

- Ozenda P (1982) *Les Végétaux dans la Biosphère*. Paris: Doin.
- Tucker CJ, Dregne HE, and Newcomb WW (1991) Expansion and contraction of the Sahara Desert between 1980 and 1990. *Science* 253: 299–301.
- Tyree MT and Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology* 40: 19–38.
- Walter H (1977) *Vegetationszonen und Klima*. Stuttgart, Germany: Ulmer.
- Whittaker RH (1975) *Communities and Ecosystems*. London: Collier Macmillan.

Physiology of Vegetative Reproduction

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Introduction

Vegetative regeneration is both a natural process and an artificial process. The artificial process is used by agriculturalists, horticulturalists, and foresters to capture and multiply individual genotypes, and so to produce cultivars and clones. Clonal approaches to forestry and horticulture have a history going back more than 800 and 3000 years respectively, originating in China. Typically the process is used to develop superior planting stock, although there are also many applications in research where clonal uniformity is a powerful tool in the separation of genetic effects from physiological and environmental impacts on growth processes in plants.

The level of understanding about vegetative regeneration using stem cuttings has progressed enormously since the 1970s, the period when clonal forestry was becoming a reality in Europe, USA, tropical Africa, and Latin America. Although the focus of this review is primarily on the physiology of rooting cuttings, some mention is also made of related issues in air-layering/marcotting, grafting/budding, and different *in vitro* propagation methods.

This contribution draws heavily on studies done with *Triplochiton scleroxylon*, a tropical hardwood of West Africa, because of the large number of relatively comparable experiments done using a similar type of material (single-node leafy cuttings) under similar environmental conditions, to seek some physiological principles of wider relevance. In addition, the review offers some suggestions on how future research should be implemented to enhance

the identification of underlying physiological principles determining successful rooting of stem cuttings. The problem that needs to be overcome is the high level of interaction between the large number of factors pre-severance, post-severance, and in the propagation environment.

Rooting Stem Cuttings

Stem cuttings can come in many forms but the two major groups are leafy softwood cuttings from relatively un-lignified, young shoots (**Figure 1**), and leafless hardwood cuttings from older and more lignified shoots which typically have already shed their leaves due to the onset of winter or a dry season. It is important to understand that the factors determining the rooting of these two types of cuttings are very different: leafy cuttings depend on current photosynthates produced in the propagation bed, while hardwood cuttings depend on the hydrolysis and availability of carbohydrates stored within the stem tissues.

When trying to root leafy stem cuttings, there are four stages when a good physiological understanding of the factors influencing rooting ability is necessary: (1) in the propagation environment; (2) post-severance; (3) in cutting origin and environment; and (4) in the pre-severance stockplant environment.

The Propagation Environment

The most important aspect of the propagation environment is that it encourages physiological activity (photosynthesis and transpiration) in the leaf to minimize the physiological stresses experienced by the tissues, from transpiration and respiration, and encourages meristematic activity (mitosis and cell differentiation) in the stem. The transport of assimilates and nutrients from the leaf to the base of the stem, and of water from the base of the stem to the leaf, are also important. Recent physiological measurements confirm general experience that the duration of physiological shock arising from severing a cutting from its stockplant and inserting it in a propagator can be minimized by controlling the propagation environment. Minimizing this shock enhances rooting.

There are many different types of propagation systems for stem cuttings, but the most common are: (1) fogging systems; (2) intermittent mist (**Figure 2**), controlled by a range of different sensors; and (3) airtight, watertight, high-humidity, nonmist propagators (**Figure 3**). These are all very effective, but vary in their cost and sophistication. The nonmist



Figure 1 A rooted cutting of *Milicia excelsa*.



Figure 2 A typical mist propagator.

propagators have the advantage of being very low cost and simple and so are highly suitable for use in developing country or rural situations where electricity and piped water are not available. The basic

principles behind all these systems are that the cuttings are well supplied with water at the cutting base while the leaves are in a cool, shady environment with low vapor pressure deficit (VPD) to



Figure 3 A nonmist propagator – a watertight, airtight box when the lid is closed. Inset: cross-section of the propagation medium showing layers of saturated gravel and unsaturated but moist rooting medium.

minimize water stress. Moist leaves also keep the cuttings cool due to the evaporation of water from the leaf surfaces. While shading is beneficial, leafy cuttings need enough light to photosynthesize. Interestingly, the highest values of photosynthesis in severed cuttings have been found at relatively low levels of irradiance.

Comparative studies between different propagation systems for cuttings (e.g., mist and nonmist) found that nonmist propagators provided as good an environment for rooting as mist, if not better. Under mist, air and leaf temperatures and VPD were consistently higher than under nonmist systems. There were also differences in the frequency of peaks in VPD associated with peaks in irradiance. Peaks of VPD can also occur as a result of misting frequency, and its spatial distribution on the propagation bed. In a second study, using cuttings of four tropical trees (two from the moist tropics and two from the dry tropics), significant water deficits did sometimes develop in the leaves of the cuttings under both systems. The patterns of variation in relative water content (RWC) were similar to those of water potential and stomatal conductance. Interestingly, the species differences in RWC and stomatal conductance seemed to be more closely related to leaf morphology than to their environment of origin.

Leaf morphology may also account for differences between the four species in optimum leaf areas, indicating the need to report full details of as many of the long list of morphological and physiological pre- and postseverance factors affecting rooting as possible if a good understanding of the vegetative propagation process is to be achieved.

Few studies have been done on the effects of the light environment on photosynthesis during propagation because of the difficulty of measuring gas exchange in cuttings with wet leaves; however, the use of a nonmist propagator has allowed measurements on the rates of photosynthesis, stomatal conductance, and chlorophyll fluorescence ratio to be made on cuttings with and without shade. A study on *Cordia alliodora* confirmed that photosynthesis does occur in severed cuttings in the propagation bed. Photosynthetic efficiency under two levels of irradiance (24–53 and 106–159 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was found to be more closely related to rooting ability than photosynthetic rate, the latter being greatest at the higher irradiance, while rooting ability was either unaffected or reduced by irradiance, depending on the cutting's leaf area and presumably the balance between photosynthesis and transpiration. The number of roots produced was, however, closely related to photosynthetic rate. Further work is required to

look at the interactions between propagation light environments and pre- and postseverance factors. The composition of the rooting medium, usually open compost or fine gravel, is often critical for rooting and can vary between species, and cultivars/clones. In addition to holding the cutting firm, it has to provide moisture and allow respiration from the tissues. Anoxia at the cutting base usually encourages rotting, so the gas-filled pore space (air-to-water ratio) of the medium needs to be optimized by the use of various-sized particles (sand and gravel) and a water-holding medium (perlite, peat, or other organic products). The oxygen diffusion rate also needs to be adequate for respiration. In *Milicia excelsa* the moisture content of the medium was positively related to the numbers of roots formed and negatively related to mortality and leaf abscission.

In temperate environments propagation beds, especially those for leafless hardwood cuttings, typically have some bottom-heat provided by heating pipes or cables to promote meristematic activity at the cutting base, while the leaves remain cool. Sprouting by cuttings in the propagation bed often has negative impacts on rooting, presumably by creating a competing sink for assimilates. Consequently a lower air temperature than bed temperature can be advantageous. This differential, although more difficult to achieve, can also be important in the tropics.

For successful rooting, cuttings have to have a positive carbon balance (i.e., producing assimilates faster than they are losing them through respiration). However, very little is known about the overall respiration rates of cuttings under different environmental conditions, or about the ways in which cutting origin, leaf area, and stem length/diameter affect respiration losses. This has, however, been investigated using an oxygen electrode to measure respiration in leafy, single-node cuttings of *Prosopis juliflora*. It was found that respiration rate per gram of dry matter decreased linearly down a shoot, as stem diameter increased. This can be attributed to an increase in nonrespiring lignified tissues, although the greater mass of cuttings with larger diameters more than compensated for these losses and the larger cuttings had a greater overall rate of respiration. Perhaps more importantly, however, the respiration rate of the cutting base (1-cm-long section) was greater than that of the stem above it. This, it has been suggested, provides a concentration gradient which drives assimilate transport basipetally to the cutting base and is a key factor in the rooting process.

Postseverance Treatments

There is probably a larger body of literature on the effects of postseverance treatments than on any other

aspect of rooting cuttings. One characteristic of this literature is the apparent lack of consistent results between, and even within, species. This lack of any clear principles defining the rooting process has led to a plethora of papers reporting apparently situation-specific results, rather than to enhanced understanding. To reverse this process it is important to seek the factors that create the variability in responses to different treatments and factors affecting rooting ability.

Probably the most important of the postseverance factors are the application of auxins, leaf area, and cutting length/diameter. Consequently, to develop a practical rooting protocol for leafy stem cuttings of a previously unstudied species, it is first desirable to determine experimentally the optimal auxin application, optimal leaf area, and optimal cutting length and, if possible, to investigate experimentally their interactions within each propagation environment.

Auxin applications The application of root-promoting growth-regulatory substances (auxins) is the most common treatment to enhance rooting in stem cuttings. It is also probably the single most effective treatment to achieve successful propagation. In addition to effects on cell differentiation, auxins promote starch hydrolysis and the mobilization of sugars and nutrients to the cutting base, although increasing auxin concentrations does not result in respective increases in cutting dry mass. However, behind this apparently 'cure-all' treatment there lies a considerable body of evidence showing that auxin applications are interactive with other treatments, types of material, and the environmental variables affecting the rooting capacity of cuttings. This high degree of interaction is probably the reason why the literature is full of apparently contradictory statements about the precise physiological role of auxins in the rooting process, a situation that cannot be resolved when authors do not present definitive information about either the physiological condition of their material or the propagation environment used.

Typically cuttings treated with auxins root more rapidly and produce more roots, usually with a higher percentage of cuttings rooted. Usually, indole-3-butyric acid (IBA) is found to be the most effective root-promoting auxin, but occasionally α -naphthalene acetic acid (NAA) can be as effective, as in *Parkia biglobosa*. However, tree species and even clones can appear to respond differently to individual and mixed applications of auxin at differing concentrations, even when many other factors are constant. Interestingly, however, clones of *T. scleroxylon*, which appeared to have different dose-response curves, all rooted equally well at 40 μ g auxin per cutting.

Leaf area Usually the rooting of softwood cuttings is dependent on the presence of a leaf, and indeed in the physiological processes of this leaf. Cuttings without a leaf very quickly become moribund, while the most common reason for these cuttings failing to root is the death of the leaf due to rotting, necrosis, bleaching, or leaf abscission. All these causes of failure are due to either the use of inappropriate tissues (too old (senescent), photosynthetically inactive (below compensation point; water-stressed; starch-filled), diseased, pest-infected), or to an undesirable rooting environment (too hot, too wet, too dry). The most common symptoms are leaf shedding, leaf rot, and stem rot.

Studies of the role of the leaf have indicated that rooting ability is maximized when the severed cutting is photosynthetically active and producing assimilates for the development and elongation of the root primordia, and when the leaf is not suffering water stress (Figure 4). Consequently, there often seems to be an optimum leaf area at which the balance between photosynthesis and transpiration is optimal. This varies between species and clones, depending on specific leaf area (leaf thickness), stomatal density, leaf morphology (waxiness, etc.) and the age of the leaf (node position). Optimizing the balance between photosynthesis and transpiration seems to be particularly important in difficult-to-root material, with easy-to-root species not being very sensitive to leaf area. Cuttings with a leaf that is too small rapidly decline in their carbohydrate (sugars and starch) contents, while those with an appropriate area increase in carbohydrate content (and hence dry matter), at least until the roots start to develop,

creating a sink for assimilates. One study has found that there is a relationship, which develops after severance, in cuttings with differing leaf areas, between rooting ability and the content of reflux-extracted soluble carbohydrates, which suggests that rooting is promoted by the production of specific sugars during the period that the cuttings are in the propagator. Cuttings with an overly large leaf suffer from transpiratory water loss and stress, and close their stomata, thereby limiting their capacity to photosynthesize, and often triggering leaf abscission. As mentioned earlier, leaf area is an important variable interacting with the level of irradiance in the propagation environment. Consequently, statements about the optimal leaf area for rooting have to be linked to statements about the specific propagation environment.

Despite the importance of current assimilates for rooting in leafy softwood cuttings, there is evidence that the level of dependency does vary between species, with some species also being able to utilize stored reserves in the same way as hardwood cuttings, perhaps reflecting differences in stem anatomy. In *Larix × eurolepis* cuttings, for example, a dual ^{13}C and ^{15}N labeling approach indicated that more than 80% of total carbon in the roots was newly assimilated carbon, while 20% was from stored reserves.

Cutting length Cuttings can either be cut to a constant length (in which case they will usually vary in the number of nodes present) or can be cut to the available internode length of a predetermined number of nodes (Figure 5). The decision about which



Figure 4 Using a 'pressure bomb' to assess the leaf water potential of *Triplochiton scleroxylon* cuttings.



Figure 5 Variation in length and diameter in single-node cuttings from a two-shoot stockplant of *Triplochiton scleroxylon*, arranged in node order from the shoot apex. Top shoot: nodes: 1–5; second shoot: nodes 1–4.

option to take will have big impacts on the rooting ability, as long cuttings usually root best. From the practical point of view, the number of cuttings rooted is maximized by using a constant length, close to the optimum. This has the additional advantage that all the cuttings will penetrate the rooting medium to the same depth and that the leaf will be held the same height above the medium. From the research point of view, however, much can be learnt about the sources of variation by using a fixed number of nodes and utilizing the pattern of variation in internode length found within a stem (Figure 5). In the latter case, it is important to remember that internode length varies sequentially down a stem and thus is not an independent variable.

Stockplant Factors: Cutting Origin and Environment

There are two major sources of variation in stockplants. These are attributable to: (1) within-shoot factors and (2) between-shoot factors, both of which are strongly influenced by the stockplant environment. Additionally, there are other endogenously controlled growth changes, such as recurrent flushing, which can affect rooting ability.

Within-shoot factors Within any shoot there are numerous gradients of variation associated with the chronological aging of shoots as they grow longer. For example, from the top to the bottom, there is a gradient in age that affects the leaf size, leaf water potential, leaf carbon balance, leaf senescence, inter-

node length, internode diameter, stem lignification, nutrient and stem carbohydrate content, and respiration. These gradients mean that no two cuttings are physiologically identical and, hence, no two cuttings have the same rooting capacity. Consequently, it is possible to use these gradients node by node as a diagnostic tool for how physiological factors affect rooting. For example, one of the unresolved issues that could be addressed is the importance of the relative concentrations of carbohydrates and nutrients in cutting tissues, which vary between node positions and over time. There is evidence of stored reserves being depleted early in the rooting process in *Larix* hybrid, and in *Khaya ivorensis*.

Comparing the typical with inverse relationships between cutting length and node position allows the study of within-shoot variation and has found that cutting length (in reality probably cutting volume) has a major influence on rooting ability. It seems that this may be due to the need for storage capacity for current assimilates until the new roots form a sink for these carbohydrates. The importance of this is supported by a negative relationship between leaf area and cutting length, suggesting that short cuttings cannot provide the storage capacity for assimilates coming from a large leaf.

Between-shoot factors Even in the simplest type of stockplant, a seedling that has been cut back once previously (Figure 6), there are considerable differences in rooting ability between the lateral shoots, with those from upper shoots being best. In *T. scleroxylon*, the percentage of cuttings rooted declines as

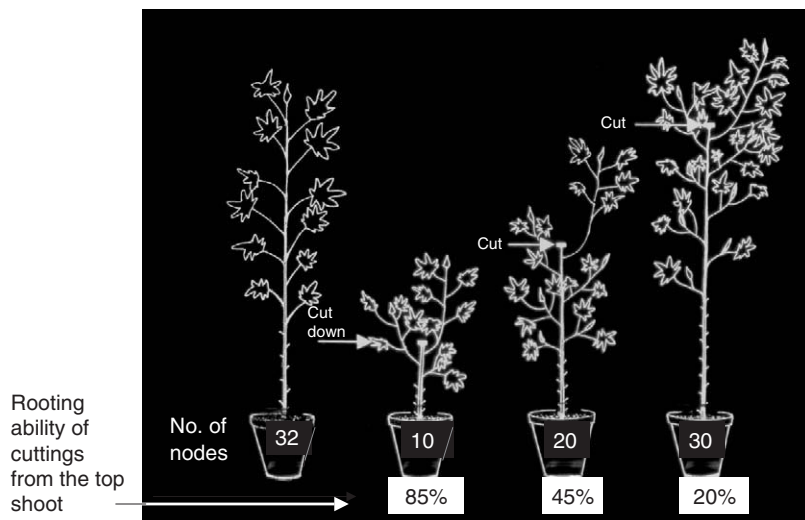


Figure 6 Effects of the number of shoots and stockplant height on rooting ability of *Triplochiton scleroxylon* cuttings from the top shoot. After Leakey RRB (1983) Stockplant factors affecting root initiation in cuttings of *Triplochiton scleroxylon* K. Schum., an indigenous hardwood of West Africa. *Journal of Horticultural Science* 58: 277–290.

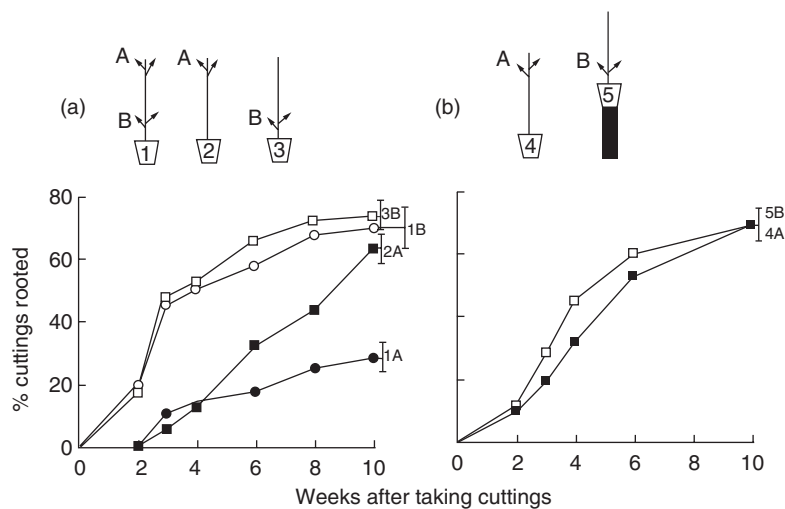


Figure 7 Effects of the number and position of shoots in stockplants of *Triplochiton scleroxylon*, relative to a light source. After Leakey RRB (1990) The domestication of tropical forest trees: a strategy for increased production and for conservation. In: Werner D and Müller P (eds) *Fast Growing Trees and Nitrogen Fixing Trees*, 1990 © Elsevier GmbH. Stuttgart, Germany: Gustav Fischer Verlag.

the height of the stockplant increases, there being a relationship between percentage rooting and the number of shoots per plant. The rooting ability of cuttings from lower shaded shoots can, however, be enhanced by the use of fertilizers, or by reorienting the stockplant (angled or horizontal) to alter the patterns of correlative inhibition. The rooting ability of cuttings from the upper shoots can be enhanced by removal of the lower shoots, implying that intershoot competition is a factor in determining rooting ability. Under situations of low but equal competition, basal shoots have a higher rooting ability than upper shoots. However, if basal and upper shoots are under

similar light environments, their rooting ability becomes very similar (Figure 7).

In more complex stockplants, cuttings from first-order lateral shoots of *Cryptomeria japonica* rooted better than those from second-order laterals, indicating the need for better physiological and morphological understanding of such structural variation.

Preseverance Stockplant Environment

As seen above, both nutrients and light have been confirmed to have major effects as preconditioning agents on rooting ability, a finding confirmed in

Albizia guachapele. When this was tested experimentally in *T. scleroxylon*, it was found that there are complex interactions between nutrients and the quantity and quality of light, which affected photosynthesis and the carbohydrate status of cuttings. Photoinhibition and high starch concentrations in cuttings appeared to inhibit rooting, while active photosynthesis was associated with good rooting. Both low irradiance and low red-to-far-red ratios independently enhanced rooting ability, but in many natural systems these characteristics of shade occur together and probably have additive benefits. The mechanisms for this enhancement seem to be both morphological and physiological; cuttings from shaded stockplants of *Eucalyptus grandis* have longer internodes, greater specific leaf area, greater codominance between shoots, lower rates of pre-severance net photosynthesis, lower chlorophyll concentration, but higher rates of net photosynthesis per unit of chlorophyll, and many other differences in gas exchange characters (Figure 8). These characteristics of pre-severance physiology and morphology subse-

quently enhanced the cuttings' post-severance physiological status and promoted high rooting ability.

In *T. scleroxylon*, analysis of deviance indicated that the effects of light quality on rooting were entirely attributable to increased internode length. The changes in these stockplant factors are largely attributable to changes in the physiological condition of the shoots and are often related to vigor; thus they can be seen as a component of physiological aging.

The effects of pre-severance light quality on rooting ability have now been demonstrated in a number of different taxa but, as expected, there are differences in stem and leaf morphology. Shoot etiolation under low irradiance and the pre-severance elimination of light from the area of the cutting base independently and additively enhance subsequent rooting ability, having histological effects on stem development and retarded sclereid development. There is also some evidence of etiolation on levels of rooting cofactors and sugar concentrations. This newer understanding of pre-severance factors is important as it involves easily overlooked differences in the ambient environment. This contrasts with the manipulative treatments like bark girdling, which have also been used to enhance rooting.



Figure 8 Using a portable gas analyzer to assess rates of pre-severance net photosynthesis and transpiration in stockplants of *Zizyphus mauritiana*.

Stockplant Management

The importance of all of the above stockplant factors clearly indicates the opportunity to enhance the rooting ability of cuttings through stockplant management (especially a combination of pruning, fertilizer use, and light management) to promote the appropriate morphological and physiological conditions of the shoots. Field trials in the tropics have indicated that using nitrogen-fixing species like *Leucaena leucocephala* to provide a shading canopy above a stockplant hedge can be very beneficial. Hedging approaches have been tested over long periods, and found to be robust with no loss of rooting ability with time, although rooting success is affected by the height of hedges and the types of shoots used.

Efforts to improve stockplant management in *Larix* have included the extension of the photoperiod with artificial illumination in the fall, but without success, and the use of cytokinins to promote the outgrowth of short shoots. In *T. scleroxylon*, however, the injection of auxins pre-severance was found to enhance rooting ability, with earlier injection dates enhancing the rooting ability of short cuttings.

Phase Change

The relative importance of ontogenetic and physiological aging is one aspect of the impact of stockplant

physiology relating to rooting ability that is unresolved. As trees grow they develop a gradient towards reproductive maturity (ontogenetic aging) and after a time reach a threshold above which the newly developing shoots have the capacity to fruit and flower, while those below the threshold are still juvenile (Figure 9). The transition from juvenility to the state of maturity is called phase change. There are large numbers of reports in the literature that cuttings from mature shoots are very much more difficult to root than those from juvenile (seedling or coppice) shoots and attributed this to phase change. Increasingly, however, there are reports of old mature trees being propagated by cuttings, with reasonable success, especially in the early spring. However, a good understanding of the reasons why mature trees are difficult has never been achieved.

The importance of physiological aging in the rooting of cuttings from mature trees is illustrated by recent unpublished data in *Prunus avium* (Figure 10), which indicate that by comparison with leafy juvenile shoot cuttings, the rooting capacity of mature softwood cuttings was limited by the availability of stored reserves, while mature hardwood cuttings were constrained by leaf abscission. Other evidence that the poor rooting ability of mature shoots can be

attributed to physiological aging rather than to ontogenetic aging is seen in the high rooting ability of ontogenetically mature and flowering plants formed when cuttings from mature tree crowns are successfully propagated and then used as stockplants (Figure 9). Although often plagiotropic, such plants have the vigor of juvenile seedlings and coppice shoots. To examine this experimentally within the crown of mature trees is difficult as it requires the formation of physiologically young shoots within an ontogenetically mature crown. This is not achieved by pollarding, but further research is needed to elucidate the relevance of phase change to rooting.

Observations of leaf shape and other morphological characters indicate gradients as trees grow older and these changes have been examined in detail, often using ivy (*Hedera helix*) as a model plant. This raises two questions: (1) are the changes in leaf shape relevant? (2) do we need to have a maturity factor, or are the conditions in mature cuttings just a severe case of the complex interactions arising from the sorts of stockplant variables examined above? Regarding leaf shape in ivy, there may be an error in the belief that the juvenile leaf form converts to the mature form as a result of ontogenetic aging, as the juvenile form is associated with the vine stems

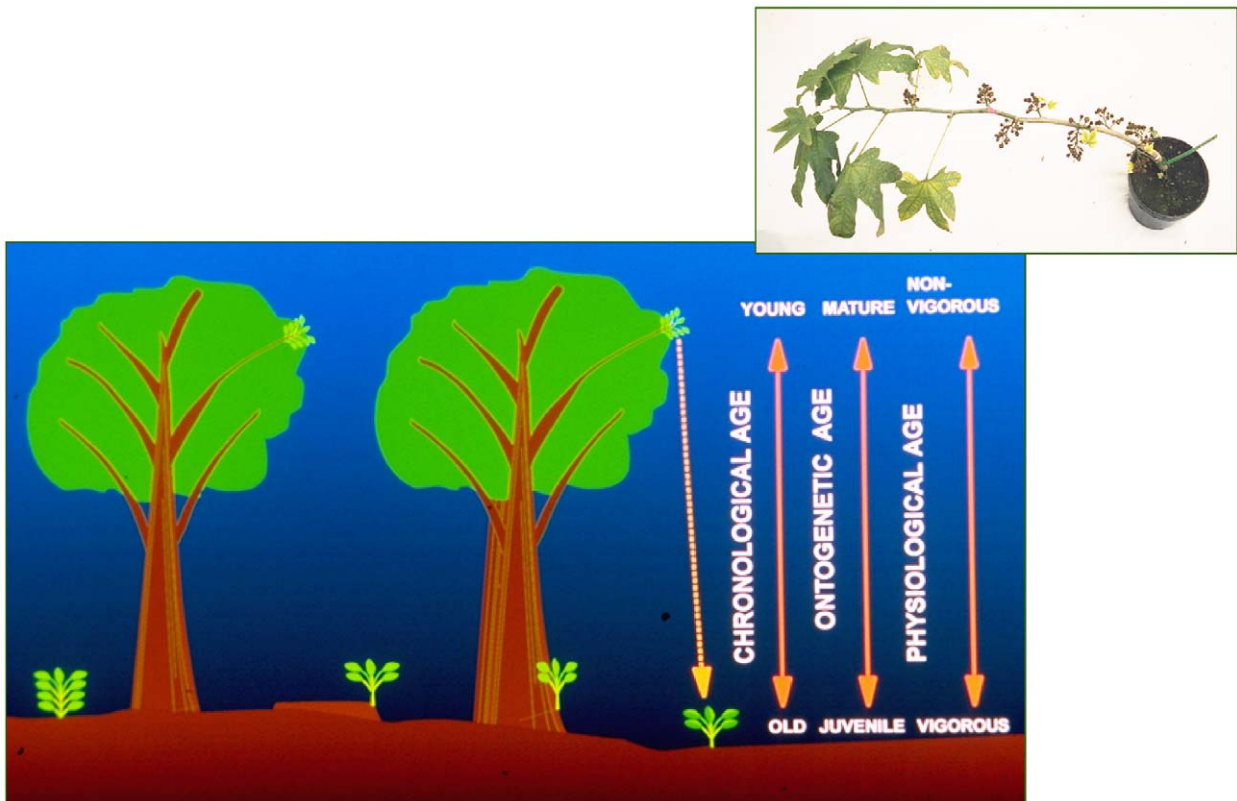


Figure 9 Gradients of aging and maturity in trees. Inset: an easily rooted mature cutting of *Triplochiton scleroxylon*, illustrating its plagiotropic habit and ability to flower.



Figure 10 Cherry (*Prunus avium*) cuttings from juvenile root suckers (1- and 2-year-old wood), young lateral softwood in a mature crown and terminal woody shortshoots in a mature crown.

(the mainstem) and the mature form is associated with free-standing branches, which happen to be where ivy, like many other woody plants, flowers. Different leaf arrangements and shapes in mainstems and branches are very common in woody plants. It is not clear therefore whether the reported differences in genetic material between these two tissue types is a result of ontogenetic phase change or to epigenetic differences between different tissues. In other species, there are changes in leaf morphology up the mainstem, as in *Acacia mangium*, in which the pinnate true leaf on seedlings changes to a mature phyllode. The unreliability of the phyllode as a marker of phase change was shown in a rooting trial from coppice stumps in which the rooting ability of cuttings with phyllodes was greater than that of cuttings with true leaves.

The felling and subsequent coppicing of mature trees are generally regarded as the best way to return to the juvenile state. However, while this was successful in *Milicia excelsa*, the rooting ability of cuttings from coppice shoots was still negatively correlated with the age of the stump. Similarly, in *Vochysia guatemalensis*, increasing stump diameter also had a negative effect on rooting, with larger

stumps producing more shoots, and intershoot competition perhaps reducing rooting success.

There are some anomalies in the phase change literature. For example, in *Picea mariana*, cuttings from flowering crowns of 9-year-old trees rooted better than those from nonflowering trees of the same age and origin, while in *Cunninghamia lanceolata*, burying mature shoots horizontally in the soil apparently results in new juvenile shoots.

This topic of how to propagate mature tissues is the major constraint to many tree improvement programs focusing on cultivar development through vegetative regeneration.

Genetic Variation in Rooting Ability

Experience has suggested that there are genetic differences between species, and even between provenances and clones within species, which result in differences in rooting ability, although more and more formerly unrootable species and clones are now being rooted relatively easily as understanding improves. This suggests that, as the within-clone factors affecting rooting ability are optimized, the apparently innate genetic differences in rooting ability are actually attributable to genetic differences in the morphological and physiological factors that govern rooting ability. This view is supported by the use of stepwise regression to analyze data from rooting experiments, which commonly finds that the factors explaining much of the variance are cutting length, leaf abscission, and leaf area, and that the genetic differences between clones explain relatively little of the variance. This conclusion is in contrast to some recent studies, which have sought to detect quantitative trait loci affecting vegetative propagation. No very clear evidence has been found to indicate that there is genetic control of rooting ability *per se*. Some trees, like many herbaceous weeds, do regenerate vegetatively naturally (e.g., from root suckers), but it is difficult to see in evolutionary terms why there would be a genetic trait for rooting ability in detached shoots of trees.

Failure to Root

To learn more about the processes affecting rooting, there is also a need to pay much more attention to the causes of rooting failure. Some cuttings, as stated earlier, display different symptoms of death from leaf abscission to different patterns of rooting, which can be attributed to water stress, photoinhibition, anoxia, and negative carbon balance. Other cuttings neither die nor root. More information needs to be collected on all these responses to attempted propagation.

Integration by Modeling

The complexity of the rooting process in leafy stem cuttings alone makes it a very appropriate subject for modeling. Based on the *T. scleroxylon* data set, a mechanistic model of carbohydrate dynamics during the rooting process provides a framework for many of the other factors discussed above to be examined and compared with research results. Hopefully in future it will be possible to use this and other models to test differences in experimental methods and materials and so interpret the often contradictory experimental results.

Apparent Absence of Principles Determining Rooting Success

Recording Materials and Methods

On top of the highly interactive nature of the multitude of factors influencing the physiological condition of cuttings, there is an overarching methodological issue that needs to be resolved. Typically, people taking cuttings do not collect their cuttings in the same way, and more importantly, do not report what they have done precisely. Because of the impacts of all the interactive processes discussed above, two people propagating the same species under relatively similar conditions can obtain results that appear to be contradictory, while in fact their results are expressions of the different physiological and morphological condition of the tissues being propagated. Researchers need to address these deficiencies in their techniques and to address the

impacts of all the variables experimentally before we can expect to understand fully the fundamental physiological principles determining the success of vegetative propagation.

Percentage Rooting – A Poor Measure of Success

To make matters worse, almost all research papers use the percentage of cuttings rooted as the prime measure of rooting success. Taking a simple example, even if auxin application, leaf area, and rooting environment are all optimized, when all the available cuttings are collected from a managed juvenile stockplant (Figure 11a), they are likely to have a fairly low rooting percentage and hence create a relatively low number of new plants. This is because of the inclusion of all of the inherent variations in cutting size and shoot position. If, on the other hand, the same people go to an identical plant and, because they know more about the species they are propagating and are aware that cuttings from the top two shoots are likely to have the greatest capacity to root (Figure 11b), restrict their collection to these shoots (so maximizing the use of their time and resources), they will root the same number of cuttings, but can claim an improved rooting percentage. In a third situation, where they have more understanding of stockplant management, and grow their stockplants under the shade of other plants and provide nutrients, the stockplant has greater codominance between shoots and produces more material to harvest. In this case, the shoots are morphologically and physiologically in a better condition to root well (Figure 11c). Consequently, more cuttings can be

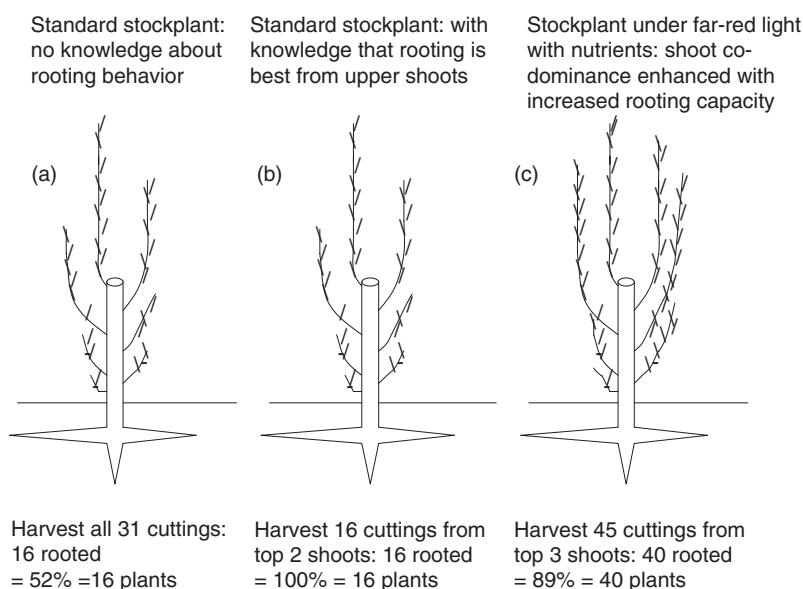


Figure 11 Diagram showing how percentage rooting varies in optimally treated cuttings, depending on which cuttings are used and on how the stockplant is managed (leaves omitted for clarity).

collected, and a third shoot can be included, resulting in a much larger number of cuttings rooted, but the percentage rooting may be lower than that in **Figure 11b**. Which of these results is of greatest practical value, and how well does the measure of percentage cuttings rooted represent the overall rooting capacity of the cuttings collected? Clearly, if the understanding of vegetative propagation is to advance, we have to be more rigorous in describing the source of our cuttings, and we have to improve the way we quantify rooting capacity.

Many authors do use additional measures of rooting success; for example, the number of roots per cutting, the mean or total length of roots produced, the mass of roots produced, and graphs often show differences in the rate of rooting. Interestingly, these measures of success are often unrelated to rooting percentage, and it is probably only when these different measures are well correlated that there is a good measure of rooting ability. These methods of quantifying rooting ability and their relationships require further research.

Other Propagation Systems

Grafting/budding, marcotting (**Figure 12**), root cuttings, and *in vitro* culture (**Figure 13**) are all systems that are used to multiply ontogenetically mature shoots that are very difficult to propagate by cuttings. This is especially important for the propagation of fruit trees or selected phenotypes in a forest

tree seed orchard where ontogenetic maturity has to be retained.

In contrast with *in vitro* systems there have been relatively few major advances in grafting and marcotting in recent years, although they are still widely applied. Nevertheless, there is a need for improvements to make them more robust and reliable as low-technology options for mature tree propagation. Probably the most important area for future research is an investigation of how to use pre-severance treatments and environment to enhance the rate and success of both the propagation and the subsequent establishment and growth of the young propagule.

Constraints on space here make it impossible to review fully the progress in other propagation systems. *In vitro* systems, which potentially have much greater multiplication rates and allow for biotechnological developments through genetic manipulation, continue to be an area of rapid development, meriting an independent literature review. Some easy rooting of shoots from mature *in vitro* cultures has been reported but the mechanism remains unclear. *In vitro* micrografting has also been used to improve the rooting ability of mature shoots. There is a need for better understanding of the use of these systems to promote easy propagation from a range of mature tissues. Evidence suggests that some physiological rejuvenation occurs after serial subculturing *in vitro* (with and without an assortment of culture medium supplements) but the physiological processes



Figure 12 Marcotting or air-layering on a tree of *Dacryodes edulis*.



Figure 13 *In vitro* micropropagation of (a) *Khaya ivorensis* and (b) *Nauclea diderrichii* showing the proliferation and rooting phases respectively.

involved are still unknown. Additionally, there is a need for more research on the role of pre-severance factors on the opportunities for more robust *in vitro* propagation. For example, light quality has been found to be important for root formation in *Betula* shoot cultures *in vitro*, while darkness was important for micrografting *Picea* shoots *in vitro*.

Against the advantages of *in vitro* systems are the facts that they are costly and require specialist facilities and staff, making them inappropriate for some developing-country applications.

Conclusions

Within any of the numerous different types or systems of propagating trees, there are large numbers of factors that determine whether or not the propagule is in a good physiological condition, to form a functional plant and grow. For example, when propagating from single-node, leafy cuttings from juvenile shoots, the factors that will determine the level of success are:

- stockplant environment × stockplant management
- × topophytic variables × node position
- × nursery management × post-severance treatments
- × propagation environment

Each of these factors are themselves multifaceted and influenced by the ambient environment (light quality and quantity, water, temperature, nutrients) of the stockplant garden, the nursery, or the propagation bench. For example, in the stockplant garden the environment (light, water, and nutrients) and the management of stockplants can have both short-term impacts on rooting ability by determining the levels of water or heat stress experienced by the tissues being propagated before severance from the stockplant, or long-term impacts on rooting ability through their effects on the morphology or physiological condition of the shoots. Similarly, once the cuttings have been severed from the stockplant the environment of the nursery and the handling of the severed cuttings before and after insertion in the propagation bed will also determine the levels of stress that the cuttings experience. In addition, the cuttings are also affected by the activities of the person doing the propagation and particularly the care taken by this person to minimize the levels of stress experienced by the cuttings (e.g., maintenance in a cool, shady, moist environment; reduction of transpiration by leaf trimming). The human element in this is what is commonly called having ‘green fingers’ and reflects the person’s sensitivity to the needs of the plant material.

See also: Genetics and Genetic Resources: Propagation Technology for Forest Trees. **Silviculture:** Natural Regeneration of Tropical Rain Forests. **Soil Biology and Tree Growth:** Tree Roots and their Interaction with Soil. **Tree Physiology:** Root System Physiology.

Further Reading

- Davis TD, Haissig BE, and Sankhla N (1988) *Adventitious Root Formation in Cuttings*. Portland, OR: Dioscorides Press.
- Dick JMcP and Dewar RC (1992) A mechanistic model of carbohydrate dynamics during the adventitious root development in leafy cuttings. *Annals of Botany (London)* 70: 371–377.
- Hartmann HT, Kester DE, Davis FT, and Geneve RL (1997) *Plant Propagation: Principles and Practices*, 6th edn. Upper Saddle River, NJ: Prentice-Hall.
- Jain SM and Ishü K (2003) *Micropropagation of Woody Trees and Fruits*. Dordrecht, The Netherlands: Kluwer Academic.
- Leakey RRB (1981) Adaptive biology of vegetatively regenerating weeds. *Advances in Applied Biology* 6: 57–90.
- Leakey RRB (1983) Stockplant factors affecting root initiation in cuttings of *Triplochiton scleroxylon* K. Schum., an indigenous hardwood of West Africa. *Journal of Horticultural Science* 58: 277–290.
- Leakey RRB (1985) The capacity for vegetative propagation in trees. In: Cannell MGR and Jackson JE (eds) *Attributes of Trees as Crop Plants*, pp. 110–133. Monks Wood, UK: Institute of Terrestrial Ecology.
- Leakey RRB (1990) The domestication of tropical forest trees: a strategy for increased production and for conservation. In: Werner D and Müller P (eds) *Fast Growing Trees and Nitrogen Fixing Trees*, pp. 22–31. Stuttgart, Germany: Gustav Fischer Verlag.
- Leakey RRB, Newton AC, and Dick JMcP (1994) Capture of genetic variation by vegetative propagation: processes determining success. In: Leakey RRB and Newton AC (eds) *Tropical Trees: The Potential for Domestication and the Rebuilding of Forest Resources*, pp. 72–83. London, UK: HMSO.
- Longman KA (1993) *Rooting Cuttings of Tropical Trees. Tropical Trees: Propagation and Planting Manuals*, vol. 1. London, UK: Commonwealth Science Council.
- Mudge KW and Brennan EB (1999) Clonal propagation of multipurpose and fruit trees used in agroforestry. In: Buck LE, Lassoie JP, and Fernandes ECM (eds) *Agroforestry in Sustainable Agricultural Systems*, pp. 157–190. New York: CRC Lewis.

TROPICAL ECOSYSTEMS

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Tropical Pine Ecosystems and Genetic Resources

Acacias

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Introduction

Acacias are emblematic landscape trees, whether they are the flat-topped trees that pepper the African savanna, the swollen thorn ant acacias of Central America or the wattles of the Australian outback.

Many acacias are adapted to poor soils and disturbed conditions, often in hostile environments, where they are colonizers. It is these conditions that are often faced by tropical foresters, especially where human activities have modified the environment. Thus, acacias, particularly the Australian species, are important forestry trees and multipurpose tree species in the tropics. Acacias belong to the speciose genus *Acacia* and the monotypic genus *Faidherbia*. It is the purpose of the present article to introduce the basic systematics and distribution of the acacias, together with data on genetic variation and hybridization. The