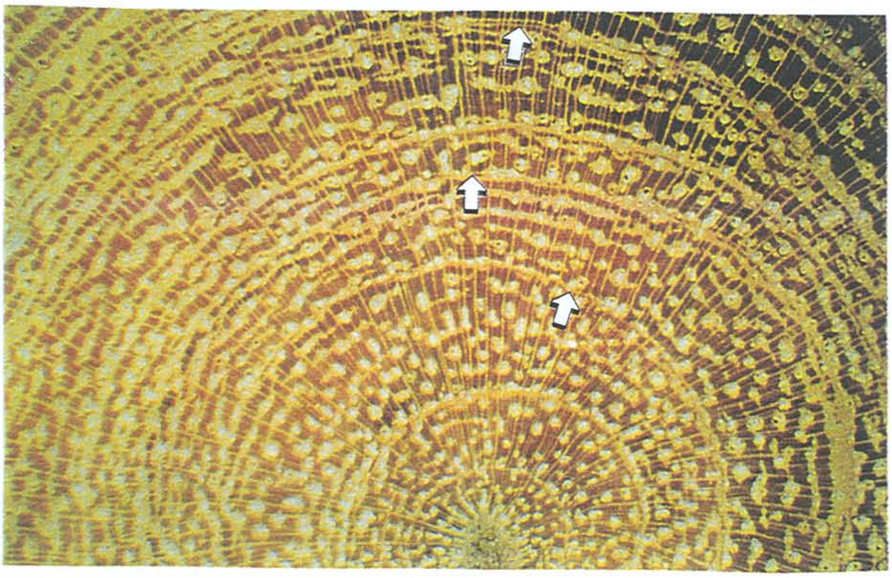

Figure 4.4 **Growth-ring boundaries (arrows) clearly visible on a transverse view of a sanded sample of *Acacia erioloba* from the Kalahari Gemsbok National Park (1x magnification).**

The IAWA Committee (1989) refers to marginal parenchyma as a form of axial parenchyma produced by some tree species in bands (a more or less continuous layer of variable width) at the beginning or end of a growth season. Gourlay (1995) describes these bands as commonly composed of less than five rows of parenchyma cells (Figure 4.5) forming a continuous layer visible on the transverse surface as a fine light-coloured band (Figure 4.6).

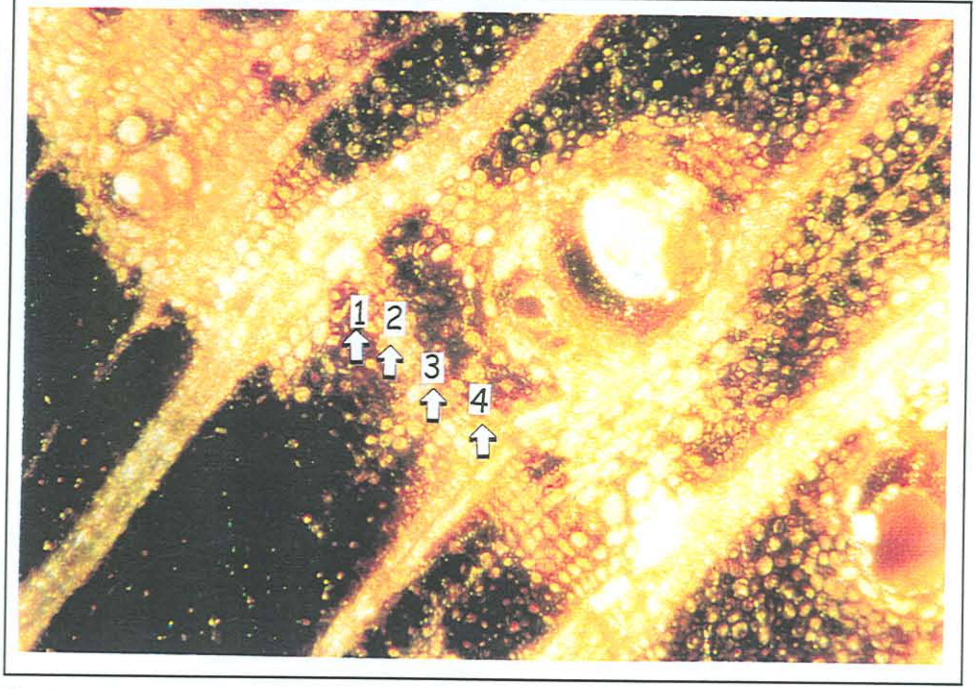

Figure 4.5 Transverse section of marginal parenchyma composed of 4-5 rows of cells (arrow) of a sample of *Acacia erioloba* from the Kalahari Gemsbok National Park (10x magnification).

Worbes (1989) recorded that particular ring types are dominant in certain families. The growth zones of all Fabaceae are for example separated by marginal parenchyma bands. In many trees of the family Fabaceae these bands of continuous marginal parenchyma are filled with amorphous substances or crystals.

Gourlay and Kanowski (1991) examined the growth-rings of six African *Acacia* species. Rings were apparent in most species as narrow bands of marginal parenchyma filled with long crystal chains. The marginal parenchyma bands are extremely difficult to detect due to the presence of aliform-confluent parenchyma, a feature common to most *Acacia* species. The broad bands often mask the finer marginal bands (Figure 4.3). A further complication sometimes arises in the form of merging and or partial rings. They also found that in *Acacia erioloba* marginal parenchyma bands were quite clear with small concentrations of crystals in the marginal parenchyma.

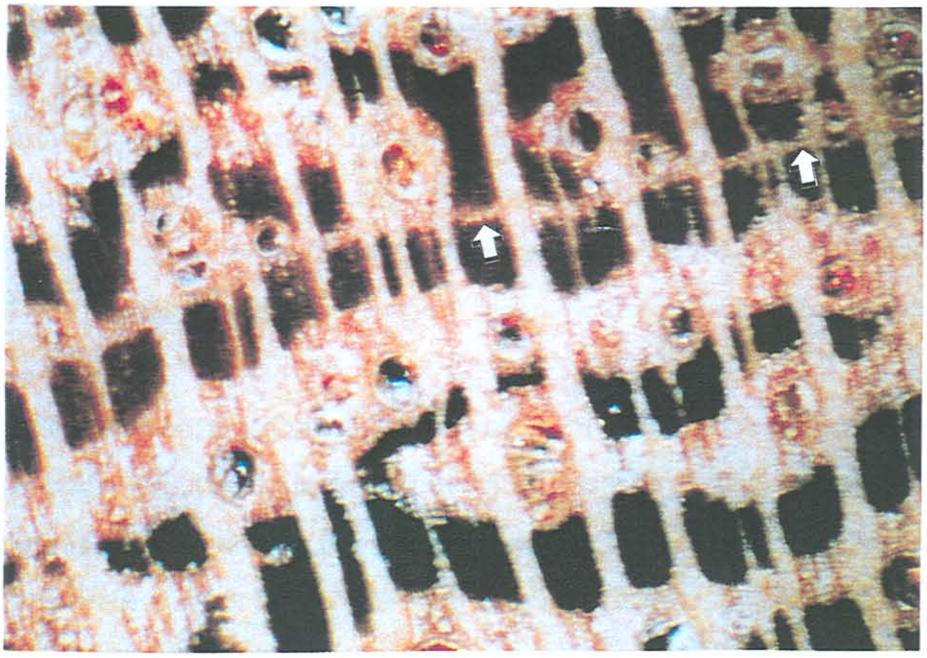

Figure 4.6 Marginal parenchyma visible as a fine light-coloured band (arrows) in a transverse view of *Acacia erioloba* from the Kalahari Gemsbok National Park (4x magnification).

A wide variety of anatomical features define the resulting growth-ring, including early wood/ late wood transitions, bands of marginal parenchyma, alternating patterns of parenchyma and fibres and ring porous structures (Worbes 1989). Détienne (1989) remarks that well-marked boundaries of annual growth-rings are those delimited by marginal bands of parenchyma. These bands are easy to detect in species having mostly paratracheal or apotracheal parenchyma in short bands.

Mariaux (1975), as quoted in Gourlay (1995), suggested that in *Acacia radiana* the real limits of growth are indicated by a very fine line of parenchyma (Figure 4.6), comprised of very flat cells which appear among the fibres where the line rejoins the paratracheal parenchyma. He found it necessary to follow the broad bands of parenchyma to assure himself that a fine line was not associated with them. The number of rings found in most trees was less than that commonly assumed for such trees in an arid environment.

Research by Wyant and Reid (1992) on *Acacia tortilis* in Turkana District, Kenya, demonstrated a significant (r = 0.90) linear relationship between ring count and known tree age. However, they did not identify the anatomical features responsible for this band or qualify its dependence on water by correlating the ring widths with rainfall. They suggested that there is a good possibility that ages of tropical trees can be determined by ring counts in ecosystems with a strongly seasonal, unimodal rainfall pattern. Even though rings may not form every year, the frequency of missing rings may be related to drought frequencies. They found approximately one missing ring for every 3-4 years of growth. This corresponded with the frequency of annual drought, as confirmed by climatic records.

Gourlay (1995) counted rings from individuals of a number of *Acacia* species of known planting date and generally found their number to be slightly less than or equal to the known age in areas with a unimodal rainfall pattern. For trees from areas of bimodal rainfall the number of rings corresponded to the number of peaks in local rainfall records.

On examining *Acacia karroo* it was established that the marginal parenchyma bands were laid down at the beginning of the dry season when wood production ceases (Gourlay 1992). This was also stressed by Ogden (1981), who pointed out that these bands could be formed during times of stress.

Kromhout (1975) described the parenchyma in 13 South African *Acacia* species, including *Acacia erioloba,* as mainly paratracheal and with an indication of marginal parenchyma.

Lilly (1977) gave *Acacia erioloba* a dendrochronological rating of 0 (see Table 4.1). She identified the following tree ring characteristics: boundary parenchyma (6), evidence of a ring structure (1), diffuse porosity (0), banded parenchyma (-2) and indistinct boundaries (-5). She concluded that *Acacia erioloba* could be of possible use in dendrochronological studies.

Robbertse *et al.* (1980) reported growth-rings, consisting of flattened marginal parenchyma or thick-walled fibres present in most species of the sub-genus *Aculeiferum* and a few species of the subgenus *Acacia*. They found banded parenchyma and growth-rings in *Acacia erioloba.*

4.4.2 CRYSTALLIFEROUS CHAINS IN PARENCHYMA

The presence of calcium oxalate crystals in woody tissue is quite common, and their size, quantity and distribution may be used in wood anatomical identification and classification (Chattaway 1956; IAWA Committee 1989; Gourlay & Grime 1994). Crystals in African *Acacia* species have been documented by several authors (Chattaway 1956; Kromhout 1975, Robbertse *et al*. 1980; Fahn *et al*. 1981; Gourlay & Grime 1994).

In African *Acacia* species where samples did not display clear bands of marginal parenchyma, it was possible to define rings by taking radial sections of the complete radius and identifying the crystalliferous chains. In a dendrochronological study of several African *Acacia* species, Crystals are more numerous in arid zone species and occur at the termination of growth periods in some species (Fahn *et al*. 1981; Gourlay & Grime 1994). These crystals proved to be of great value in establishing the presence of a growth-ring in samples where clear bands of marginal parenchyma are not displayed (Gourlay & Grime 1994). By means of a scanning proton microprobe the crystals were subsequently identified as calcium oxalate (CaC_2O_4). The presence of crystals is apparently associated with certain plant families. In the Cactaceae and Chenopodiaceae, the content can reach more than 10% of the dry weight of the wood (Fahn *et al*. 1981).

Prior and Cutler (1992) suggested that the presence of oxygen-bearing calcium oxalate crystals in Zimbabwean *Acacia karroo*, *Acacia tortilis*, *Colophospermum mopane* and *Combretum apiculatum* is a key factor in wood quality and has an important influence on the fire retardant properties in these species as it acts as a flame retardant and promotes a glowing combustion. Calcium oxalate (CaC_2O_4) crystals are formed when tree roots absorb salt-rich water from the soil. The tree removes any excess calcium ions, which combine with oxalic acid, a constituent of cell sap, to produce insoluble calcium oxalate. The calcium oxalate is then stored as large prismatic crystals in many parts of the plant. The presence of calcium oxalate crystals also makes tropical trees less palatable to termites.

John (1990), as quoted by Gourlay (1995), found that, in *Acacia nilotica* subsp. *kraussiana* from Swaziland, growth-rings were sometimes indistinct, although usually marked by a band of marginal parenchyma. The late wood was frequently rich in crystalliferous cells. She also found that the chemical composition or the physical structure of fibre walls often changed abruptly at growth-ring boundaries. The quantity of crystals appeared to increase in the late wood and also in samples from sites with a high level of exchangeable calcium. However, crystal numbers per unit area varied even on some sites with similar soil types and with the same levels of calcium and magnesium in the soil. The only observable difference in these sites appeared to be water availability. She also noted that the crystals increased in quantity with the dryness of the site. At sites where the crystals were more numerous, growth-rings were more clearly defined.

4.5 RELATIONSHIP BETWEEN WOOD ANATOMY AND CLIMATIC VARIABLES

A primary cause of annual ring variations in trees is climate. If the climate is consistent over large enough areas, trees will cross-date over distances from tens to hundreds of kilometres (Jacoby & Wagner 1993). A problem in studying environmental effects on growth is that the relative importance of an environmental factor can change during the growing season (Kramer & Kozlowski 1979). Conditions preceding the growing season sometimes have a greater influence on ring width than conditions during the growing season. The relative effects of these factors on growth vary with latitude, altitude and environmental factors at the site. Climatic factors are sometimes directly related to the growth and at other times are inversely related to growth. Statistical methods are employed for ascertaining these differences in the climatic response of trees from different sites (Fritts 1971; Kramer & Kozlowski 1979).

An abrupt change in the environment does not alter growth similarly in all trees of the same species in a stand. This may be the result of differences among trees in exposure, crown size, depth of rooting, inherent growth characteristics, and other causes, including micro-environmental heterogeneity (Kramer & Kozlowski 1979).

Numerous studies applying dendrochronological techniques to temperate species suggest that wood anatomy provides a lasting and reasonably accurate record of trees' reaction to the environment (Schweingruber 1988). The reaction mechanisms in trees are very complicated (Figure 4.7). Chain reactions are set up between the influencing environmental factors and the parts of the tree which react to these influences (Fritts 1971).

University of Pretoria etd – Steenkamp, C J (2000)

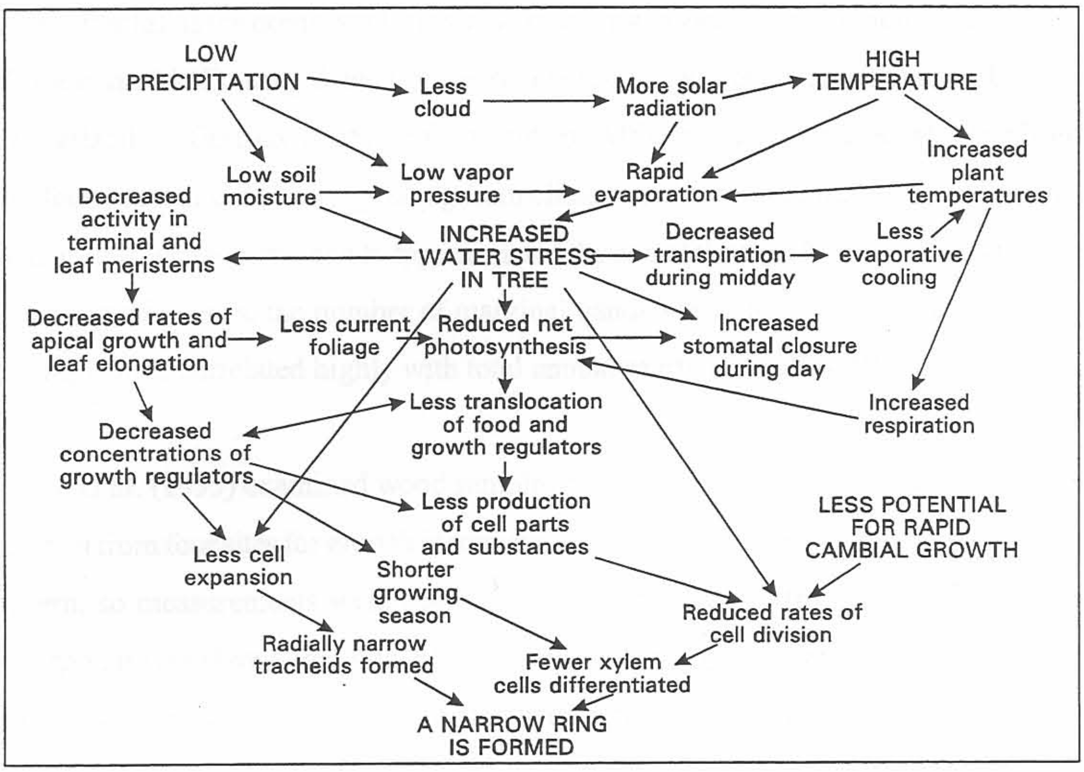

Figure 4.7 **Physiological model illustrating how low precipitation and high temperature during the growing season (season of cambial activity) may cause a ring to be narrow for conifers growing on semi-arid and warm sites** (after Fritts 1971).

Physiological processes initiated by a change in the environment eventually become directly measurable as a growth change or evident in the variation of such features as tree ring width. Growth-rings can therefore be used to investigate relationships between tree growth and climate by comparing annual variations in ring width with annual variations in the climate of the area of study (Fritts 1976). Schweingruber (1988) agrees that the growth-rings of trees are of ecological significance because of the periodicity of their formation. Growth-rings can therefore be related to age.

Although periodic cambial growth in tropical trees is genetically determined, it can be influenced by climate. While the phenological patterns of shoot development are linked to periodicity of cambial activity, the exogenous influences, other than temperature, are only likely to affect the cambium directly. Of all the climatic factors, temperature plays the major role in regulating the cambial activity and phenological events. In desert conditions however, the amount of water in the soil becomes the limiting factor (Mushove *et al.* 1995).

In general rainfall is the dominant factor in determining growth in arid regions (Fahn *et al.* 1981; Mushove *et al.* 1995). Ring formation in *Acacia* species is closely associated with changes in water availability (Gourlay 1995). In their study of African *Acacia* spp., Gourlay and Kanowski (1991) found that in samples originating from climatic zones with a single wet season, the number of marginal parenchyma bands approximated the age of the tree. In samples originating from bimodal climatic zones, the number of marginal bands were more or less twice the age of the tree. Ring widths correlated highly with total annual rainfall (Gourlay 1995).

Mushove *et al.* (1995) examined wood samples of *Colophospermum mopane* and *Combretum apiculatum* from four sites for growth increments. Increments were small and sometimes difficult to discern, so measurements were made to the nearest 0,1 mm. In contrast to the studies on *Acacia* spp., it was shown that rainfall and its corresponding interactions with site and species were of no significance in explaining differences in tree ring widths.

Gourlay and Kanowski (1991) stress that the development of ecological understanding and sustainable management practises for the natural tropical forests depend partly, on reliable means of estimating the age and growth rate of trees, but are quick to point out how difficult the identification of growth-rings in certain tropical species can be. Others working on the wood anatomy of tropical trees also agree that it can be difficult to establish whether all visible growth-rings in tropical trees correspond to annual increments (Lilly 1977; Ogden 1981; Van Daalen *et al.* 1992).

The primary problem in tropical tree ring analysis is the frequent lack of well-defined cyclical growth-rings. Absence of seasonality (which induces dormancy and associated anatomical change) is the main reason for this problem. Temperatures are relatively uniform throughout the year and the daily temperature fluctuations often exceed the annual fluctuations. There is no annual cold season to induce dormancy in the trees (Fritts 1976).

Boundaries of annual growth-rings are always formed during the longest dry season and clearly express the rhythm of cambial activity. The appearance and nature of these growth-rings vary according to genera rather than types of climate (Détienne 1989).

The widths of growth-rings in woody plants can serve as natural records of climate when they vary as a function of some limiting factor. In arid and semi-arid regions, ring widths have been shown to vary directly with the intensity and duration of drought. In mature trees on arid sites a growth layer may have approximately the same average width throughout the main stem except in the uppermost, exposed portions of the tree where it is often narrower (Fritts 1971).

In cases where rings are not formed every year, the frequency of missing rings may be related to drought frequencies. Extensive cross-dating should account for missing rings (Fritts 1971).

Tree rings are the most geographically widespread entity that can provide actual year-to-year-dating of current and prehistoric environmental changes (Jacoby & Wagner 1993).

4.6 ALTERNATIVE METHODS OF DETERMINING AGE

4.6.1 STEM DIAMETER AND HEIGHT

In most studies of forest tree dynamics it is common practise to age a sample of the trees studied. Using the resultant age-diameter relationship, the ages of the remaining trees are then estimated based on their diameters. There are, however, some serious limitations associated with this approach. Because of the considerable uncertainties involved in determining the age of individual trees, an unavoidable error is built into the age-diameter model. The magnitude of this error is usually unknown (Norton & Ogden 1990).

In many cases age and diameter are not closely related. This arises largely because competition among trees causes marked differences in growth rates and is often best seen in even-aged stands where a wide variation in diameters can be found. Clearly there are very real limitations in the use of size class data to determine age structures. Even if the relationship between age and diameter is statistically significant, as it often is, it may still be misleading to predict age from diameter because of the large variance in age for any diameter class (Norton & Ogden 1990).

Phenological observations may be very helpful in denoting species and locations where a definite cessation of growth would be likely to produce an anatomical feature marking dormancy and restart of radial growth. Some phenological studies include recordings of diameter growth, although diameter changes often respond to hydration and dehydration rather than cell division. Hydration and dehydration can occur on a daily and seasonal basis and such variations must be considered in diameter growth studies (Jacoby 1989).

Early work on diameter measurement and anatomical studies is reviewed by Mariaux (1981) and Fahn *et al.* (1981).

Nicholson (1965), as quoted by Ogden (1981), stressed that in natural forest stands radial growth increments vary greatly between individuals within species and size classes. He reasoned that a more reliable estimate of age might be obtained by averaging only the fastest growing individuals in a size class in proportion to their representation in the size class above.

In their study of *Acacia tortilis* in South Turkana, Kenya, Wyant and Reid (1992) found that although the correlation between basal stem diameter and known age is high, stem diameter may be useful only for predicting the age of young trees. After about 10 years the scatter around the regression line becomes large.

These difficulties clearly highlight the need for careful sampling and sample analysis in age determinations. Where possible the utilization of cross-dating techniques will greatly increase the accuracy of the age estimates. These will assist in obtaining more accurate information on the ecology and dynamics of forest trees (Fritts 1971; Norton & Ogden 1990).

4.6.2 RADIOCARBON DATING

During an international workshop entitled "Age and growth rate of tropical trees: New directions for research", Stuiver *et al.* (1981) proposed the use of radiocarbon to establish age and growth rates in tropical trees.

There are three isotopes of carbon which occur in nature: two stable isotopes, ^{12}C and ^{13}C and the unstable or radioactive isotope ^{14}C. The latter is produced in the atmosphere by cosmic rays and,

University of Pretoria etd – Steenkamp, C J (2000)

after oxidation, is mixed with the carbon dioxide in the air. Through photosynthesis this isotope mixture is incorporated into living plants and, subsequently through consumption into the bodies of animals (Vogel 1969). The organic compounds in living organisms thus acquire a defined relative concentration of radioactive ^{14}C. The ^{14}C level of the carbon in such compounds will then slowly decrease by radioactive decay with a half-life of 5730 years. This forms the basis of the radiocarbon dating technique. By measuring the ^{14}C level in such material the age can be calculated. The statistical uncertainty of the age is normally ±50 years or in the case of high-precision dating ±20 years can be achieved.

Initially it was assumed that the cosmic ray flux and therefore the ^{14}C level in the atmosphere had remained constant in the past. It was found, however, that fluctuations did occur through time and adjustments need to be made to the radiocarbon ages to arrive at the historical date (De Vries 1958). For trees older than 350 years this calibration is usually straight forward, but in the period between 1650 and 1955 relatively large variations did occur and a precise date cannot be given. In the ageing of a tree calibrated dates can, however, be obtained by analysing two or three samples at increasing radial depth through the trunk (Talma & Vogel 1993). The calibration curve for this time-period is shown in Figure 4.8.

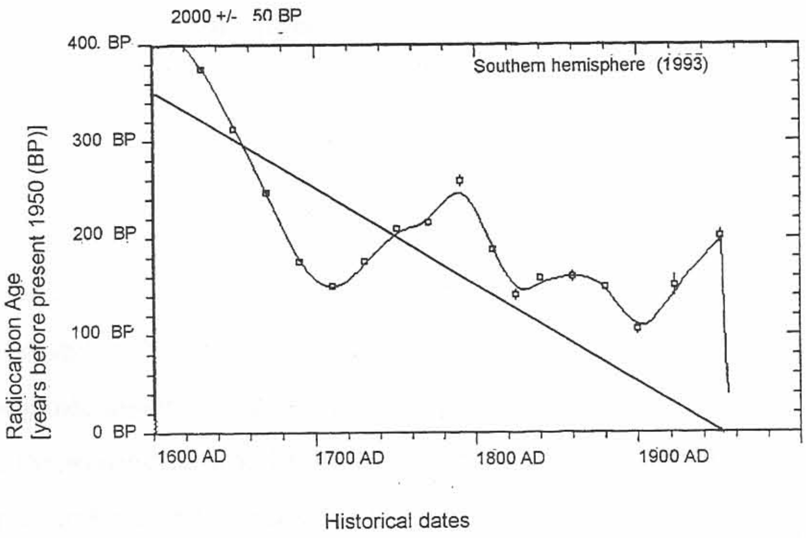

Figure 4.8 Calibration curve for ^{14}C age in years before present (BP) 1950 for the southern hemisphere. (The diagonal line gives the expected correlation between historical dates and ^{14}C age in the case of a 1:1 correlation. The curved line shows the actual calibration curve for the period 1600 AD to 1950 AD).

In the second half of the 20th century the situation changed completely. The atmospheric nuclear weapon tests conducted between 1954 and 1962 drastically increased the ^{14}C content of the environment. The effect of this artificial ^{14}C on the carbon dioxide in the air is shown in Figure 4.9. In the southern hemisphere the level reached a value of 65% above normal in 1965 and has subsequently gradually decreased to about 10% above normal in 1998 (Vogel 1971; Vogel *pers. comm.* 1998[1]). Using this curve for calibration, material in this time range can be dated to ±1 year (Figure 4.9).

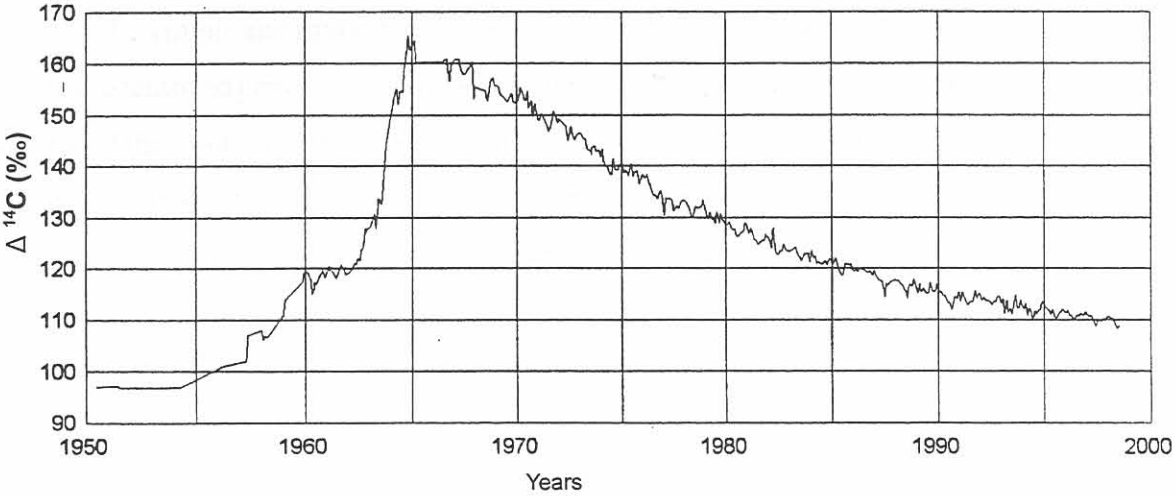

Figure 4.9 ^{14}C content of atmospheric carbon dioxide in recent years, expressed in per mille above normal, extended (after Vogel 1971).

Owing to the variations in the atmospheric ^{14}C level briefly outlined above, radiocarbon dating of plant material may involve considerable effort. In determining the age of a tree the first step would be to date the inner annual growth-rings of the trunk (Vogel 1971; Ogden 1981). If the age lies between 130 and 230 years, two or three further samples along the radius would indicate which of the possible historical dates actually apply to the core. With sufficient measurements one can locate the individual wood sample on the ^{14}C curve for recent decades. One can also place the samples in time and interpolate or extrapolate for ages of other portions on the same radius of the sample. If one assumes a relatively uniform, or at least predictable, growth rate

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[1] Vogel, J.C. Quaternary Dating Research Unit, Division of Water, Environment and Forestry Technology, CSIR, Pretoria, South Africa

University of Pretoria etd – Steenkamp, C J (2000)

through time, the age of the tree can be estimated. ^{14}C measurements are expensive and it is possible to estimate growth rates by using only two samples of the same radial dimension (Jacoby 1989). Lacking this, other considerations may be used to arrive at the "most probable" age for the specimen.

With the dating of wood there arises a further complication in that the sample may contain organic matter that is younger than the annual rings themselves. During the formation of the heartwood, organic substances that are up to 20 years younger than the annual rings are deposited in the cells. If this organic carbon derives from after 1957 this would significantly increase the ^{14}C level of the sample and make it appear younger. As a rule all organics that are soluble in acid and alkali are removed prior to analysis (AAA method), but this may not be adequate in all cases. The degree of this contamination depends on the species and is not yet well known. The problem can be overcome by preparing pure cellulose from the sample, since this carbon definitely dates to a single year (Van Daalen *et al.* 1992; Kromer & Becker 1995).

Archaeologists have always favoured wood as material for radiocarbon measurement. In theory at least the carbon in each annual ring in wood largely represents the production of photosynthesis for that year. Some material is transported in wood rays from the phloem to older wood where it contributes to the formation of heartwood. There may be some synthesis of cellulose in the formation of tyloses in the heartwood formation zone in some genera (e.g. *Quercus* species), but most of the material transported to the heartwoods is in the form of tannins, gums and resins. Most radiocarbon studies of wood employ some form of extraction to remove tannins and resins. Although the ^{14}C activity of each annual ring may thus be specific to the year of formation, problems do occur, as in the case of dendrochronology where missing rings and decayed sapwood must be taken into account.

Radioactive isotopes can be used in many ways to help determine growth rates in trees lacking annual or seasonal growth-rings (Jacoby 1989).

The major disadvantages of the ^{14}C dating technique are the high cost and the time needed for analysis (4 months). It does, however, provide a reliable method for dating tropical trees where rings are often missing or false.

University of Pretoria etd – Steenkamp, C J (2000)

4.6.3 CAMBIAL WOUNDING OR DYE-INJECTION

One of the safest, but most time consuming ways of dating wood is marking by mechanical wounding (Mariaux 1976, as quoted in Worbes 1989) or poisoning of the cambium. The tree is then felled after some years and the number of rings can be compared with the time difference between marking and felling (Détienne 1989; Worbes 1989).

The marking of growth layers by scarring or dye-injection permits precise determination of seasonal changes in radial growth. Periodic sampling of the outermost layers also preserves a record of cambial activity. Subsequent anatomical analysis of samples from either procedure can reveal the sequence of radial growth during a year or preferably years (Jacoby 1989).

Shiokura (1989) describes a method whereby four nails are driven into a tree in a zigzag pattern, one every 3 months (Figure 4.10), at breast height. One year after the first nail was inserted the trees are felled and the amount of wood (barrier zone) formed subsequent to nailing is measured in an area about 1 centimetre above or below the site where the nails were driven in. Due to the distinctness of the cambial response to nailing this method appears to be a simple and effective method for measuring radial increment in tropical trees.

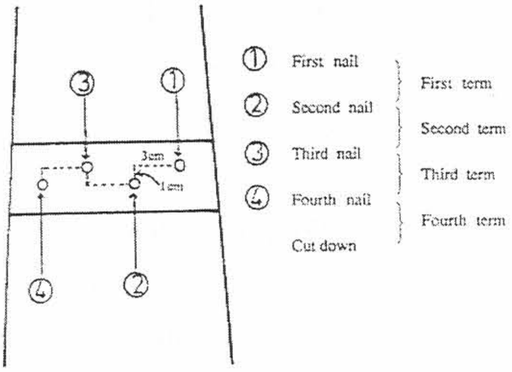

Figure 4.10 Arrangement of nailed locations (after Shiokura 1989).

Results from a periodic wounding study performed by Gourlay and Grime (1994) on *Acacia* species indicated that the marginal parenchyma/crystalliferous band was produced at the onset of the dry season and, therefore, the tree did not produce wood during the dry winter period.

University of Pretoria etd – Steenkamp, C J (2000)

4.6.4 XYLEM VESSEL DIMENSIONS

Carlquist (1977) found that xylem vessel diameter decreased with decreasing water supply and suggested that a correlation exists between xylem anatomy and habitat (see also Zimmerman *et al*. 1971; Baas *et al*. 1983). February (1993) investigated the above using *Protea caffra* and *Combretum apiculatum*, and while he did find a relationship to rainfall, he could find no relationship to temperature in either of these species.

Gillespie *et al*. (1998), in a preliminary investigation of xylem vessel diameter and area as a tool for tree ring identification and age determination in *Breonadia salicina*, found patterns of radial vessel diameter across tree rings related to each other. A climatic variable can also be related to this same pattern of xylem vessel diameter thereby making it possible to estimate tree age. Radial vessel diameter was found to be the most sensitive to annual rainfall but there was no correlation between mean annual temperature and vessel diameter.

4.6.5 DENSITOMETRY

Densitometry as it pertains to tree ring analysis is the measurement of variations in wood density on an intra-annual and annual basis (Jacoby 1989). According to Jacoby (1989) densitometry has not yet proven to be very useful in species other than conifers and further efforts are needed to evaluate this method with regard to tropical trees. Gourlay (1995) also pointed out that the relatively high density wood of *Acacia* species (> 1.0 g/cm^3), and the presence of gum, contribute to the lack of growth-ring definition by densitometric analyses.

4.6.6 PHENOLOGY

There have been more phenological studies of tropical trees than tree ring studies. These phenological studies are encouraging in that many of them document definite seasonality of growth changes. Seasonal flowering, fruiting, flushing, and leaf fall all indicate a rhythm that could be accompanied by radial growth cycles. In the transitions between the phases of the cycles there may be identifiable changes in the anatomy of the radial growth (Jacoby 1989). The phenological observations may be very helpful in denoting species and locations where a definite cessation of growth would be likely to produce an anatomical feature marking dormancy and restart of radial growth. Some of the phenological studies include recordings of diameter growth, although diameter changes may often be responses to hydration and dehydration rather than cell division (Reich & Borchert 1984).