

Chapter 2

Biology of Plantation Growth

Growers want their plantations to be healthy and to grow as rapidly as possible. To appreciate how plantation silviculture can achieve this, it is necessary first to understand how plantations grow and what resources they need to do so. Forrester et al. (2010a) have reviewed the relationships between plantation growth and silvicultural practice, with particular reference to eucalypt plantations; much of what they say will apply equally to other plantation species.

This chapter describes the growth of normal, healthy plantations. It concentrates on **monocultures**, that is, plantations of a single **tree** species, since these are the most common types of plantations grown commercially. **Mixed-species** plantations, that is, those that contain two or more tree species, behave differently in some respects from monocultures and are discussed in [Chap. 13](#). Much of the information in this chapter will be referred to in later parts of the book, as the various aspects of plantation silviculture are discussed in detail.

2.1 Basic Plant Biology

For readers without any detailed biological knowledge, this section describes briefly the biology of plants in general and trees in particular. Standard texts on plant biology can be consulted for more details. More advanced texts, such as the excellent volume by Atwell et al. (1999), provide much more scientific detail of plant biology.

2.1.1 Tree Requirements and Characteristics

In common with all plants that grow on land, trees have certain fundamental needs that they must obtain from the environment around them. In particular, they need:

- Sunlight.
- Carbon dioxide from the air.

- An appropriate air and soil temperature.
- Water and **nutrients** from the soil.

Each of these will be discussed in more detail later. As long as they are all available, trees have anatomical, physiological and metabolic characteristics that allow them to live and grow. For the present discussion, the most important of these characteristics are:

- Leaves that take in carbon dioxide from the air and convert it chemically to food for the tree, using energy from sunlight in the process.
- Branches that support the leaves high in the air to intercept sunlight.
- A stem that supports the tree upright, and through which water and nutrients are transported up from the roots to the leaves and down which food is transported from the leaves to the roots.
- Large, woody roots that transport water and nutrients to the stem and anchor the tree firmly in the ground.
- Living, fine roots that are located at the extremities of the root system and take up water and nutrients from the soil. Usually, they are defined in practice as roots less than about 2 mm in diameter, but perhaps up to 5 mm (da Silva et al. 2009; Douglas et al. 2010).

Other land plants have leaves, branches, stems and roots, but what distinguishes trees in particular is that they are tall. The tallest in the world, the redwoods (*Sequoia sempervirens*) of California and the eucalypts, mountain ash (*Eucalyptus regnans*) and Tasmanian blue gum (*Eucalyptus globulus*) of southern Australia (Potts and Reid 2003), may grow to over 100 m. Most tree species grow to much lesser **heights** and the definition of what is then a tree and what is a shrub becomes rather arbitrary.

The key to the great height of trees is that they have massive stems made of wood. Wood is a strong material, its strength coming from the particularly thick walls of the microscopic plant **cells** of which it is made. Wood consists mainly of dead tissue. That is, the cells have been emptied of their living contents, so the tree needs no longer to supply them with food. Not only do tree stems contain wood, but branches and large roots also do.

Wood serves two purposes. It provides strength and is also the pathway through which water is transported from the roots to the leaves. The dead, empty wood cells can be thought of as a system of interconnecting pipes, through which water passes up the whole length of the tree, a process known as **transpiration**. The tissue that transports water in plants in general, not just trees, is known as **xylem** and wood is one such tissue.

A thin, outer layer of living tissue (known as **phloem**) surrounds the wood of roots, stems and branches. Food is transported down through the phloem from the leaves to the living fine roots, at the extremities of the root system. Between the phloem and the wood is a very thin layer of tissue called the **cambium**. When cells in the cambium divide, they form new wood cells towards the inside of the stem or new phloem cells towards the outside. Outside the phloem is the **bark** that

consists also largely of dead tissue and serves to protect the thin layer of living tissue beneath it; bark is often 2–3 cm thick.

Speaking ecologically, the great height of trees allows them to carry their leaves high in the air. This gives them an advantage in that they can receive the sunlight they need and deny light to the smaller, shaded plants below. A tree stem can be considered as an engineering structure, in fact simply as a tall, tapered pole. That pole must be strong enough to support both its own weight and the weight of the branches and leaves it carries. It must also be strong enough to resist the **stresses** to which it is subjected as the wind blows on the tree **crown** (a term used for the foliage and branches of an individual tree). Engineering theory shows that the taller a pole, the larger must be its diameter at its base for it to remain upright. So is it for tree stems (King and Loucks 1978; King 1981, 1986; Osler et al. 1996b; Lundström et al. 2008; Meng et al. 2008; Schelhaas 2008; Zenner 2008; Aiba and Nakashizuka 2009; King et al. 2009) and very tall trees must have very large stems. The tallest trees have girths at the base of their stems of 20–30 m.

2.1.2 Photosynthesis and Water Use

The surfaces of the leaves of plants that grow on land are covered by microscopic holes called **stomata**. These have a special structure that allows them to open and close. When they are open, carbon dioxide may enter the leaves from the air. Then, within specialised cells in the leaf, a complex sequence of chemical reactions occurs. Using energy from sunlight, these reactions chemically convert carbon dioxide and water into sugars that are energy-containing food for the plant. Sucrose (the chemical name for table sugar), glucose and starch are all sugars produced by plants; both sucrose and starch can be converted into glucose, the form of sugar that plants use ultimately as food.

This whole process of food production by plants is known as **photosynthesis**. A by-product of photosynthesis is oxygen that is released from the leaves into the air through their stomata. Animals then breathe this oxygen; animal life as we know it on earth is possible only because oxygen is released by plants through photosynthesis.

The ultimate result of photosynthesis, and use by the plant of the food it produces, is that plants grow and increase their **biomass**. The word biomass means the weight of a living organism. It may include the water in the organism, when it is referred to as fresh biomass. However, since plants take up water from the soil, they do not have to produce it chemically; all the other tissues of which plants consist derive ultimately from food produced through photosynthesis. Because of this, the **oven-dry biomass** of plants is referred to commonly in biological science. This is the tissue weight after the water has been removed by drying; it is a measure of what the plant has actually produced through its **metabolism**.

Unfortunately for plants, not only does oxygen escape from leaves through their stomata, but water does also, as water vapour. The living tissue of the leaves

needs water to stay alive, but the presence of the stomatal holes in the leaves means that a lot of water is evaporated from them. On hot, dry days or during droughts, plants close their stomata to prevent excessive water loss. However, as long as their stomata are closed, they cannot take in carbon dioxide from the air and are unable to produce food through photosynthesis. As will be discussed in more detail later, the availability of water from the soil is often the most crucial environmental factor that determines how well plants grow on any particular **site**.

2.1.3 Temperature

As temperature varies from season to season and from time to time during any day, it affects the rate of metabolism of plants, that is, the rate of the chemical reactions within cells that provide the energy and the materials for their growth, maintenance and reproduction. If the temperature is too low or too high, the chemical reactions cannot proceed and the plant stops metabolising.

Within this range from too low to too high temperatures, a plant has some temperature at which its metabolism and, hence, its growth is maximised. Both the temperature at which this maximum occurs and the temperature range within which any growth occurs vary from plant species to plant species. Some species are adapted to grow better in cooler climates, whilst others grow better in warmer climates. Plants do not tend to occur naturally on earth in places where the annual average air temperature is outside the range of about 5–45 °C.

2.1.4 Nutrients

Nutrients are chemical elements that play a wide variety of roles in the metabolism of plants; without them, plants cannot survive. There are 15 nutrient elements believed to be essential for plants. Table 2.1 lists them and the minimum **concentrations** (averaged over plants generally) at which they need to be present in actively metabolising leaf tissue for plants to function normally (the concentration of something is the proportion it makes up of the whole of which it is part). For nutrient elements in plants, their concentration is usually expressed as a weight of the element per unit weight of the oven-dry biomass of the plant.

It is obvious from Table 2.1 that the amount of each nutrient required for plant metabolism varies enormously, from 25,000 mg/kg of nitrogen to 0.1 mg/kg of nickel and molybdenum. Because the first six nutrients are required in much larger amounts than the others, they are referred to commonly as macronutrients. The last nine are called micronutrients.

Plants take up virtually all their nutrient requirements from the soil. They do so through the living, fine roots at the extremities of the root system. For nutrient elements to be taken up by fine roots, they must be dissolved in the water that fills the

Table 2.1 The chemical elements considered essential nutrients for plants

| Element | Chemical symbol | Concentration (mg/kg) |
|-----------------------|-----------------|-----------------------|
| <i>Macronutrients</i> | | |
| Nitrogen | N | 25,000 |
| Potassium | K | 10,000 |
| Magnesium | Mg | 2,000 |
| Phosphorus | P | 2,000 |
| Calcium | Ca | 2,000 |
| Sulphur | S | 1,000 |
| <i>Micronutrients</i> | | |
| Sodium | Na | 500 |
| Chlorine | Cl | 100 |
| Iron | Fe | 100 |
| Manganese | Mn | 20 |
| Zinc | Zn | 20 |
| Boron | B | 12 |
| Copper | Cu | 3 |
| Nickel | Ni | 0.1 |
| Molybdenum | Mo | 0.1 |

The chemical symbol by which each element is known is shown, together with the minimum concentration (averaged over plants generally) at which each needs to be present in actively metabolising leaf tissue for plants to function normally. The concentrations are shown as milligrams of the chemical element per kilogram of oven-dry weight of plant tissue. The elements required in higher concentrations are known as macronutrients and those required in lower concentrations as micronutrients (*Source*—Atwell et al. 1999)

spaces between the particles that make up the soil. Both nutrients and water are then taken up together by fine roots.

It is believed that the uptake of water and nutrients is aided by a symbiotic relationship between fine roots and certain types of **fungi** ([Sect.11.1](#)), known as **mycorrhizas**. In a symbiotic relationship, both organisms involved derive benefit from their association. In the case of a plant and a mycorrhiza, the plant is believed to benefit from improved water and nutrient uptake, whilst the mycorrhiza is provided with food by the plant.

There are many types of mycorrhizal fungi and they are associated with a large proportion of tree (and other plant) species throughout the world (Brundrett 2009). There are two principal groups of mycorrhizas, ectomycorrhizas that form a sheath of fungal tissue around fine roots and vesicular arbuscular mycorrhizas that grow within the root. Both extend an extensive fine web of filaments (known as hyphae) beyond the roots into the soil; effectively, they increase greatly the surface area of the plant root system for uptake of water and nutrients. Many plant species are unable to grow and develop adequately unless they have a mycorrhizal association with their roots. Various works give more information about mycorrhizas and their importance in forests (Vogt et al. 1997; Siddiqui et al. 2008; Smith and Read 2008; Bâ et al. 2010; Brockwell et al. 2011; Cairney 2011; Mukerji 2011;

Robson et al. 2011; Southworth 2012). In their review of the function of ectomycorrhizas, Lehto and Zwiazek (2011) suggested that, in large trees, rather than mycorrhizas generally aiding water and nutrient uptake, their principal role may be to assist nutrient uptake during and after periods of reduced water availability in soils, such as drought periods or when the soil has been frozen.

Once water and nutrients have been taken up by the fine roots, both are transported into the woody roots, then into and up through the wood of the stem and branches to finally reach the leaves. This transport of water and nutrients from the roots to the top of even the tallest trees is powered directly by energy from sunlight. The sunlight evaporates water from the leaves, through their stomata, and a continuous stream of water is literally pulled right up the length of the tree from its fine roots to its leaves. Thus, trees do not have to use any energy from the food they have produced through photosynthesis to raise water and nutrients to their tops.

2.2 Principles of Plantation Growth

Consider a newly established forest plantation. Tree seedlings have been raised in a nursery (Sect. 5.2) and planted out (Sect. 5.3). Usually, the trees will have been planted in rows, typically with 2–3 m between each row and 2–3 m between each tree in a row (Sect. 7.2). The soil has been prepared for planting by some form of cultivation (Sect. 5.1). **Weeds** that might compete with the seedlings have been controlled (Sect. 5.4). Various other treatments may have been applied also to give the seedlings their best chance to survive and grow rapidly.

Because of their small size at the time of planting, the seedlings are vulnerable. They face hazards such as hot, dry weather, insect infestation (Sects. 10.2, 10.3), browsing by larger animals (Sect. 10.4), frost or competition from vigorous weed growth (Sect. 5.4). Often, it is accepted as normal in plantation **forestry** that 5–10 % of the seedlings will die from one or other of these causes over the first year or so after planting out.

Assuming it survives these early hazards, each seedling will then start to grow. During the first year or so, seedlings are so small that their requirements for nutrients and water from the soil are correspondingly small. As the trees continue to grow, the biomasses of their leaves, branches, roots and stems all increase. Also, the trees increase in height and their crowns increase both in length and width. Their root systems grow deeper into the soil and spread in width. As the biomass of the principal living tissues, the leaves and fine roots, of each seedling increases, the amount of water and nutrients the seedling requires to keep it alive also increases; the expansion of its root system will allow it to take up the extra water and nutrients it needs.

Eventually, the root systems and crowns of the individual trees expand to such an extent that they meet those of neighbouring trees. The individual tree crowns then form a closed **canopy**, that is, a more or continuous layer of leaves and branches covering the whole plantation area. Below ground, the root systems will be spread also more or less continuously over the entire area.

On some sites, the canopy may become sufficiently dense that it intercepts nearly all of the sunlight falling on it, leaving the ground heavily shaded. When this happens, there would obviously be no advantage to the trees to increase their leaf biomass any further, because there would be no additional sunlight for those leaves to intercept. This will happen only on sites that are supplied so plentifully with water and nutrients that there is more of both available than the trees can use.

On drier or less fertile sites, the root systems of the trees will continue to expand until they can gather all of the water and nutrients available to them from the soil. Once this happens there will be no opportunity for the trees to increase their leaf and fine-root biomasses any further. Under these conditions, the canopy will be less dense than on sites where there is more water and nutrients available than the trees can use.

It follows from this discussion that there will be a limit to the biomasses of the principal living tissues that can be supported on any site. This limit will be determined by the availability of sunlight, water or nutrients. In fact, whichever of those three is in least supply will determine the limit for a particular site. From a forestry point of view, this limit is extremely important. It will determine the amount of photosynthesis that can occur on a site at any time, hence, the rate at which the trees will grow and so, ultimately, the amount of wood available for harvest at any time in the future.

One of the vital resources from the environment required for plant growth, carbon dioxide ([Sect. 2.1.1](#)), has not been mentioned as one of the factors that could limit plantation growth. The amount of carbon dioxide available does not depend on the properties of a site, because carbon dioxide is obtained from the air. Fresh supplies are brought continuously to any site with the wind. The last environmental factor that affects plant growth, temperature ([Sect. 2.1.3](#)), will affect the rate at which photosynthesis, hence growth, may occur at any time of day; maximum growth rate will occur when the temperature is optimal for the plant species concerned.

2.3 An Example of Plantation Growth

The principles of plantation growth established in [Sect. 2.2](#) will be illustrated with an example. This is taken from an experimental plantation of flooded gum (*Eucalyptus grandis*) in south-eastern Queensland, Australia. Flooded gum has been an important plantation species in subtropical, eastern Australia and elsewhere in the world. The experimental details and some results from the first few years of growth were given by Cromer et al. (1993a, b). To provide the information for this example, I used those results with a forest growth modelling system (adapted from the system of Running and Coughlan 1988 and Running and Gower 1991) to predict how the experimental plantation would have grown from 1 to 20 years of age.

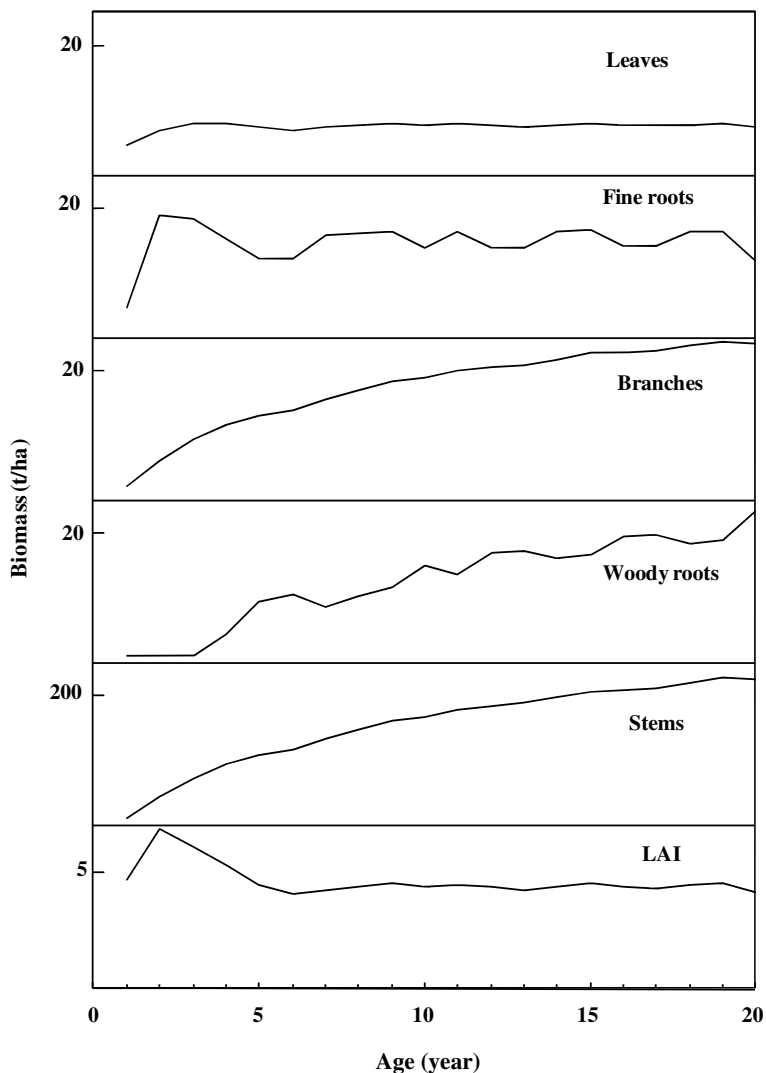


Fig. 2.1 The change with age in the stand oven-dry biomass (tonnes per hectare) of leaves, fine roots, branches, woody roots and stems and of the stand leaf area index (LAI, m^2/m^2) of an experimental plantation of flooded gum (*Eucalyptus grandis*) established in south-east Queensland, Australia (derived by the present author, based on results of Cromer et al. 1993b for plantations that had been fertilised heavily)

The results are shown in Fig. 2.1. Note that they are shown as **stand** results, that is, as the weight of oven-dry biomass of all the trees per unit ground area they occupy (the units used are tonnes of oven-dry biomass per hectare of ground area). Stand is a peculiarly forestry term that refers to a more or less homogeneous group of trees in a forest in which an observer might stand and look about him or her.

2.3.1 Leaf Development

Figure 2.1 shows that, over the first 3 years, the stand leaf biomass increased steadily until it reached a maximum approaching 8 t/ha. This was the period during which the small planted seedlings were growing and expanding their crowns, until they formed a continuous canopy over the entire plantation area. Thereafter, the leaf biomass stayed more or less constant from year to year, with an average biomass of about 7.6 t/ha. That is, after 3 years of age, the canopy of the plantation had reached its limit of leaf biomass. That limit will have been determined by the availability at the site of water, nutrients or sunlight (Sect. 2.2). In this case, it was probably sunlight; the plantation was growing in a region with a high annual rainfall (1,440 mm/year) and had been heavily fertilised to ensure there was an adequate supply of mineral nutrients.

This development of leaf biomass was matched by a corresponding development of the surface area of the leaves. This is illustrated in the bottom section of Fig. 2.1 that shows the change with age in **leaf area index** (often abbreviated to LAI) of the stand. Leaf area index is the area of the leaves of the canopy expressed per unit area of the ground they cover (the units used in Fig. 2.1 are square metres of leaf area per square metre of ground area covered by the canopy). Leaf area is defined as the area of the shadow that the leaves would cast if they were laid flat and lit vertically from above; by using a shadow area, scientists can define readily the areas of leaves with either flat surfaces or needle shapes. There are various instruments and techniques available to measure the leaf area index of plantations at any time during their life. Texts on forest measurement should be consulted to learn more about these methods (e.g. West 2009).

As can be seen in Fig. 2.1, the leaf area index of the plantation rose to a peak of $6.9 \text{ m}^2/\text{m}^2$ at 2 years of age, then declined to a more or less constant value that averaged $4.4 \text{ m}^2/\text{m}^2$ over 5–20 years of age. Leaf biomass did not show a similar peak, although Ogawa (2012) has suggested that it may do so in some plantations. In this case, the peak in leaf area index seems largely to reflect the fact that leaves of very young eucalypt seedlings are often much thinner than leaves of more mature trees (Doley 1978; Linder 1985; Beadle and Turnbull 1986; Cromer and Jarvis 1990; West and Osler 1995; Whitehead and Beadle 2004); the balance between increasing leaf biomass with age and increasing thickness of the leaves leads to the peak in leaf area at 2 years of age in Fig. 2.1. Such a peak often seems to occur in plantations at about the age the individual tree canopies meet to form a closed canopy over the whole plantation (Pinkard and Beadle 2000; White et al. 2010).

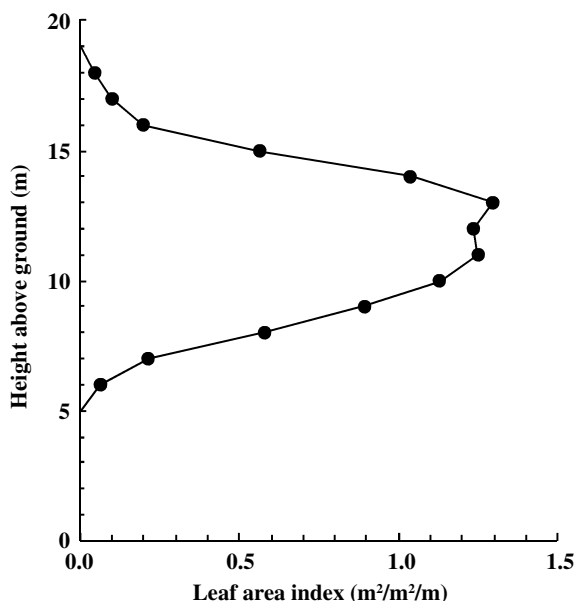
Results have been shown here for leaf area index and leaf biomass because both are important in understanding how the canopy of a plantation develops. Leaf biomass represents the amount of living leaf tissue in which plant metabolism can occur. Leaf area index is important because it is the surface area of the leaves that intercepts the sunlight falling on the canopy. The larger the leaf area

index of a stand, the more sunlight will the leaves be able to intercept and, hence, the more photosynthesis will they be able to undertake. In fact, considerable research has shown that the rate of growth of forests is directly proportional to the amount of sunlight their leaves intercept (Atwell et al. 1999, p. 405 et seq.; Landsberg and Gower 1997, p. 136; Whitehead and Beadle 2004; Stape et al. 2008; Binkley et al. 2010). This fact has been used as the basis of many mathematical modelling systems that have been, and continue to be, developed to predict how forests grow (Bartelink et al. 1997; Le Roux et al. 2001); it was an important part of the model system that I used to obtain the results in Fig. 2.1. Also, leaf area index is important in determining the amount of water that may be evaporated from the vegetation canopy and the amount of carbon dioxide that may be absorbed during photosynthesis; it has become one of the most useful measures available to help describe the behaviour of vegetation in relation to climate (Asner et al. 2003).

The leaf area indices reached by plantations vary widely both for different species and on different sites. Asner et al. (2003) compiled leaf area index data collected from forests around the world. For plantations, leaf area indices varied over the range 2–18 m^2/m^2 . The highest value they reported for any forest type was 47 m^2/m^2 for some needle-leaved, evergreen **native forests** from temperate regions of the world. The leaf area index of 4.4 m^2/m^2 attained by the plantation considered in Fig. 2.1 is consistent with the figure of 4–6 m^2/m^2 considered typical as the long-term, constant leaf area index of highly productive eucalypt plantations (Beadle 1997; Whitehead and Beadle 2004). Just as with canopy leaf biomass (Sect. 2.2), the availability of water and nutrients will be the principal factors determining the leaf area index that the canopy attains on a particular site (White et al. 2010).

Figure 2.2 shows how leaf area index usually varies at different heights down through the canopy of a plantation. As the trees grow in height, new leaves develop at the top of the canopy but have not yet reached their full size. Thus, leaf area index increases progressively from the top down to the mid-levels of the canopy, where the leaves have developed fully. Leaves higher in the canopy then shade those below that are reaching the end of their lifespan in any case. They can no longer carry out any appreciable photosynthesis and are shed, so reducing the leaf area index near the base of the canopy. This pattern of leaf distribution is similar both in individual trees and down through the canopy as a whole (Vose 1988; Hashimoto 1990; Osawa 1990; Wang et al. 1990; Mori and Hagiwara 1991; Pulkkinen 1991; Medhurst and Beadle 2001). However, differences in the way leaves are distributed in the canopy can then lead to further variations in leaf area index in different species. In some species, leaves are held rather more in clumps than in others. In some species the leaves hang more vertically than in others. These leaf arrangements affect the amount of sunlight the leaves can intercept. In turn, that determines the total leaf area index of the canopy required to intercept the sunlight available (Fleck et al. 2003; Niinemets et al. 2004).

Fig. 2.2 The leaf area index, over 1 m height intervals, at various heights through the canopy of a 25-year-old plantation of Douglas fir (*Pseudotsuga menziesii*) grown near Florence, Italy. The leaf area index of the entire canopy of this plantation was a little under $9 \text{ m}^2/\text{m}^2$ (adapted from Fig. 2.4 of Borghetti et al. 1986)



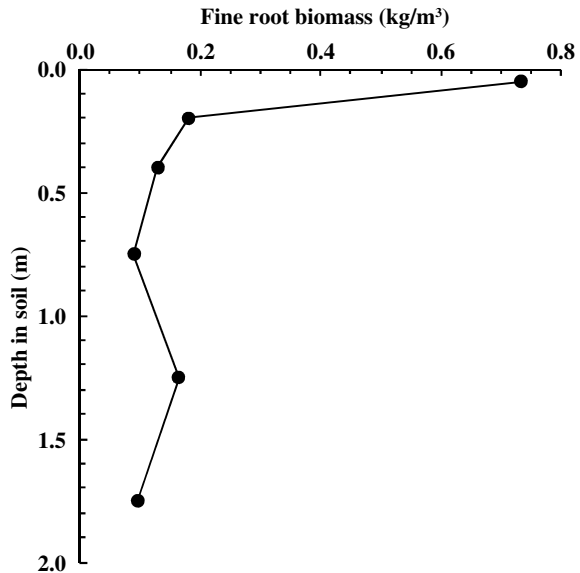
2.3.2 Root, Branch and Stem Growth

It can be seen from Fig. 2.1 that the biomass of the fine roots followed a pattern similar to that of leaf biomass. Fine-root biomass eventually reached a more or less steady amount, of nearly 15 t/ha after about 5 years of age. This is consistent with the earlier discussion (Sect. 2.2) that fine roots will reach a steady, long-term stand biomass so they can continue to supply water and nutrients to the steady, long-term stand leaf biomass.

The example in Fig. 2.3 came from a flooded gum (*Eucalyptus grandis*) plantation growing in Brazil and illustrates the distribution of fine roots commonly found in forests down the soil profile. By far the greatest proportion of the fine roots was located in the top 10 cm or so of the soil. This is the ‘topsoil’, where water from rainfall will be found most readily as will nutrients released by the breakdown of leaf litter from leaves that have been shed from the canopy. Thus, fine roots tend to be concentrated where the resources they take up from the soil are concentrated; however, the potential for nutrient uptake by roots at different depths may vary from nutrient element to nutrient element (da Silva et al. 2009). Similar patterns of fine root distribution occur in other forest types (Valverde-Barrentes et al. 2007; Zhou and Shangguan 2007; Bakker et al. 2009; Douglas et al. 2010; Krasowski et al. 2010; Persson and Stadenberg 2010; Asaye and Zewdie 2013; Konôpka and Lukac 2013).

By comparison with the leaves and fine roots, the stand biomasses of woody roots and branches in Fig. 2.1 continued to increase continuously with age, well after the stand biomasses of leaves and fine roots had become more or less steady.

Fig. 2.3 The change with depth down the soil profile of the fine root oven-dry biomass in a 2½-year-old plantation of flooded gum (*Eucalyptus grandis*) growing in Brazil. Fine roots were defined as roots less than 2 mm in diameter. The average height of the trees in the plantations was about 14 m (Laclau et al. 2008) (adapted from Fig. 4 of da Silva et al. 2009, using data for the 100 % flooded gum plantation)



Their need to do this follows from the fact that some trees die as the plantation grows (Sect. 2.4). Despite the loss of those trees, the biomasses of both the leaves and the fine roots in the plantation will remain the same; their amounts will continue to be determined by the availability of sunlight, water and nutrients from the site.

To make up for the deaths, each surviving tree will need to increase its leaf and fine-root biomass. In addition, it will need to spread further both its crown and its woody root system, to support the additional leaves and fine roots. The spread will occur into gaps left by the dead trees. Because of the spread, both branches and woody roots will have to become longer. Engineering theory shows that, as this happens, they will need to become disproportionately larger in diameter, hence biomass, to maintain the strength they need to support the weight of the leaves or to ensure the tree remains anchored securely in the ground. The increase in branch and woody root biomass across the whole plantation will more than offset the corresponding biomass lost through tree deaths. Thus, both branch and woody root stand biomasses will continue to increase with time.

The stand biomass of stems also continued to increase continuously with time. This occurred because trees grow continuously in height. The diameter of their stems, and hence their biomass, will have to increase also, or the stem will have insufficient strength to support the tree upright (Sect. 2.1).

2.3.3 Growth Variations and Leaf and Root Turnover

There are several other features of the results of Fig. 2.1 that are worth noting. First, it is obvious that the long-term leaf and fine-root biomasses were not exactly

constant from year to year. Nor were the increases in branch, woody root and stem biomasses consistent from year to year.

These variations reflect the fact that weather conditions vary from year to year. If one year is slightly warmer than another, it might be expected that growth rates might be a little different in that year than in the other. If rainfall was particularly low in one year, there might be a shortage of water available from the soil, at least for some part of the year. The plantation would respond to the lack of water by losing some of its leaves and reducing its leaf area index to a value consistent with the reduced water availability; fine-root biomass would be expected to change accordingly in that year, to correspond with the change in leaf biomass. Almeida et al. (2004b) have given an interesting example for flooded gum plantations in Brazil that illustrates how variable plantation growth can be from year to year as weather conditions vary. Various authors have shown how leaf area index may vary seasonally and annually in a plantation (Almeida et al. 2007; du Toit 2008; Stape et al. 2008; White et al. 2010; Sprintsin et al. 2011; Guiterman et al. 2012).

Second, it should be realised that the leaves and fine roots that make up the leaf and fine-root biomass are not the same leaves and fine roots all the time. After the canopy has reached its maximum size, leaves are shed from its more shaded base and progressively replaced by new leaves at its better lit top. There are several reasons for this continual turnover of leaves as follows:

- On highly productive sites, such as the one considered in this example, the leaves absorb most of the sunlight falling on the canopy. Thus, shaded leaves near the base of the canopy no longer receive sufficient sunlight for them to carry out photosynthesis. As they then no longer have any use, they are shed by the tree and replaced by new leaves near the well-lit top of the canopy.
- On less productive sites, where the availability of nutrients from the soil is relatively low, trees may recycle nutrients from the more shaded leaves near the base of the canopy to better-lit leaves near the top of the canopy. Those leaves near the top are then positioned better to carry out photosynthesis than shaded leaves. The now nutrient deficient leaves near the base of the canopy would then be shed.
- Living tissue, such as leaves, has a limited lifespan. For leaves this is often around 2–3 years, but may be less than 1 year or as long as 10–12 years (Ashton 1975; Muukkonen and Lehtonen 2004; Whitehead and Beadle 2004; Harlow et al. 2005; Muukkonen 2005; Laclau et al. 2008; Stape et al. 2008). When they die, leaves are shed and replaced by new leaves. The turnover of leaves may vary seasonally also, so that the total biomass of leaves on a tree will differ from season to season during a year (Sampson et al. 2003; Roig et al. 2005). Of course, in deciduous forests leaves have a lifespan of only 1 year and are all shed and replaced annually.

Fine roots too have a limited lifespan that can be as short as a few months but can be more than 1 year (Santantonio and Santantonio 1987; Fahey and Hughes 1994; Rytter and Rytter 1998; Mäkelä and Vanninen 2000; Baddeley and Watson 2004; Kern et al. 2004; Tingey et al. 2005; Valverde-Barrantes et al. 2007; Xiao et al. 2007; Andersen et al. 2008; Jourdan et al. 2008; Hodge et al. 2009;

Krasowski et al. 2010; Persson and Stadenberg 2010). Thus, they are continually turned over, as some die and are replaced by new ones.

After they have been turned over and replaced, the dead leaves and fine roots rot away in the soil. As they do so, the nutrients they contain are returned to the soil. The living fine roots then take up those turned-over nutrients from the soil and make them available to new leaves and new fine roots as they develop. The importance of this process of nutrient cycling will be discussed in [Sect 6.3](#).

2.4 Growth of Individual Trees

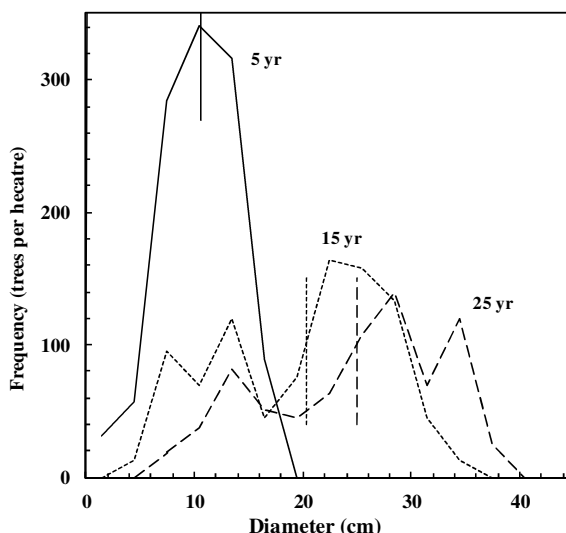
The discussion in [Sect. 2.3](#) concentrated on the growth of plantations as a whole, that is, when the total plantation growth is considered over all the individual trees that make up the plantation. From a forestry point of view, this is obviously important: on sites where more of the resources necessary for growth are available to the trees, plantations will produce more wood over any given time than on sites where lesser amounts of resources are available.

However, it is not only the total amount of wood that is produced by plantations that is important to forestry. Wood is sold from plantations as logs that have been cut from the stems of the individual trees. There are certain minimum sizes logs must have before they are large enough to be sawn to produce any of the various types of sawn **timber** (or lumber as it is termed in the USA) used in building and for many other purposes ([Sect. 3.3](#)). Larger logs are able to produce larger timber sizes that generally attract higher prices at sale. Hence, it is not only the total amount of wood produced by a plantation that is important in determining its value, but also the sizes of the stems of the individual trees in the plantation. This section describes how individual trees grow in plantations and how their sizes are determined.

After planting, each tree seedling in a plantation starts to grow using the sunlight, water and nutrient resources available in its immediate vicinity ([Sect. 2.2](#)). However, different seedlings will grow at somewhat different rates for two reasons. First, each seedling has its own **genetic** characteristics that will determine its inherent growth capability (von Wuehlisch et al. 1990). Second, the availability of water and nutrients from the soil may vary quite appreciably from metre to metre across the site (Thomson 1986; Phillips 2001; Guo et al. 2004; Hutchings and John 2004; Phillips and Marion 2004; Roy et al. 2004; Pollock and Reid 2008). These micro-site variations occur for several reasons:

- Small-scale variation in the topography of a site influences how water moves through the soil and just how much is available to a tree at any particular point.
- Variation in the soil parent material (the underlying rock from which soil is formed) may influence nutrient availability at any spot.
- The spatial arrangement of the trees and other vegetation on the site leading to varying water use from spot to spot.
- Vegetation that grew on the site before the plantation was established may have affected the site, the effects of which will vary from spot to spot.

Fig. 2.4 The frequency distribution, at 5 (—), 15 (---) and 25 (—) years of age, of stem diameter at breast height over bark in a plantation of flooded gum (*Eucalyptus grandis*) growing in subtropical, eastern Australia. The short, vertical lines show the average diameter of the trees in the plantation at each age (derived using an unpublished plantation growth and yield model developed by the present author)



By the time the seedlings have grown sufficiently large that their canopies and root systems have spread to make contact with neighbouring trees, these differences in individual growth rates will ensure that some are already taller and larger than others. At that stage, the trees start to interact with each other and to compete for the sunlight and soil resources available for growth (Sect. 2.2).

Considerable research has been undertaken to understand how trees compete with each other in monoculture plantations. Above ground, the principal competitive process is for taller trees to shade smaller trees and deny them sunlight for growth (Weiner and Thomas 1986; Hara 1986a, b; West et al. 1989; Schwinning and Weiner 1998). This type of competition is known as asymmetric competition; since taller trees can shade smaller ones, but not vice versa, the taller plants obtain a disproportionately large share of the available sunlight (Schwinning and Weiner 1998; Park et al. 2003). Below ground, there is symmetric competition between the trees for water and nutrients; since the roots of each tree occupy a volume of the soil that is proportional to the size of its root system, each tree can take up amounts of water and nutrients that are proportional to its size and, hence, its metabolic needs (Bartelheimer et al. 2008). These competitive processes between individual plants become rather more complex in vegetation that contains a mixture of species (Li et al. 2012; Xu et al. 2012).

In monoculture plantations, the result of the asymmetric competition for sunlight is that taller trees are able to grow disproportionately faster than smaller trees. This will lead to an ever-increasing range of tree sizes within the plantation. Eventually, some of the smaller trees will be shaded so heavily that they will be unable to continue to grow and will die.

The effects of this asymmetric competition are illustrated in Fig. 2.4. It shows results, for a plantation of flooded gum in subtropical eastern Australia, of the

frequency distribution of individual tree stem diameters at **breast height** over bark (forest scientists conventionally measure tree stem diameter at breast height, that is 1.3 m above ground, or 1.4 m in some countries). Results are shown at three different ages of the plantation (it is not the same plantation as that in Fig. 2.1, but the results were determined using other information available to me for such plantations).

Frequency distributions are used generally in science to show the distribution of sizes amongst a group of things (stem diameters amongst a group of trees in this case). Tree stem diameter is shown here because it is used commonly in forest science to represent the overall size of any tree; research by forest scientists over many years has shown that there is a close correlation between the overall biomass of trees and their stem diameters (West 2009).

The results of Fig. 2.4 illustrate how the competitive processes in a monoculture plantation affect the development of individual trees. On average, the trees increased in size as the plantation grew; their average diameter increased from 11 cm at 5 years of age, to 20 cm at 15 years of age and then to 25 cm at 25 years of age. At 5 years of age, the plantation contained 1,119 trees per hectare. As larger trees suppressed smaller ones through asymmetric competition, and some of the smaller trees died, this **stocking density** was reduced to 929 trees per hectare by 15 years of age and then to 759 trees per hectare by 25 years of age.

What is most striking in the figure is how the spread of diameters was affected as the plantation grew. At 5 years of age, the range of diameters was 1–17 cm. This had spread to 6–34 cm by 15 years of age and, by 25 years of age, even further to 7–39 cm. This reflects the disproportionately larger growth rates of the taller trees as they shaded the smaller ones.

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