GENERAL PRINCIPLES OF TREE GROWTH

General principles of tree growth — C 10
- *introduction: how trees grow*

How do trees grow?

By using the energy of sunlight to make organic matter out of simpler substances.

Does the sunlight just warm them up?

No, although it does do that. Like all green plants, trees contain a pigment called *chlorophyll* which absorbs some of the sunlight, allowing part of its energy to be turned into a chemical form.
During the second stage of this process of *photosynthesis*, the chemical energy is used to build in *carbon dioxide* absorbed from the air to form sugars (D 10 in Manual 4).

What happens to these sugars?

Of the large amount produced in a tree, some sugars are:

(a) **broken down again** in the process of *respiration*, providing useful chemical energy throughout the tree (and releasing carbon dioxide again);
(b) **built up** into many other chemical substances that allow it to live, grow and form roots, trunks, branches, leaves, flowers, fruits and seeds; ***and***
(c) **stored**, often as starch.

Does the tree keep on storing more and more?

Yes it may do so, if there is enough light. However, quite a lot of its sugars, starch and structural parts are:

(1) eaten by animals, which cannot produce their own food; ***or***
(2) shed from the tree as dead leaves and other parts, and ripe fruits. These form *litter*, which is then broken down by *decomposers* (D 13 in Manual 4).

Tropical trees are often the main **producers** in the **food chains,** on which all the **consumers** (most other living organisms) depend (D 10).

But what has all this got to do with tree nurseries?

Growing good trees successfully is determined by the general principles which control tree growth. Practical experience is important too, but it is most effective when combined with a grasp of the basic elements of tree biology.

How does a tree actually get bigger?

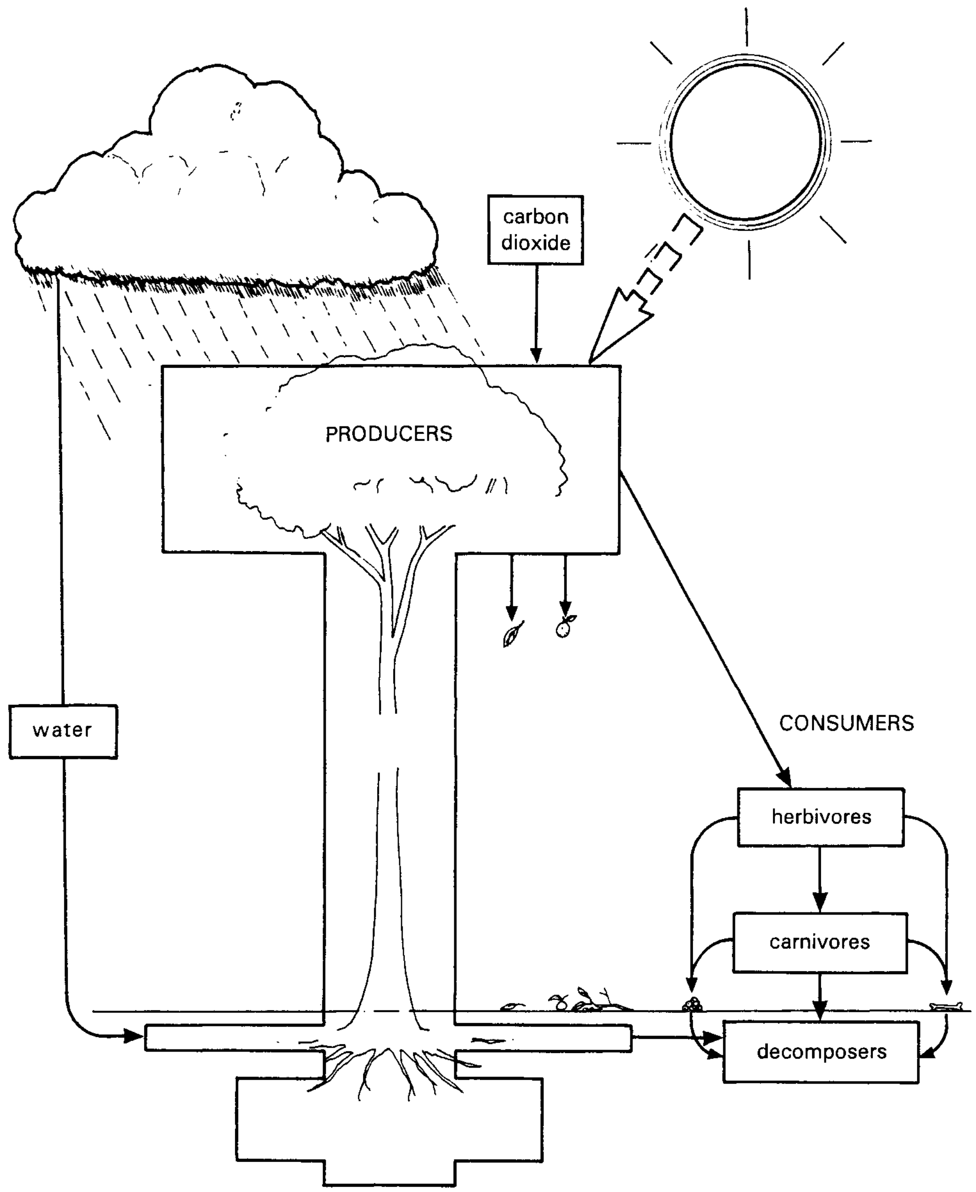
It does so because some of its *cells:*

(A) ***divide*** into two, making more cells, some of which may themselves divide; ***and***
(B) ***increase in size*** considerably, so that they become much bigger.

What are cells?

They are the living units of which the tree is made, which often:

(a) expand mainly ***in one direction,*** causing that part of the tree to grow in a specific way;
(b) ***become specialised,*** so that groups of them look different and have a variety of functions; ***and***
(c) can ***continue*** to function even ***when dead.***



Note: All living organisms release carbon dioxide to the air as they break down organic matter to release energy.

And what are they like?

(1) Cells are typically very small (frequently much less than 1 mm across);
(2) They contain a complete set of 'instructions' for ***all*** the things which can be done by that individual tree (C 17); ***but***
(3) They carry out only some of these functions.

For example, the cells in the root possess all the instructions for making fruits, but these remain unused.

Why is that important?

Because it means that:

(a) damaged parts of the tree can often be repaired;
(b) stem cuttings can produce new roots (Manual 1); ***and***
(c) cut stumps can produce coppice shoots.

In theory, any living cell could be turned into a whole tree.

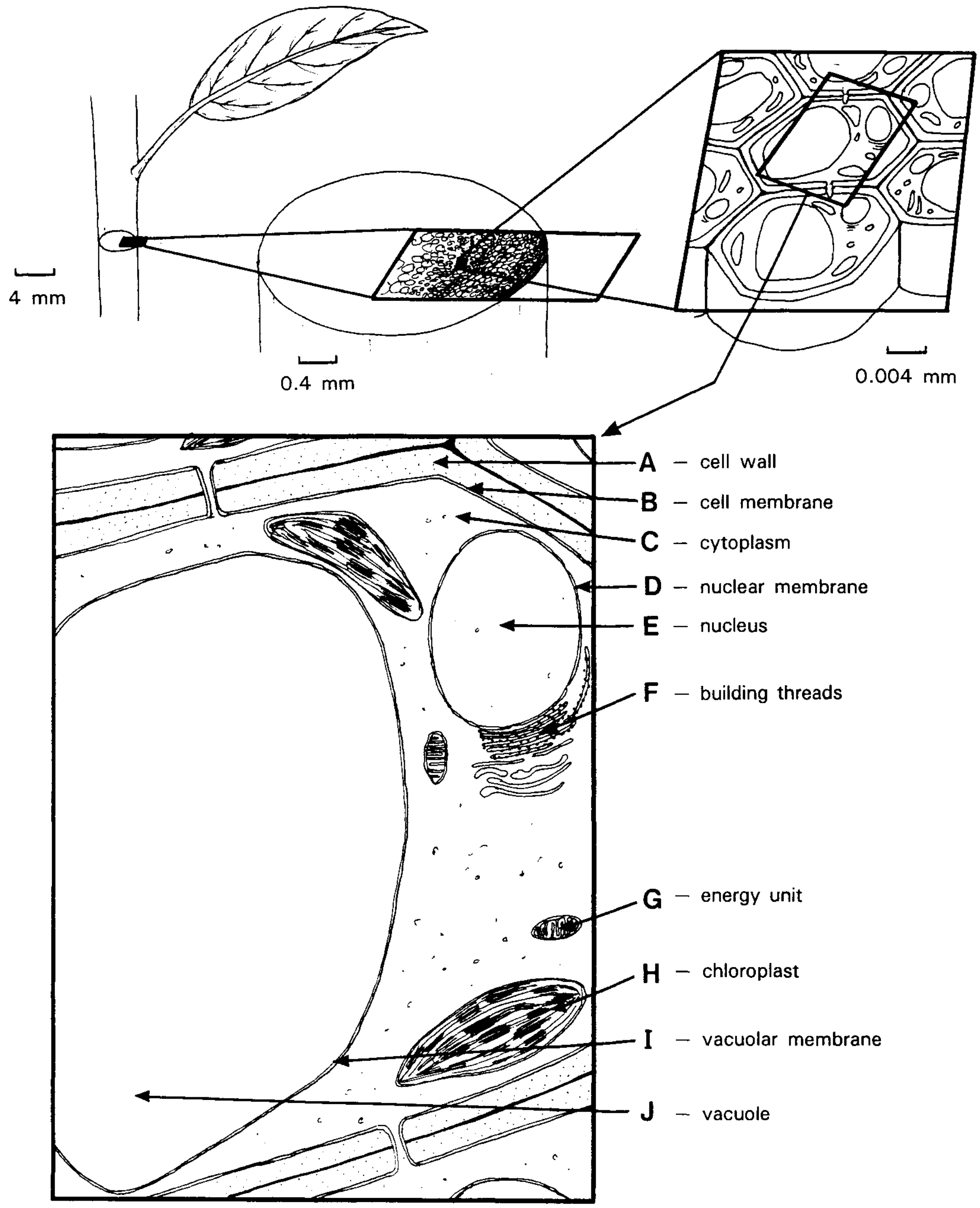
How many cells are there in a big tree?

A single leaf can contain several hundred, and a large tree many millions.

Well, why not turn a good tree into millions of young ones?

Unfortunately, there are a lot of barriers to such *micropropagation* (A 5 in Manual 1). For example:

(A) many of the cells in a large tree are dead, while others have lost the ability to divide;
(B) most of the living cells could not be separated from one another without killing them;
(C) cells taken higher than a metre or two above the ground are probably no longer *juvenile* (C 5; and A 21 in Manual 1), and therefore might not produce good trees;
(D) culturing individual cells and persuading them to produce a lot of new *plantlets* is not always easy; ***and***
(E) there can be genetic changes and losses of parts of the instructions during this kind of micropropagation.



Cross-section through young elongated stem.

Does that mean that micropropagation can't help?

No it doesn't, because:

(1) culturing **detached shoot tips** appears to have better prospects than starting with individual cells, and problems (D) and (E) appear to be less serious; ***and***

(2) the potential for multiplying the numbers of young trees for planting could still be large in tree species that produce a lot of shoot tips, and in those which can be persuaded to form many shoot tips or *somatic embryos* in culture.

However, for most tree species the best prospects are to root leafy, juvenile cuttings in a shaded poly-propagator (Manual 1), and grow them on in a tree nursery, because this approach:

(a) can easily be fitted into existing nursery practice;

(b) does not need expensive facilities or depend on an assured electricity supply;

(c) makes it easier to use superior selections to produce clonal planting stock (C 5).

What are cells like inside?

The living part usually includes:

(1) **the cell membrane,** a very thin layer on the outside which governs the movement of substances into and out of the cell (C 14);

(2) **a nucleus,** which contains the genetic instructions, and controls the activities of the cell;

(3) **cytoplasm,** which carries out the first part of respiration, and contains various structures including:

- (a) **energy units,** which perform the second part of respiration, releasing useful chemical energy;
- (b) **building threads,** where the essential *proteins* are made.

Cells may also contain:

(5) **a vacuole,** an inner sac of water and dissolved nutrients that often takes up most of the space; ***and***

(6) **chloroplasts,** which are the green, chlorophyll-containing units that carry out photosynthesis.

Outside is the **cell wall,** which limits the tendency of the living part to go on getting bigger, and if strengthened may give support to the tree even after the cell has died.

How do cells divide?

The instructions in the nucleus are copied **exactly,** the two versions separate, and new cell membranes and walls are formed between them. Most cell divisions result in two identical daughter cells, one of which often continues dividing while the other expands and becomes specialised.

Can any cell divide?

Any living cell can theoretically do so, but in practice most cell division happens:

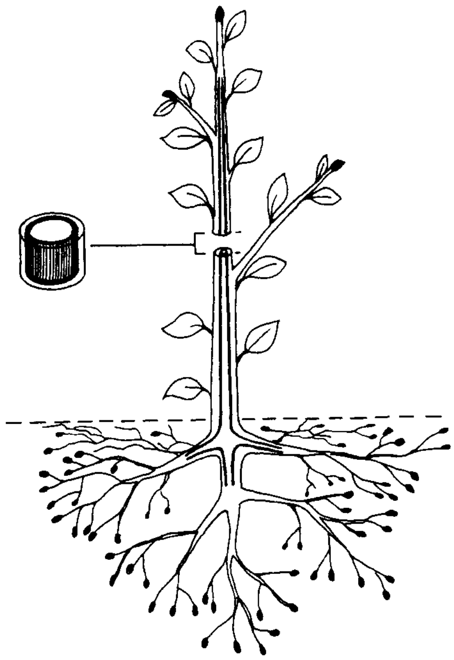
(a) in the growing points at the tips of roots and shoots, making them get longer;

(b) between the wood and the inner bark in main stems and branches (C 12) and in some roots (C 11), making them thicker.

Cell division also occurs in other young, rapidly growing parts of the tree, such as elongating fine roots, extending stem internodes and expanding young fruits. It also takes place when new growing points are formed, and in response to damage.

How do cells enlarge?

Water tends to enter the cell more strongly than to leave it. The pressure this exerts stretches the new thin cell wall, making the cell bigger until the strengthening wall and neighbouring cells restrain the enlargement.



Where most cell division happens. Stylised young tree, showing many root tips, three shoot tips, and the layer between wood and inner bark.

What kinds of specialised cells are formed?

Some common examples are:

(1) **sugar-making cells,** which contain a lot of chloroplasts, and are found especially in leaves and near the surface of young stems and unripe fruits;

(2) **sugar-conducting cells,** which are long tubes that remain alive for some time. They connect up different parts of the tree, and are common in the inner bark;

(3) **water-conducting cells,** which quickly die and lose their contents, often becoming like long narrow pipes. They also connect different parts, and are present in large numbers in the sapwood of roots, trunk and branches;

(4) **surface cells,** that:

(a) *in the fine roots* often absorb water and nutrients from the soil (C 16); ***and***

(b) *in above-ground parts* restrict drying up of the tree, but permit carbon dioxide and oxygen to enter (C 12);

(5) **storage cells,** which can be full of starch grains, and in seeds may also contain stored proteins and fats; ***and***

(6) **strengthening cells,** whose walls are often thick and strong.

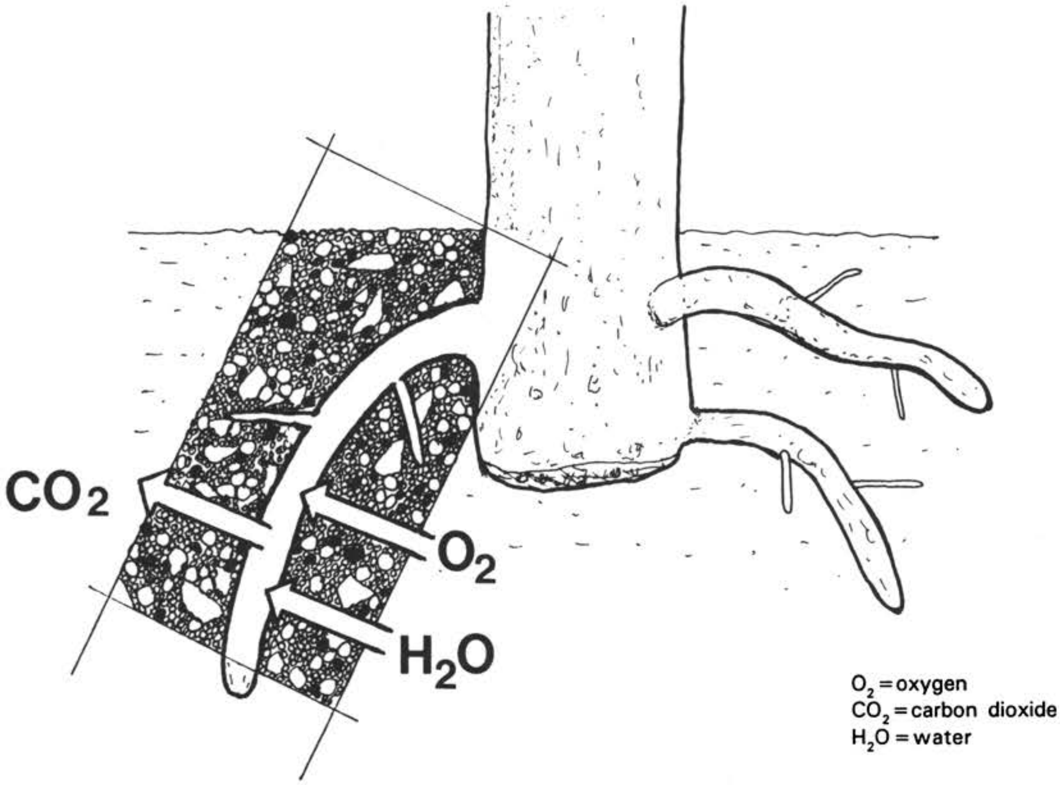
Don't things go wrong sometimes?

Yes, occasionally a cell is formed that has incorrect instructions. However, in most cases there are specific structures in the cytoplasm which destroy such faulty cells. The contents are broken down and other cells take over.

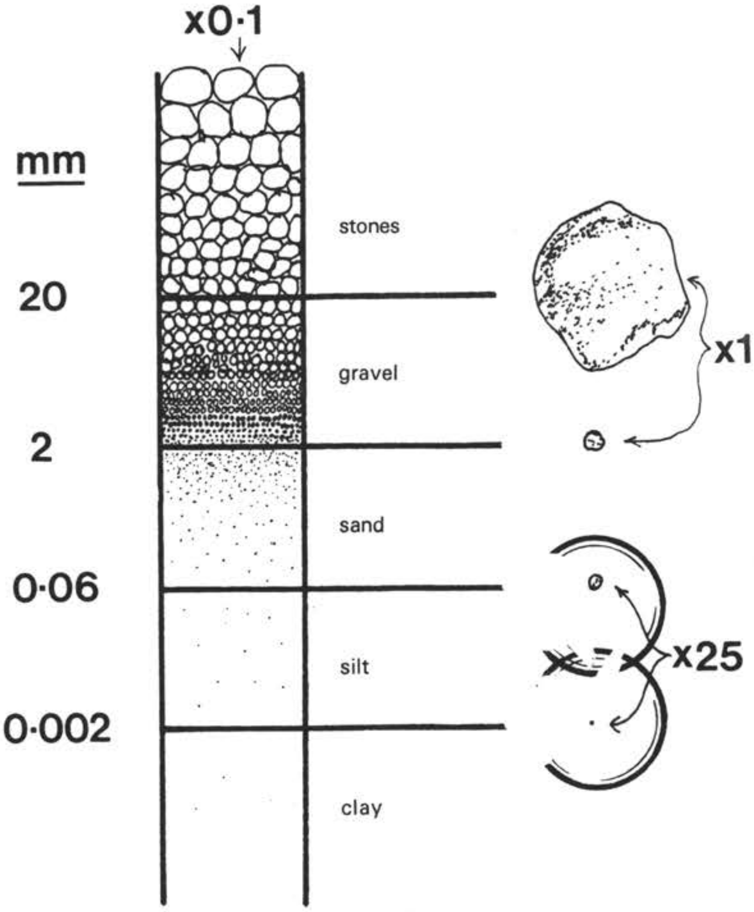
What affects growth and division of cells?

(A) Where they are situated within the tree;
(B) Its hormonal control systems;
(C) The availability of water, oxygen, sugar and nutrients;
(D) Temperature; ***and often***
(E) Light.

Some of these effects will be mentioned in sheets C 11-15 and C 34.



CO_2
O_2
H_2O
O_2 = oxygen
CO_2 = carbon dioxide
H_2O = water



x0·1
mm
stones
20
gravel
x1
2
sand
0·06
silt
x25
0·002
clay

General principles of tree growth - *expanding root systems* C 11

What kinds of roots do trees have?

In a young nursery tree, the root system generally consists of:

(1) **main roots,** including the taproot and others arising from the root collar or the base of the stem;

(2) **branch roots** formed at the sides of the main roots, which in turn branch frequently.

In a larger, well-established tree, there are often:

(a) thickened **structural roots** in the soil, going downwards but also spreading sideways;

(b) fine **absorbing roots,** growing and branching repeatedly in the top 10 cm;

(c) many **mycorrhizas,** close associations between fine roots and fungi (C 30-31).

In some tropical trees part of the root systems are above-ground, for example as *stilt roots* or as *'breathing' roots,* found especially when the soil is waterlogged.

How does a root grow?

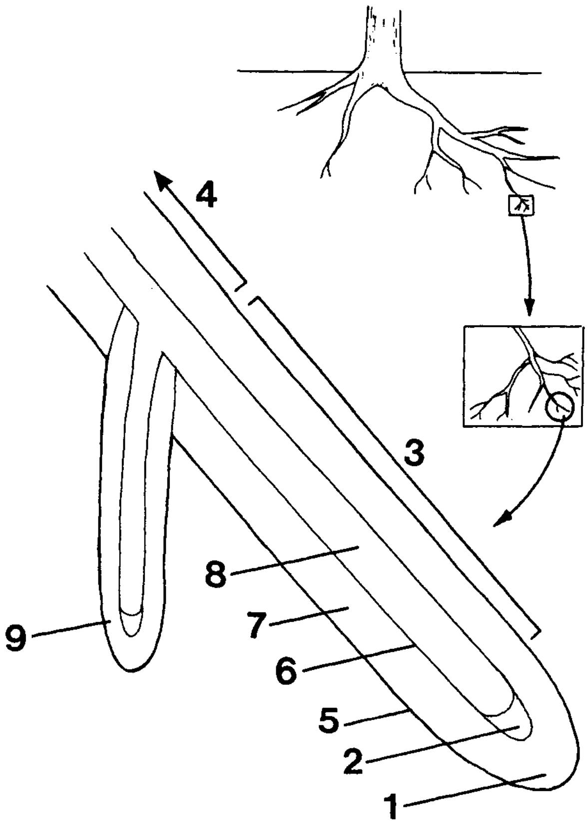
By some of its cells dividing, becoming larger and more specialised (C 10). Within one actively growing root, there are usually zones where cells:

(1) **are continually being formed,** in the root tip, just beneath the root cap;

(2) **elongate greatly,** while some of them continue to divide. This zone, about 2-20 mm behind the root tip, pushes it forward through the soil;

(3) **absorb water and nutrients,** in the parts that are no longer extending, often in association with fungal threads running through the soil, and sometimes root hairs. Branch root tips are often formed in this part; ***and***

(4) **conduct water and dissolved substances,** in the parts that are becoming thicker and no longer absorb from the soil.



Section through a young root.

1 — root cap. 2 — cells dividing.
3 — cells dividing, elongating and becoming specialised.
4 — zone no longer elongating.
5 — surface cells. 6 — boundary cells.
7 — storage cells. 8 — conducting cells.
9 — branch root.

Do all roots start off the same?

In some tree species, young root tips are of two distinct types:

(A) **thick roots** (1-2 mm in diameter), which may become structural roots and continue to grow in diameter; ***and***

(B) **thin roots** (less than 1 mm in diameter), which may function as short-lived absorbing roots that remain thin but branch frequently.

In seedlings (Manual 2), the first root is generally thick, making branch roots that may be thick or thin;
In cuttings that have been treated with *auxin* (A 40 in Manual 1), both types may be formed, but without added auxin only thin roots may sometimes be produced.
In palms, the roots are usually very thick when formed, and remain the same diameter, without branching.

How do the roots of other trees get thicker?

By producing a cylindrical layer of cells that then divide continually, forming water-conducting and strengthening cells to the inside and sugar-conducting cells to the outside (C 10). Because this layer of dividing cells lies deep inside the tissues, the root can actually get thinner as the outer parts are lost, before thickening later on. Like stems (C 12), thickened roots also produce bark to the outside.

And how do branch roots form?

A small group of cells divide and form into a root tip, which then grows in the normal way, bursting out into the soil through the outer tissues of the original root. Older, thickened roots can also produce branch roots, especially after disturbance or injury.

When cuttings form roots (Manual 1), a similar process happens near the base of the stem, which is stimulated by adding small amounts of auxins.

Can I increase root growth by adding auxins?

No, applying these hormones will make root *elongation* slow down or stop altogether.

Do roots normally grow all the time?

Growth in length of roots is often continuous in the tropics, though with periods of faster and slower growth. Similarly, there are often peaks in the formation of new thin roots. However, roots might stop growing completely if subjected to:

(A) **serious wilting** - when water has been lost from the shoot faster than the root system can absorb it (C 13). If the shoot is beginning to wilt, the root cells will also be short of water, and may also produce different hormones (C 14); ***or***

(B) **chilling injury** - if soil temperatures fall to around 10°C, the root cells of lowland tropical trees may be seriously damaged (C 41; and D 11 in Manual 4).

Is growth in thickness of roots continuous?

It generally is, unless the trees become leafless (C 12).

What influences how fast the roots grow?

In the nursery, root growth is likely to be most rapid when:

(1) both the species and the genetic origins are suited to the locality;
(2) the soil conditions are favourable to root growth (C 6, C 23);
(3) the tree has had time to become established in a bed or container;
(4) it is receiving sufficient light (C 41) and nutrients (C 33-34), is being carefully watered (C 43) and well looked after (C 40, C 48).

What other things slow down root growth?

Root growth will tend to decrease or even stop if, for example:

(A) the trees are kept in such dense shade that sugar production in the shoots barely exceeds what is used up or lost by the whole tree (C 10);

(B) the tree is subjected to a lot of *stress*, for instance from lack of or too much water, low or very high temperatures, strong winds or toxic chemicals (C 41);

(C) roots are badly damaged during potting up (C 42); ***or***

(D) the roots in a container become *pot-bound,* just going round and round outside a poor or exhausted potting soil (C 6).

Why is too much water bad for root growth?

Because the water drives out the air from the spaces between the soil particles, so that the root cells run short of oxygen. Such conditions can also favour micro-organisms that cause diseases (C 45). Waterlogging can happen if:

(1) the drainage holes in pots are too small (C 6), or get blocked by soil or roots;

(2) the potting soil contains a lot of clay;

(3) it becomes compacted inside the container; ***or***

(4) a newly-potted young tree is subjected to prolonged rainfall or is over-watered.

Tree species from mangrove woodland, freshwater swamps, and seasonally flooded forest and savanna generally thrive in soils liable to flooding. Some of them have:

(a) aerial 'breathing' roots reaching above the water level;

(b) air-conducting passages that allow oxygen to reach the root system; ***or***

(c) other special adaptations for coping with lack of oxygen.

But isn't the purpose of roots to supply water?

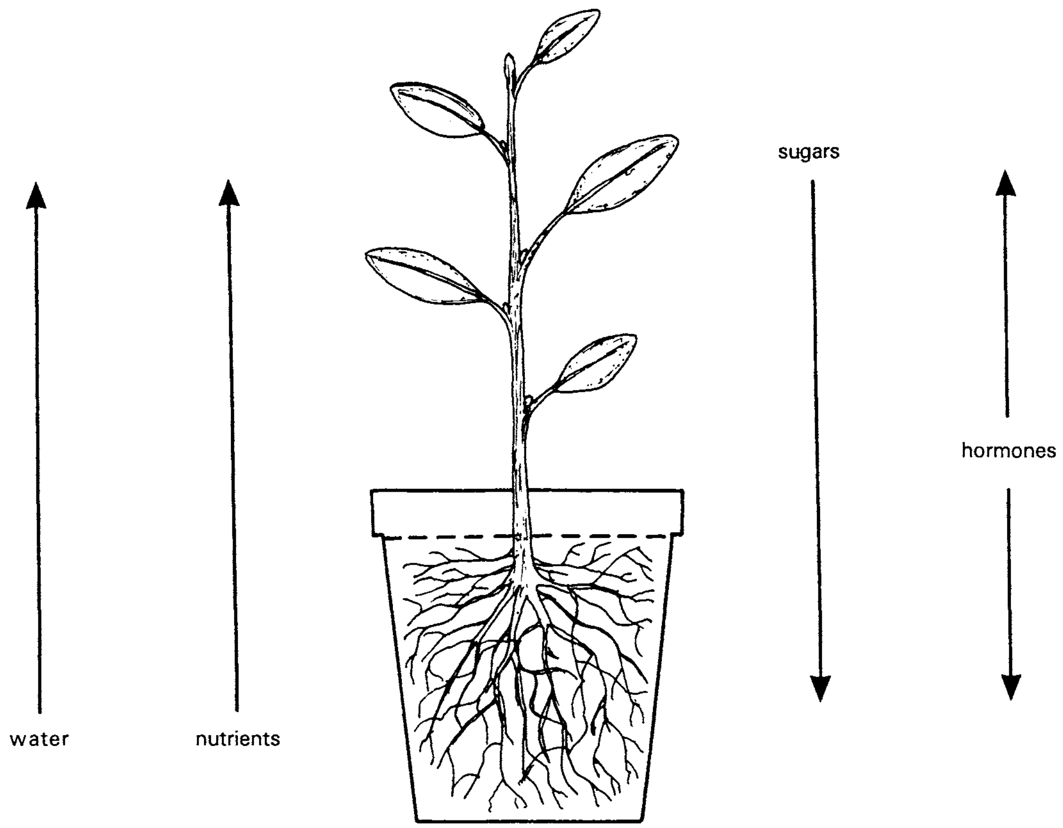
Well, it is one of their four vital functions, which are:

(A) taking up water;

(B) absorbing nutrients;

(C) manufacturing substances; ***and***

(D) anchoring the tree into the ground.



How is the water actually taken up by the tree?

When a fine, absorbing root is in close contact with small, moist soil particles, it is easy for water to pass through the thin walls of its surface cells. Because of the dissolved substances they contain, water is then taken up strongly through their cell membranes (C 10). Most of it moves from cell to cell into the water-conducting 'pipes' of the root, and then into the shoot system.

Water may also pass into the roots from the extensive network of fungal threads of mycorrhizas (C 30-31).

Are nutrients taken up the same way?

If the nutrient is dissolved in water, it can enter the cell walls easily. However, the next stages are different (C 14), because:

(1) the cell membrane is **selective,** not taking up nutrients in proportion to their concentration in the soil solution; ***and***

(2) uptake of nutrients requires the use of chemical **energy** (C 10) to transfer them across the cell membrane.

Once absorbed, the nutrients may be:

(a) used for growth in the root;

(b) stored; ***or***

(c) transported to the shoot either in the water- or sugar-conducting cells.

What sort of substances are manufactured in the roots?

Using sugars arriving from the leaves, the root system usually:

(A) produces the many chemical substances for the new root cells;

(B) stores starch in some of them;

(C) makes specific hormones that help to correlate the growth in the shoots with that in the roots (C 14).

How about anchorage?

Starting in the nursery, the root system also serves to fix the tree into the ground, keeping it upright and stopping it from being blown over (and in flooded sites from being washed away). When the tree is older, a set of large near-horizontal roots with *sinkers* may anchor the tree firmly, while in other tree species stilt-roots may assist in stability.

Aren't nursery root systems too weak to give much stability?

Young trees do need shelter (C 25, C 46), and could still be damaged by occasional fierce storms (C 3). However, their roots generally soon provide anchorage because:

(1) root numbers increase rapidly;

(2) roots branch in many different directions through the soil; ***and***

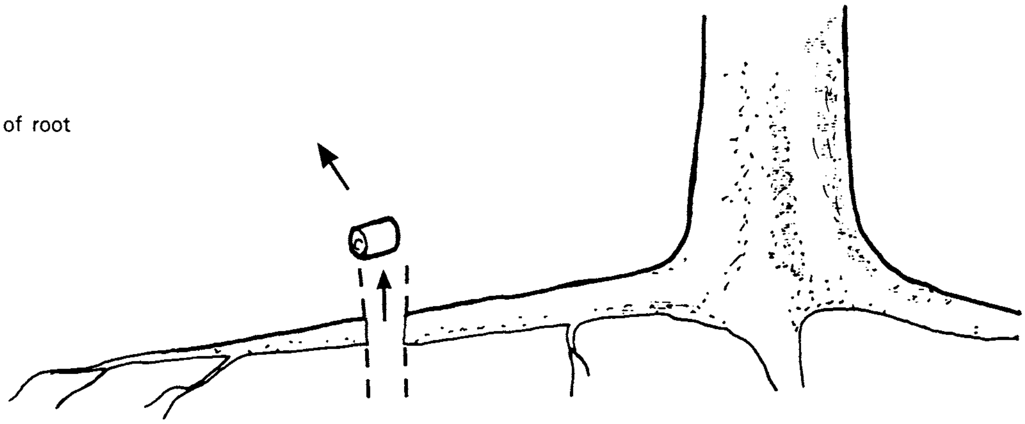
(3) the thicker ones are quite strong and flexible when pulled.

Poor, diseased or spindly trees are more likely to prove unstable than good planting stock (C 4).

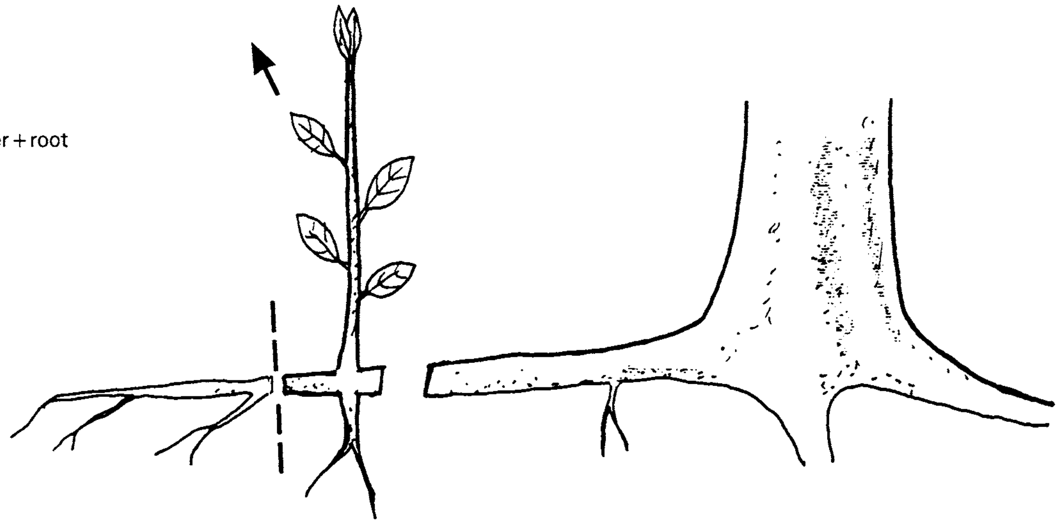
Do roots ever turn into shoots?

Root tips do not turn into shoot tips.
Certain cells on older roots occasionally form buds (suckers), for example in *Milicia (Chlorophora)* and *Cordia alliodora* (A 3 in Manual 1).

Remove section of root



Dig up sucker + root



Can root systems exist by themselves?

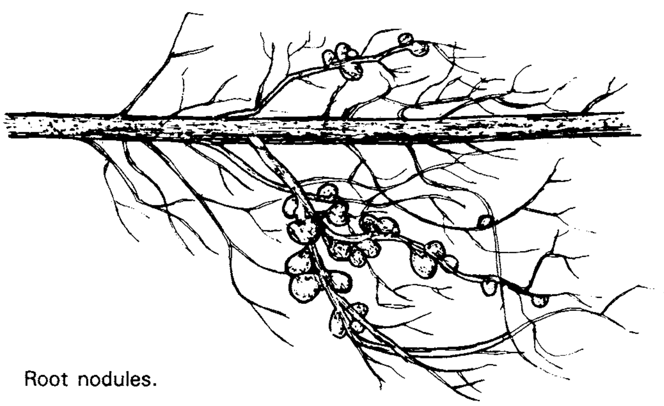
Only in the laboratory, and when provided with a sugar supply. Roots usually contain few or no sugar-making cells (C 10), and so are just as dependent upon photosynthesis in green shoots as are humans, other animals and decomposers (D 10 in Manual 4).

Does that mean that the shoots are more important?

No, because:

(a) they in turn are dependent upon the roots, both for supplies of water and nutrients and for stability; ***and***

(b) a good nursery root system is more crucial to tree survival after planting than the sort of shoot (C 34).



Root nodules.

General principles of tree growth C 12
- growing stems, leaves and branches

How do shoots differ from roots?

In the way they are organised, how they grow and what they do.

Do they have the same kinds of cells?

Sugar-making cells are found in large numbers in the shoot, and only rarely in roots. Many of the other kinds of cells are found in both.

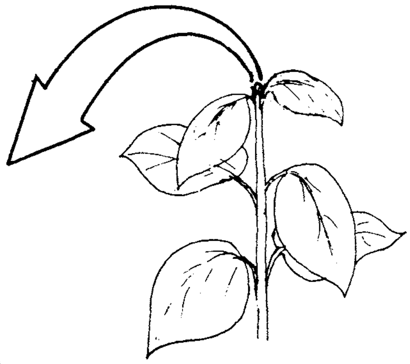
What differences in organisation are there?

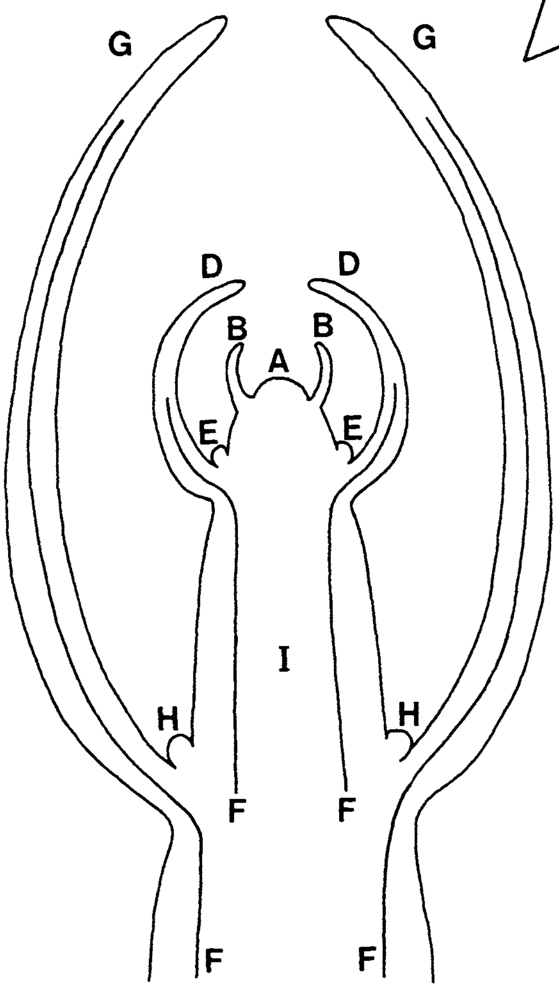
The chief points are that:

(A) shoots consist of **stems** and **leaves,** with buds and branches formed at the points where the leaf is attached to the stem (the *node*); ***whereas***

(B) roots are variations on one kind of structure, and can branch more or less anywhere.

In addition, shoots have a much thicker waxy covering on surface cells (C 10), which reduces water loss.





Section through a young shoot.

A – shoot tip. B – first pair of leaf projections. D – third pair of young leaves *(the second [C] cannot be seen)*. E – third pair of young buds. F – conducting cells. G – fifth pair of leaves expanding. H – fifth pair of buds. I – third and fourth internodes extending.

How do stems and leaves grow?

They are both formed at shoot tips, which have zones of:

(1) **actively dividing cells** at the tip, which from time to time form small projections that become leaves;

(2) **dividing and elongating cells** behind the tip, which form the new *internodes* of the stem, extending and pushing the shoot tip farther away from the roots, and also expanding the leaf; ***and***

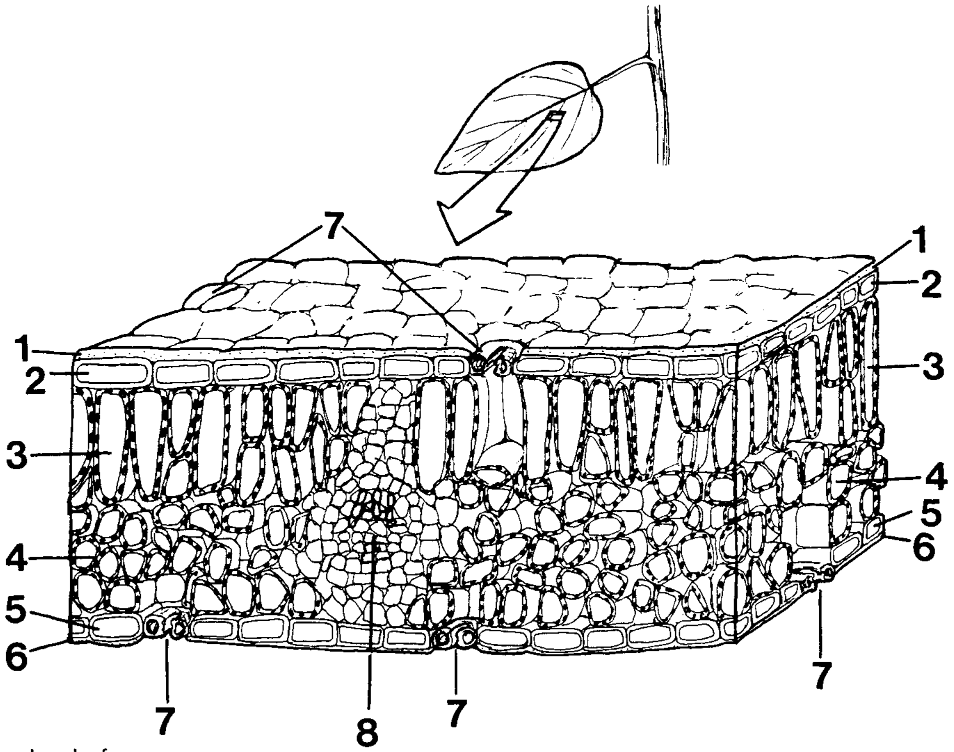
(3) **specialising cells** (including sugar- and water-conducting cells) in the leaves and the parts of the young stems that lie behind zone (2) and have ceased to extend.

What makes stems and leaves different?

Although both of them arise from the same growing point, they differ because:

(A) **leaves** are temporary organs that are typically predetermined as to their maximum size, and can seldom form a new stem; ***while***

(B) **stems** can usually continue to grow indefinitely, producing more stems and leaves. Some become progressively thicker, forming the trunk and major structural branches.



Section through a leaf.

1 — thick waxy layer. 2 — upper surface cell. 3 — upper sugar-making cell. 4 — lower sugar-making cell. 5 — lower surface cell. 6 — thin waxy layer. 7 — guard cells and holes. 8 — conducting cells.

Don't they also differ in what they do?

Yes, that is so. Generally:

(1) leaves are primarily organs of photosynthesis. They contain many sugar-producing cells and also special surface cells *(guard cells)* that regulate the movement of gases through the leaf surface (C 10, C 13); ***whereas***

(2) stems have several functions, including providing a strong above-ground structure that:

- (a) displays a succession of leaves, and later on flowers;
- (b) conducts water, nutrients, sugars and hormones around the tree; ***and***
- (c) stores starch and other substances.

However, most young stems also contain some chloroplasts and guard cells, while in a few tree species, such as *Acacia mangium,* short flattened stems act in place of leaves.

What happens to the leaf projections at the shoot tips of trees?

They may:

(1) develop into full-sized leaves at once, by continued cell division, expansion and specialisation;
(2) grow a little and then remain within a bud for a time, and then expand rapidly when the bud *flushes* later on;
(3) become a small bud scale around an inactive bud; ***or***
(4) never get much bigger, and soon fall off.

What about the shape of leaves?

This varies greatly between different species, to some extent from one tree to another of the same species, and even within a single tree. For example, leaves may have:

(1) **stalks** that are long, short or absent altogether;
(2) **blades** which are divided up into separate leaflets, or not;
(3) **margins** that are deeply lobed, finely toothed, wavy or uncut;
(4) **surfaces** which are flat or undulating, hairy or smooth; ***and***
(5) **texture** that is tough and hard, or thin and delicate.

Many features of leaf shape are useful in identifying one tree species from another.

How big can leaves get?

Their final length can vary between a few millimetres (for instance in *Casuarina* and *Cupressus*) and several metres (for example in palms). Widths range from about 1 mm to 1 m.
In mountains, tree leaves are usually smaller than at lower elevations, and the same is often true in drier compared with wetter environments.

Which features of leaves are the most important?

The **number of leaves** and the **leaf area** are usually key points, whether for a single leaf, a tree crown or an entire stand.

What determines leaf area?

Besides the genetic potential of the individual tree (C 5), many other factors influence the number of leaves formed and how big they grow. These often include:

(A) ***in the aerial environment*** (D 11 in Manual 4):
- (1) the air temperature, during the night as well as the day;
- (2) how much light falls on the leaves during an average day;
- (3) the *quality* of this light, and the day-length;
- (4) the drying power of the air (determined by temperature, humidity and wind speed);
- (5) competition with the shoots of other plants;

(B) ***in the soil:***
- (1) the physical and chemical nature of soil components (D 12-13 in Manual 4);
- (2) soil temperature;
- (3) the supply of water to the tree, compared with the amount the shoots are losing (C 13, C 43);
- (4) the availability and balance of nutrients (C 14, C 33);
- (5) the presence of close associations between micro-organisms and the tree's root system (C 30-32);
- (6) competition with the roots of other trees and weeds (C 44); ***and***

(C) ***within itself:***
- (1) how big the crown is, whether the leaf is on the main stem, a large branch or a small twig, and where it is positioned on the particular shoot;
- (2) the interplay (past and present) between root and shoot, and between vegetative and reproductive activity; ***and***
- (3) the presence of stored reserves of sugars and nutrients.

Do I want the leaves to be as big as possible?

Yes, in a well-established tree, growing in the ground; ***but***
No, in a young tree in the nursery (C 34).

How long do leaves live?

Usually between 3 and 15 months, although in a few tree species they may last for several years. In a rapidly growing nursery tree, some of the first-formed leaves may live for only a few weeks.

What happens to their contents when they die?

(a) Normally, when old leaves start to change colour, some of the sugars and nutrients in them are transported out into the stem. Then the leaf is actively cut off by the tree and falls to the ground, where it adds to the litter (D 13 in Manual 4); ***but***
(b) Under stress conditions, leaves may just wilt and shrivel up, often staying hanging on the tree.

In a few species, such as some palms, it is normal for the bottoms of dead fronds to remain attached to the trunk.

Why do some trees naturally lose all their leaves at once?

This is a common feature of:

(1) many trees and shrubs in savanna and dry forest areas;
(2) some of the taller trees in humid forests.

Deciduous trees shed all their leaves well **before** they produce any new ones, so that the tree stands leafless for weeks or months;
Leaf-exchanging trees shed their leaves at about **the same time** that they produce new ones, so the tree may be leafless for a short time only;
Evergreen trees never stand leafless, because they either:

(a) shed their old leaves well **after** new ones are formed; ***or***
(b) grow **continuously,** producing new leaves and shedding old ones all the time.

Is it drought that makes leaves fall off?

Although many leaves may fall during the early part of the dry season, there are probably several other factors at work, such as:

(1) other small changes in the environment;
(2) the leaves may be near the end of their natural life-span, with other more recent leaves 'taking over'; ***or perhaps***
(3) monkeys or a swarm of insects might have eaten most of the leaves.

Poor watering, rough handling or sudden changes in the amount of light reaching nursery trees can sometimes be followed by a lot of leaf shedding (C 40-43, C 47).

So shoots don't necessarily grow all the time?

Shoot growth is **continuous** in young trees of a considerable number of species; ***but***
Some seedlings and most saplings and older trees show **periodic flushing,** followed by one to eleven months in which no new leaves are expanding or stems extending.

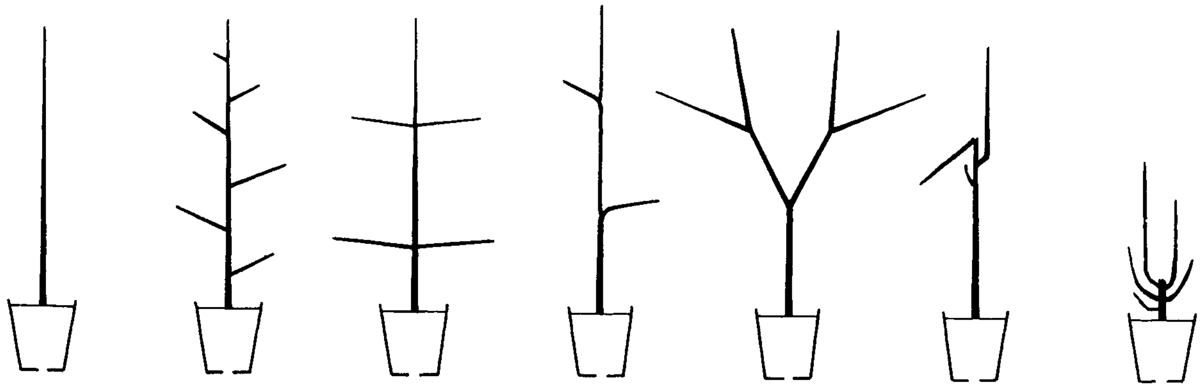
Is it rainfall that starts shoots growing again?

Perhaps yes in a few species, especially in dry areas; ***but***
Probably no in many others, because flushing commonly occurs before the first rains.

Do all the buds grow into branches?

No. Some buds may:

(1) never grow any bigger;
(2) remain small and inactive unless the shoot is damaged;
(3) turn into flower buds (Manual 2);
(4) become *dwarf shoots* of limited growth potential. For example, the needle-like leaves of *Pinus* are produced on a tiny shoot, while the leafy, budless branchlets of *Taxodium* are shed like leaves.



Common types of branching.

Which buds become branches?

Trees generally have regular patterns of branching that produce a growth habit and crown shape that are characteristic of the species, and sometimes of the individual clone (A 11-13 in Manual 1).

Does this matter much?

Yes it does, because different branching habits and crown shapes are best for trees needed for shade, shelter, wood production or fruits.

For instance, straight stems are valued for timber, pulpwood and poles (C 36-38 in Manual 4), but undomesticated tree species (C 5) often contain stems that are crooked, forked or even grow as multiple stems. Some may have large branches that leave big *knots* in the wood, reducing its strength and value.

How do stems get thicker?

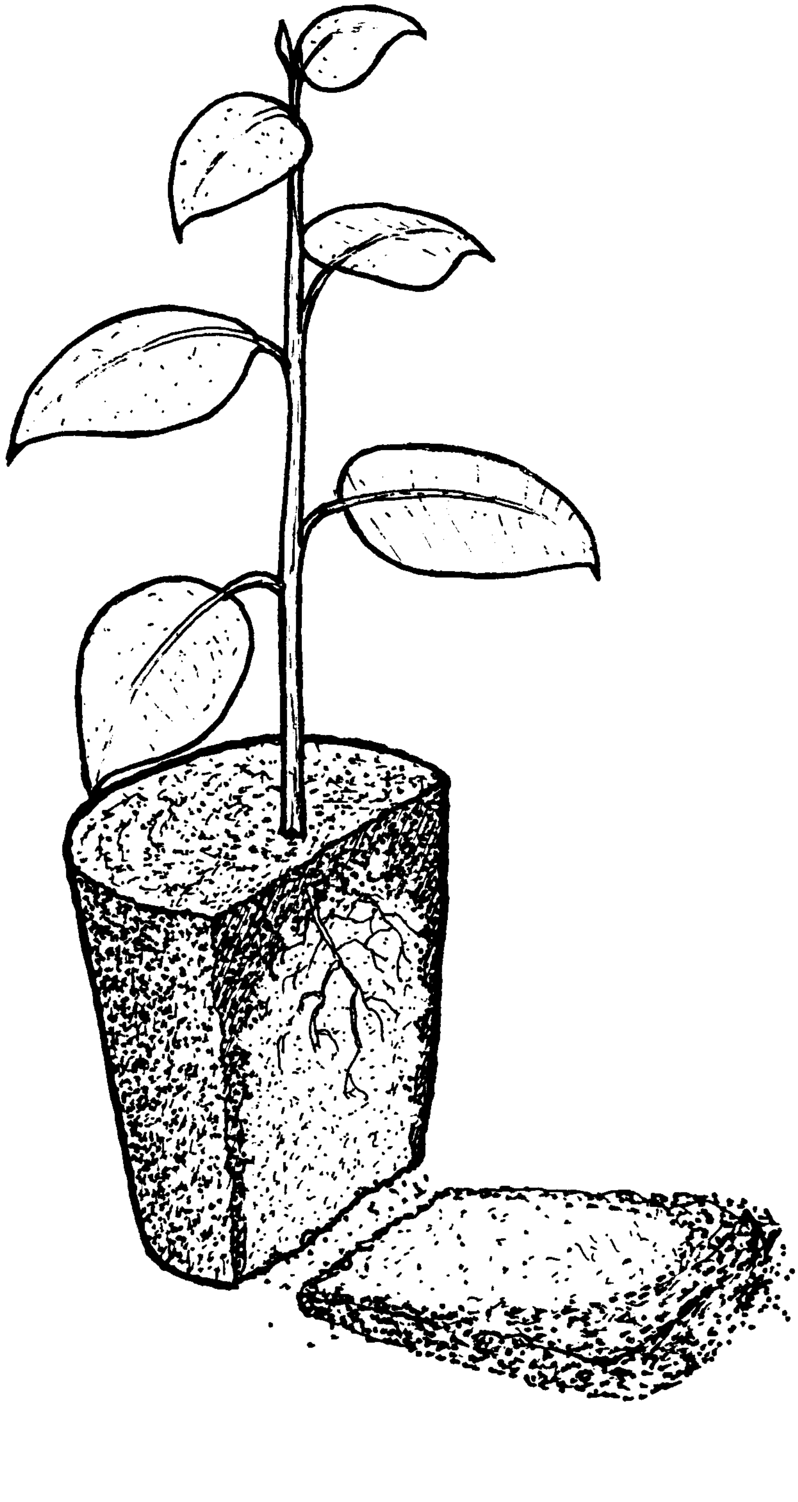
By division of a cylindrical layer of cells lying nearer the outer surface than in roots (C 11). The cells it produces on the inside become specialised as wood cells (water-conducting, strengthening or storage), while those formed to the outside are sugar-conducting or strengthening cells (C 10).

Will all these cells stay alive?

Dividing layers and storage cells may live for many years, and sugar-conducting cells for a shorter time, but many of the other kinds die quickly. The outer part of the wood *(sapwood)* contains some living cells, but in the inner *heartwood* they are all dead, though they generally remain strong.

What happens to the surface of the tree when it grows?

When a **leaf** falls off, its *scar* has usually been already protected.
As a **stem** grows in thickness, a second layer of dividing cells is formed nearer its surface. This produces the bark, and the original surface cells die. The bark may become smooth, ridged, scaly or peeling, but looser areas remain that allow some continued gas exchange.



Cutting a test plant shows that water did not reach all the soil.

General principles of tree growth C 13
- *maintaining the water balance*

What is meant by the water balance?

Trees contain large quantities of water, but if they **lose** more than they **gain,** there may soon be problems.

How much water is there in a tree?

A considerable proportion of it consists of water. For example:
(a) a thin leaf might be about 90% water by weight; ***and***
(b) an expanding root cell could contain as much as 95% of water.

Is it important that there should be so much?

Yes, because:
(1) many of the activities of living cells (C 10, C 14) are carried out in very dilute watery solutions;
(2) water is needed for the new cells in young stems, leaves and roots to elongate;
(3) plenty of water is required to maintain considerable pressure inside living cells (C 10), giving support to expanded leaves, young stems and flowers;
(4) trees that are in leaf generally lose large amounts in a single day, and need some water in reserve.

What happens if a tree runs short of water?

It is under *water stress* (C 41). Moderate, temporary water stress is normal, but a lack of substantial amounts of water for longer periods can lead to premature leaf-shedding, shoot die-back or death of the whole tree, unless it:
(a) is of a species and genetic origin that comes from a drought-prone area;
(b) has had time to form a well-established root system (C 11, C 42); ***and***
(c) has been *hardened* before being exposed to full light and drying winds (C 47).

And if not, it wilts?

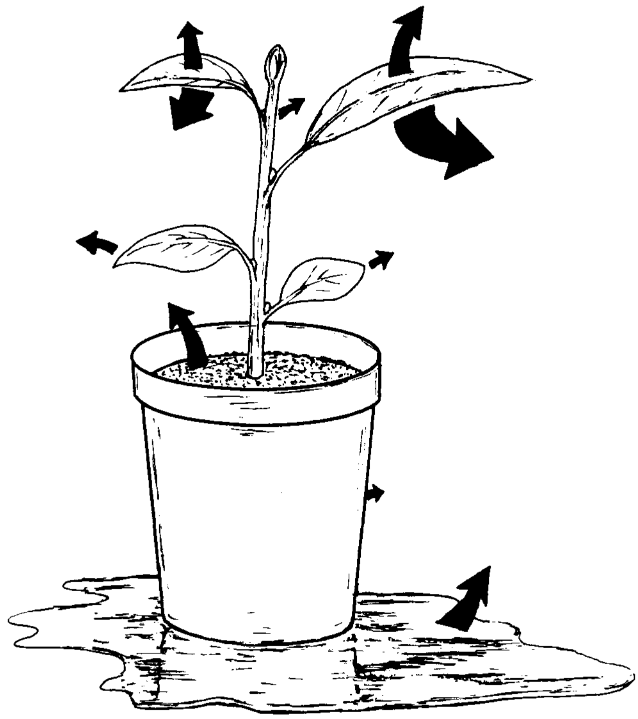
If nursery trees wilt, it means that the water shortage is decreasing the pressure in the cells. This should be avoided, as they are already under severe stress, leading to a check in growth, damage or even death.
Note: young trees with thick, leathery leaves and tough stems may not wilt although suffering from pronounced water stress.

Why do trees in leaf lose such a lot of water?

Because it *evaporates* so easily from leaves, especially from their moist **internal surfaces.** Perhaps only around 10% is lost from the outer surfaces of leaves, stems, aerial roots, flowers and fruits, because:
(a) the surface cells are covered by a waxy substance that restricts evaporation;
(b) thicker stems generally develop bark (C 12), which has a similar effect.
Less than 1% is actually used up in photosynthesis and other chemical reactions.

How does such a lot come from inside the leaves?

Because there are:
(1) a series of interconnected air-spaces inside the leaves, filled with moist air;
(2) a lot of sugar-producing cells exposed, which lose water easily; ***and***
(3) many small holes between the surface cells (C 10), which let carbon dioxide enter freely, but also let water vapour escape rapidly.



The bigger the arrow, the more water is evaporating.

Can they be closed?

Yes, each small hole can be opened or closed by two special *guard cells.* Generally the holes are ***open*** during daylight hours, ***but closed:***

(a) during the night, when photosynthesis cannot occur; ***or***
(b) if the tree is suffering from pronounced water stress.

It is also common for many of the holes to close around midday during sunny weather.

But isn't that when sugar production could be fastest?

Yes it is. Light levels are often greatest then, but with higher air temperatures evaporation will also be very rapid. A balance is struck by the plant, capturing carbon dioxide but stopping excessive water loss.

In practice, unshaded or lightly shaded leaves in the nursery can receive plenty of light for photosynthesis from about 0800-1200 and 1500-1700.

What influences how much water is lost by a tree?

(1) The amount of sunshine reaching it;
(2) The temperature and humidity of the air;
(3) How strong any wind or air currents are;
(4) How many leaves there are on the tree, whether they are hairy or not, the angle they are held and whether they are folded or rolled;
(5) Whether most of the small holes in them are open or closed.

How quickly can water be lost from leaves?

If you break off a leaf and keep it in the sun, it may be only a minute or two before it wilts. Water has been lost so rapidly that most cell activities will already have been affected. Unless the water balance is quickly restored, the leaf will soon die.

How much water does that mean in a day?

Each attached leaf could lose many times its own weight in water in a single hour. So a small tree may lose litres a day, and a big emergent tree in the canopy of a tropical forest might be losing hundreds of litres an hour.

Where does all this water come from?

It has to come from the soil, by way of the root system, trunk, branches and twigs.

However does it get up a tall tree?

Most of the water travels in the dead water-conducting cells (C 10), which are like long, miniature pipes.

Aren't they too small to carry all that water?

No, because there are a lot of them, all the way from the absorbing zones in young roots (C 11) to the small veins in the leaves.
Their diameter is usually much less than 0.5 mm, but this and their wall structure help these tiny water columns to travel up and not break.

How do the roots pick up so much water from the soil?

A well-developed root system has a very large *surface area* of fine, growing roots in contact with moist soil particles. Water enters the root easily because:

(a) the **cell walls** of the surface cells of the root offer little or no barrier to its movement; ***and***

(b) their **cell membranes** tend to pass more water in than out, because of the dilute solution inside them.

The surface area of the root system may be enlarged still further by:

(c) thousands of fungal threads from mycorrhizal associations (C 30-31); ***and sometimes***

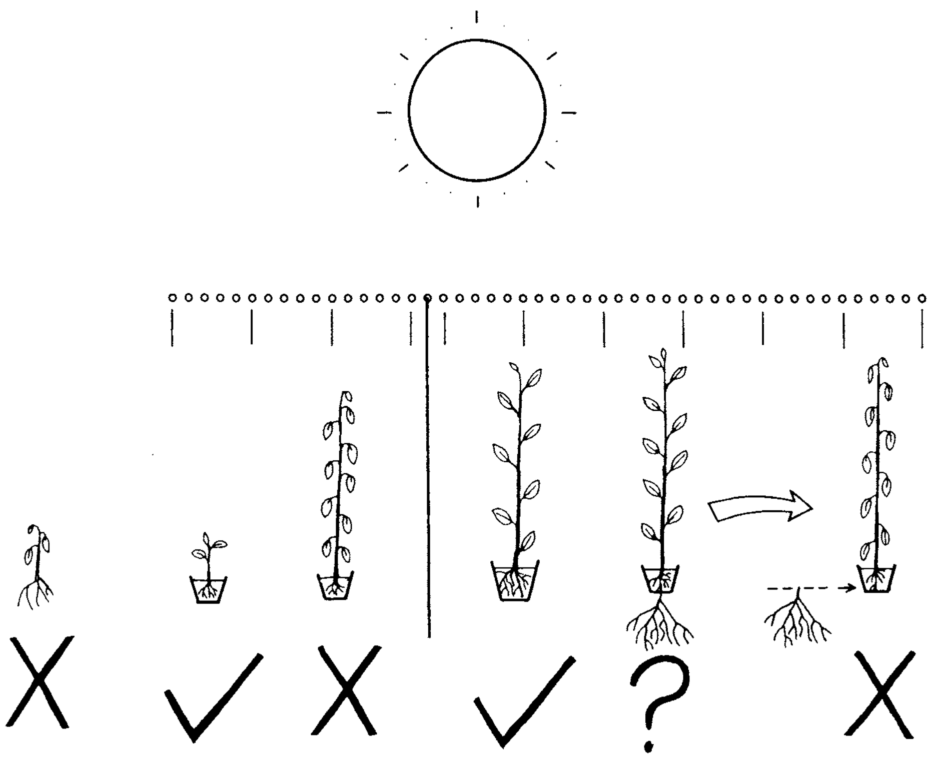
(d) root hairs, which are temporary extensions of the root surface cells.

What affects how fast it comes in?

The rate at which water is taken up by the root system depends primarily on how much water is being lost from the shoots of the tree, which draws it up from the roots. However:

(1) water loss may exceed uptake during the day-time, in which case the trunk of a large tree can shrink measurably, as water reserves inside it are depleted; ***but***

(2) water uptake continues during the night, often restoring these lost water reserves by 0600 hrs, allowing the trunk to return to full size.



But is there enough water in the soil?

For an established tree there may be, but its root system must be able to:

(a) keep growing and branching into new soil, maintaining a large surface area of absorbing roots; ***and***

(b) take up water from the soil even when it is getting dry.

For a young tree in a container, a good root system (C 4) and adequate watering (C 43) are clearly vital. If the potting soil becomes dry, water may still be lost rapidly unless most of the small holes in the leaves have closed.

Is there any way of saving young trees that are wilting severely?

(A) Reduce water loss immediately by shading plants growing in beds, and moving containers to a humid, shady and protected place (ideally a poly-propagator, see A 31 in Manual 1); ***and***
(B) Water the plants if the soil is dry.

Note: *do* ***not*** *water if the soil is moist, because it will not help, and it could cause harm by waterlogging the soil (C 11), and encouraging root diseases (C 45).*

Can shoots take up any water directly?

Generally no, because rainfall does not normally enter the small holes in the leaves.
Occasionally they might do so, for example when the soil is very dry, and:

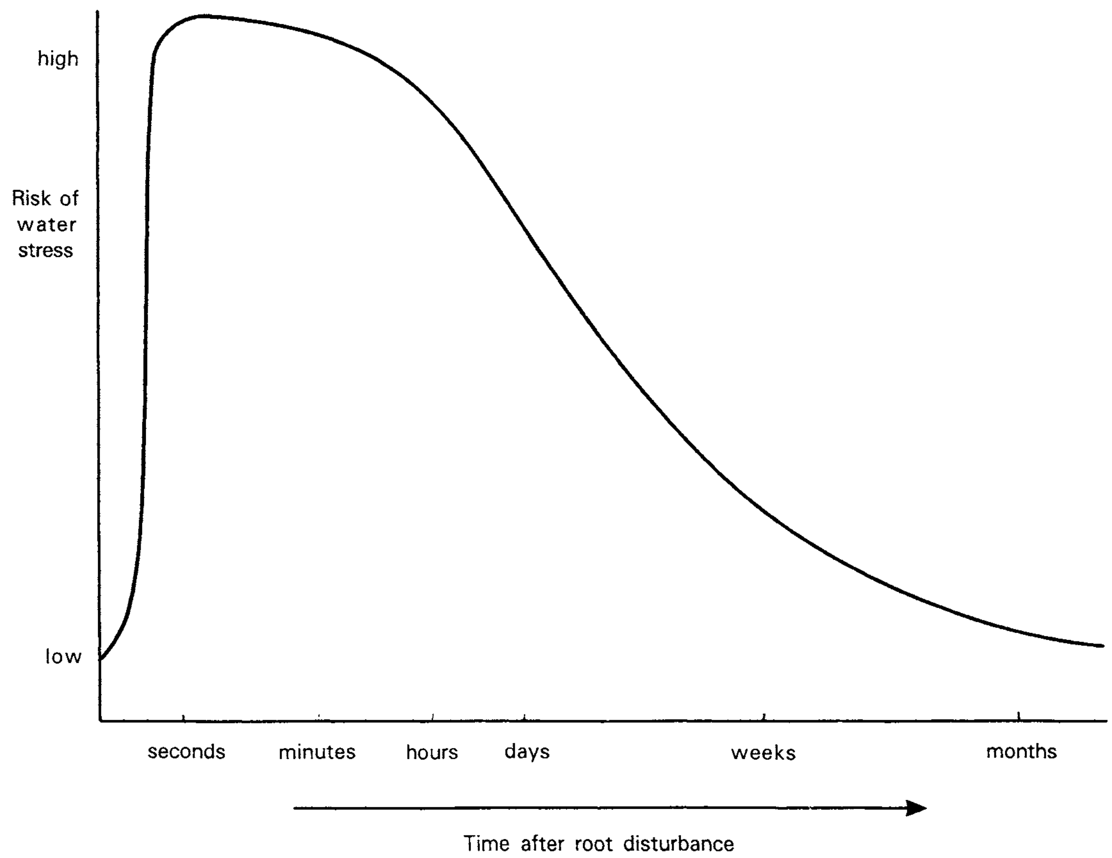
(a) mist or dew moisten the shoots;

(b) the leaf surface is specially adapted, or aerial roots are formed, making above-ground water absorption possible.

Although leaves and young stems depend on rain taken up by the roots, if water fills their internal air spaces they cannot function properly.

What about trees which have shed their leaves naturally?

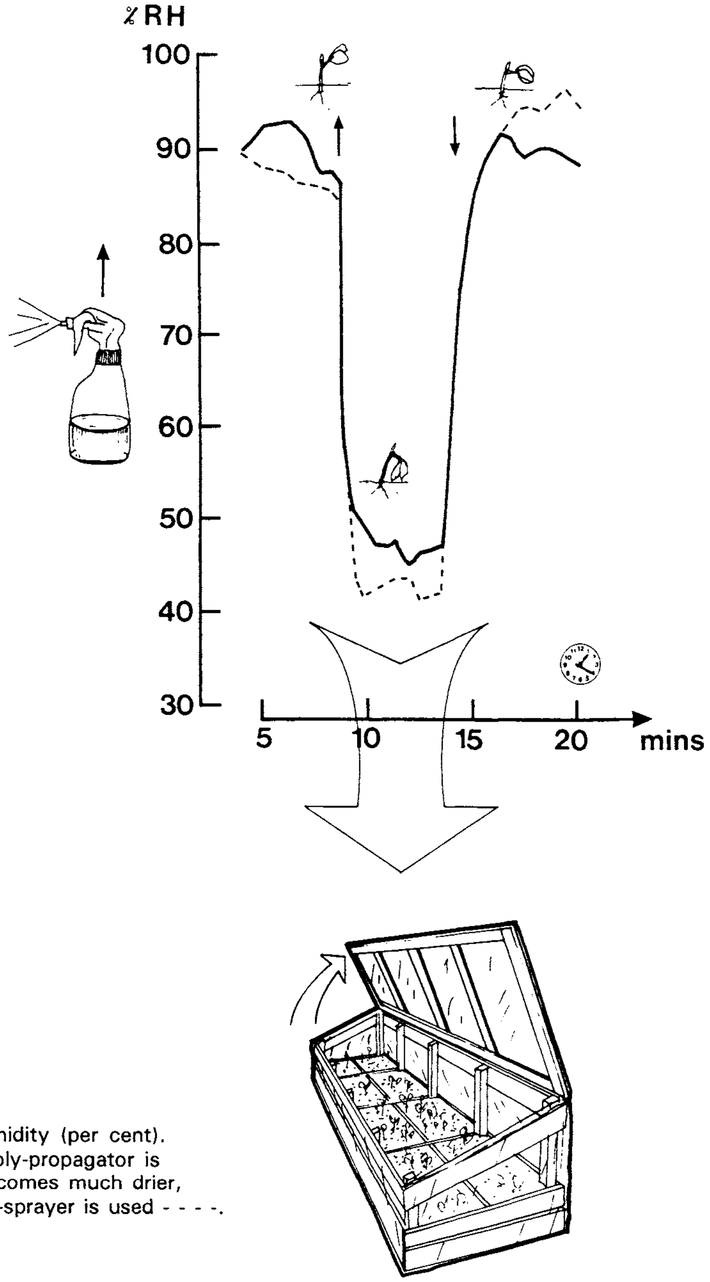
These lose much less water than leafy plants, and may even contain sap under pressure. They should be watered sparingly (C 43), but not allowed to dry up.



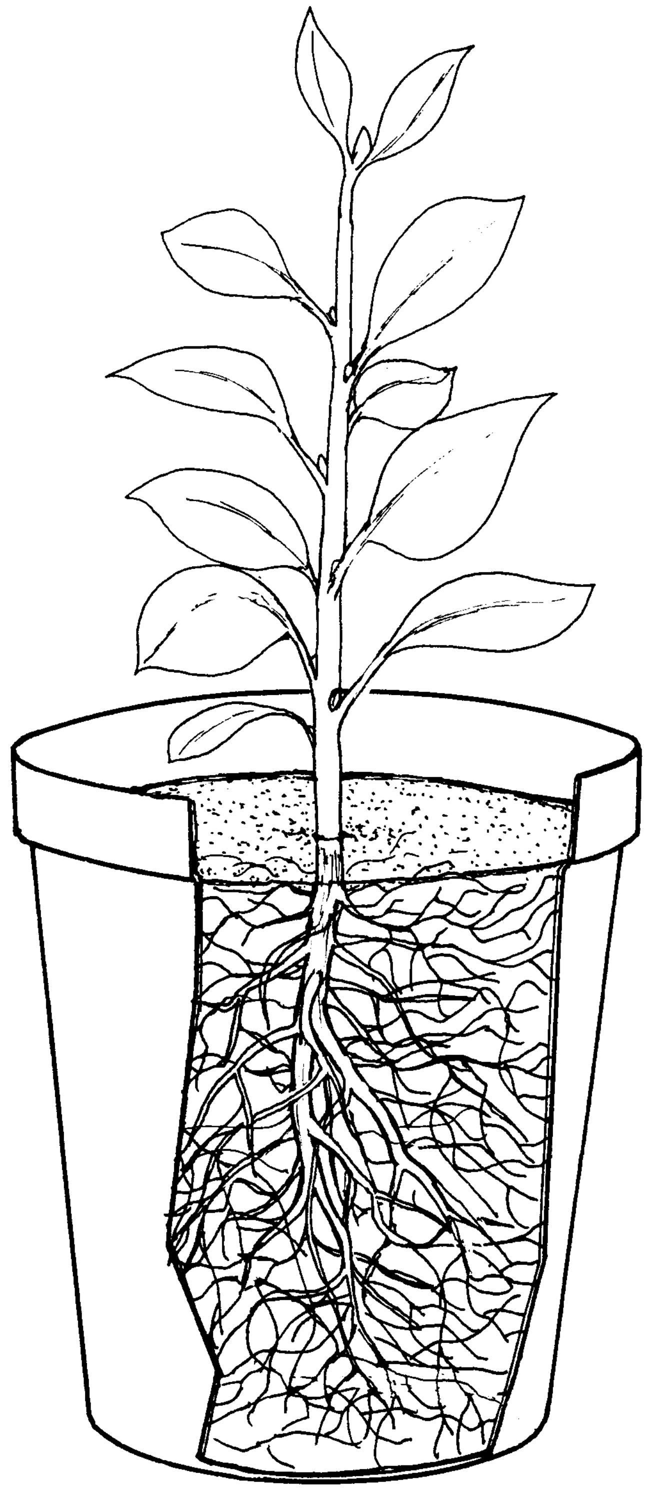
Are there some other practical guide-lines about water balance?

(1) Young trees, even of hardy species and local origin, are very liable to run short of water when their root systems are disturbed, so damage needs to be kept to a minimum when they are potted up (C 42) or moved to different conditions (C 41).
(2) Unrooted and newly rooted cuttings (Manual 1) and germinating seedlings (Manual 2) require special care because they are particularly liable to water stress.
(3) Most tree species need shading (C 41) at some stages while in the nursery, and careful watering (C 43) is needed by all young trees, especially in containers (C 6).
(4) Growing a good root system (C 4, C 11) is more important than having a big shoot (C 12) on a nursery tree. Similarly, large leaves are undesirable on planting stock (C 34).
(5) Young trees need 'hardening' before going to the planting site, so that the newly planted tree can grow "from a position of strength" (C 47; and Manual 5).
(6) The chief function of a tree nursery is to produce planting stock that can maintain its water balance when planted out.

Other suggestions for maintaining the water balance are found elsewhere in the Manuals.



%RH = relative humidity (per cent). Immediately the poly-propagator is opened, the air becomes much drier, even when a hand-sprayer is used - - - -.



General principles of tree growth C 14
- *absorbing, making and moving substances*

What kind of substances does the tree absorb?

(A) **Water,** mainly taken up by the roots from the soil (C 11, C 13);
(B) **Nutrients,** also chiefly from the soil; ***and***
(C) **Carbon dioxide,** as a gas which passes in the air into the leaves (C 10).

Some **pollutants** can also be absorbed by the shoots of trees (D 16, D 26 in Manual 4).

What are nutrients?

Simple chemical substances that are important to or essential for the growth of all living organisms (D 13 in Manual 4).

Which are the main nutrients?

(1) **Nitrogen (N),** occurring in soluble compounds such as urea, nitrates and ammonium salts, and in a less easily dissolved form within organic matter;
(2) **Phosphorus (P),** usually in an insoluble form, but more soluble when it occurs as various kinds of phosphates; ***and***
(3) **Potassium (K),** usually as fairly soluble salts.

Relatively large amounts of these three nutrients are required for good growth of both young nursery plants (C 33-34) and older trees (D 13 in Manual 4).

Are other nutrients needed as well?

(a) Moderate quantities of substances containing **calcium (Ca), magnesium (Mg)** and **sulphur (S);** ***and***
(b) Very small amounts of *micronutrients,* from chemical compounds containing **boron (B), chlorine (Cl), cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), molybdenum (Mo)** and **zinc (Zn).**

Where do all these chemicals come from?

(1) **Litter:** nutrients are released by the decay of organic matter:
- (a) on the surface of and within the topsoil (D 13); ***and***
- (b) when used as an important component of potting mixtures (C 6);

(2) **Soil particles:** some nutrients become available as any stones and gravel (D 12) are very gradually broken down into smaller sizes by *weathering* ;
(3) **Air:** a few nutrients come from gases in the air, and from dust and other tiny particles that can settle or be brought down in rainfall.

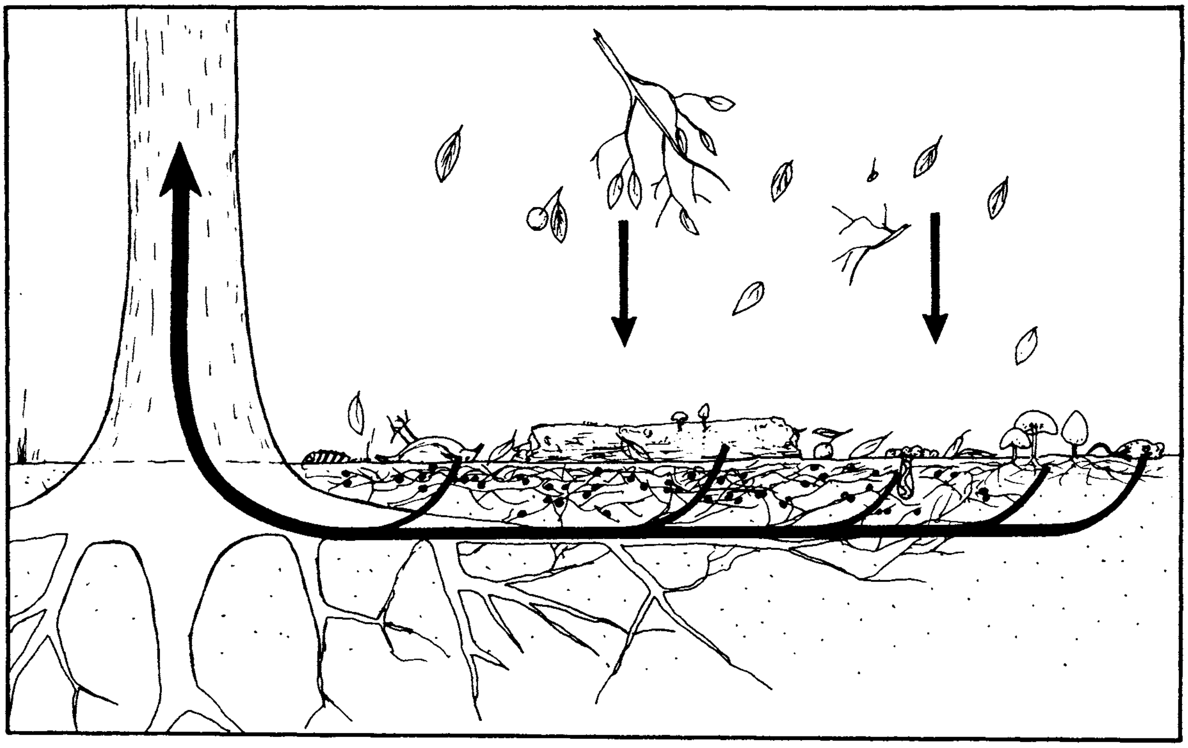
Which is the most important source?

Under trees, the **litter** is usually by far the most important. Most nutrients are very efficiently recycled in natural woodland ecosystems, so that they are used over and over again, with only very small losses in *run-off* and *leaching* (D 13).

What happens when the trees are cut down?

Nutrient supply generally becomes a serious problem, because:
- (a) most nutrients are very easily **lost** from land that is bare, farmed without shade trees or planted with a single species of tree (Manual 4);
- (b) many tropical soils contain **limited supplies** of nutrients; ***while***
- (c) **growth** of plants can be **greatly retarded** if even one kind of nutrient is in short supply.

So recycling of nutrients is one of several important reasons for having plenty of different kinds of trees (C 1; and D 30 and D 53 in Manual 4) in managed ecosystems.



Recycling of nutrients.

But does this apply to young trees in the nursery?

Young nursery trees start off with a supply of nutrients stored in the seed, or present in the cutting when it is taken. But sooner or later they depend for nutrients on what is available in the potting mixture or nursery bed.

What about adding fertilisers?

If a *balanced* fertiliser (C 33-34) is added to a poor soil, the young trees may be able to take up more nutrients and grow better, unless:

(a) these are rapidly washed out of the pots, or *leached* too deep for the roots;
(b) the soil is too acid or too alkaline (C 6);
(c) there is still a lack of one or more individual nutrients; ***or***
(d) there was plenty of a particular nutrient already in the soil, and there is now too much, damaging the roots or hampering the uptake of another nutrient.

It is generally better to concentrate on choosing good nursery soils (C 23) and preparing favourable potting mixes (C 6).
Use cheap and readily available materials like composts and wastes (C 33), and avoid expensive fertilisers except when they are specially needed.

How do nutrients actually get into the tree?

(1) They must dissolve in water, even if sparingly;
(2) The solution enters the network of cell walls in the outer parts of the absorbing regions of fine roots (C 11);
(3) Specific nutrients are actively transferred across the cell membrane (C 10) into the living cell, while others are excluded or absorbed in smaller quantities; ***and***
(4) They pass an inner boundary layer and can move to the rest of the tree.

Small amounts of nutrients can also be absorbed by leaves, if for example a foliar feed is sprayed on to them.

What about mycorrhizas?

Yes, these are very important in the uptake of nutrients (C 30-31; and D 32 in Manual 4), because the fungal threads can:

(a) form a very extensive network that captures and recycles a lot of nutrients;
(b) often release P and other nutrients that are in an insoluble form in the soil; ***and***
(c) pass nutrients into the tree's root system.

How about nitrogen-fixing trees?

These form nodules with closely associated micro-organisms that have the unique capacity to fix N from the air, where it is very abundant, into nutrient form (C 32 and D 32).

Are sugars also nutrients?

No, they are more complex **organic** substances that green plants ***manufacture*** from simple chemicals containing **carbon (C),** using the energy of sunlight (C 10).

Does that include carbon dioxide?

Yes, the energy that is captured during photosynthesis is used to make sugars by adding more carbon to organic acids, which also contain **hydrogen (H)** and **oxygen (O).** Some of the latter is released into the atmosphere.

What other kinds of substances do trees manufacture?

Amongst the most important are those used in:

(1) making **cell membranes** (C 10);
(2) building **cell walls,** including *cellulose* and various substances that strengthen and join cells together;
(3) copying the **genetic instructions** during cell division;
(4) providing nitrogen-containing building blocks for making the ***enzymes*** **(proteins)** that allow specific chemical reactions to take place rapidly;
(5) creating the phosphate-containing substances that allow **easy transfer of chemical energy** to drive chemical reactions, including photosynthesis;
(6) storing **starch, fats** and other substances for later use.

Do trees make anything else?

Yes, a very large number of different chemicals. Some have been widely studied, while many others are yet to be identified. For example, some may:

(a) discourage most kinds of animals from eating the leaves or bark (D 10 in Manual 4);
(b) give an attractive odour to flowers or flavour to edible fruits (D 33);
(c) contribute to the strength or durability of timber (D 36);
(d) provide useful substances that can be used for raw materials (D 37), medicines (D 33) or veterinary purposes (D 39).

How do these substances move around in the tree?

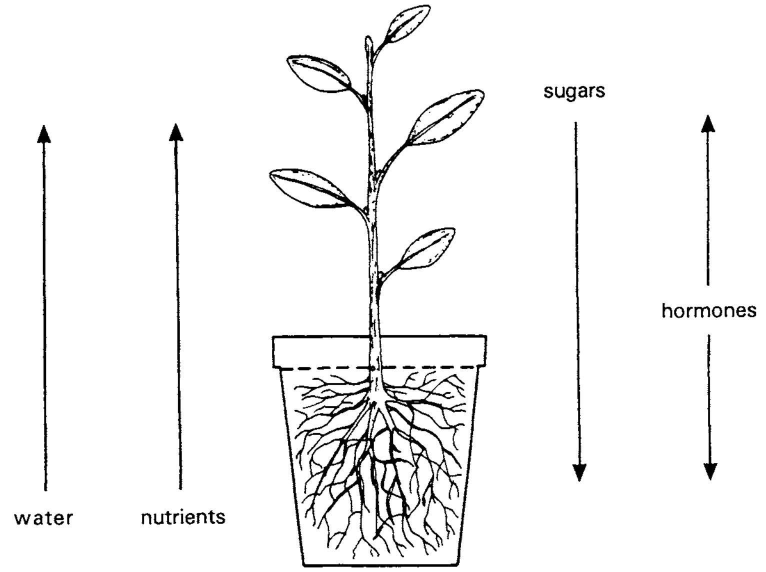
Those that do so will move:

(A) from one living cell to the next through tiny connections;
(B) along the fine tubes formed by the elongated water- and sugar-conducting cells.

Some substances are formed, broken down and reformed many times over.
However, others are made within a cell and never move, becoming part of the permanent tissues of the tree.

Where do sugars move?

From the sugar-making cells in the leaf and stem to neighbouring cells, and then through the sugar-conducting cells to all other cells in the shoot and the root system.



What are they used for by the tree?

Besides storage, sugars are broken down *(respired)* (C 10) in each living cell, releasing energy for:

(a) its own maintenance and manufacture of chemicals;
(b) cell division and expansion in the growing zones of the tree, and repair of damaged parts; ***and***
(c) driving the active uptake of nutrients and the transport of organic substances.

How do nutrients move?

Simple nutrients, once through the inner boundary layer of an absorbing root, travel mainly through the water-conducting cells to other parts of the tree.
Organic nutrients, already partly built up, may pass either by the same route or through the sugar-conducting cells.

How is all this controlled?

In at least 3 ways:

(A) through the **genetic instructions** contained in the nucleus of each cell (C 10), which accurately control the production of enzymes and thus of other substances;
(B) by the **position within the plant** that a cell occupies, which narrows the wide potential for activities it possesses; ***and***
(C) by **plant growth hormones** which are manufactured in one part of the tree and often move to another.

For example, when a leafy stem cutting is detached from a stockplant (Manual 1), the natural auxins (produced by the shoot tip and moving towards the base) can help to regenerate a complete plant by stimulating cells there to form new root tips. Synthetic auxins applied to the base can often increase this process (A 40).

What else do plant hormones do?

Various hormones appear to help keep a balance between the two parts. For example:

(1) poor root systems generally lead to poor shoot growth;
(2) very rapid shoot growth may coincide with reduced root activity, followed by the reverse;
(3) poor shoot and root growth may follow heavy fruiting.

Are hormones well understood?

Although control over the growth and development of large trees is a central part of biology, there is still much to be learnt. Much more research is needed (C 7, C 15).

General principles of tree growth C 15

- *experiments with young trees in pots*

What experiments can be done in pots?

Many different kinds. It is often best to concentrate on those which are:

(1) fairly straightforward to do; ***and***

(2) likely to help increase understanding of tree growth and to improve nursery practice.

Are there some examples?

(A) Discovering more about the various **factors that affect tree growth** (C 10-14, C 62);
(B) Comparing different **growing conditions** for a batch of trees;
(C) Seeking to resolve **nursery problems** that have been experienced (C 3, C 60-61);
(D) Testing **tree species** and **genetic origins** (C 5) that are unfamiliar;
(E) Trying out a new **technique** or **timing.**

What is the main aim of basic studies of tree growth?

To add a bit to our understanding of some of the complex **interactions** (C 69-K) between:

(a) the genetic potential of the individual tree (C 5);
(b) internal factors dependent on the size and age of the tree (Manual 2);
(c) the non-living part of the local environment;
(d) competition and collaboration with other plants and micro-organisms;
(e) effects of animals, especially humans.

How would I discover better growing conditions?

By using the most successful local techniques, and then:

(A) Setting up an experiment, in which you could for instance compare:

(1) different types or sizes of containers (C 6);
(2) contrasting potting mixes;
(3) soils inoculated for mycorrhizas (C 30-31) or nitrogen-fixing nodules (C 32), compared with uninoculated control trees;
(4) differing watering regimes (C 43);
(5) degrees of shading, or rates of reducing it (C 41);

(B) Trying out the most successful treatments on some spare batches of trees; ***and then***
(C) If appropriate, modifying current nursery methods accordingly.

What about problem-solving?

Some nursery problems can be tackled by:

(a) thinking about the general principles that control the growth of trees (C 10-14), and spotting which conditions might be unfavourable;
(b) using a check-list (D 60); ***or***
(c) checking with a more experienced grower or with research workers (C 53; and D 5 in Manual 4).

Other problems may need formal or informal experiments to find out what might be wrong.

Is it possible to test out a new tree species in pots?

Yes, this is often a useful first step, ***before*** trying them out in field trials (D 29 in Manual 4). One might discover, for instance:

(1) if the new trees can thrive under nursery conditions that suit other species, or whether they may need special environments (C 48);
(2) what their growth rates are like; ***and***
(3) if they are particularly liable to damage by stress (C 41) or from insect pests or diseases (C 45).

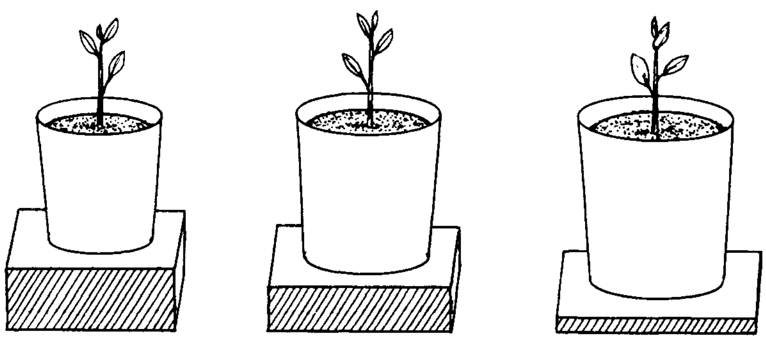
Before writing off the species as a failure, remember that it could be the provenance, seed-lot or clones used (C 5) that were unsatisfactory.

How would I set about doing an experiment?

(a) Grow enough young trees to a suitable size under uniform conditions in containers (C 6-7), allowing for some spares;
(b) Decide on the particular topic for the experiment, and what treatments to apply (D 6 in Manual 4);
(c) Get together all the materials and tools you are going to need (C 24, C 51, C 61-B), including labels, pencil and paper;
(d) Choose enough uniform, undamaged plants out of the batch to use, or *grade* them if numbers are short (A 45 in Manual 1), and allot them to treatments without bias;
(e) Apply the treatments, if possible all on the same day, label the young trees clearly, and make a simple record of the date, treatments, number of plants and their origin (C 54);
(f) Arrange the containers in a suitable layout (C 62-F; and D 55 in Manual 4);
(g) Look after the trees well (C 48);
(h) Note down (with the date) any differences you observe, and assess the experiment at appropriate intervals (C 55, C 67-68); ***and***
(i) Draw valid conclusions from the results, analysing them where appropriate (C 69).

Supposing I want to compare pots of different sizes?

They should preferably be:
(1) all made of the same kind of material, with a similar shape; ***and***
(2) filled with the same batch of well-mixed potting soil; ***but***
(3) sufficiently different in size for any effects to have a chance of showing up.



How many treatments would be needed?

Between two and four is often a good idea, rather than making the experiment too large.

And how big should the different pots be?

The most important aspect of pot size is the **volume** of soil within, which will provide both rooting space and a nutrient supply for the young tree. So you could choose convenient pot sizes that:
(a) range either side of a container of medium size;
(b) involve two- to three-fold differences between treatments.

What would that mean in practice?

If, for instance, you chose tapered pots where the diameters at the level of the soil at the top were 9.5, 12.25 and 15.5 cm, this would give soil volumes for the root systems of about 450, 900 and 1850 cubic centimetres. The medium-sized pots would hold about twice the soil of the small ones; and similarly the large containers would have about double the contents of the medium-sized pots.

How can I check the volume of my containers?

See sheet C 63-D for this.

Should all the containers have the same number of holes?

No, the medium-sized pot would need to have more holes than the small one, so that excess water drained off in a similar way. The large containers would need even more holes to maintain comparable conditions of soil moisture.

How would I set about grading the young trees?

Supposing you have decided to have 25 *replicates* for each of the 3 treatments:

(a) first arrange the 75 plants in *triplets* of similar height, branching habit, vigour or other features;

(b) next *randomly* assign the 3 plants of the first triplet to each of the 3 treatments. (You could do this by withdrawing small, similar-sized, numbered pebbles in turn from a bag, after mixing them together); ***and***

(c) repeat for the other 24 triplets.

What about applying the treatments?

Some important points to plan for are:

(1) Reduce to a minimum the time that root systems are exposed to the air;

(2) Pot up the whole experiment on the same day, or if this is not possible, complete a certain number of triplets, not treatments; ***and***

(3) Try as far as possible to keep conditions the same for all the young trees, except for the pot size. Avoid favouring any particular treatment, as this would *bias* the results of the experiment, perhaps giving you false ideas about the most suitable pot size. For example, try not to damage roots more when putting them into small pots.

How about labelling and records?

The best way is to:

(A) label each plant with numbers and/or letters that identify it uniquely; ***and***

(B) note down the details of the experiment straightaway, including the date and the origin of the plants which were used (C 54).

Are individual labels really necessary?

Although in this experiment you can easily see which treatment is which, remember that:

(1) knowing which trees were in which triplets can improve the analysis of the results (C 69-F, I);

(2) labelling trees individually will mean that their performance can continue to be followed after they have been planted out.

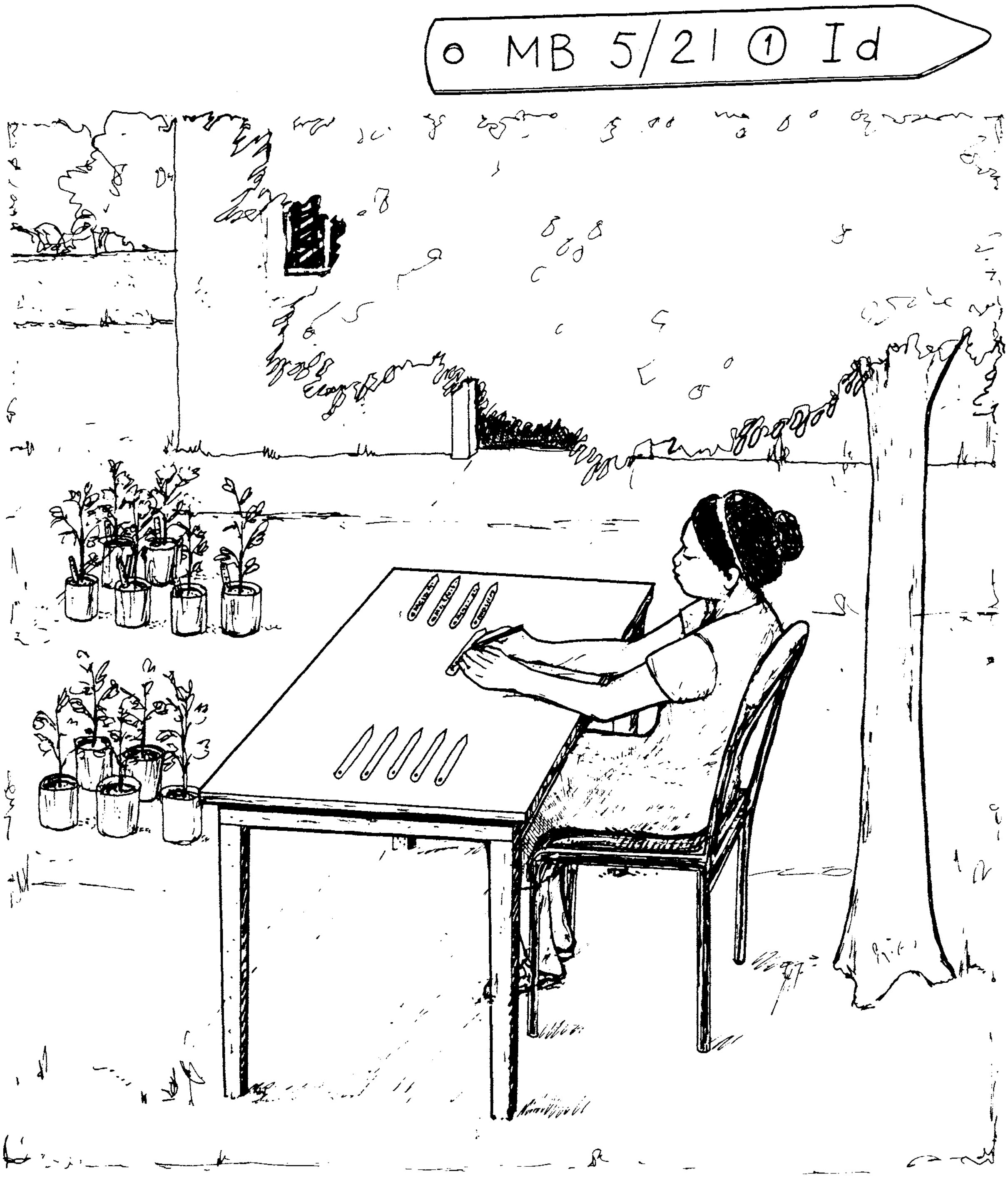
Note: experiments using clonal plants (Manual 1) can give greater precision than those with seedlings, provided that the trees of each clone are allocated equally to the 3 treatments. In such cases you might perhaps write the treatment details on the label bearing the clone number.

Where should the pots be kept?

(a) In as uniform conditions of light as possible; ***and***

(b) Where you can water (C 43) and check the experiment regularly (C 40, C 48).

It may be useful to put an extra line of similar trees in pots around the experiment, so that none of the treated trees are 'edge plants' subject to different conditions.



How should the experiment be laid out?

In such a way that no treatment (or genetic origin) is specially favoured. To avoid bias it is often recommended that a completely random arrangement of the pots should be used. However, you also need to take into account the following points:

(1) Trees in smaller pots are liable to be shaded by larger containers, especially if the trees in the latter are stimulated to make more rapid growth.

(2) Small pots mixed with larger containers can easily fail to get enough water, and they may also dry out more rapidly. Thus care is needed to prevent additional water stress (C 41) occurring in some treatments.

(3) With complete randomisation, several replicates of one treatment may happen to be allocated to one small part of the area.

For problems (1) and (2), a compromise might be to randomise short *lines* of trees of the same treatment and pot size. Layouts such as *Randomised Blocks* (D 55 in Manual 4) can reduce problem (3), and *Latin Squares* can avoid it altogether.

What would the Blocks consist of?

In the pot size experiment, five triplets could be randomly assigned to each of 5 Blocks, making five sets of 15 plants. Each Block would be laid out together in a convenient and compact pattern within the whole experiment.

But supposing all the pots won't fit into one place?

If necessary, some of the Blocks could be put in one area, and the rest in a second place, according to the available space. As long as the whole Block is kept together, it would even be possible to put each Block in a separate place, as long as they were all reasonably similar.

Do experimental trees need special care?

Yes they do (C 48), in order to:

(a) avoid introducing extra, unnecessary sources of variation; ***and***

(b) lessen the risks of damage to individual trees, or of losing the whole experiment.

How about assessing and analysing the results?

In order to be able to judge properly (C 55, C 67-69), it is important:

(A) to **observe** frequently (and make brief notes about) what is going on; ***and***

(B) to **measure** or **count** some aspects of growth (C 67-68).

Some research workers **decide beforehand** what should be assessed, but others prefer to **choose at the time** what to measure and when to do it. If combined with regular observations, the second approach may allow one:

(1) to assess what looks particularly relevant to your experiment;

(2) to measure when differences between treatments are just becoming marked; ***and***

(3) to decide on priorities that are achievable with the people, equipment and time available.