Chapter 3 How a tree grows, becomes old and decays

3.1 Tree growth

This section outlines the principles of tree growth that have consequences for management techniques. It is not the intention to give a detailed account of the physiology of trees.

3.1.1 Tree growth

A cross section of a tree (Figure 10) illustrates some of the features important for growth. The **bark** forms a protective, waterproof layer, and actually consists of several layers, the innermost of which is the **phloem**, which transports food from the leaves to the rest of the tree. Inside the phloem is the **cambium**, which is the region of growth, or meristematic, cells. These cells divide, forming phloem to the outside and **xylem** to the inside. The xylem is where the water is transported from the roots to the leaves and forms the wood of future years. The outer bark usually remains a relatively thin structure (although it can compose up to 10% of the radius in veteran trees) but the wood builds up so that the overall girth of the trees gets bigger each year as well as the tree, usually, increasing in height. Trees are not perfect cylinders however; they taper towards the top and the higher up a tree a cut is made across it, the fewer the rings that can be counted.

Recently formed xylem (sapwood) consists of conductive pipes surrounded by living parenchyma (packing) cells. In some tree species (eg beech) the living cells progressively die over a period of years and the tissue becomes non-conductive. This older, non-conductive wood is then called **ripewood**. In other species (eg oak) the living xylem cells are genetically programmed to die after a certain period of time (approximately 10 years in oak) and after this is termed **heartwood**. Heartwood may contain substances that increase its resistance to decay. The variation in wood formation and structure between different tree species has consequences for the rotting processes and the organisms associated with rotting and also the longevity of the tree.

3.1.2 Annual growth

Living trees always add annual increments of sapwood, although their width may vary according to growing conditions and the age of the tree. Trees in Britain hardly grow in the winter months. In the spring they grow very fast; the wood produced has large cells with thin walls and is the **earlywood**. Later in the year, when the growth is slower, **latewood** results, with smaller cells and thicker cell walls. These differences in growth are seen as rings in the wood when a tree is felled. (False rings can occur some years due to **lammas** (late summer) **growth** or after a stressful weather event such as a drought). The relative widths of the annual rings can give an indication of the growth rate of the tree in a particular year. There may, though, be variation between branches on the same tree eg one side may be growing more quickly than the other, and this can give rise to eccentric rings.

Pollarding has a considerable impact on annual rings and tree growth. After cutting, the crown is reduced in size, so for the first few years the trunk of the tree expands slowly and the rings are narrow. The width of the rings gets gradually wider (varying of course with other local conditions) until either the tree is cut again, or it resumes the growth rate of a maiden uncut tree.

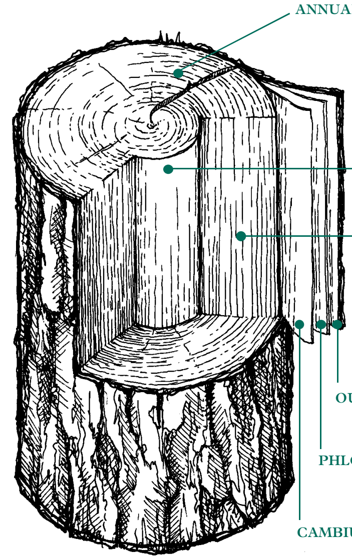


Figure 10. *Diagram of the internal structure of a tree.*

3.1.3 Forming new branches

There are two different processes by which a tree can produce new branches from old stems: from dormant buds (also called epicormic growth) and as adventitious growth. In addition the growth of existing small stems may increase, relative to others, following tree surgery or damage.

3.1.3.1 Epicormic growth from dormant buds (Figure 11)

Dormant buds form from the growing stem or branch of the tree, but do not develop any further at that time. They become embedded in the bark but, by growing a small amount each year they are able to maintain their position and not become completely engulfed by the wood as the tree expands in thickness. Sometimes they can divide to form additional buds that also remain dormant.

Hormones, such as auxins, from the crown of the tree probably keep the buds in a suppressed condition, but if some change in the root to foliage ratio occurs in the tree this alters the balance of the hormones and the dormant buds may start to grow. The types of change that stimulate growth include ring barking, severe pruning, exposure of the tree to increased light levels and water-logging.

Some species of tree lay down more dormant buds (eg oak, lime, English elm, poplar species,ash) than others (eg beech). Dormant buds can survive in a suppressed condition for many years and then grow when conditions are favourable. However their viability does decline over long periods of time. The longevity of buds is believed to be in the region of 100 years for oak, 60 years for hornbeam and sweet chestnut and less than this for beech and willow. This is one of the reasons why old trees are less able to respond to cutting than young ones. It is also thought that, as the trunk of the tree has only a fixed number of dormant buds, repeated pollarding will eventually exhaust the supply. Trees cut repeatedly at short intervals, such as street limes and planes have shown a decline in response to cutting over a long period of time, which may be due to the fixed number of dormant buds. Thus, leaving some young growth on the tree may increase the chance of viable dormant buds being present and hence the chance of regrowth. Dormant buds are not usually distributed evenly over the surface of the tree but form in clusters. Rough bark or burrs may indicate a higher density and trees that have these features may respond better to cutting than smooth barked trees. Some epicormic shoots grow from the buds as soon as they are formed, ie the buds do not have a dormant period.

In many situations epicormic growth is viewed as a detrimental characteristic. Where shoots occur they cause knots in the wood and this reduces the timber value of trees such as oak. They are potentially hazardous in street trees where lots of small branches projecting from the main stem can damage cars and hurt pedestrians. There may also be a genetic component in the production of such growth habits. **For the success of pollarding , however, the more dormant buds the better the chance of regrowth and survival.** Perpetuating the genetic stock of trees on sites where pollarding has been carried out in the past may be better than planting commercial stock, which is likely to have been selected because it produces high quality timber with few knots and therefore few dormant buds.

3.1.3.2 Adventitious growth

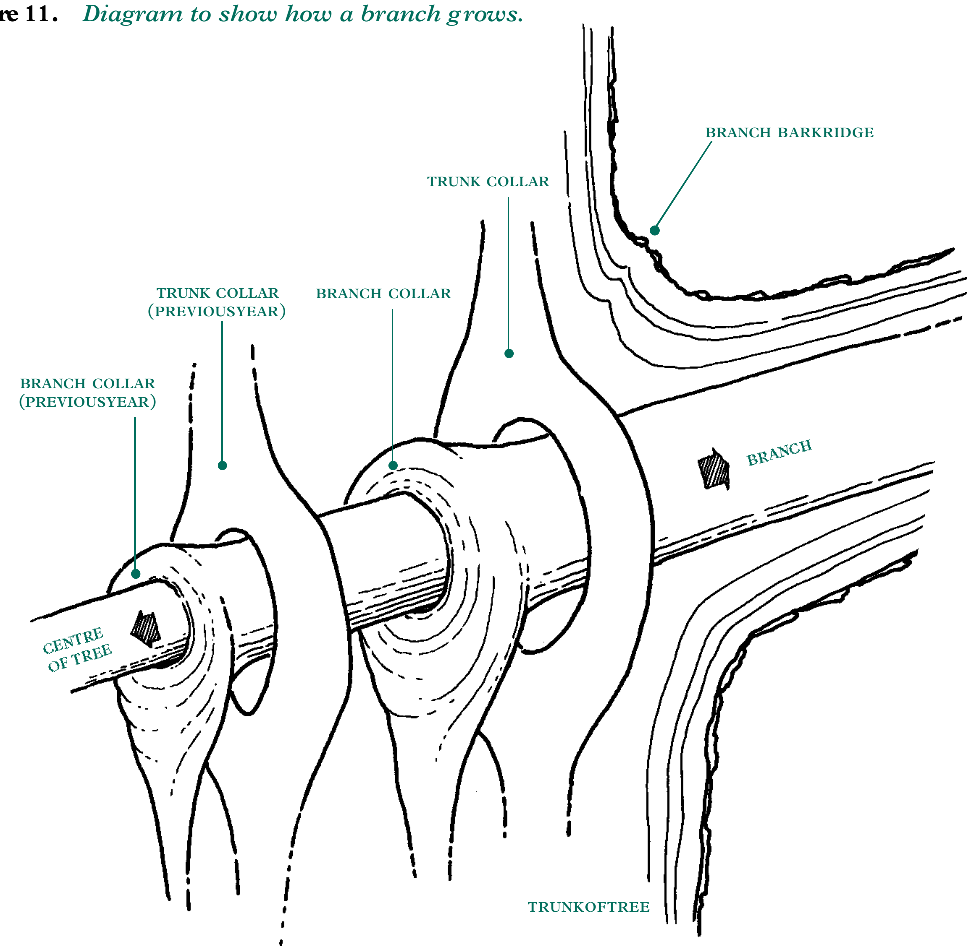
Adventitious buds form when a tree is damaged. They result from injury or pruning, developing from the callus tissue that forms at the point of damage. Typically a cluster of small shoots develops but it is unusual for them to persist for many years.

While growth from dormant buds arises from a deep-seated connection to the trunk of the tree, adventitious growth is much more superficial. As a result it is not as strong and is more easily broken. The presence of adventitious growth on old trees is encouraging but often of less value than growth from dormant buds in the long term. Again, some species of tree are better at producing adventitious growth than others. Oak is generally poor, beech is often cited as being good, but recent experiences at Burnham Beeches and Epping Forest with both old and young trees has not borne this out. Adventitious growth *may* develop better from natural tears rather than saw cuts, owing to the increased exposure of the cambium.

3.1.3.3 Growth of existing branches

Crown reduction in old trees may produce a third form of growth as a result of light reaching retained branches that were previously receiving low levels of light. As a consequence, small existing shoots grow rapidly into the light. As the years progress,they become the major branches. This type of growth is characteristic of trees that generally respond poorly to being pollarded (eg conifers and beech), and this is how the classic candelabra-shaped beech pollards arise.

Figure 11. *Diagram to show how a branch grows.*



3.1.3.4 Repeated cutting

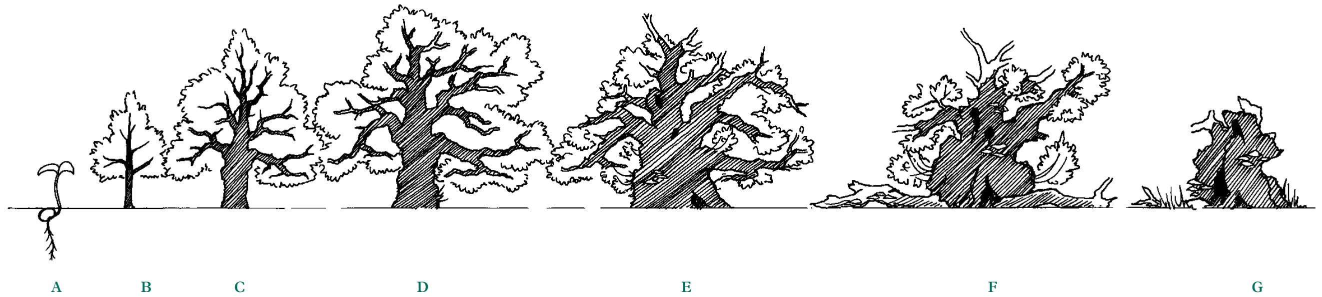
Repeated cutting back to the same point may result in swollen areas. This can be seen in old trees and also younger street trees which have been cut many times. This has been attributed to the active growth points attracting a good supply of food, which results in excessive wood production and/or reaction wood, the result of loading from developing branches.

3.2 The stages in the life of a tree

Trees do not have a fixed life span; some die before reaching veteran status, others will become veterans at a much earlier age than might be expected. There is considerable variation both between and within different tree species. The life of a tree in natural conditions may pass through three main stages (Figure 12):

1. **Formativ e** - *This is the stage when most of the energy produced by a tree is used for growth. There is a rapid increase in size as it grows from a seedling to a fully mature tree. Crown size and leaf area increases each year, until the canopy is fully developed. The widths of the annual rings are similar each year but because the whole tree is getting bigger, the cross-sectional area covered by each successive ring is greater.*
2. **Full to late maturity** - *This starts when the optimum crown size is reached. The amount of food produced from the leaves remains much the same each year and results in a more or less constant volume of wood being laid down. However, as the tree gets ever larger, this volume is spread increasingly thinly, thus the rings in the stem decline in width.*
3. **Ancient (Veteran stage)** - *This is the stage reached when the successive increments added to the tree, seen as the rings of wood, have a reducing cross-sectional area, but the tree is still increasing in girth. The crown dies back and branches may be lost, damage and decay also reduces productivity. The result is that as the leaf area declines, less new photosynthetic material is produced each year and the tree is even less able to maintain a complete cover of woody material over the whole stem area. This process is called retrenchment and is seen most visibly as 'stag-headed' trees (Figure 13), typically in oak.* This does not mean that the tree is about to die, *it is a condition that can persist for many decades or even centuries. Retrenchment is not the only cause of stag-headed trees, it can also occur in younger trees, brought on by drought,disease, insect damage, root disturbance or pollution. The response of the tree results in a new balance between the area of woody material and that of the leaves. A tree in the last phase of its life that has retrenched can be very healthy and vigorous despite extensive decay and dieback. This stage may be also be the longest in the life of the tree.*

Figure 12. *The stages in the life of a tree.*



STAGES				*IDEAL NATURAL STATE: OPTIMUMGROWTH* GERMINATION	
FORMATIVE	A - B	INFANCYPRE-SEXUAL MATURITY:	YOUNGTREE, HIGHVITALITY GROWTHENHANCEDBY MYCORRHIZAL ROOT ASSOCIATES		
	B - C	JUVENILE TO EARLY MATURITY:	CONTINUED FAST GROWTH NETINCREASEINANNUALINCREMENT LOW VOLUMEOF DYSFUNCTIONALTISSUE	LOW HABITAT CONTRIBUTION	HIGHVITALITY
FULL TO LATE MATURITY	C - D	FULL TO LATE MATURITY:	GROWTH TO PEAKCROWNSIZE COLONISATION BYSAPROXYLIC (DEADWOOD) INVERTEBRATES MAXIMUMPOLLINATIONANDSEED CAPACITY ONSETOF NATURAL LIMBLOSS INCREASEOF DYSFUNCTIONALTISSUE ACCELERATED FUNGAL COLONISATIONAND ACTIVITY		
ANCIENT	D - E	EARLY ANCIENTSTAGE:	RETRENCHMENTOFCROWN: REDUCTIONINNETANNUALINCREMENT CONTRACTIONOFLIVECROWN INCREASEDVEGETATIVEVITALITYINLOWERCROWN INCREASEDFUNGAL ACTIVITYAND WOODDECAY INCREASEDCOLONISATIONBYFLORAANDSAPROXYLIC FAUNA		
	E - F	LATEANCIENTSTAGE:	ADVANCEDRETRENCHMENT DECLINEIN CROWNSIZEANDANNUALINCREMENT EXTENSIVE HOLLOWING CROWNCOLLAPSE DECLININGVITALITY ADVANCED HEARTWOOD DECAY AND HOLLOWING ADVANCED ACTIVITYBY FAUNAAND FLORA	INCREASING NUTRIENT STATUSOF TREEFOR COLONISERS INCREASING HABITAT	GRADUAL DECLINE INVITALITY
	F - G	SENESCENT:	TERMINALDECLINE: TREEDEATH CONTINUING FUNGAL ACTIVITY PEAKOF SAPROXYLIC ACTIVITY NUTRIENTRECYCLING	DEATH	

Figure 13. *Sweet chestnut trees at Croft Castle Herefordshire). A standing dead tree is in the foreground and stag headed trees behind.* *(see colour plate page 84).*

The ancient stage can be further subdivided into three phases.

- Early ancient. **When, over a period of years, there is a trend for the amount of dieback to exceed growth.**
- Mid-ancient. **When the annual rings cannot form all the way round the stem and some discontinuities start.**
- Senescent. **The terminal decline of the tree, leading to death.**

Tree species vary in the proportion of time they spend in each of these phases. Willow and birch tend to have an extremely short 'mature phase' whereas others, such as yew can grow in cycles, passing from ancient back to formative growth. All the stages are a continuous process and of variable length. Once a tree has reached the middle ancient stage, nothing should be done to encourage the speeding up of the ageing process and the aim should be to keep it in this phase for as long as possible. When discontinuities in the annual rings develop, the tree is at its most vulnerable stage.

3.2.1 Other aspects of the veteran stage

Veteran trees that are retrenching tend to show a diminished growth rate and a drop in reproductive output. They are also slower to occlude wounds if damaged. They tend to develop other features and characteristics to a greater extent than younger trees (eg cavities in the trunk, seepages, dead loose bark, dead wood in the canopy and physical damage). One important point to note is that, **as the tree ages it becomes more valuable for a wide range of other organisms and its habitat value increases**.

3.3 Assessing the age of a tree

Assessing the age of a veteran tree is not an easy task and is usually, at best,an estimate. There are a number of methods that can be used, however.

- **Taking a core** is one option but many veteran trees are hollow or rotten to a greater or lesser extent. Coring is also detrimental as it can cause damage in an undesirable place (Shigo, 1986a illustrates the possible consequences of taking a core from a tree in terms of the rot induced.) Felling a veteran tree to count the rings should, of course, never be done! Counting the rings on major branches (cut during the course of work or fallen) from veteran trees can sometimes give an indication of age. An allowance of years for the tree to produce the branch should be added to the ring count.
- **Age based on tree girth I.** Because of the variation in growth rate throughout the different stages in the life of a tree, caused by differing conditions of soil type, nutrient status, rainfall etc and the even greater variation between different species it is difficult to extrapolate age from girth measurements. There are some rules of thumb that can help. Mitchell (1974) states that one inch (25 mm) of girth (at breast height, 1.2 m from the ground) is equivalent to one year's growth for a free standing tree and 1/2 inch (13 mm) in a tree within a woodland setting. This approximation of age is only helpful for some species of tree (eg oak) that are in middle age and have not been cut. It is of very limited value with regard to old trees.

- **Age based on tree girth II** This is a more accurate (and thus more complicated) system also based on tree girth developed by J. White. It has been calibrated using a variety of older trees where the planting date is known and provides the best estimates of age available. (For a description of methods and the relevant tables used for calculation see White, 1998.)
- **Age/size ratios within species** . Different species of tree grow at very different paces but it is possible to build up a table of girth sizes and estimated age for a particular species, though even within a species there is considerable variation. Yew has been studied with this aspect in mind (Baxter 1992).
- **Site-specific information.** It is possible to draw up a table for a particular species on a particular site that allows figures for girth to give an estimate of age and which may be able to take into account the effects of historical management such as pollarding (eg Le Sueur 1931). These may not correlate well with data from other sites.

As a general principle it is almost impossible to age pollards, or trees that have undergone natural crown loss, by the methods given above.

3.4 Why does pollarding or cutting cause trees to live longer?

A normal tree reaches the veteran stage when the size of the crown is not large enough to produce enough food to maintain the same cross-sectional area for each annual ring. During the process of retrenchment the photosynthetic area is reduced, as is the surface area of the woody branches, so that less food is required by the tree.

Reducing the size of the crown at intervals delays the veteran stage in a tree's life when the demand for water and nutrients outstrips its ability to increase the root area to absorb them. A reduced crown also reduces the risk of wind throw, owing to the relatively low stature (short 'lever-arm') and small 'sail area', but a long abandoned pollard with a large sail area may become particularly vulnerable.

In addition, the multiple branches from the top of the bolling produce a larger number of vascular connections into the trunk than in a normal tree. These, in effect, form separate compartments and it is less easy for pathogenic agents, or aggressive decay fungi, to spread through the entire tree.

Severe wounding of a tree is similar to pollarding and has four main effects:
- exposure of cut surfaces to micro-organisms;
- drying out of wood from the cut surfaces;
- reduction in the volume of foliage and sapwood in the tree and thus its existing stores of carbohydrates and the capacity to replace them;
- loss of shoot tips which disrupts hormonal co-ordinating signals and affects growth.

Wounds result in the drying out of an area of wood, causing decay. The larger the amount of wounding (as on an old tree with all branches removed) the more drying out and dieback with the increased chance of infection by micro-organisms. The ability of the tree to compartmentalise (see section 3.5.1) will be reduced because of its severely reduced photosynthetic area. It seems that a few trees are able to cope with this situation although willows can grow new shoots from an old bole. If some branches are retained on the tree, the amount of exposure, drying out, and infection by micro-organisms is decreased. However, these areas will be restricted to strips of xylem and phloem associated with the cut branches. For this reason (and to keep the sap wood active) it is best to retain good connections of xylem and phloem throughout the tree,thus maintaining 'channels'of living tissue between the roots and shoots. In some old trees that have been cut back heavily on one side this connection has been broken and the tree has died back completely thus resulting in a 'lop-sided' tree. Leaving branches, at least small ones, all round the bolling is therefore advisable.

The value of pollarding and working trees

When humans started clearing the forest they removed many of the conditions that saproxylic species (or wood decay communities) required such as dead wood on the ground and within trees and standing dead trees. While this must have been detrimental to many populations of saproxylic species the human management of the trees eg pollarding and coppicing, created very similar conditions in a different way. Almost all trees may, at one time, have been used or managed and these can be referred to as 'working trees'. The increased life expectancy of working trees and the characteristics they developed enabled the perpetuation of suitable niches for a range of species in the wood decay community despite the change in the landscape that resulted.

3.5 The decay process

The process of decay in wood is a complex subject and the details are only just starting to be understood. There are many different agents involved, which make it very difficult to establish the relative importance of each. What is clear however, is that fungi have a fundamental role in the process. The work of A. Rayner, L. Boddy, A. Shigo, F. Schwarze and D. Lonsdale has helped enormously in establishing how fungi behave within living trees and dead wood and how the tree responds. The following sections summarise the crucial points with respect to living trees. Section 7.5 considers the conservation of fungi in relation to veteran trees.

3.5.1 Compartmentalisation

Trees have no wound healing processes, as animals do, but they do have a way of limiting any damage caused. If a tree has been damaged and is then cut some years later it can be seen to have dried out,the dysfunctional area of wood extending back from the wound. This area often has a sharp boundary wall between it and the rest of the tree as shown by a difference in the colour of the wood (Figure 14). This process of boundary setting has been termed compartmentalisation.

The sharp boundary results from a response of living cells to the ingress of air and/or micro-organisms and may represent a barrier between healthy and damaged areas. If a tree is badly damaged it spends energy in compartmentalising, leaving less for growth, which can result in a smaller annual ring. The more areas that are 'sealed off', the less tissue is available for the tree to distribute food and water to its various parts. Eventually, when there are too many dysfunctional compartments and the distribution of new sapwood becomes discontinuous, the tree is unable to maintain vital functions and death results. However, the more compartments there are in a tree, the more structural diversity there is and so the larger the number of niches and habitats for other organisms. The exact processes by which compartmentalisation and barrier formation occurs remains unclear.

Figure 14. *See colour plate page 84.*

3.5.2 Fungal colonisation

It seems likely that fungi colonise living trees in two main ways:
- from the outside. In the simplest scenario, physical damage to a tree weakens its physical defences and makes conditions suitable for the fungus to colonise,become established and grow;

- **from the inside. The fungus makes use of the tree's own plumbing system (xylem and phloem) to reach different parts of the tree via the sap stream; this can occur at any stage in the life cycle. The fungi often remain in a latent (inactive) state without any noticeable impact on the tree until conditions within the wood change enough to activate them, eg drought, ageing process.**

It is thought that the sapwood of a healthy tree has such a high moisture content that it is unsuitable for the growth of most fungi. However, when the tree is mechanically damaged or is stressed in some way, parts of it may become more suitable for fungal growth. Loss of a branch, for example, allows air in and causes drying out of the wood around the wound and enables fungal growth. Stress brought on by drought or the severing of roots may cause the tree to stop producing food (photosynthesising) from a branch. This branch then dies back and dries out because the flow of sap is no longer as strong as normal. The drier conditions activate some of the latent fungi or fungi entering via the dead or broken wood.

Most of the fungi capable of causing extensive decay depend on wounds or dead branches or roots as entry points. Some of these species grow only in heartwood, while others are confined to sapwood or are able to colonise either. A wide range of factors determine whether or not decay becomes extensive enough to weaken the tree significantly.

Some pathogenic fungal species are able to cause death or dysfunction to parts of the tree even without stress or major injury (eg some honey fungus species or the fungus that causes Dutch elm disease). This relative minority of species are a primary cause of dysfunction in the sapwood or of death of the cambium.

As the fruiting bodies of the fungi are the only parts that are usually noticed they are often misinterpreted. A small number of species (eg some species of honey fungus) can cause the death of a tree but a much larger number produce fruiting bodies only when the tree (or that part of it with fungal fruiting bodies) has died from other causes (ie they are saprophytic). This leads to many misconceptions as to the role of fungi.

The means by which fungi colonise sapwood

- **Root coloniser s.** Species that colonise intact roots and then spread throughout the cambial zone of the tree. They may kill the tree by girdling it or killing too many roots, eg *Armillaria mellea.*
- **Sapwood colonisers I.** Species that enter the tree through a wound or other open entry point on the tree. Most species decay parts of the tree without killing it but sometimes the decay parts of the tree without killing it but sometimes the decay is so extensive that very little functional sapwood is left, eg most *Ganoderma* species.
- **Sapwood colonisers II.** These species also enter the tree through wounds but are more aggressive and may kill the host, eg *Chondrostereum purpureum.*
- **Deadwood coloniser s.** Species that can colonise sapwood only after it has died as they are unable to overcome the active defences of the tree, eg *Daedaleopsis confragosa.*

Note that the behaviour of fungi covers a spectrum and that a particular species may fall in between the categories presented here.

3.5.3 Fungi growing within the heartwood

Some fungal species are able to grow in the innermost part of the tree, which consists of dysfunctional wood. It is usually drier than the outer sapwood and so is more suitable for the growth of fungi if they are present. Species that rot the heartwood such as *Laetiporus sulphureus* (Figure 15) break down only the dead wood. This decays the centre of the tree but leaves the outer, living layers intact. While this may not be desirable from the point of view of a commercial forester, the tree is not harmed and may actually benefit. Decay and hollowing are part of a nutrient recycling process.The tree can make use of the products of wood decay within the trunk by producing aerial roots from its above ground parts, which grow into the rotting stem. A hollow tube may respond differently from a solid trunk in high winds and is not necessarily more likely to snap provided its walls are not so thin that buckling occurs.

Figure 15. *See colour plate page 84.*

3.5.4 Types of deca y

There is a wide range of variables influencing decay. The result of this is a tremendous range of potential niches available to organisms such as invertebrates that make use of the rotting process and its products. Premature decay in a tree is not necessarily detrimental, either to the tree or to its wildlife value. Young decaying trees can be very valuable, on sites with veterans, in providing suitable conditions for the saproxylic organisms. Decay is dependent on many factors:

- **age of tree;**
- **presence of heartwood. (Those species of tree, eg birch and beech lacking durable heartwood tend to decay quicker that those that do, eg oak);**
- **type of wound or stress agent;**
- **species of fungi involved and stage of growth within the tree;**
- **species of invertebrate involved;**
- **species of vertebrate involved;**
- **position of wound;**
- **whether the wound collects water or not;**
- **whether the wound is enclosed or open to the air;**
- **whether the wound is permanently covered by water (becoming anaerobic);**
- **ability of the tree to respond to damage (ie to form reaction zones and to occlude wounds);**
- **outside factors (eg dung, rotting carcasses, aerial pollution).**

There are three main types of rot caused by fungi:

- **White rot** - When the lignin and cellulose are both broken down. In **simultaneous white rot** the lignin and cellulose are broken down at approximately the same rate causing loss of both stiffness and strength, which, in the advanced stages of decay produces a thick porridge-like substance. In **selective delignification** (or **stringy white rot**) the lignin is broken down first and the cellulose degrades more slowly. Initially the result is soft material that is still quite strong, the colour and weight of balsa wood. White rot is more common is broadleaved than coniferous trees, eg rot produced by some *Ganoderma* species.
- **Brown rot** - When the cellulose is degraded and the lignin is left intact. The initial results of the decay are brittle but rigid. It does not bend much before breaking but may break into cubes known as cubical brown rot. Eventually a rich, humus like, substance may result (red wood mould) usually after having passed through the guts of many invertebrates. Brown rot is more common in conifers than broadleaved trees. It is produced by, for example *Fistulina hepatica* and *Laetiporus sulphureus* in oak trees.
- **Soft rot** - This is when the cellulose is degraded, as in brown rot, but the fungi invade the cell walls in a very different way. Many white rots and some brown rot fungi can behave like soft rot fungi in living trees, but 'classic' soft rots are caused mainly by specialised ascomycetes which grow in the surface layers of dead wood or timber under very wet conditions.

Different invertebrate species and communities are associated with each of these types of rot.

> ***Decay detectors***
>
> *There is a range of devices available for the detection and assessment of decay. Some of these can help to determine whether there is significant weakening, by providing information on the position and extent of decay. Interpretation of such information is, however, often difficult and should be attempted only by a suitably qualified practitioner who will make a visual inspection in the first instance, and will use the resulting observations to decide which parts of the tree, if any, could be usefully probed, using a particular diagnostic device. The number of probes should be kept to a minimum, as all currently available devices are invasive to a greater or lesser extent.*

3.5.5 The value of dead wood

It is important to encourage a variety of types of rot so that suitable conditions are provided for a range of the more specialised invertebrates. The more dead wood a tree contains the more valuable it is. Thus, a living veteran tree is better than a dead one because it will continue to produce more dead wood. Old dead trees left standing are usually better than those in younger growth phases. Damaged young trees may also have valuable areas of rot (natural or even artificially induced).

Trees containing a higher volume of wood have a higher wildlife value, which is why old pollards are generally more valuable than old coppice stools. The latter may have a range of niches, but the sheer volume of wood is considerably less than in most old pollards.

3.5.6 The role of organisms other than fung i

Although fungi have the fundamental role in the decay process in trees, they are not the only active organisms. Many invertebrates assist in the breakdown of wood by boring into it and feeding on the comparatively softer and more nutritious bits. They also enable fungal mycelia to penetrate the wood more easily along the sides of burrows. Some species of insect have nitrogen-fixing bacteria in their guts, which enhance the nutritional value of their faeces which may be re-ingested by other species.

Wood has a very complex chemical structure and is very indigestible. Many of the invertebrates rely on fungi to break the wood down into simpler molecules so that they can take advantage of it. Ambrosia beetles (family Scolytidae) even have fungi associated with them, which they carry between trees to perform this function.

Birds such as woodpeckers may contribute to the process by actively hollowing out areas for nesting, their nests and holes may then be inhabited by other animals. The faeces and dead bodies that build up in the tree holes contribute to the nutrient status of the rotting wood. There are even secondary fungal colonists whose fruiting bodies are found in cavities created by the primary decay fungi.

Further reading: Beckett (1975), Boddy & Rayner, (1983), Coder (1996), Dolwin *et. al* (1998), Graham (undated), Green (1993, 1994, 1996a), Le Sueur (1931, 1934), Lonsdale (1996, 1999), Mattheck & Breloer (1994), Mitchell, A. (1974), Mitchell, P. (1989), Patch, (1991), Patch Coutts & Evans. (1986), Rackham (1986, 1990, 1991), Shigo (1986a, 1986b), White (1996, 1998),Wignall, Browning & Mackenzies (1987).