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Literature review of bark characteristics, wound response and harvesting

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Synopsis

Bark refers to two complex layers of tissues outside a tree's vascular cambium: the secondary phloem (innermost layer) and the rhytidome (outermost layer). Both layers include living and dead parts. The sieve-tubes of the older secondary phloem become non-functional, die and collapse. In the rhytidome of most species, most cells are dead. Among the fully formed cells, only the youngest cork cambium (phellogen) cells and their recent derivatives are living.

The bark knowledge base remains fragmentary and unconsolidated despite quite a number of review documents. There is no comprehensive, generally accepted framework of bark types based on internal bark characteristics beyond the separation of ring barks from scale barks. There is no accepted framework of grouping trees according to their response to bark wounds. Confirmation is required of the wider applicability of a tentative opinion that healing is more rapid in thin-barked than thicker-barked species. A complication in assessing wound response is lack of standardization for wounding limited to the vascular cambium and/or the tissues external to it. Drill wounds are becoming a uniform approach for studying deeper wounds. Additional complications are inconsistencies in the timings of wounding and variability in the vigour of the trees studied for response.

Under natural conditions wound healing is generally from the wound margin over the face of the wound, but is likely to be halted if there is a roughened, exposed wood surface. In some species, healing may possibly not progress on to the wound from its margins, or mechanisms other than callus spread to cover the wound surface may operate. After initial post-trauma changes at cellular level adjacent to the injury, tissue replacement starts with callus formation. Over a time period that varies from a matter of days to one or two months, meristematic tissue forms as a replacement of the vascular cambium (if this had been destroyed) in the inner part of the callus or as a phellogen (cork cambium) in the outer part of the callus. Soon after formation these meristems produce derivative tissues – xylem to the inside and phloem to the outside of the vascular cambium and phelloderm to the inside and phellem to the outside of the phellogen.

Where bark is harvested as a product of commercial significance, harvesting is destructive and the shoots are harvested with the bark except in the case of cork oak and, under some current management systems, *Prunus africana*.

Preamble

Overall, there is a wealth of published reference to bark, even excluding brief comments routinely included in tree description. However, despite the extent, this is essentially a fragmentary knowledge base with relatively few reviews of aspects directly concerning bark as a resource, and a striking lack of reports suggesting basic and generally applicable classifications of bark structure to enable potential management groupings. Comment here is restricted to dicotyledons.

On-line facilities have been used to explore the range of published information on bark to generate a context, and define the state of knowledge, for cyclic bark harvesting from wild African trees. Note is taken of a range of descriptive morphological and anatomical studies, including several comparing large numbers of taxa on this basis (Zahur, 1959; Roth, 1981; Outer, 1983, 1993). Integrated accounts of bark and stem tissue structure and function, notably the phloem, available as review papers (Srivastava, 1964; Borger, 1973; Cronshaw, 1981), or benchmark texts (Metcalfe & Chalk, 1979, 1983; Dickison, 2000) complement the more restricted view with a broader perspective.

The second aspect explored in the existing literature is that of tree (bark) damage and how the affected individuals respond. Published information is very diverse in emphasis and much is presented in a pathological context, or in relation to the economic implications of logging, fire or animal damage, and lacks detail of the wound repair process. However, there have been some broad reviews: Bloch (1941, 1952), Lipetz (1970), Noel (1970), Borger (1973), Vasiliauskas (2001).

A further aspect of the current state of knowledge which has been considered is the bark harvesting process in major bark product species. These, in the main, however, are managed on a destructive total harvest basis (e.g. quinine bark, *Cinchona*; black wattle, *Acacia mearnsii*; babul, *Acacia nilotica*). Cork oak (*Quercus suber*) and *Prunus africana* are the only major sources of bark harvests carried out under management practices involving repeated bark harvesting from the same stems.

Descriptive morphological and anatomical studies

A varied terminology has been applied to the outer tissues of what Dickison (2000) terms the "secondary plant body". As a recent statement, Dickison's interpretation of bark is generally followed for present purposes and regarded as consistent with the more comprehensive definitions of terms provided by Trockenbrodt (1990). Bark is regarded as the complex of tissues exterior to the vascular cambium. The two principal zones of this complex consist of the secondary phloem, situated immediately outside the vascular cambium and, beyond this, the rhytidome, which is usually a complex mixture of dead secondary phloem and a series of specialized structures termed periderms. In some woody species, primary tissues, the original epidermis and cortex may persist outside the secondary phloem. The relative prominence of different bark tissues, and their uniformity and form, and the nature, abundance and distribution of the cell types which compose them, vary with species. Not all the tissues are always clearly distinguishable.

The vascular cambium

The vascular cambium, being meristematic, generates tissues that build-up to result in the tree's diameter increment. Secondary xylem is added internally by the vascular cambium and secondary phloem to the outside. It is customary to regard the vascular cambium in the strict sense as a single layer of cells tending to form a cylinder within the tree bole, with a few layers of cells within it and outside it from which distinctive xylem (within) and phloem (outside) tissues are

directly derived. Consequently, it is convenient in practical terms to recognize a cambial zone or region of several layers of cells. Two types of cambial cells are distinguished – fusiform initials and ray initials. A range of elongated specialized cells characteristic of xylem (vessel cells, fibres, axial ray parenchyma) and phloem (sieve elements, phloem fibres and axial phloem parenchyma) are derived. From the ray initials, aggregates of parenchyma cells (xylem wood rays, phloem rays) are derived. It has been suggested that the length of the fusiform initials reflects the extent to which the vascular structure has become specialised. Long initials (mean length *ca* 890 μ m) indicate a relatively unspecialised and more primitive structure, while short initials (mean length *ca* 250 μ m) arranged in regular horizontal rows (“storeyed” appearance) indicate an advanced structure. Where the initials are long, the xylem vessels derived from them have scalariform pitting on their end walls. Where the initials are short, the vessels derived have simple pits or no pits in the terminal cross walls. Initials with mean length (*ca* 410 μ m) represent an intermediate state of advancement.

The secondary phloem

In secondary phloem, sieve elements and parenchyma are consistent cell types. If fibres are present, they may occur in aggregates forming, in transverse section, distinctive patterns, particularly if fibrous bands of tissue alternate with aggregates on non-sclerified cells. The distribution of parenchymatous cells in the phloem may also be distinctive. The sieve elements are units within sieve tubes and the sieve tubes function as the channels whereby carbohydrates and nitrogenous food materials produced by leaf activity are distributed to other metabolically active parts of the plant. Parenchyma cells occur in the secondary phloem in several situations. Some axial parenchyma cells are closely associated with the sieve tubes, both in derivation from the same cambial initials and in the mutual exchange of metabolites. These and parenchyma cells elsewhere within the phloem may accumulate products of various kinds (including energy-rich materials and tannins). Other parenchymatous cells may contribute mechanical support within the tissue, particularly if cellulose deposition increases wall thickness and rigidity. Regardless of where they occur or their arrangement, fibres are most important for their mechanical, strengthening role which is a result of various degrees of lignification of the cell walls. In the past, fibres were generally considered to lose their protoplasts during differentiation but it is now recognized that, in at least a proportion of species, fibres are nucleated living cells which store starch. A further type of cell with lignified walls is the sclereid which, in contrast to the typical fibre cell, is of secondary derivation – from axial and ray parenchyma cells. Sclereids often occur as isolated cells and in addition to having lignified walls are often noteworthy for containing stored starch, tannin or aromatic compounds.

It is usual for only the recently formed secondary phloem to be fully functional – the conducting role of a phloem sieve element rarely continues for more than a year or two. As the conducting role transfers to cells recently derived from the cambium, the older cells, further from the cambium, become non-functional. The secondary phloem is divided into functional (inner) and non-functional (outer) zones to indicate this process. The outer of these zones is recognized through the collapsed state (seen in transverse section) of the sieve elements. Sieve element collapse results from pressures exerted by the addition of newly formed phloem tissues nearer the vascular cambium and enlarging parenchyma cells. Parenchyma cells remaining alive in the non-functional phloem accommodate the increase in size of the axis through division, often forming wedges of parenchyma (dilatation tissue) which alternate with aggregations of other types of cells (fibres and collapsed sieve elements).

Rhytidome

The boundary between the secondary phloem and the rhytidome is indicated by the presence of a periderm. In most trees, there is a series of periderms between the secondary phloem and the external surface of the tree's axis, developed successively over time and increasing in age from the inside to the outside. The periderm is a very distinctive structural element of bark, variation in periderm activity, and in the character of the tissues which form it, often accounting for the diagnostic features allowing separation of different tree species on bark surface and blaze appearance. Three intimately related tissues form a periderm, one of these, the phellogen, being a lateral meristematic tissue. The cell proliferation taking place in the periderm provides a mechanism for the tree to retain its form as it increases in diameter. At the same time, the presence of phellogens ensures that the internal tissues are protected from excessive lateral moisture loss to the atmosphere and the ingress of antagonistic organisms. In some environments, protection may also be against fire-damage.

Phellogen cells are formed by the dedifferentiation of living mature cells that resume division and become converted into a cambium. The initial periderm may be from the epidermal or cortical parenchyma cells of the young shoot, and forms around its entire circumference. With time, however, the cells of the original epidermal and cortical tissues of the shoot die and are shed as the axis increases in diameter. Protection of tissues within the axis is maintained through the development of one or, more commonly, a series of replacement periderms. The later periderms arise from the dedifferentiation of phloem parenchyma cells. As the axis grows, additional periderms periodically arise, each interior to the previous one produced. A concentric series of replacement periderms, continuous around the bole, arises in trees with so-called "ring bark". In most trees, however the new periderms take the "scale bark" form - of separate, but imbricated and overlapping, tangential patches within which is the cambial layer (phellogen). There may be numerous periderms with an active phellogen within a tree's trunk at any point in time. The older periderms, nearer the bark surface, will have died and many of their cells will be suberized or lignified. When the cells are in this state they are regarded as contributing significantly to the tree's protection against microorganisms, insects, water loss and the resultant desiccation, and external temperature extremes.

Phellogen cells are of only one type, typically rectangular and radially flattened in transverse section. Divisions of phellogen cells produce a few rows of living parenchymatous cells, sometimes with chloroplasts, to the inside, as the phellogen. To the outside, phellogen activity produces the phellem, a tissue of cells that are non-living when their differentiation is completed. Many of these are cork cells - cells containing suberin and other waxes, and lignin in quantity, making the phellem impervious to the passage of gases and liquids, and providing insulation from external extremes of temperature. Cells of other types may be dispersed among the cork cells, notably phelloids (which lack suberin), and sclereids with thick lignified secondary walls.

Bark chemicals (Srivastava, 1964; Martin & Crist, 1970)

Different tissues of bark vary in the relative proportions of extractives. The periderm fractions of the rhytidome show higher concentrations of waxes and fatty materials than do secondary phloem fractions. Conversely, the secondary phloem fractions tend to be richer in alcohol- and water-soluble extractives than rhytidome tissues. Different tannins may be associated with different tissues and vary widely with species. It has been suggested that water-soluble tannins are present in the cambium and functional phloem but that condensed tannins are

more typical of the rhytidome. The nature of carbohydrates also varies with the tissue. Hemicelluloses are characteristic of secondary phloem while periderm tissue is where suberin content is especially high, and lignin levels are high in the other rhytidome tissues. Cellulose accounts for around 20% or more of all the tissues except periderm, where it is less than 10%.

Bark tissue prominence and habitat (Roth, 1981)

A consensus has gradually developed over several apparent correlations of bark characteristics and the broad tropical habitat categories of humid forest and savanna. Within the latter group there are further contrasts depending on whether there is regular exposure to fire and whether there is a major benefit from water storage in the bark tissues.

In the humid forest habitat, barks are much more likely to display cellular and chemical characteristics associated with resistance to decay and reduction of damage from pathogens or herbivores. Sclerenchyma is abundant, and may be lignified. Tannins and tannin-like substances occur in quantity. Secretory cells and canals contain materials, including gums and resins, with disinfectant qualities, but tissues with water-storing characteristics tend to be lacking. The presence of cork cells is usual.

In the savanna habitat, anatomical characteristics associated with water storage are commonplace, and there may also be tissues where, under favourable conditions, reserves of starch or sugar accumulate which can be mobilized under stressful circumstances. Water storage tissue may be developed in persistent epidermis tissues, typically thin-walled phloem (and other) parenchyma, and as (among other materials) gums in secretory cells and cavities. Protection from herbivores is relatively less important, so levels of chemicals with disinfectant qualities are low, or they are absent, and sclerenchyma is much less prominent. Under very dry conditions, there may be a distinctive persistent or partly persistent epidermis if the bark has a major photosynthetic function – in which case a rhytidome is absent and there is very reduced formation of cork. However, in trees typifying savanna subject to regular and frequent intense ground fires both thick cork and a well-developed rhytidome, of many periderms, are often present, giving a measure of fire-tolerance.

Phylogenetic trends

Published work on bark morphology and anatomy mostly centres on providing basic descriptions (*e.g.* Richter, 1990; Richter & Wyk, 1990), and on determining characteristics for distinguishing different species on the basis of their bark (*e.g.* Rollet, 1980-1982; Furono, 1990). Identifying features particularly associated with families presumed primitive or advanced on traditional morphological grounds has been an additional aim of studies of bark (Roth, 1981), and secondary phloem (Zahur, 1959; Outer, 1983, 1993). The last of these approaches has met with little success. Outer (1993) examined a wide range of secondary phloem features but describes the relationship between these and the traditionally accepted phylogenetic arrangement of plant families (*e.g.* Hutchinson, 1973; Takhtajan, 1980) as "absent or scarce". It is nevertheless improbable that the revised interpretations of angiosperm phylogeny based on molecular investigations (*e.g.* Angiosperm Phylogeny Group, 2000) will change the situation. It seems that complications of secondary specialization correlated with habit and environmental conditions obscure any phylogenetic patterns when taxonomically, morphologically and ecologically diverse sets of species are evaluated.

Despite failure to relate bark characteristics to current understanding of phylogeny, the studies involving significant numbers of species (423 species – Zahur, 1959; 264 species – Roth, 1981; 463 species – Outer, 1993) have supported the much older view of primitive and advanced forms of sieve-tube, and intermediate conditions. Outer (1993) links primitive, intermediate and advanced sieve-tube character with a range of other secondary phloem characteristics to separate three bark structural types: a *Tilia* type, a *Populus* type and a *Datura* type. In a more elaborate categorization of barks into 10 types, Furono (1990), takes account of how phloem fibres, fibre-sclereids and sclereids are arranged, and features of ray and axial parenchyma cells. However, the utility of Furono's scheme is effectively restricted to the 55 species he included, as emphasis is on diagnostic group features and no key is provided.

Interpreting sieve-tubes as primitive, advanced or intermediate depends primarily on their length and the nature of the sieve plates and the sieve areas within the sieve plates. An advanced state is indicated by short (100-300 μm) sieve-tubes, with sieve plates (containing relatively few sieve areas) mainly or exclusively on slightly oblique or transverse end walls. A primitive state is indicated by long (>500 μm) sieve-tubes having very oblique end walls with sieve plates containing 10 or more sieve areas, and additional well-developed sieve areas on the side walls.

Outer (1993) was able to describe combinations of secondary phloem characters typifying his three bark structural types but found no consistency between the degree of specialization of cell types/tissue organization and presumed evolutionary trends for plant families. The prominence and organization of transporting (sieve-tubes, axial parenchyma, rays) and mechanical (fibres, sclereids) tissues is the basis of Outer's distinctions. Comments below refer to the arrangements of tissues as revealed in transverse section. In the *Tilia* type, the organization is considered advanced: well-developed tangential bands of fibres/sclereids alternating with bands of axial phloem parenchyma surrounding small groups of sieve-tubes with companion cells. Transport is presumed to involve all of sieve-tubes, axial parenchyma and rays to an appreciable extent. The sieve-tube and companion cell characteristics are advanced. The banding of the mechanical tissue is regarded as a primitive arrangement. In the *Populus* type, intermediate between the *Tilia* and *Datura* types, narrow tangential bands of fibres and/or sclereids alternate with narrow bands of axial parenchyma and bands of sieve-tubes. Transport is presumed to involve mainly the sieve-tubes and axial parenchyma. The sieve-tube characteristics are intermediate. In the *Datura* type, the organization is considered primitive: axial parenchyma constitutes a ground tissue within which groups of sieve-tubes and companion cells are dispersed. Mechanical tissues are represented as scattered, isolated cells. Transport is presumed to be exclusively or primarily via sieve-tubes which are interconnected to form a network. Sieve-tube and companion cell characteristics are primitive; the representation of mechanical tissue as fibre-sclereids and/or sclereids is regarded as advanced.

Bark damage and post-trauma responses

There is a long history of interest in events following the wounding of trees (Noel, 1970; Dujesiefken *et al.*, 2001), particularly when crowns have remained alive long after (sometimes many years) complete girdling. While the literature relating to wounds on tree boles is extensive, it represents investigations undertaken through a wide range of approaches. Experimental situations have been important in studies of tree wounds. However, while experimental prescriptions eliminate some potential sources of variation, allowing clearer and more informative analysis of data recorded, there is little standardization or consistency

of approach among researchers, even when pursuing closely similar objectives. Experimental convenience has also sometimes led to artificial wounding without parallels in typical tree environments, as Basham (1978) points out. A fragmentary and widely scattered literature selectively explores aspects ranging from physiological cell responses (*e.g.* Lipetz, 1970), through interactions with pests (*e.g.* Harmon & Dixon, 1984) and pathogens (*e.g.* Okey *et al.*, 1995) and the identification of arboricultural best practices (*e.g.* Neely, 1991) to basic descriptive studies (*e.g.* Noel, 1968a) and economic implications (*e.g.* Vasiliauskas, 2001). Unfortunately, even the reviews (Bloch, 1941, 1952; Lipetz, 1970; Noel, 1970; Vasiliauskas, 2001) fail to provide overall categorizations of trees that can be readily applied to any species based on the bark morphology, taxonomic position or ecology. Emphasis remains on comparative studies of small numbers of species growing under limited ranges of environmental conditions and on monitoring reactions to wounding of particular species within restricted areas. For present purposes, attention centres on biological aspects. Tree responses to bark wounds are considered in terms of the causes and nature of wounds, the sequence of events involved in healing at tissue level and rates of wound closure.

Causes and nature of bark wounds

Wounds to tree bark arise from both natural causes and from the intentional human actions. In forest ecosystems, a major natural cause of mechanical damage is identified by Schoonenberg *et al.* (2003) as falling forest debris which strikes and abrades or gouges the stem surface. In cold climates such falls of debris may be due to ice or snow overloading, and seasonal low temperatures may also be associated with recurring deep cracks induced by frosts (Neely, 1988). Other natural causes are fire (Pinard & Huffman, 1997; Smith & Sutherland, 1999), lightning (Taylor, 1969) and animals (Coetzee *et al.*, 1979; Malan & Wyk, 1993).

Human action may inflict damage as a side-effect of felling operations (Vasiliauskas, 2001) or prescriptively. Prescribed damage includes the girdling of boles or branches for tree elimination (frequently combined with fuelwood collection), or to induce horticulturally desired changes such as the onset of a reproductive event or root development at the proximal end of a branch section (which can be detached and used in propagation). Some less drastic prescriptions entail specific and localized injuries triggering production of a product in a conveniently harvested form (*e.g.* latex and gum tapping) or initiating events in the crown by temporary severance of the conducting pathway (Soe, 1959). Another relatively less drastic form of damage is associated with insertions or injections into the bole for nutritional, prophylactic or therapeutic purposes (Neely, 1988). More drastic prescriptions are represented by total rotation-end bark harvesting (*e.g.* Flach & Siemonsma, 1999).

Damage arising in different ways creates a range of injuries. Those involving fire are manifested in tissue death from high cambial temperatures (Pinard & Huffman, 1997) below the exposed area of bark. Over the affected tissues, the bark surface may survive unbroken, although charred, preserving some protection against pest/pathogen ingress for the freshly killed tissue beneath. Most injuries, however, are mechanical, with bark detached to varying extents. Mechanical damage due to natural causes, or as a side-effect of felling, produces wounds irregular in surface area, shape and depth. Vasiliauskas (2001), reviewing felling damage, draws attention to several reports revealing that only some 20% of wounds sustained during logging operations (in temperate, mostly coniferous, stands and forests) penetrated as deeply as the wood. Damage from natural windfalls and limbfalls in unlogged forest is probably much less than that arising when logs are hauled through stands. Death and fragmentation *in situ*

mean that debris tends to have lost weight, tends to be small and tends to fall vertically to the ground at source.

Damage inflicted by animals seems to vary with bark structure (Malan & Wyk, 1993). Bark may be stripped or gnawed from a tree's bole or branches. Stripping is associated with larger herbivores, notably elephants, and gnawing with smaller species, particularly rodents. Bark detaches relatively in long axial strips if it has high breakage and bending strength, qualities attributed to high content of gelatinous fibres with only slight wall lignification. In contrast, brittleness increases as fibre walls become more heavily lignified or when there is increasing abundance of sclereids. Large scars result if long strips of bark are torn away. With brittle bark, relatively small, compact pieces tend to be individually detached.

The time of year may affect the tissues removed and the extent of damage. Vasiliauskas (2001) points out that damage in the non-growing season of the northern hemisphere winter is less than at other times, partly because the bark adheres more tightly to the sapwood. Malan & Wyk (1993) consider damage more extensive when mammals detach it at times of elevated cambium activity (annual period of tree growth – especially at the beginning of this) and it is common for the cambium to be removed, exposing the wood. At this time, it has been suggested, animals may be selecting bark as food because sugar contents in its conducting tissues are high. Other explanations not associated with seasonal changes in the trees have also, however, been put forward: bark as a calcium source; bark as the most accessible nutritive dry season foodstuff; bark as an essential fibre source.

Prescribed bark damage may be intended to inflict temporary or permanent damage. Temporary damage may be external to the vascular cambium, taking the form of localized blazes as in frankincense tapping (Gebrehiwot, 2003), or shallow excavated channels as in rubber tapping, or scoring (which is a deeper wound made to sever the conducting tissues each side of the cambium but involves no bark removal). Tapping measures release exudates for collection by cutting across canals in the bark and the tree's recovery from the wound is by inclusion of a resting phase in the tapping cycle or a periodic switch to a different area of the bole. Scoring has been used to interrupt phloem transport to induce earlier and more prolific flowering and fruiting (Soe, 1959), typically for a few weeks until healing has taken place. Girdling describes the removal of a complete ring of bark from a tree's axis. Researchers vary in whether only tissues external to the cambium are detached or if cuts are made through the cambium into the underlying wood. Deeper, more severe, girdling is used to bring about crown death while the cambium is meant to be left undamaged if a short-term effect is sought and the girdle itself is then narrow. Wide girdles have been used to regulate downward movement of products making the lower parts of trees attractive to destructive insects and for various other exploratory silvicultural initiatives (Noel, 1968b, 1970). Injection/insertion wounds are inflicted using low-speed drills. Neely (1988) refers to bits 9-17 mm in diameter, and Martin & Sydnor (1987) to a penetration of 20 mm (through the bark, into the wood). Comparable wounds have been adopted as convenient standards for various experimental studies of reaction to injuries (Guariguata & Gilbert, 1996); these experimental wounds may be more superficial (Schoonenberg *et al.*, 2003 – penetrating only to the vascular cambium). Rotation-end total bark harvesting entails bark removal without regard to which tissues are collected; depending on the species and the season the vascular cambium may be stripped with the remaining bark tissues or may remain on the stripped axis.

Experimental initiatives to gain clearer understanding of the impact of bark damage on trees have involved attempts to inflict injuries broadly matching types mentioned above under varying degrees of control. In most cases the responses of different species have been compared, although not always according to a robust protocol. Systematic approaches have been best developed for fire, blaze and injection damage.

Fire damage has been simulated through burning wicks (Pinard & Huffman, 1997) and copper plates (Basham, 1978; Schoonenberg *et al.*, 2003) attached round the bole. The effect of the burning wick is considered comparable to exposure to a burning natural fuel bed around the tree. The copper plates are heated with blow torches with the aim of raising cambial temperatures to 45°C (low intensity fire simulated) or 70°C (high intensity fire simulated).

Blaze damage is experimentally simulated with the removal of long axial strips of bark 25-50 mm wide (Basham, 1978) or variously shaped panels of bark up to 50 mm wide and long (Noel, 1968a; Neely, 1988). The aim has been to compare sensitivity of a species to damage in different seasons or under different site conditions (Basham, 1978), or to compare the recovery process in different species (Noel, 1968a, Neely, 1988), sometimes with seasonal comparisons also included. Basham also compared reaction between trees where only the outer layers of bark were stripped (leaving an inner layer protecting the vascular cambium), and trees stripped to the surface of the wood. Not surprisingly, recovery was superior in the latter group.

Drill wounds are easy to inflict and the resultant wounds can be kept consistent in diameter and depth terms. This offers obvious advantages in the generalized study of tree response to bark/outer wood damage. Studies involving drilled wounds compare response over time (2 months – Schoonenberg *et al.*, 2003; a growing season – Martin & Sydnor, 1987, and Neely, 1988; two growing seasons – Guariguata & Gilbert, 1996). Coupling the experimentation with imposition of size uniformity among treated individuals eliminates or significantly reduces a major complication in interpreting recovery data. Wounds inflicted for prophylactic or therapeutic purposes are associated simultaneously with mechanical damage and phytotoxicity damage, as the chemicals applied have phytotoxic properties (Neely, 1988). To separate these effects, recovery from wounds involving no chemical insertion/injection has to be gauged. The experimental use of wounding drills enables this.

The wound healing process

General summaries of the sequence of events in wound healing have been provided by Hudler (1984), Shigo (1989), Dickison (2000) and Schoonenberg *et al.* (2003). Following the wounding, the most superficial cells die (Noel, 1970). It is events beneath and behind these, in intact living cells, that initiate the recovery process, Shigo (1989) refers to electrical and chemical changes. Through the chemical changes, stored energy reserves in parenchyma cells are mobilized and defensive chemicals are formed and deposited in cells around the wound.

The replacement of lost tissues starts with callus formation. Where callus develops depends on the conditions to which the wound is exposed. If the xylem surface left after bark removal remains moist, uniform wound callus develops across the entire wound surface (Dickison, 2000), and this seems to be a universal response among species (Dujesiefken *et al.*, 2001). With the less favourable circumstances under which most wounds heal in nature, callus mostly grows from the wound periphery. Callus cells are produced from de-differentiating xylem ray and axial parenchyma, in a process involving auxins and cytokinins

(Dickison, 2000), and as callus accumulates the more peripheral layers of cells become suberized. From the phellem of the surrounding intact bark, a new cork cambium develops in the wound area, while at greater depth a new vascular cambium forms and progressively extends across the wound. Cambial activity initially generates cells by irregular cell division. With time, however, normal secondary tissues are produced. In those tissues, phloem parenchyma and direct cambial derivative cells may themselves differentiate to form more callus. In the wound environment, however, xylem cells (tracheids, vessels) differentiated from callus cells may become lignified and produce ribs of woundwood around the wound (Shigo, 1989).

Rates of healing

The literature indicates much variation in the detail of the healing process but no general categorization for species groups has so far emerged. Noel (1970), in the particular context of girdling wounds, distinguished four patterns according to the relative prominence of the scar tissue masses formed at the upper and lower edges of the girdle. Guariguata & Gilbert (1996) also associated different amounts of callus production with different species. They speculate, however, that the pioneer species included in their study may have been entering senescence and that the responses noted would not apply for younger individuals. Dickison (2000) stresses that the way in which new secondary tissues differentiate, and the rate with which this takes place, is influenced by which tissues are exposed at wounding and the ambient conditions prevailing during recovery. In seasonal climates, time of year also affects response. In general, studies in which healing is compared among species indicate similar sequences of events but variation in rates overall and for different phases of the repair process. Schoonenberg *et al.* (2003) found some evidence of more rapid formation of the defensive, suberized, zone in thin-barked species.

Descriptions of wound healing achieved in time by different species refer occasionally to tissue differentiation events (Soe, 1959; Noel, 1968a), but more frequently to gross surface response (Martin & Sydnor, 1987; Neely, 1988; Guariguata & Gilbert, 1996). Tissue differentiation is rapid – new callus has been detected as early as 3-6 days after incision damage (Soe, 1959) and in only 20-30 days after the more drastic impact of removing a 50 mm x 50 mm bark panel (Noel, 1968a). In these two studies cambial tissues were noted to re-form in 6-9 days and in 1.5-3 months, respectively.

Some monitoring of healing concerns wounds resulting from the physical removal of the protective bark layer to the wood surface (Noel, 1968a; Neely, 1988). In other cases the wounds are inflicted with drills, so that both the bark and some wood are removed (Martin & Sydnor, 1987; Neely, 1988; Guariguata & Gilbert, 1996). By maintaining moist, dark conditions over experimental wounds, Noel (1968a) was able to promote the differentiation of replacement bark simultaneously across 50 mm x 50 mm wounds to *Trema orientalis* in about 6 months. More commonly, no protection is given to the wound surface and bark replacement depends on spread across the wound surface from its margins. A field estimate of this process for *Sclerocarya birrea* (Coetzee *et al.*, 1979), expressed on an annual basis, is 28.5 mm from each lateral margin.

Studies involving drill wounds have generally anticipated and monitored closure by callus formation visible at the mouth of the wound. Martin & Sydnor (1987) record 10 mm wounds closing in 3-6 months. Guariguata & Gilbert (1996) noted, however, not only that 7 mm wounds consistently took over 3 months to heal but that callus formation was not necessarily the only mechanism involved. They

found that in trees able to produce latex or resin these materials contributed to healing the wounds – in some cases without a contribution from callus.

Neely (1988) ascribes differences in the rates, and times to completion, of wound closure to wound size, species, tree vigour and season. He undertook a comprehensive initial study of three temperate hardwood species over three years, concluding that closure rate correlated most closely with tree vigour. In the light of this finding, he criticises the past tendency to use inappropriate measures and provide inadequate supporting information in reports of healing. He questions the utility of values expressed simply as linear measures linked to a time interval, even with tree age or diameter also disclosed. His recommendation is that wound closure should be expressed in relation to a standard of radial increase in the wounded tree. Estimates he gives are in the order of 2-6 mm closure per 1 mm of radial growth.

Harvesting of bark and products from bark

The bark of an enormous number of woody species is valued as a source of useful products but very few of these are recognized as major resources associated with an established trading infrastructure, even at local level. In some cases interest is in products tapped from the bark (gum arabic, frankincense, rubber); in other cases the bark itself is removed as a bulk product to be processed for subsequent use (cork, cinnamon sticks) or as raw material from which flavourings (quinine), tannin (wattle) or medicinal compounds (*Prunus*) can be extracted with appropriate processing.

Gum arabic (Gibbon & Pain, 1985; Booth & Wickens, 1988)

The species is *Acacia senegal* (Leguminosae: Mimosoideae). Wild trees are opportunistically tapped but there are also stands which are managed. The latter, even if spontaneously regenerated from dispersed seed rather than planted, are of known age and management determines a rotation period, trees eventually being felled at 15 years of age. Tapping begins when trees are 4-5 years old, is annual, and is a dry (relatively cool) season activity. Strips of bark are peeled back, often with a special tool, leaving axial scars some 75 cm long, along which gum exudes and forms nodules in 3-8 weeks. Opportunistic exploitation is by making incisions and returning on a later date to gather the hardened globules of the gum exuded from the wound. The wood and bark anatomy of *Acacia senegal* have been described by Ghosh & Purkayastha (1962).

Frankincense (Gebrehiwot, 2003)

The species is *Boswellia papyrifera* (Burseraceae). The trees tapped are wild. Tapping involves shaving off thin (1 mm) patches (each 25 mm x 25 mm) of bark at a number of points with a chisel-like tool. The number of points tapped depends on the size of the tree but all the wounds are created at the same time, early in the dry season. A series of collections of the exuded resin takes place, the first some 3 weeks after wounding. At collection, the wound is enlarged to stimulate further exudation. By the end of the dry season, resin will have been collected about 11 times. Tapping ceases in the rainy season but resumes in the dry season each year for five years. Three year total resting periods separate five year harvesting phases.

Rubber (Webster & Baulkwill, 1989; Delabarre & Serier, 2000)

The species is *Hevea brasiliensis* (Euphorbiaceae). This is a plantation species, increasing areas of plantation being established using grafted stock. The tapping

procedure is based on opening the laticifers, which are organized in rings within recently formed phloem, so that latex is exuded and can be directed to collecting receptacles via the inclined shallow grooves in the bark that are cut to release the latex from the laticifers. Well-applied tapping is restricted to the outermost laticifers. When cut, the laticifers release latex under pressure, pressure maximal early in the day which is when tapping takes place. Tapping is applied to half the tree's circumference, is generally on alternate days and begins at a height of about 160 cm when trees are 15-20 cm in diameter and 4-7 years old. Daily opening of further sets of laticifers lowers the level of the channel draining the latex by 18 mm per month, forming a tapped panel. The individual operation to open further laticifers lowers the channel by around 1.5 mm, maintaining a constant 25° slope, and penetrates to within 1.5 mm of the vascular cambium. It takes some 5 years for the panel to be tapped to its lower limit, the union of the graft. Tapping then switches to the untapped side of the tree and continues there for the next 5 years. At the end of this period, bark recovery where tapping started has been in progress for 10 years and the original panel is re-opened. Tapping life overall is 25-30 years. Tapping in accordance with the specified criteria of angle, penetration and rate of lowering is skilled work and essential to avoid wound impacts that reduce yield. Special tapping knives and gouges are used.

Cork (Cooke, 1961)

The species is *Quercus suber* (Fagaceae). The commercial source areas of cork are forests which have been intensively managed for centuries, and rejuvenated as necessary through planted seeds or transplanted or, less often, nursery-raised seedlings. Harvesting starts as trees reach 20 cm in diameter, at which stage their age is around 20 years, and is a summer (growing season) operation. If harvesting is correctly timed, the outer bark (which constitutes the harvest) separates from the innermost phellogen leaving this, and the secondary phloem tissues internal to it, on the tree. Bark collection is effected when the tree is actively growing as the separation of the harvest from the tissues within is easiest at this time. Nevertheless, the initial seasonal pulse of vigorous sap flow is allowed to pass before harvesting, which is completed before onset of the windy period later in the year. As trees attain the size and age permitting harvesting only the bark of the lower 75 cm of bole is collected. A further four harvests follow at 6-10 year intervals, on each occasion combining re-harvest from the previously de-barked area and the next 50 cm up the bole. The harvest is gathered as large detached sheets, detached through careful use of specially designed hatchets. Circular cuts penetrating only to the innermost phellogen are made at the upper and lower limits of the harvested part of the bole and then connected with a vertical incision to the same depth after which the whole bark cylinder is peeled away. If carried out skilfully, this leaves a smooth, uninjured surface ensuring that subsequent bark regeneration will be even and as a continuous cover.

Cinnamon sticks (Flach & Siemonsma, 1999)

The species is *Cinnamomum verum* (Lauraceae). The marketable product is the inner part of the bark so the entire bark is removed and the outer layer removed and discarded later. In terms of the shoots stripped of their bark this is a destructive process and further harvests are from replacement shoots and not of bark regenerated on a previously harvested axis. Harvesting is a wet season activity as at this time the bark is most easily separated from the wood. Management promotes the development of clumps of multi-stemmed plants, and regrowth as new shoots replacing those harvested. Clump size is maintained at 4-6 shoots by removing others. Harvesting is carried out when shoots reach 2-3 m

height and 1-5 cm diameter. Shoots in central parts of clumps are cut near ground level but peripheral shoots are cut higher up, a procedure encourage regrowth to be concentrated around clump boundaries. If clumps are established from seedling material 3 years elapses before harvesting but transplanted rootstocks allow harvests in half this time. Regrowth shoots are harvested at two year intervals and clumps remain productive for as long as 40 years.

Quinine (Williams *et al.*, 1980; Gibbon & Pain, 1985)

The species is *Cinchona ledgeriana* (Rubiaceae). This species is grown in plantations to an age of 10 years, with an early harvest from thinned stems extracted at an age of 4-6 years. Harvesting is a destructive operation, trees being uprooted and bark stripped from the stem and the larger roots. The bark is not readily detached and is beaten while on the felled stems to make it more easily removed.

Wattle (Sherry, 1971; Wiersum, 1991; Wulijarni-Soetjpto & Lemmens, 1991)

Wattle species from which bark is harvested for tanning material are *Acacia mearnsii* and *Acacia nilotica* (both Leguminosae: Mimosoideae). In both cases harvesting is a destructive operation carried out at the end of a rotation of 8-10 years (*A. mearnsii*), or 15 years in the case of *A. nilotica*, where bark is a by-product to timber or fuelwood harvesting. Initial bark removal of *Acacia mearnsii* is from standing trees. Conventional tools are used to sever the bark near the tree base and at about 1.5 m, with a further vertical cut connecting the two. The band can be prised from the bole and then the whole cylinder loosened and detached. Further bark sections are removed after felling. Downward working from the lower cut permits collection of bark from the upper parts of large roots. Unnecessary impacts on the park must be avoided to maintain its quality. The crop is replaced by new individuals grown from seed. With *A. nilotica*, bark harvesting follows tree felling. The bark is loosened by beating with wooden mallets before it is detached as strips.

Prunus africana (Hall *et al.*, 2000)

Prunus africana (Rosaceae) bark is currently exclusively harvested from wild trees. Removal is as panels of complete bark, leaving the vascular cambium of the tree exposed and relying on even sheet recovery across the entire wound. The habitat in which *Prunus africana* grows ensures a more or less continually moist atmosphere. Harvesting is carried out over most of the year, being suspended only during the wettest periods. There are specially designed tools for bark removal but cutlasses are widely used. Guidelines to minimize inadvertent destructive practices in harvesting and maximize prospects for successful bark regeneration have been drawn up. These specify the minimum size of tree to be harvested (30 cm dbh), the parts of the tree from which bark can be removed (from a height of 1 m upwards to the first major branch), the circumferential proportion of the stem that can be stripped (not exceeding 50%) and whether this should consist of two (trees <50 cm dbh) or 4 (trees >50 cm dbh) panels. Further provisions define when root bark can be included in the harvest and the interval (4-5 years, although extension to 8 years has been urged) that should separate successive harvests from the same tree. The process of bark removal is careful prising away of sections of panels 50 cm long. Heavy stakes are used for judicious knocking of the panel to loosen it before final separation with a cutlass. A major consideration in the management of the *Prunus africana* resource is the CITES listing (Appendix II) of the species. The bark harvests are for the extraction of internationally traded pharmaceutical substances and any

exportation requires licensing which is conditional on the application of sustainable management practice to the resource base.

Points relevant for FRP Project R8305

Only weak relationships between bark structure and habitat have been detected in previous studies, and they are not well defined. The most noteworthy trend involves the prominence of sclerenchyma in the mechanical tissues (prominent in the bark of many forest trees, and less prominent in the bark of many typical savanna trees).

Phylogenetic patterns of bark variation have not been convincingly demonstrated – this means assumptions of similarity between species in related families cannot be made. Even within genera, there may be wide variation from species to species. Given the present state of knowledge, each species of interest to the project needs an anatomical assessment in its own right, and when the project's bark recovery data have been collected attempts should be made to relate structure and response.

The bark injury studies relevant for the project are those which involve mechanical (not heat) damage to tissues outside the vascular cambium, inflicted by detaching panels of secondary phloem and rhytidome. It would be useful to establish for each of the project's study species the bark breaking and bending strength. This could have implications for harvesting (brittle bark: highly lignified, or with abundant sclereids - in small units; pliable bark: with little lignification in long strips). Project results may well be affected by the timing of bark removal from the experimental trees, and as much by the vigour of treated individuals as by their size categories. With some species, growing season bark harvesting is favourable to easy separation of inner from outer bark (cork oak) or all bark, and the vascular cambium, from the wood (cinnamon). In the cases of the project species it would be useful to know if, at any particular time (season) of year, separating the bark from the vascular cambium without damage to the latter is easiest.

Precautions keeping the wound surface moist and dark after bark is harvested might favour simultaneous and uniform recovery over the whole exposed wound surface if the vascular cambium has been left undamaged.

The responses of any species releasing latex or other exudates in quantity when bark is removed merit close study and protocols for harvesting bark from such species may need to differ from protocols for species releasing little or no exudates.

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