Lesson 2

TREE PHYSIOLOGY

Aim

Explain tree biology, including morphology, anatomy and physiology, as it relates to arboriculture.

TREE GROWTH

Tree growth is a response to the environment and to the tree's genetic make-up. The environment is made up of such factors as water, light, air, temperature and cultural practices. This has an impact on the physiological processes that lead to growth, such as photosynthesis, which take place within every plant. A tree's genetic make-up will also influence its growth and responses to the environment in which it is growing. If a tree is growing in a favourable environment and its genetic make-up also favours that environment it will be healthy and grow to optimum size and shape.

PHOTOSYNTHESIS

Photosynthesis is fundamental to life on earth. It is the process of converting the sun's energy into useable chemical energy. From this process, we obtain the source of all our food, much of our fuel, and all the other plant derivatives that we rely on to preserve life, as well as oxygen, a waste product of the process. *Trees grow through photosynthesis.*

During photosynthesis, green plants take in CO_2 (carbon dioxide) and water. In the presence of light, plants are able to manufacture carbohydrates (comprised of carbon, hydrogen and oxygen) and oxygen is released into the atmosphere. The general equation for photosynthesis is:

$$nCO_2 + nH2O + \text{Light} \rightarrow (CH_2O)n + nO_2$$

In other words, photosynthesis = carbon dioxide + water + light energy → glucose + oxygen

Photosynthesis occurs in two stages: a light dependent stage (the "light reactions") and a light independent stage (the "dark reactions"). During the light reactions, water is split into hydrogen and oxygen, and the energy from the splitting of the molecule is stored in chemical form. The oxygen is released into the atmosphere. During the dark reactions (also known as the Calvin cycle), CO_2 from the atmosphere is combined with the hydrogen from the split water molecule to form carbohydrates.

RESPIRATION

Respiration involves the breakdown of carbohydrates to release energy for cellular activities. That energy was originally captured and stored through the process of photosynthesis. In a broad sense, respiration is the reversing of the photosynthesis process.

Respiration occurs both in plants and animals – the only difference is that plants manufacture their own carbohydrates, whereas animals consume the carbohydrates that are the substrate for respiration.

During respiration, carbohydrates (eg. sugar) react with water and oxygen to produce energy plus carbon dioxide and water. (NB: the amount of water produced is greater than what is started with.) This occurs in the mitochondria of plant cells. Sugar is the usual substrate for respiration, but it is worth noting that other compounds such as fats and proteins can also be used.

In its most basic form, respiration is similar to combustion of sugar – the exception being that respiration releases the energy much more slowly than combustion does. Respiration is a relatively slow step-by-step chemical process where the degradation of carbohydrate occurs slowly, releasing small amounts of energy in each step, slowly over a period of time. The general equation for respiration that you must know is:

glucose + oxygen → carbon dioxide + water + energy

This can also be written as:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{Energy}$$

TRANSPIRATION

Transpiration is the loss of water vapour through the stomata of the leaves. Stomata are small openings in the leaf surface which have guard cells either side. The guard cells can facilitate the openings to be open or closed controlling the flow of water and gases into or out of the plant.

The movement of water from the roots through the xylem and up to the leaves is called the "transpiration stream", because transpiration is the main reason for movement along that pathway. This works as follows:

- Water evaporates and is lost through stomata on the leaves.
- This creates a change in pressure or a lower pressure in the upper leaves, which is evened out by water under higher pressure (further down the plant) moving upwards.

Water will always diffuse or move from cells which have more water into cells with less water. A chain reaction set in motion by the evaporation from the leaves thus causes movement right along the transpiration stream, which results in lower levels of water in the roots - which tends to cause water to be absorbed (or sucked) into the roots.

EFFECT OF TEMPERATURE ON GROWTH AND FLOWERING

Each species or variety has a set of conditions relating to temperature which determine its growth and development. Plants have a **minimum temperature**, below which they will not growth; an **optimum temperature** (or range of temperatures) at which they growth at a maximum rate; and a **maximum temperature**, above which they will not grow and may die.

Critical steps in the plant's life cycle are triggered in response to certain temperature treatments. Other environmental factors such as light, photoperiod and moisture availability interact with temperature to initiate the plant's developmental responses.

Vernalisation

Some plants require a period of vernalisation to initiate flowering. Vernalisation is the induction of flowering by low temperatures. The temperature range needed for vernalisation varies according to the species or cultivar, but is usually in the range of 0°C and 10°C.

Most woody perennials do not require low temperatures for flower induction, but many do need low temperatures to overcome the rest period.

Deciduous fruit trees require a period of low temperature over winter to initiate flowering; and in turn, fruiting.

WHAT MAKES FOLIAGE CHANGE COLOUR IN AUTUMN?

Deciduous plants shed their leaves in autumn or early winter, and are fully or partially devoid of foliage over the colder months of the year. This is an adaptation that allows the plant to better survive unfavourable conditions (such as extreme cold).

Prior to leaves dropping they undergo a period of senescence.

Senescence is the period during which leaf cells progressively die

Over this senescence period, tissue at the leaf base progressively dies, until finally a complete section of tissue between the leaf and the stem is dead (At this point there is nothing left to hold the leaf to the stem; so it detaches and drops to the ground.)

As senescence occurs, the amount of chlorophyll in the leaf (which gives it the normal green colour) reduces. Chlorophyll is actually only one of many pigments that generally occur in leaves; but it is usually the strongest pigment, and for that reason alone, most leaves usually appear green if the plant is healthy.

Other types of pigment chemicals commonly found in leaves include:

- Anthocyanins – Reds, Blues and Purples
- Carotenoids – Yellows and Oranges

Generally carotenoids also decompose rapidly in autumn, but anthocyanins break down much more slowly.

Often anthocyanins can still be at close to 100% normal levels when only 40% of normal chlorophyll and carotenoids remain. Anthocyanins are produced through chemical processes, from excess sugars in the leaves, particularly in the presence of bright light. In view of this fact; the level of anthocyanins will be stronger if the plant has been actively photosynthesising (producing sugars) over summer, combined with lots of bright autumn days (if weather is frequently overcast and dull in late summer and autumn; the production of anthocyanins is decreased).

Lower temperatures in autumn reduce the movement of sugar around the leaf, so if the weather changes from warm to cool fast, the leaf sugar remains high and anthocyanins build up; otherwise the levels of these pigments might not be so high. High levels of anthocyanins will generally result in more vivid autumn foliage colours.

Variations

Autumn colour can still vary from plant to plant within a species. Variations include:

- the time at which colour occurs (some produce colour earlier, others later)
- the duration of colour (some maintain good colour for longer periods)
- the intensity of colour

Such variations can be affected by:

- duration of seasons
- severity of seasons
- whether climatic changes are gradual or more abrupt
- aspect (whether it faces north or south, east or west
- degree of protection (whether it is exposed or protected by walls or other plants)
- genetics
- sex (eg. parentage of cutting/grafting material can have a significant effect in some plants)

TREE PHYSIOLOGY

To understand and practise arboriculture successfully requires an understanding of how plants grow.

Trees have four main parts:

- Roots - the parts which grow below the soil
- Stems - the framework
- Leaves - required for respiration, transpiration and photosynthesis
- Reproductive parts - flowers and fruits.

Roots

Soil provides the plant with:

- Nutrients
- Water
- Air
- Support

Roots absorb nutrients, water and gases transmitting these "chemicals" to feed other parts of the plant. Roots hold the plant in position and stop it from falling over or blowing away.

Stems

The main stem and its branches is the framework that supports the leaves, flowers and fruits. The leaves, and also green stems, manufacture food via the process known as photosynthesis, which is transported to the flowers, fruits and roots. The vascular system within the stem consists of canals, or vessels, which transfer nutrients and water upwards and downwards through the plant (this is equivalent to the blood system in animals).

Leaves

The primary function of leaves is photosynthesis, which is a process in which light energy is caught from the sun and stored via a chemical reaction in the form of carbohydrates such as sugars. The energy can then be retrieved and used at a later date if required in a process known as respiration.

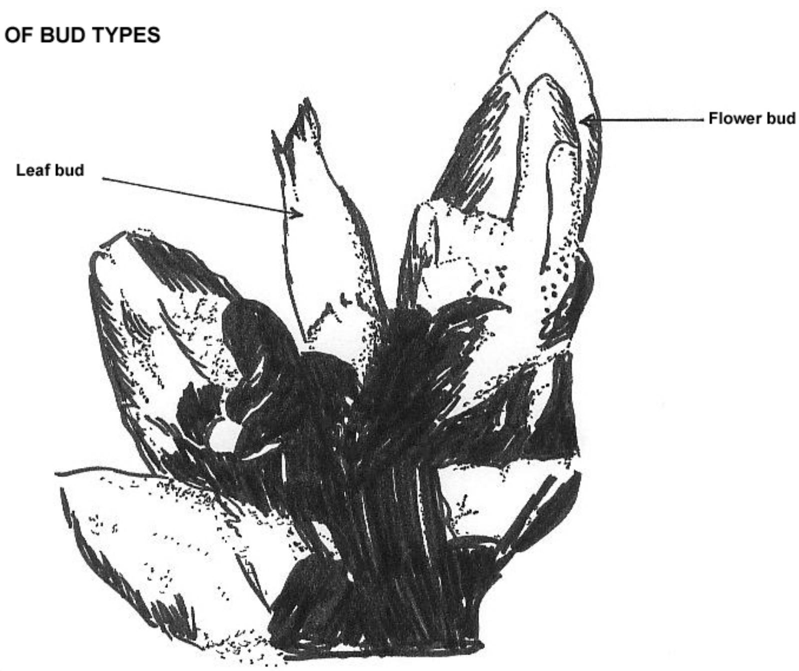
Leaves are also the principle plant part involved in the process known as transpiration whereby water evaporating, mainly through the leaf pores (or stomata), sometimes through the leaf cuticle (or surface) as well, passes out of the leaf into a drier external environment. This evaporating water helps regulate the temperature of the plant. This process may also operate in the reverse direction whereby water vapour from a humid external environment will pass into the drier leaf. The process of water evaporating from the leaves is very important in that it creates a water gradient or potential between the upper and lower parts of the plant. As the water evaporates from the plant cells in the leaves then more water is drawn from neighbouring cells to replace the lost water. Water is then drawn into those neighbouring cells from their neighbours and from conducting vessels in the stems. This process continues, eventually drawing water into the roots from the ground until the water gradient has been sufficiently reduced.

As the water moves throughout the plant it carries nutrients, hormones, enzymes etc. In effect this passage of water through the plant has a similar effect to a water pump, in this case causing water to be drawn from the ground, through the plant and eventually out into the atmosphere.

Reproductive Parts
These reproduce by pollen (ie. male parts) fertilising an egg (ie. female part found in the ovary of a flower). The ovary then grows to produce a fruit and the fertilized egg(s) grow to produce seed.

There can sometimes be difficulty in obtaining a good crop because insufficient pollen reaches the female parts, resulting in insufficient fruit forming.

DIAGRAM OF BUD TYPES



Flower and leaf buds of almond (Prunus amygdalus)

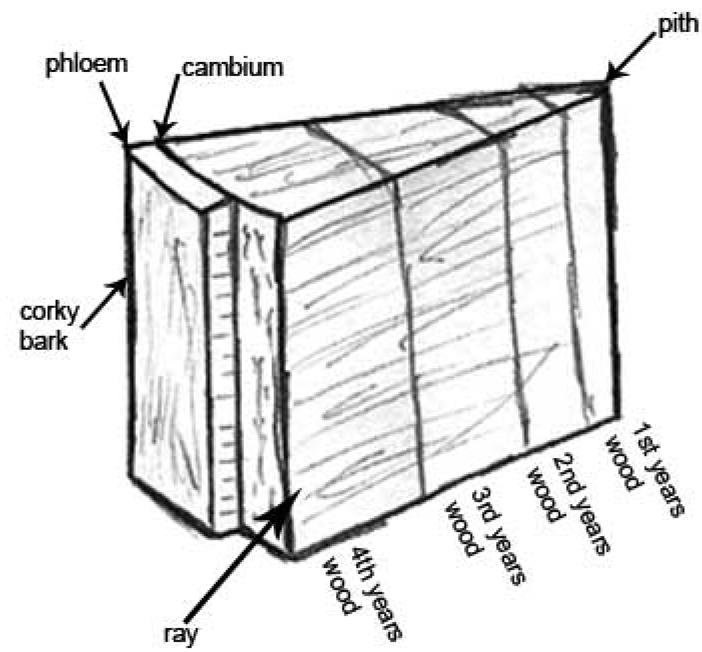
HOW A TREE GROWS

Like all living organisms, trees are composed of cells with specialised functions. Actively dividing cells, called meristematic cells, are found in the tips of roots and shoots. The plant elongates at these points as the meristematic cells divide and multiply. All plants undergo this process of primary growth. However, when trees and other woody plants reach a certain length, another type of growth occurs – this is known as secondary growth. Secondary growth results in the development of new secondary vascular (conducting) tissues, such as the secondary xylem and secondary phloem. Secondary growth occurs at the lateral meristems, which are cylinders of meristematic tissue, and as the cells there continue to divide, the girth of the plant increases.

Secondary growth only occurs in certain plants such as gymnosperms and woody angiosperms. There are two types of lateral meristems:

1. The vascular cambium – this produces thick accumulations of secondary xylem and phloem.

2. The cork cambium – this produces the outer layers of the bark in both the roots and shoots of plants.



Section of a Mature Woody Stem

More on Secondary Growth
Cell division in the cambium, results in an increase in diameter of a plant organ through the formation of secondary tissues, ie. secondary xylem, secondary phloem, phellem and phelloderm. The mature parenchyma cells in the medullary rays (between the adjacent vascular bundles) become meristematic and form what is known as the fascicular cambium. The fascicular cambium forms a continuous ring of cambium between the xylem and the phloem. The ring undergoes division to form secondary phloem to the outside and secondary xylem to the inside as concentric cylinders on either side of the cambium ring.

Vascular rays are formed at certain points through the secondary xylem and phloem by the cambium in the form of parenchyma. Due to this the stems thicken as the primary xylem and phloem are pushed further and further apart (the pith remains alive).

Growth Rings
Seasonal increases in stem girth are responsible for the development of growth rings. Trees growing in temperate regions usually produce one annual ring of wood each year. During spring and early summer, when the tree is actively growing, large xylem cells are formed. This xylem tissue becomes the early (porous, light-coloured) wood. Later in the season, growth slows and the xylem cells become denser and smaller, forming dark-coloured wood. Trees that grow year-round in tropical regions do not produce annual growth rings.

Heartwood and Sapwood
As some trees age, the older xylem cells become darker and heavier. Lignin, tannins and resins impregnate the cells, making them stronger and more durable, providing support for the tree stem. The old cells commonly referred to as the 'heartwood', become less porous and are non-conductive. Although they are physiologically inactive they can respond to wounding and pathogen attack.

The outer xylem elements, which are still actively conducting water and minerals, are commonly called the ‘sapwood’.

COMPARTMENTALISATION - HOW A TREE ROTS

The process of compartmentalisation refers to how a tree naturally resists pathogen attack. It was first described in the 1970s and 1980s by an American scientist, Dr Alex Shigo. He described it as the CODIT system: compartmentalisation of decay in trees. The following is a summary of this process.

If a tree is healthy it has a natural tendency to contain the spread of wood rots as explained below:

- Tree trunks and branches are made up of a series of "compartments”. The compartment walls are not actual anatomical features, but are naturally occurring boundaries within woody stems.

- Disease/wood rots find it more difficult to break through one compartment into the next than spread within a compartment.

- When microorganisms first attack a tree, chemicals are deposited around the wound which create a barrier to the spread of infection.

- Some microorganisms can grow through this barrier, allowing other microorganisms to move in behind the first invaders. A snowball effect can occur, with successions of microorganisms causing further damage, and making the spread of infection difficult to contain.

- Another "compartment" which acts to prevent the spread of decay is the "wall" of new wood and bark tissue which is produced each year. (ie. each ring you see in the cut section of wood is a barrier to infection).

- Wood rots thus move up and down a trunk (within a tree ring) than they do further into the centre of the tree.

The Importance of Compartmentalisation to Arborists

Trees vary in their ability to compartmentalise decay. Some species do not readily form compartments, for example, *Populus* (poplar), *Salix* (willow), *Brachychiton*, *Erythrina* (coral tree) and *Liriodendron* (tulip tree) species.

Tree vigour, pathogen virulence and the effects of further wounding are also important factors. Tree surgery practices such as pruning, bracing and cavity treatment, which inflict further wounds on trees, may interfere with this natural process and cause the decay to spread to new wood. For this reason, cavity drilling and rod bracing of cavities are no longer standard arboriculture techniques (see next section on Tree Surgery Techniques).

WATER AND PLANT GROWTH

Water is a major component of all plant growth. In succulent, leafy plant material the water content may be as high as 85 - 95%. Of all materials taken in by a plant, water is absorbed in the largest quantities. Generally less than 5% of the water taken in by the plant is used within the plant. In some cases the amount used is as little as 1%. The water remaining in the plant is used mainly in the cell tissue which are 75 - 90% water, as a carrier of foods and growth regulators from the leaves via the phloem, and in very small quantities as part of the photosynthetic process.

The remaining 95% or more acts as a carrier of nutrients. Once it has carried these nutrients up through the plant, it becomes surplus and is disposed of to the atmosphere through the leaf stomata. This loss of water also helps to keep the leaf canopy cool reducing the likelihood of leaf burning or desiccation. This upward movement of water from the roots through the stems via the xylem to the leaves is sometimes known as the transpiration stream.

Transpiration is the principal method of water movement into and through the plant. This is a physical process powered by the evaporation of water as a vapour into the atmosphere from the plant leaf. This water is lost from the outer surface of the leaf mesophyll cells. As the water is lost the cells become dehydrated. This creates a potential difference between the dry mesophyll cells and adjacent moist ones. Because of waters strong cohesive property (strong resistance of water molecules to be pulled apart) water from the adjacent moist cells diffuses through the cell walls into the dehydrated cells thereby relieving the pressure differential. The continued loss of water molecules from the leaves by evaporation creates a continual flow of water throughout the plant. This results in the pulling of replacement water from the soil via the roots and up the plant stem into the leaf.

Evaporation from the crown of the plant is roughly proportional to the size of the crown. Wind is the major cause of evaporation as it removes the moisture-laden air around the leaves creating a strong gradient between the moisture laden leaf and the drier atmosphere surrounding the leaf. Increasing temperature will also increase the rate of evaporation. During winter transpiration is generally small, however in spring and early summer the amount of water transpired can be very large. If the availability of soil moisture is high and other conditions (eg. light) are favourable the transpiration will be high. If either water supply is limited or other conditions are not favourable then transpiration will be greatly reduced. On a sunny spring day, mature trees can use 250 or more litres of water a day. One hectare of forest in a medium rainfall area may use the equivalent of 1000mm of rainfall per year. In high rainfall areas, such as tropical rainforests, over 2500mm per year may be transpired. In low rainfall areas the figure may be only 250mm per year (500mm of rain per hectare is equivalent to about 5 million litres).

Conifers and evergreen plants generally use less water than deciduous plants, even though in winter deciduous plants only use about 1% of their annual consumption compared to about 18 to 20% for the conifers and evergreens. Generally it will take about 200 to 300 litres of water to produce 1 kilogram of dry wood. For some agricultural crops, such as maize it may take 3500 to 4500 litres to produce 1 kilogram of dry matter.

In cities and other built up areas water use is generally higher than in open areas due to the amount of light and heat reflected from surrounding structures or paved areas.

Heat absorbed by dark paved surfaces also heats the underlying soil, promoting root growth, and therefore increased water absorption. The burning of fossil fuels also helps to raise temperatures, and increase carbon-dioxide levels in cities. This can also promote growth, increasing the amount of water required.

When there is adequate water in the soil and conditions are favourable for evaporation at the leaf surface then water moves easily into the roots from the soil and up into the plant via the xylem. As the soil dries the water remaining in the soil is held more tightly to the soil particles. If evaporation through the leaf continues then there is insufficient water to replace that lost through evaporation. Water stress then occurs in the plant and wilting may occur. In severe cases wilting may be permanent resulting in permanent damage to the plant, even death.

In times of water shortage stomata may only open late at night or early in the morning when humidity is high or dew is present. If water stress continues for a prolonged period then the stomata may only open for short periods to allow the discharge of waste gases (eg. oxygen) and to take in carbon-dioxide. There will be little growth at these times.

Too much water in the soil can also be a problem for healthy plant growth. While some plants are adapted to growing in waterlogged soils, or directly in water, the majority require sufficient levels of oxygen in the root zone to maintain healthy growth. If a soil is poorly drained or becomes flooded in some way then the water will displace all air in the soil leaving insufficient oxygen for the plant roots to metabolise the carbohydrates they require for energy and growth. The root tissue will die leaving no way for water to move from the soil to the upper parts of the plant, which will subsequently wilt from a lack of water.

To the horticulturist then the maintenance of sufficient, but not too much, water for healthy plant growth is extremely important.

FACTORS AFFECTING THE RATE OF PHOTOSYNTHESIS, RESPIRATION and TRANSPIRATION

Rate of Photosynthesis

The rate of photosynthesis is affected by the following factors:

- Carbon Dioxide
  As CO_2 increases, so too does photosynthesis.

- Temperature
  The light reactions of photosynthesis are not temperature dependent, while the dark reactions of photosynthesis are temperature dependent enzymatic processes. This means that at high temperatures, the rate of photosynthesis decreases. Different plant species have different levels of optimum temperatures for photosynthesis depending on the climate they are adapted to.

- Light
  As a general rule - as light increases so too does photosynthesis; plants can be classified according to their light needs, such as high, medium and low light requirements. Low light levels reduce photosynthesis but shade plants for example require less light than plants adapted to high light conditions. Under high light, a plant can increase photosynthesis up to the maximum level, but further increases in light will not further increase photosynthesis.

- Water
  Plants under water stress close their stomata to prevent further water loss, which prevents gas exchange and limits photosynthesis.

- Leaf Age
  As the leaf becomes older, the photosynthetic capacity of the leaf decreases.

- Environmental History
  Longitude, latitude and elevation all affect the rate of photosynthesis.

Photosynthesis occurs in a series of reactions summarised as:

$$6\ CO_2 + 12\ H_2O \xrightarrow[\text{light energy}]{\text{green plant}} C_6H_{12}O_6 + 6\ H_2O + 6\ O_2$$

Rate of Respiration
The rate of respiration is affected by the following:

The rate of respiration is affected by the following factors:

- Oxygen Available
  At lower oxygen levels, there is a lower rate of respiration. Fruits and vegetables are sometimes stored in environments where the oxygen in the air has been lowered (through pumping in nitrogen or carbon dioxide). This reduces the respiration rate, hence preserving carbohydrate in the tissue and helping the produce to be kept longer.

- Temperature
  Respiration is slower at lower temperatures. At 0°C respiration occurs at less than half the rate it does at 10°C. Most plants grow better if night temperatures are lower than day temperatures because at night respiration slows allowing more of the energy stored by photosynthesis during the day to be retained.

- Soil Moisture
  If a soil is overly wet, the water reduces the oxygen available to plant roots which in turn reduces respiration in the roots and results in poor growth.

- Light Intensity
  In shaded conditions plants generally have lower respiration rates because:
  - lack of light reduces photosynthesis, thus reduces the carbohydrate produced
  - in turn, if there is less carbohydrate, there are fewer carbohydrates available for respiration

The overall reaction is written as:

$$C_6H_{12}O_6 + 6\ H_2O + 6\ O_2 \text{ --> } 6\ CO_2 + 12\ H_2O + \text{energy}$$

Environmental Factors that Affect Transpiration and Water Uptake

Solar Energy

- Wavelength variations affect photosynthesis, transpiration and morphology. As radiation increases, so too does transpiration, limited by irrigation availability.
- Variations of season, and of the plant itself.

Atmosphere Humidity

- As humidity increases, water uptake and transpiration decreases.

Wind Velocity

- As wind velocity increases so too does transpiration.

Temperature

- Temperature of the plant affects evaporation.
- Temperature of the atmosphere - if high, so too is water uptake.

Stomatal Aperture

- Stomatal aperture (size of opening) is dependant on light, plant water status, carbon dioxide concentration and the temperature.

Available Soil Water

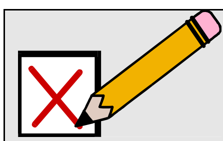
- This is affected by soil type.
- This affects turgidity which controls stomatal aperture thereby affecting photosynthesis and production.

TERMINOLOGY

Learn the following terms:

Abscission: natural shedding of plant parts, including bark, leaves, flowers and fruits.
Apical dominance: influence exerted by a terminal bud in suppressing the growth of lateral buds.
Bark: secondary tissues in woody plants from the cambium outwards.
Branch-bark ridge: zone of raised bark on the upper side of the branch/trunk union.
Bark cambium: thin layer of dividing cells responsible for the formation of phellem (cork).
Branch collar: a collar of tissue formed early in the season, at the base of a branch.
Bud: embryonic shoot protected by modified leaf scales, with the potential to develop into flowers and/or leaves.
Butt: base of a trunk or branch.
Callus: mass of large parenchyma cells that develop as a response to wounding.
Cambium: thin layer of actively dividing cells responsible for the formation of vascular tissue.
Compartmentalisation: process by which trees resistant decay.
Crotch: junction of two or more branches.
Crown: part of the tree where the main limbs originate.
Epicormic: growth that develops from a dormant or latent bud.
Fastigate: upright or conical tree growth habit.
Heartwood: central part of the secondary xylem in some woody plants which is no longer conductive but provides support to the tree and responds to wounding.
Internode: region of a stem between two successive nodes.
Main leader: lateral that terminates a main limb.

Main limb: a main branch in a tree’s framework.
Meristem: actively dividing cells capable of developing into specialised tissues.
Node: part of a stem where one or more leaves are attached.
Phellem (Cork): external, protective secondary tissue in woody plants, impermeable to water and gasses.
Phloem: tissue through which synthesised organic food is conducted from the leaves to other parts of the plant. Phloem consists of sieve tube cells, companion cells, phloem parenchyma and fibres.
Sapwood: outer functional part of the secondary xylem in woody plants.
Scaffold limbs: main limbs.
Secondary limbs: limbs arising from main limbs.
Sucker: adventitious shoots arising from the rootstock or base of a plant.
Tissue: group of cells of similar structure that perform a special function.
Tracheid: elongated, tapering xylem cell with lignified pitted walls responsible for conduction and support.
Trunk collar: late season trunk tissue that forms around a branch collar, at the base of a branch.
Xylem: vascular tissue that conducts water and dissolved ions from the root system to the leaves and strengthens and supports the stem.
Vascular cambium: thin layer of dividing cells between the xylem and phloem responsible for the formation of vascular tissue.
Wood: secondary non-functioning xylem tissue in perennial (woody) shrubs and trees.

	**SELF ASSESSMENT** Perform the self assessment test titled ‘Self Assessment Test 2.1’. If you answer incorrectly, review the notes and try the test again.

SET TASK
Find some wounds on trees. Using some firm wire, a chisel and any other tools you might find appropriate, prod into the wound to see what wood is infected. How far does the rotten wood go into the main trunk or the main part of the branch? How far does the rot move up or down the length of the stem or branch? If you can - cut a rotten section out of a tree to see exactly where the rot has occurred; what is the pattern of the rot?

	**ASSIGNMENT** Download and do the assignment called ‘Lesson 2 Assignment’.