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THE DEVELOPMENT OF THE TREE TRUNK IN RELATION TO APICAL DOMINANCE AND OTHER SHOOT ORGANISATION CONCEPTS

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NG, F. S. P. 1999. The development of the tree trunk in relation to apical dominance and other shoot organisation concepts. Trunk development is an expression of tree architecture. All trees begin as seedlings with a simple unbranched shoot. Trees that remain unbranched throughout their whole lives are referred to as unbranched trees. Trees which eventually branch to produce multiple shoots, all of one type, are referred to as 'monomorphic' trees. In the next class, branch shoots are differentiated from the leader (trunk) shoot, the most important difference being that branches are designed to be shed, while the trunk is permanent; such trees are 'dimorphic' because they consist of two types of shoots. In the fourth class (containing most of the big timber trees of the world), trees grow through the seedling unbranched phase, followed by an intermediate dimorphic phase (with sheddable branches), followed by a 'metamorphosed' phase in which the crown is made up of limbs that do not get shed; such trees are 'metamorphosed'. The fifth class of trees are 'plagiotropic' because their apical buds grow sideways, but an erect trunk is formed because the leader shoot straightens up by secondary erection. The trunk height of unbranched and dimorphic trees is indeterminate because the upper limit of the trunk moves up as leaves or branches are shed. The trunk height of monomorphic trees is determined by the onset of branching, that of metamorphosed trees by the onset of metamorphosis, and that of plagiotropic trees by the cessation of secondary erection.

Key words: Apical dominance - tree architecture - orthotropy - plagiotropy - metamorphosis - maturation - rejuvenation - secondary thickening - wood

NG, F. S. P. 1999. Kaitan perkembangan batang pokok dengan konsep keunggulan apeks dan susunan pucuk yang lain. Perkembangan batang menunjukkan binaan pokok. Semua pokok bermula daripada anak benih dengan pucuk tunggal yang tidak berdahan. Pokok yang kekal tidak berdahan di sepanjang hayatnya dipanggil sebagai pokok tidak berdahan. Pokok yang akhirnya tumbuh dahan dan mengeluarkan pucuk berganda yang semuanya sama jenis dipanggil pokok 'monomorf'. Dalam kelas seterusnya, pucuk dahan dibezakan daripada pucuk (batang) anjur, iaitu perbezaan yang paling penting di mana dahan akan digugurkan, manakala batangnya pula kekal; pokok seperti ini dipanggil dimorf kerana ia mengandungi dua jenis pucuk. Dalam kelas keempat (mengandungi kebanyakan pokok balak yang besar di dunia), pokok tumbuh menerusi anak benih di peringkat yang tidak berdahan, diikuti dengan peringkat dimorf pertengahan (dengan dahan yang boleh gugur), diikuti dengan peringkat metamorfosis di mana silaranya daripada dahan yang tidak gugur; pokok seperti ini adalah metamorfosis. Kelas kelima pokok adalah plagiotropik kerana tunas apeksnya tumbuh mengiring tetapi membentuk batang yang tegak kerana pucuk anjur diluruskan dengan penegakan sekunder. Had ketinggian batang pokok yang tidak berdahan dan pokok dimorf tidak dapat dipastikan kerana ketinggiannya akan dipanjangkan mengikut kadar keguguran daun atau dahan. Ketinggian batang pokok monomorf ditentukan melalui permulaan pendahanan, manakala pokok metamorf melalui permulaan metamorfosis, dan pokok plagiotropik pula melalui penghentian penegakan sekunder.

Introduction

A few years ago, I visited a famous teak plantation, where I saw magnificent 'plus' trees, over 80 years of age, with immensely tall, straight, cylindrical trunks. Buds had been taken from the crowns of these trees for cloning. However, instead of trees with tall straight trunks, the plantlets had grown into crowns with large limbs. By pruning the lower limbs, a short trunk could be produced, but this is an artificial way of producing a trunk, not nature's way (Figures 1 and 2).

In cloning, it is usually assumed that clones replicate in totality the organisms from which they are derived. For trees, this assumption is incorrect. In *Araucaria*, it has long been known that rooted cuttings from an erect (orthotropic) stem will produce erect plants, but cuttings from the sideways-growing (plagiotropic) branches will produce plants that grow like branches (Bonga 1982). In fruit orchards, trees cloned by air-layering of shoots of the mature crown may have little or no trunk-forming ability; instead, they tend to replicate the mature crown. In forestry, cuttings taken from coppice or epicormic shoots induced from the trunk will grow into trees with trunks, but cuttings from the mature crown may fail to develop a proper trunk. Hence clones derived from different parts of the same tree may look and behave very differently from each other.

Without its trunk, a tree would resemble a shrub. The trunk, being the main source of the world's supply of timber, is the focus of production forestry, and great emphasis is placed on improvement of trunk length, diameter, straightness, circularity and so on. However, some purposes are better achieved by getting rid of the trunk or minimising it, e.g. to gain easier access to the crown for harvesting fruits and seeds or to carry out controlled pollination. Furthermore, the time saved in trunk-building might contribute to earlier productivity in the case of fruit and seed orchards. Hence it is of economic as well as scientific interest to understand the mechanisms involved in trunk development.

The unique set of properties which define a tree trunk can be summed up in three words: *single, erect, woody*. These three properties are reviewed here, in relation to the theories or concepts that have evolved around them. Shrubby trees (having multiple erect stems) are excluded from this review.

The excellent classification of tree architectural models by Halle, Oldemann and Tomlinson (1978), which I will refer to as Halle *et al.*, provides a good basis for probing the relationship between trunk-building and apical dominance. Halle *et al.* recognised (1) trees built by one meristem, (2) trees with modular construction, (3) trees with trunk-branch differentiation, and (4) trees with changes in orientation of axes. These four 'trunk' classes were further subdivided into over 20 models based on details of branching. In this paper I shall refer to the four 'trunk' classes, (but using a simpler set of labels), and propose an additional one.

In 1967, Brown *et al.* came to the conclusion that the classical work of Thimann and Skoog in the 1930s on apical dominance in *Vicia faba* had been applied too uncritically to the interpretation of form in woody plants. Brown *et al.* attempted to reinterpret the form of trees, but limited themselves to a few temperate species. The present review takes a more global approach.

Lateral bud control: inhibition or stimulation?

For a review of the history of ideas on the mechanisms of apical dominance, readers are referred to Hillman (1984). Hillman listed four themes that have been brought under the umbrella of apical dominance: (a) inhibition of lateral buds, (b) suppression of subordinate shoots, (c) influence on positioning and behaviour of other organs such as leaves and roots, and (d) influence on nutrient transport and cellular differentiation. Hillman's review dealt mainly with the first theme: the inhibition of lateral buds. In this review, I will emphasise the first and second themes and draw attention to a fifth theme: secondary thickening, which has been neglected in the development of the theory of secondary thickening. These are the themes that are most relevant to trunk-building.

It has been established by common observation and many experiments carried out in the past 100 years that the removal of the apical bud results in the activation of dormant lateral buds below the apex. This is the main basis of the theory of apical dominance: that the apical bud actively inhibits the lateral buds. If the apical bud is destroyed, a lateral bud is activated and becomes the new apical bud. The role of dormant lateral buds is therefore to provide insurance against the loss of the apical bud.

Until the 1930s, the mechanism of lateral bud inhibition was thought to be competition for nutrients between the apical bud and the lateral buds. The actively growing apical bud was thought to act as a nutrient sink, inhibiting the lateral buds by depriving them of nutrients. Later, with the discovery of auxins, the idea of inhibitory hormones gained ground. Growing apical buds were thought to produce hormones, which moved basipetally to inhibit downstream lateral buds. However, this simple model of hormonal inhibition suffers from some serious deficiencies.

Upon removal of the apical bud, only the upper lateral buds respond, but if a shoot is divided into serial segments, (as in cuttings for vegetative propagation), the uppermost buds of each segment will respond. The simplest explanation for this is that injury of the stem *stimulates* the dormant buds below the level of the injury. Indeed, a well-known way to induce coppice shoots is to make a wound in the trunk above the desired level of coppicing. Removal of the apical bud can be viewed as a specific case of stem injury which fits easily into the general case.

If a shoot cutting is planted upside down, new shoots arise from the *lower* end of the cutting, which is the end closest to the original (morphological) apex of the shoot, rather than from the upper end of the cutting. The reversal of the cutting does not result in reversal of flow of the hypothetical inhibitory hormone. This polarity in shoot behaviour is illustrated in Hartmann and Kester (1968, Figure 9-17) with *Ribes sativum.* Here in Figures 3 and 4, I use the familiar tropical examples of a well-known single-stemmed erect plant, the cassava, *Manihot esculenta,* and a slender climber, *Ipomoea congesta.* The latter shows that polarity is not peculiar to trees. The observed facts on polarity indicate that the mechanism of apical dominance cannot be a hormone moving by gravity. The exact mechanism of activation of dormant buds must therefore remain open to question.

Under the inhibition concept, we would have to assume that the default condition of a bud is to grow unless actively inhibited. Under the stimulation concept, we would have to assume that the default condition of a bud is stay dormant unless stimulated. There are hundreds of published papers on the inhibition as well as the stimulation of vegetative buds by the application of physiologically active substances, a new review of which would be desirable but beyond the scope of this paper. However, it is pertinent to note that two systems of buds are known to coexist in many trees. Buds of one system grow without resting (sylleptic buds) while buds of the other system stay dormant unless stimulated to grow (proleptic buds).

Apical dominance and the unbranched tree

If all the lateral buds of a shoot stay dormant, the result would be an unbranched tree. Such trees are well known in the palm family. We can surmise that in palms, apical dominance is effective throughout the life of the tree; indeed, over-effective, because vegetative lateral buds seem to be totally suppressed or absent (Tomlinson 1990) on the aerial stems of palms. If the apical bud is destroyed, the palm dies. However, palms rarely die in this way because the palm apex is well-protected under many layers of leaf sheaths.

The unbranched tree corresponds to "trees built by one meristem" in Halle *et al.* In principle, a meristem can be replaced by an equivalent meristem in linear succession to build an unbranched tree, with apical dominance ensuring a one-for-one succession, hence 'one meristem' cannot be taken literally. It can be easily demonstrated in unbranched trees that have dormant but functional lateral buds (e.g. the easily available papaya, *Carica papaya,* or cassava, *Manihot esculenta*) that stem injury results in the activation of dormant buds below the point of injury. Such trees can be cut down and restarted from coppice shoots, and such new shoots replicate the performance of the original shoot.

In an unbranched tree, the height of the trunk is indeterminate, because the boundary between the crown and the trunk is a moving boundary defined by leaf-abscission. This boundary moves up as leaves are shed. In some palms, the height of the trunk is determined by terminal flowering. This may be regarded as an exception to the rule.

In propagation, any bud from an unbranched tree, if it can be made to grow, may be expected to produce a whole tree, because there is only one kind of bud.

Apical dominance and the monomorphic tree

Some trees build a trunk by going through a prolonged unbranched phase. After a significant height has been achieved, a crown is formed by the outgrowth of lateral buds at the top of the shoot. These branches resemble the original shoot, and they remain unbranched for some time before they branch again. Good examples are mahogany and *Hevea* rubber. Other examples abound in the families Anacardiaceae, Burseraceae, Leguminosae, Meliaceae, Sapindaceae, Simaroubaceae, Verbenaceae, etc., which are characterised by large or compound leaves. We might surmise that in these trees, the role of apical dominance is to establish the singular trunk, and the internal relaxation of apical dominance results in the development of a multi-stemmed crown.

The branched monomorphic tree corresponds to "trees with modular construction" in Halle *et al.* The branches of a monomorphic tree are similar to the original stem, which becomes the trunk. Since the branches resemble the trunk and there is no differentiation between the two, the shoot system is monomorphic, i.e. there is only one form of shoot.

In a monomorphic tree, the height of the trunk is fixed by the point at which branching first occurs.

In propagation, any bud from a branched monomorphic tree may be expected to produce a whole tree, because there is only one kind of bud.

Apical dominance and the dimorphic tree

The dimorphic tree begins as an unbranched seedling, after which, branching occurs regularly. Such branching may occur at every node, or intermittently to form tiers of branches, or in a diffuse manner up the trunk. Trunk singularity is established by the *shedding of branches.* The branches of a dimorphic tree are reminiscent of the large leaves of an unbranched tree such as a palm or a papaya. In *Anthocephalus* (Figure 5), *Diospyros, Duabanga, Hopea* and *Garcinia,* the branch systems are applanate and hence their physical resemblance to compound leaves is quite close. *Terminalia catappa* is also a dimorphic tree, but it takes more imagination to see the relationship between the branch system of a *Terminalia* and a compound leaf.

The dimorphic tree corresponds to "trees with trunk-branch differentiation" in Halle *et al.* The differentiation of the shoot system into a vertical permanent trunk and lateral ephemeral branches constitutes a clear case of shoot dimorphism. When such trees are young, we refer to the juvenile trunk as the leader shoot. The leader shoot is erect (orthotropic) while the branches are non-erect (plagiotropic), but the essential difference is that a branch has limited secondary thickening compared to the leader shoot.

In a dimorphic tree, the boundary between the crown and the trunk is a moving boundary defined by branch abscission. Since this boundary moves up as branches are shed, the trunk height is indeterminate. Eventually height growth does come to an end and growth activity is concentrated in the topmost branches, which grow longer and thicker, but eventually drooping under their own weight.

If the apical bud of a dimorphic tree is damaged, a dormant bud on the trunk, below the wound, is stimulated to grow into a replacement leader shoot. The branches continue as branches.

The significance of two different kinds of lateral buds: buds which are dormant until stimulated to grow, and buds which grow without passing through a period of dormancy, was highlighted by Tomlinson and Gill (1973). The former are called 'proleptic' buds and the latter 'sylleptic'. In my experience, proleptic buds, if activated, grow into leader shoots while sylleptic buds give rise to branches. Apical dominance takes on a new meaning in dimorphic trees: (a) it controls the development of proleptic buds, and simultaneously (b) it limits secondary thickening in the (sylleptic) branches so that such branches can get shed.

In the family Dipterocarpaceae, and especially in the genera *Shorea, Dryobalanops, Anisoptera* and *Hopea,* all axillary buds are sylleptic, which means that a branch grows out from every node, but alongside each axillary bud is a practically invisible dormant bud. These proleptic buds belong to a bud system which I have called an *accessory* bud system (Ng 1976, Ng 1981) to differentiate it from the axillary bud system. The word was borrowed from Jacobs (1955) who had earlier found a similar system in *Eucalyptus.* In Halle *et al.*, accessory buds are called 'supernumerary' buds.

The discovery of the accessory bud system in the family Dipterocarpaceae was made in experiments involving the removal of the apical bud of the leader shoots of *Shorea* saplings. (It should be noted that the species I worked on actually belong to the next group, *metamorphosed trees,* but metamorphosed trees pass through a dimorphic crown phase in which they behave like dimorphic trees.) I found that branch shoots had no ability to become leaders. Replacement leaders could only arise from the accessory buds. Since then I have checked the behaviour of dimorphic crowns of many other families of trees and found this to be the general rule. The only exception I know of is *Symintonia populnea* (Hammamelidaceae) (Ng 1979) in which, if the leader apex is damaged, an upper branch assumes an erect position and takes over as the new leader.

Apical dominance and the metamorphosed tree

In the family Dipterocarpaceae, which is the dominant timber family of Southeast Asian forests, the trees that eventually form the canopy of the high forest pass through three stages of crown development. First is the unbranched phase found only among seedlings. Then comes a dimorphic phase similar to that described above for dimorphic trees. This is followed by the final crown phase in which the branches are not shed (Figure 6) and the distinction between trunk and branches is lost. I will refer to these co-equal stems as 'limbs'. If limbs break, they leave large stubs behind. The change from a dimorphic crown, in which the trunk is differentiated from the branches, to the final crown in which all the limbs are co-equal, was given the name 'metamorphosis' by Halle and Ng in 1981.

There is an intermediate zone in which the change takes place. In the lower part of this zone, some branches get thickened and become limbs, while others are shed. Branches that receive more light are more likely to be retained as limbs, and a good indicator that a branch is about to become a limb is when its distal parts turn upwards, marking a change from plagiotropic to orthotropic growth.

The metamorphosed tree is the commonest type among big trees, and it is not restricted to the tropics nor to dicots. I have seen it in species and locations as far apart as *Eucalyptus regnans* in Tasmania and *Pinus sylvestris* (Figure 7) in Sweden. In the Mediterranean region, the stone pine, *Pinus pinea*, is better known for its metamorphosed umbrella-crown than for its pre-metamorphosed dimorphic 'Christmas tree' crown phase. Lanner (1989) concluded that loss or weakening of apical dominance in the stone pine is responsible for the development of the umbrella crown. I agree. He thought this crown shape may be an adaptation for dispersal by birds of the large near-wingless seeds. This latter hypothesis is not true for all metamorphosed trees, because metamorphosed trees occur in practically all families of big trees and their fruits and seeds are dispersed in every possible way, from *Koompassia excelsa* (Figures 8 & 9) with light, winged fruits, to durians (*Durio zibethinus*), with fruits that drop heavily to the ground.

The metamorphosed tree was not described in Halle *et al.* Its recognition came three years later (Halle & Ng 1981).

The loss of control over secondary thickening of the branches in the metamorphosed crown fixes the upper limit of trunk development. This loss of control appears to be the main reason why in clonal propagation, buds from such crowns, even if they produce erect trunk-like leaders, have difficulty shedding their branches. If the branches are not shed, the erect central stem cannot be considered to be a proper trunk.

Apical dominance and the plagiotropic tree

I use the term 'plagiotropic trees' for those trees in which the leader shoot and all the branches terminate in plagiotropic buds. Such buds are oriented sideways, and the shoots they produce are bilaterally symmetrical, i.e. their leaves and lateral buds are arranged left and right along the stem. The leader shoot becomes erect through a process of self-straightening or 'secondary erection' (Halle *et al.*) at some distance behind the terminal bud (Figure 10). Branches are those stems that do not undergo secondary erection. There seems to be no other difference between a branch and a leader. Examples of plagiotropic trees include the temperate beech, *Fagus sylvatica* and numerous tropical examples such as *Mezzetia* (Annonaceae), *Muntingia* (Tiliaceae), *Pterocarpus* (Leguminosae), *Wrightia* (Apocynaceae) and *Xanthophyllum* (Polygalaceae).

The plagiotropic tree corresponds to "trees with changes in orientation of axes" in Halle *et al.* The leader or trunk may be built up by the continuing process of secondary erection along one stem axis, or by adding up the erect parts of a succession of shoots to make a composite stem axis.

The limit of trunk development appears to be fixed by the cessation of secondary erection. After this, the distinction between trunk and branches is lost, resulting in a crown of co-equal plagiotropic limbs. Branches below this level are shed.

In vegetative propagation, any bud of a plagiotropic tree seems able to produce a plagiotropic tree, because there is only one kind of bud. A well-known example of a plagiotropic tree that is propagated almost exclusively by vegetative means (stem cuttings) is *Pterocarpus indicus*, and such trees grow just as vigorously, if not more vigorously than seedlings. It would appear that secondary erection capability in the branch of a plagiotropic tree is not lost but merely kept dormant until a bud is isolated and enabled to develop into an independent tree.

What are branches?

In a general sense, a branch shoot is any shoot that grows out from a pre-existing shoot. However, it is worthwhile, for analytical purposes, to think of branches in a more restricted sense, as throw-away shoots which are going to be shed. Stems that are not shed are trunks, forks (replicates of the trunk) or limbs (co-equal members of the crown). A branch so defined is like an organ of limited growth, somewhat like a leaf, but with a longer life span and more autonomy to compete ('forage') for light. Under this restricted definition, branches exist only in dimorphic trees and in the dimorphic crown phase of metamorphosed trees. Cuttings made from such branches normally grow into plants with the form of branches rather than leaders.

Greenwood (1995) has concluded that in vegetative propagation, a bud will behave according to the kind of shoot it is taken from. However, in recent (unpublished) grafting experiments on *Garcinia* and *Pachira*, I found that if I replace the apex of a leader shoot with the apex of a branch, the branch apex in its new position acts as a leader shoot. These experiments indicate that buds in dimorphic crowns may not be as rigidly pre-programmed as often thought.

The restoration of leader-shoot singularity

Tropical rain forests are characterised by the abundance of erect stems, ranging from saplings to poles to immense columnar trunks. Close examination of saplings and poles of dicot trees, in which the scars of interrupted growth can still be detected, reveals that there are practically no cases in which a trunk has developed from the uninterrupted growth of a single apical bud. Instead, the scars on the young trunk indicate that the apical bud is lost periodically (due to breakage from falling branches, grazing by animals, or dieback by various causes), yet a continuous trunk is developed, by a succession of replacement buds.

As the leader shoot grows and thickens into a trunk, any unused dormant buds, including accessory buds if any, remain embedded in the bark (Fink 1983). Such buds may be called into service to produce coppice shoots when the tree trunk topples over or is cut. Coppice shoots are typically leader shoots, not branches. The coppice shoots described by Tolkamp (1996), arising from the stumps of felled 6-y-old *Shorea* trees undoubtedly originate from accessory rather than axillary buds because there are no unused dormant axillary buds in *Shorea*. The coppice system used in Brazil for propagation of *Eucalyptus* by cuttings seems also to be based on the stimulation of accessory buds.

Whenever several leader shoots are stimulated to grow, one shoot soon dominates and the others die. The shoot that prevails is the most vigorous one [as reported in e.g. *Eucalyptus pilularis* by Curtin and King (1979)] or the uppermost one [e.g. *Triplochiton scleroxylon* by Leakey and Longman (1986)]. If for some reason the reduction of competing leaders fails to work, the tree becomes permanently forked. This happens in *Nauclea diderrichii*, a tree with opposite (paired) leaves and therefore paired axillary buds (Leakey 1990). However, my impression is that forking is very uncommon even among trees with opposite leaves.

Restoration of leader shoot singularity or *suppression of subordinate shoots* is one of the themes attributed to apical dominance. This mechanism is obviously indispensable for trunk building.

Juvenility, maturity, and rejuvenation

In general, living organisms pass through a non-reproductive phase before they become reproductive. The onset of reproduction provides the basis for dividing the life cycle of such organisms into a juvenile versus a mature phase. In annual plants, and some trees (e.g. *Corypha*), such a division exists, but in the majority of trees, the onset of reproduction does not signal the end of vegetative growth. On the contrary, vegetative growth continues and reproduction becomes a series of repeated events within the continued vegetative development of the tree. However, trees grow through changes in vegetative expression and references to juvenility and maturity in trees are usually made in relation to such changes, which include changes in leaf shape, slowing down of vegetative growth, loss of rooting ability of cuttings, and increased plagiotropy of shoots. The various rates of change are not correlated with each other and the observed changes are not highly generalisable (Borchert 1976, Hackett 1985). There has also been a misunderstanding of plagiotropy, which has been given an undeservedly bad reputation [e.g. Pierik's (1990) phrase 'the unpleasant phenomenon of plagiotropy']. Some reviewers (e.g. Bonga 1982) have assumed that trees get more plagiotropic as they mature and have linked this to loss of rooting ability. However, cuttings from plagiotropic trees are not more difficult to root than cuttings from other trees. Also, in comparisons between orthotropic and plagiotropic shoots from the same dimorphic crowns, the plagiotropic shoots are not less able to root than the orthotropic shoots. There is also no evidence from tree architecture that plagiotropy increases as trees mature. The biggest change in the form of a big timber tree as it matures is the change from the dimorphic to metamorphosed crown phases, and this change does not involve increased plagiotropy. Quite the reverse! The lower limbs of a metamorphosed crown are often branches that have turned upwards, displaying increased orthotropy.

From the perspective of tree architecture, the most mature crown form is the metamorphosed crown form, characterised by the decline and loss of trunk-forming ability.

Halle *et al.* promoted the concept of reiteration, which may be regarded as an expression of rejuvenation. They defined a reiteration as a shoot that repeats the model of a tree. All trees can be reduced to one super-model, the trunk-forming super-model, and a reiteration is any shoot, apart from the trunk, that has the potential to form a trunk. This covers all examples of reiterations: coppice shoots, replacement leader shoots, and shoots that spontaneously change from lateral to erect growth behaviour. A reiteration may be considered equivalent to a seedling in so far as ability to form a trunk is concerned.

The development of wood

There are examples of plants which cannot grow into a trees in spite of having the architecture of a tree. One well-known example is *Phyllanthus niruri*, which is distinctly dimorphic, with a single leader, clearly defined branches, and a system of accessory buds. Yet this plant rarely can attain 30cm in height before it topples over. The causal factor appears to be the inability to develop and accumulate wood and thereby to maintain a rigid trunk.

The accumulation of wood is dependent upon two processes. One is the development of secondary thickening and the other is the maintenance of the wood that is produced. The process of secondary thickening is well understood and is adequately described in textbooks on plant anatomy. *Phyllanthus niruri* is unable to grow erect because of the absence of secondary thickening.

The processes of maintenance of wood in the living tree are not so well known, and will be elaborated upon here, because wood is the main economic product of trees.

In 1976, Janzen commented that a tree does not need to have a solid trunk of wood. All it needs is a living peripheral layer of wood for transportation of water. The wood at its core could be allowed to rot and provide a site for animal nests, defecation, and microbial metabolism, that would supply nutrients to the tree. Why have a solid trunk when a hollow trunk would be better? We do not have an answer. Most trees are solid rather than hollow and this suggests that there are advantages in being solid.

Basically, there are three ways in which trees deal with wood in excess of the peripheral sheath of wood needed for transportation of water (Ng 1986):

By conversion of the core wood to dead 'heartwood' loaded with chemicals that act as preservatives. The durability of timber is related to the durability of such preservatives. When the chemicals are broken down and leached out, the wood will be susceptible to rot. The most durable timbers in the world belong to this class. In Malaysia, the premier timber in this class is *Neobalanocarpus heimii* (chengal), the wood of which has been shown to last about 100 years. Characteristically the large chengal logs that are exploited from natural forests are hollow, indicating that such trees are old and slow-growing, and certainly more than 100 years old since the core has had enough time to become susceptible to rot.

By the maintenance of all the wood as living tissue. The proof of this remarkable phenomenon was established with *Dyera costulata* (Figures 11 & 12), one of the largest trees in Malaysian forests [2.5 m in diameter recorded by Setten (1956); 62.5 m tall recorded by Vincent (1963)]. This species has white latex in all living parts of the tree, including the bark, leaves, flowers and roots. When trees are felled, latex oozes from the pith and the ray parenchyma running between the bark and the pith, i.e. across the entire woody trunk. The denaturation and hardening of exposed latex takes many hours. Latex has been shown to contain nuclei, mitochondria, endoplasmic reticulum and ribosomes, and is therefore a form of cytoplasm (Gomez & Moir 1979). Jelutong in the form of timber (dead wood) has practically no natural durability. Its very high starch content attracts fungi and insects. Yet the trunk of the living tree is always sound, from the bark to the pith. One does not see a hollow jelutong.

By doing neither. In such trees, the core will rot if fungi and insects can find a way in through the peripheral sheath of bark and living sapwood.

The production of wood and its role in the life of the tree is still highly mysterious. Wood anatomists have not filled in the gaps in knowledge because they have concentrated on the properties of timber, which is wood that is no longer living. Wood as living tissue has amazing properties. The cells of the pith and the rays, if alive, must be the longest-lived cells in the world.

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Figure 1. An 80-y-old 'plus' tree of teak, *Tectona grandis*, in Java, with a long clear trunk

Figure 2. Trees cloned from crown buds of teak 'plus' trees. Note that large branches (limbs) had to be pruned to artificially make short clear trunks.

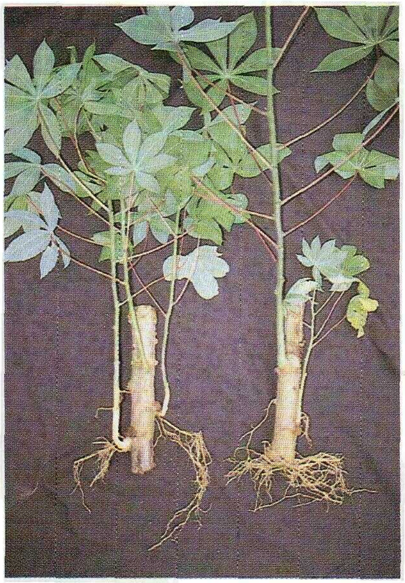

Figure 3. Polarity in stem cuttings of the cassava, *Manihot esculenta*. The cutting on the right was planted in the natural orientation: the distal (upper) bud/shoot dominates over the proximal (lower) one, and roots arise from the base of the cutting. The cutting on the left was planted upside down: the distal bud/shoot still dominates over the proximal, and roots emerge from near the bases of the new shoots.

Figure 4. Polarity in a stem cutting of the morning glory *Ipomoea congesta*, planted upside down: the distal bud develops while the proximal one remains dormant, and roots develop from near the base of the new shoot.

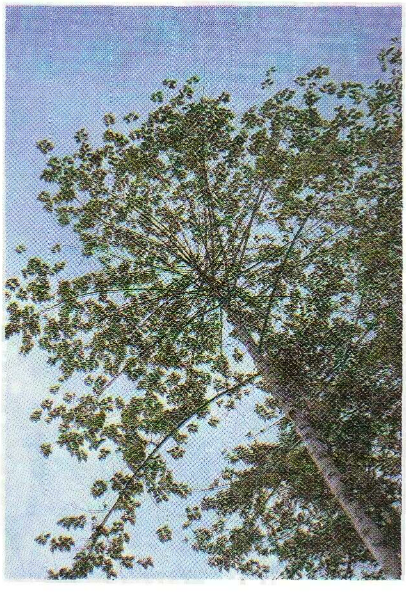

Figure 5. The dimorphic crown of *Anthocephalus* (*Neolamarckia*) *cadamba*. The branches are shed like compound leaves, and the trunk/crown boundary moves up as branches are shed.

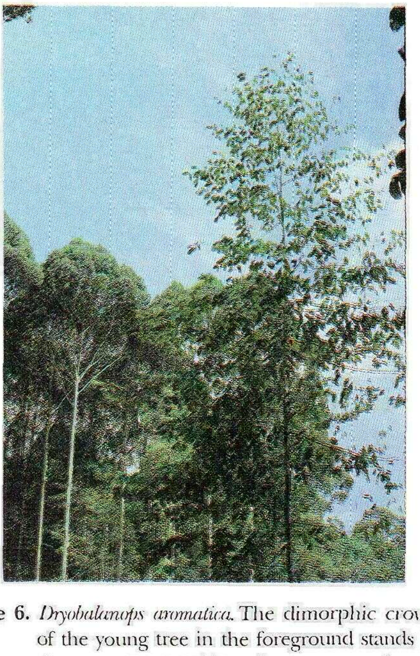

Figure 6. *Dryobalanops aromatica*. The dimorphic crown of the young tree in the foreground stands in sharp contrast against the metamorphosed trees in the background. The main differences are in branch angle, branch size, leaf arrangement, and most significantly, in branch shedding. The metamorphosed crown also breaks up into distinct crownlets. The trunk is clearly the product of the dimorphic crown phase, and its upper limit is fixed by the onset of metamorphosis.

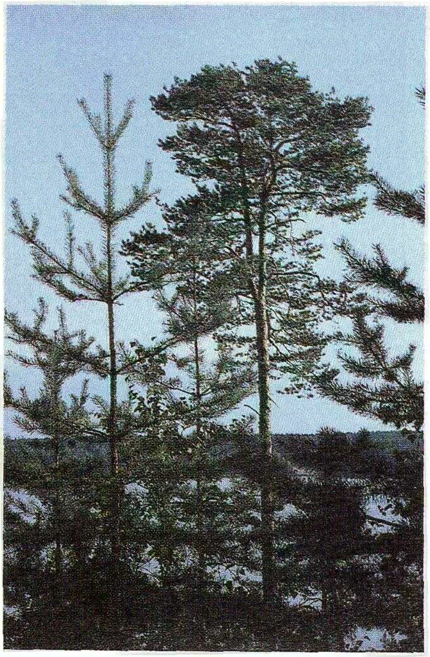

Figure 7. *Pinus sylvestris.* A metamorphosed tree stands out among the dimorphic crowns of younger trees.

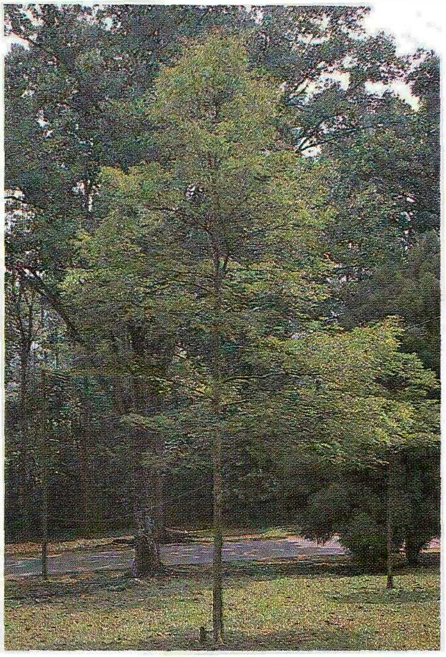

Figure 8. A young tree of *Koompassia excelsa*, with dimorphic crown

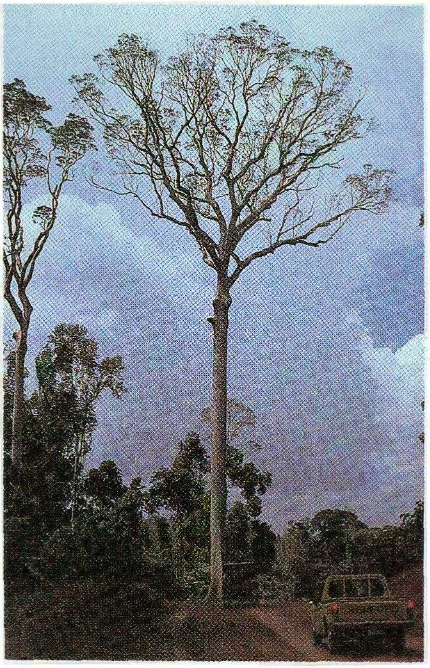

Figure 9. A metamorphosed tree of *Koompassia excelsa*, with limbs that are not shed but may be broken to leave large stubs

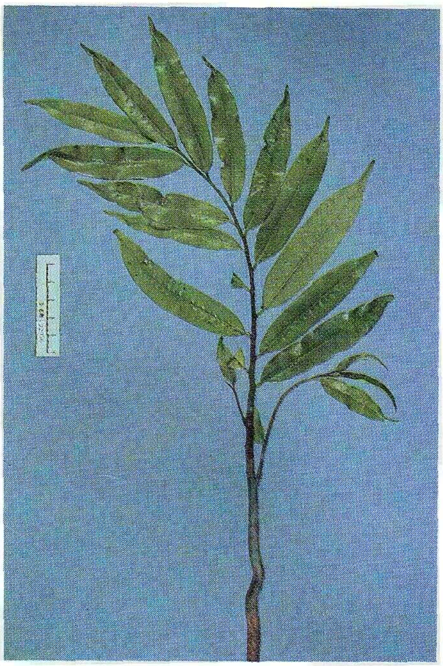

Figure 10. A seedling of the plagiotropic tree *Mezzetia leptopoda*, showing secondary erection behind the apical bud, which creates an upright leader stem

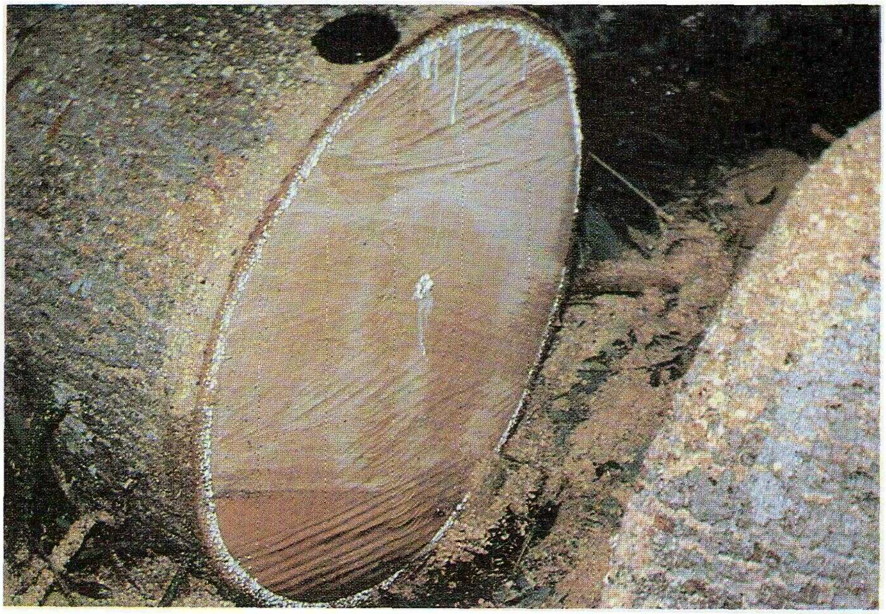

Figure 11. A trunk of *Dyera costulata*, transversely cut and oozing latex (a form of cytoplasm) from the bark and pith

Figure 12. A trunk of *Dyera costulata*, split radially, releasing latex from the ray parenchyma tissues