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Article

Revisiting phase change: Ontogenetic and physiological ageing in vegetative propagation

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Abstract: For centuries, stem cuttings harvested from sexually mature trees have been recognized to be more difficult to root than those from juvenile shoots. This has been poorly understood and attributed to a combination of ontogenetic and physiological ageing. The recent suggestion that micro-RNA may play a key role in phase change has stimulated a re-examination of some old data that identified pre-severance light x nutrient interactions affecting the rooting ability of stem cuttings. This was linked to vigorous growth and active photosynthesis without constraint from accumulated starch. Support for the prime importance of physiological factors was also obtained when seeking to induce physiological youth in the crowns of ontogenetically mature trees by the induction of roots within the tree crown. Meanwhile, at the other end of the phase change spectrum, floral initiation occurred when the opposite set of environmental conditions prevailed so that growth was stunted, and carbohydrates accumulated in leaves and stems. A re-examination of this literature suggests that rooting ability is driven at the level of an individual leaf and internode emerging from the terminal bud affecting both morphological and physiological activity. In contrast, flowering occurs when internode elongation and assimilate mobilization were hindered. It is therefore suggested that the concepts of juvenility and ageing are not relevant to vegetative propagation and should instead be replaced by physiological and morphological 'fitness' to root.

Keywords: rooting ability; pre-severance stockplant management; floral initiation; juvenility; maturation

1. Introduction

Conventional understanding in horticulture for centuries has recognized that stem cuttings harvested from sexually mature trees are much more difficult to root than those from juvenile seedlings, coppice shoots and managed stockplant hedges [1,2]. Numerous studies over recent decades have tried to explain this relationship, which has been described as Phase Change (e.g. [3,4]. Many of these have examined apparent linkages with phyllotaxis, leaf shape, topophysis, mitosis and growth regulators *vis à vis* rooting ability, with some suggesting that two factors are important: ontogenetic ageing (sexual maturation) and physiological ageing [5].

In the past, misunderstandings have clouded the debate about maturity and shoot/leaf morphology in woody perennials. For example, ivy (*Hedera helix*) was seen as a model species [6] without recognition that flowering and fruiting only occurs on plagiotropic sylleptic branches with distichous leaf phyllotaxis. In contrast, the mainstem and proleptic branches with characteristic "juvenile" leaf shape and radial phyllotaxis can climb up trees, walls or cliff faces to heights well above the sylleptic branches [7]. Typically, good rooting ability was attributed to mainstem-type 'juvenile' cuttings, while poor rooting ability was attributed to 'mature' cuttings taken from sylleptic branch type cuttings. This misunderstanding brings into doubt the usefulness of the ‘ivy model’.

Practical progress has been made over recent years seeking a better understanding of the effects of pre-severance stockplant management on the complex morphological and physiological factors affecting rooting ability in leafy stem cuttings [8]. This specifically illustrates that, even in a small managed stockplant, rooting ability can be both very poor and excellent depending on stockplant management. It now seems clear that there are ‘within shoot’ variables such as internode length, stem diameter/volume, associated with the storage of carbohydrates and nutrients, that play a critical role. These factors are then complicated by ‘between shoot’ variables that are associated with inter-shoot competition, position on the mainstem, and the stockplant environment [8]. While these are highly interactive, it seems that access to nutrients (especially nitrogen) and light (both quality and irradiance) dominate these interactions with profound effects on phytochrome-mediated stem and leaf morphology with impacts on the physiology of photosynthesis and transpiration [9–11]. Superimposed on these requirements is the need to avoid water stress while in the propagator. This can be achieved by optimizing the leaf area to ensure a balance between the benefits of photosynthesis and the reduction of water loss due to transpiration [12]. It is also important to ensure that the rooting medium has a good air:water ratio to avoid anoxic conditions.

Recent studies have examined the role of genetic material in phase change (e.g. [13–16]. These studies have identified a role of micro-RNA associated with plant development phases controlled by endogenous and environmental factors, with carbohydrates having significant effects on transcriptional and post-transcriptional regulatory mechanisms. However, there is still some element of mystery engrained in this aspect of horticultural tree domestication.

2. Physiological ageing

The concept of physiological ageing arises from the work of Wareing [17] and is well illustrated by the variation in rooting ability that can occur in variously managed juvenile and mature stockplants [8,18].

2.1. In juvenile stockplants

The management and manipulation of shoot growth can strongly influence rooting ability (physiological age) of stockplants.

2.1.1. Within-shoot factors

Juvenile shoots typically develop a gradient of internode length within an individual shoot which results in single-node cuttings of increasing length. Generally, the longer cuttings from shoots of under one metre root best [19], but there are many parallel gradients in these stems, such as: stem diameter, extent of secondary thickening and lignification, and leaf size, making it difficult to know the true effect of cutting length. Interestingly, however, when a reverse gradient was cut in stems of *Triplochiton scleroxylon* (a west African timber tree), it was clear that the positive relationship between rooting ability and cutting length/stem volume, remained significant (r = 0.80) and strong [19]. This indicates that the other within-shoot gradients are much less important for successful rooting. These results suggest that in leafy stem cuttings the storage capacity of these cuttings for current assimilates was a dominant influence on rooting ability. Hence, stockplant management should seek to maximise internode lengths.

When physiological studies investigated the interactions between node position and leaf area [12], node position affected increments in dry weight, carbohydrate content and leaf water potential. Interestingly, however, rooting ability was not related to initial (day 0) carbohydrate content, suggesting that rooting is dependent on carbohydrates formed after severance. This supports the suggestion that the storage area of the stem portion of cuttings for current assimilates has importance in rooting ability. Other studies indicate that the stockplant light environment can negatively influence rooting ability through the storage of starch in stem portions [9].

2.1.2. Between-shoot factors

Several follow-up studies in *T. scleroxylon* then identified that competition between the shoots of juvenile stockplants also affected rooting ability.

(a) Effects of stockplant height

When unbranched, 30-node *T. scleroxylon* plants were cut to heights with 10, 20, 25 and 29 nodes (with an undecapitated control) they developed proleptic lateral shoots with shoot number increasing with increasing height [20] 2.4, 4.7, 5.3 and 6.9 shoots = 21–24% of the buds present sprouted). Cuttings taken from the top shoot of each treatment differed greatly (20–84%) in their % rooting success (**Figure 1**), with the stockplants with greatest number of shoots rooting less well than the Control (43%). Thus, there was a strong negative relationship between shoot number and rooting ability ($r^2 = -0.96$), indicating that competition between shoots affects rooting ability. Stockplants with 20 nodes had higher total carbohydrate content (% of dm) than those with 10 nodes, with lower nitrogen content (% of dm) and hence a higher carbon:nitrogen ratio.

(b) Effects of applied nutrients and pot size

When 10-node decapitated unbranched stockplants were grown in different sized pots +/- added nutrients, rooting ability has greater (40–45% v. 23–25%) in plants with added nutrients regardless of pot size. However, the effect of added nutrients was almost entirely found in the greater rooting ability of basally positioned lateral shoots [20].

(c) Effects of manipulated shoot number

In an experiment to test the effects of between shoot competition bud were removed from 12-node decapitated unbranched stockplants to manipulate shoot number to one, two or four shoots: with undecapitated plants as the Control. Cuttings were then only harvested from the top shoot [20]. Rooting success was greatest from 2-shoot stockplants and declined with increasing number of shoots (**Figure 1**). This supports the suggestion that competition between shoots strongly affects rooting ability.

(d) Effects of manipulated shoot position and shoot number, and applied nutrients

Both shoot position and shoot number affected rooting success when buds were removed from 10-node decapitated unbranched stockplants to allow lateral shoots to form at two basal nodes, two apical nodes, or at both two apical and two basal nodes.

Shoot position was tested at two levels of applied nutrients. Rooting ability was enhanced in all positional treatments by the higher level of nutrients. Importantly, however, at both levels of nutrition, the rooting ability of cuttings from basally-located shoots was significantly greater than those from apically-located shoots (**Figure 1**). In addition, apical shoots rooted better when without competition from basal shoots. The speed of rooting was also significantly greater in cuttings from basal shoots at the higher level of nutrients [20]. Thus, it appears that localized micro-environments, especially shade light, and its interaction with soil nutrients, play a role in the effects of shoot position and competition on rooting ability.

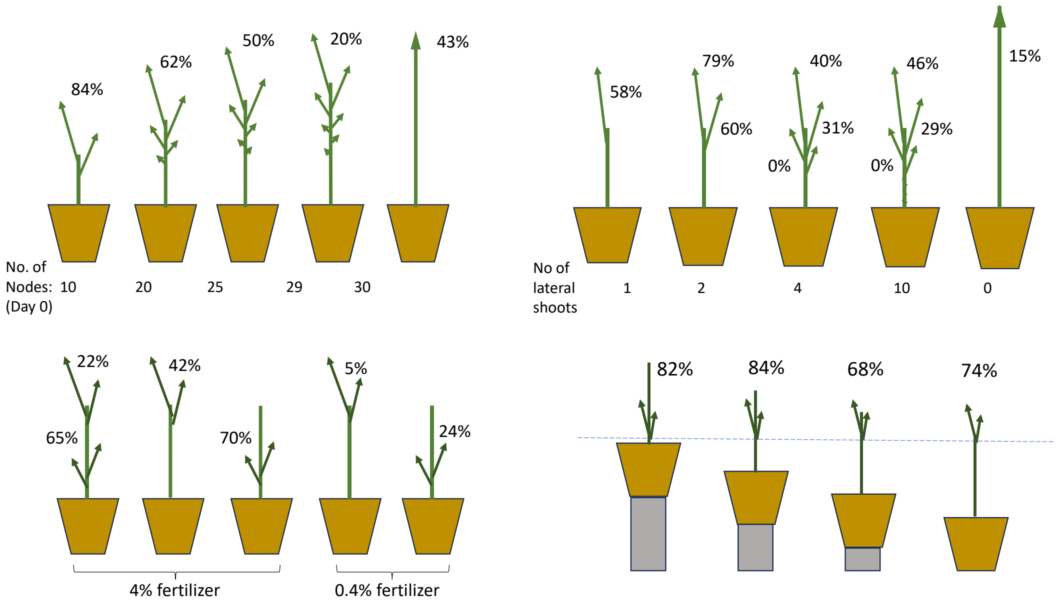


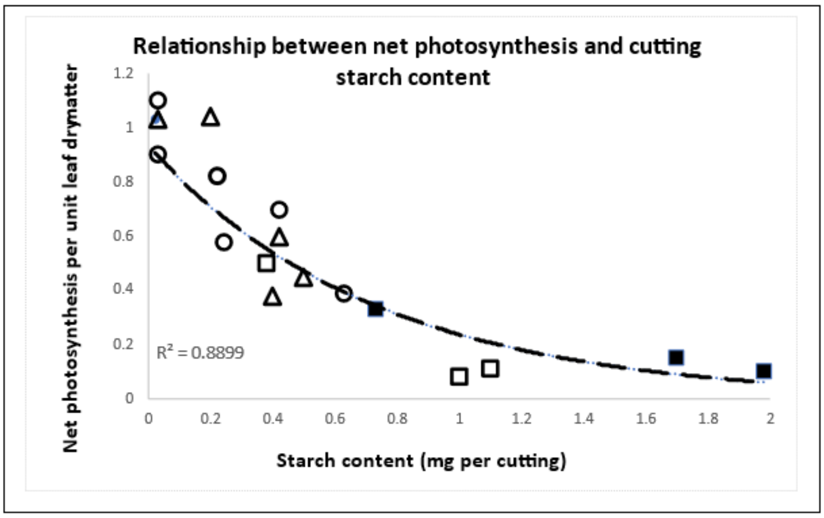
Figure 1. Effects of stockplant manipulation on rooting ability (%) of leafy single node cuttings.

(e) Effects of manipulated shoot position and the light environment

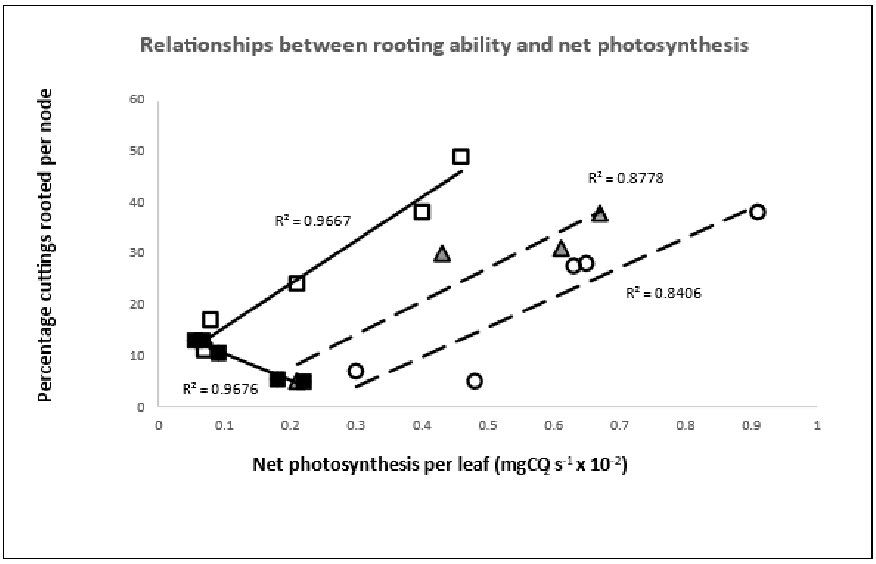
When lateral shoot formation was manipulated to four different node positions (nodes 3/4, 5/6, 7/8 and 9/10) in decapitated unbranched stockplants with 10 nodes and then the plants elevated so that the shoots were in the same light environment [20], the effects of shoot position were relatively similar (**Figure 1**). This seems, therefore, to support the suggestion that the micro-light environments associated with shoot position and mutual shading (reduced irradiance and lower R:FR ratios) are indeed important in the determination of rooting ability.

(f) Effects of irradiance on shoot and leaf morphology

When controlled-environment growth experiments investigated the effects of irradiance (106, 202, 246 μmol $m^{-2}s^{-1}$ at constant light quality) on growth of two-shoot stockplants there were significant and inverse effects on the lengths (and internode length) of both shoots [9]. This affected the shoot dominance ratio (3.4, 3.7 and 2.6 respectively) and the rooting ability of subsequently harvested cuttings (54%, 47% and 32% respectively). A second experiment then tested two levels of irradiance (250 and 650μmol $m^{-2}s^{-1}$ at constant light quality) at two levels of nutrients and measured rates of net photosynthesis per unit of leaf area. Greater levels of photosynthesis were recorded at the lower irradiance, with very low rates of photosynthesis in plants from high irradiance and low nutrients [9]. These rates of net photosynthesis were strongly related to stem starch content (**Figure 2**). There were strong positive relationships between rooting ability and rates of net photosynthesis per leaf (r^2 = 0.841 to 0.967 for both light qualities with high levels of nutrients, and for low nutrients with R:FR = 1.6. Conversely, there was a strong negative relationship (r^2 = −0.968) for low nutrients and a R:FR of 6.3 [9]. This negative relationship is indicative of end product inhibition. It seems likely that similar interactions may explain the earlier mentioned stockplant effects of shading (both R:FR ratio and irradiance) on rooting ability.



(a)



(b)

Figure 2. Relationships between: **(a)** Net photosynthesis per unit of leaf dry matter ($mgCO_2\ g^{-1}\ s^{-1} \times 10^{-2}$) and stem starch content (mg/cutting) and **(b)** Percentage cuttings rooted per node and net photosynthesis per leaf ($mgCO_2\ s^{-1} \times 10^{-2}$).

(g) Effects of light quality (R:FR ratio) on shoot and leaf morphology

A follow-up experiment examined the effects of two light qualities (R:FR 1.6 and 6.3) at constant irradiance (294 μmol $m^{-2}s^{-1}$). Again, internode length and rooting ability were significantly affected with longest cuttings having greater rooting ability (92% *versus* 55%), indicating that inter-shoot shading probably has additive effects on rooting. This is consistent with the passage of light through green leaves which both reduces irradiance and modifies light quality: lowering R:FR ratio [9, 21].

In a more detailed study on growth and gas exchange of *Eucalyptus grandis* stockplants set in growth cabinets set at a photon flux density (PFD) of 200 μmol m^{-2} s^{-1} and R:FR ratios of 0.4, 0.7, 1.3, 3.5 or 6.5. Light quality did not affect the total shoot dry weight (DW), root DW or shoot to root ratio of stockplants, or their total leaf area [10]. However, there were significant effects of light quality on: (i) plant height, (ii) partitioning of DW between leaves and stems, (iii) partitioning of DW and leaf area between the most dominant shoot and all other (non-dominant) shoots; and (iv) specific leaf area. In addition, while photosynthetic rate per unit leaf area and leaf chlorophyll concentration significantly increased with increasing R:FR ratio, light quality did not significantly affect photosynthetic rate per leaf or per unit dry weight. However, there were significant effects on transpiration, stomatal conductance and water use efficiency. Thus, light quality affected dry matter partitioning and gas exchange in ways that changed the size, number, morphology and physiology of subsequently collected cuttings. These pre-severance morphological and physiological changes subsequently had highly significant effects on internode length and volume. In turn, cutting length was strongly related (r^2 = 0.96) to rooting ability of 2-node cuttings [11] and to cutting mortality (r^2 = 0.89). Rooting ability was also strongly related to post-severance net photosynthesis per unit leaf area and per leaf (r^2 = 0.74 and 0.54 respectively).

Generally, rooting ability was associated with low pre-severance starch and water-soluble sugar concentrations, and well-maintained carbohydrate content during the propagation period. Rooting percentages at 35 days after severance were positively and linearly related to net photosynthetic rate and stomatal conductance. Thus, the significantly modified cutting morphology and physiology and the dynamics of stored and current photosynthates led to the significant influence of light quality on rooting ability.

2.1.3. Inter-shoot factors: mature stockplants/crowns

Do the same environmental, physiological and morphological factors that affect rooting ability apply in sexually mature (ontogenetically old) plants? If so, this raises the question can physiological youth (‘juvenility’) be triggered in sexually-reproductive shoots (‘mature’)? This question has not yet been adequately addressed, but some indications suggest that the answer may be positive.

(i) Comparisons between juvenile sucker and mature crown shoots from the same tree

Cuttings were taken from the current year’s lateral ‘long-shoots’ and multi-year terminal ‘short shoots’ of sexually mature crown of *Prunus avium* trees (over 20 years old) and from the current (softwood) and previous year (woody) juvenile root suckers of the same tree in early summer [18]. Cuttings from these four origins were morphologically significantly different (P=0.05) in internode length, stem diameter and leaf area and, consequently, in cutting volume. Juvenile sucker cuttings rooted well (65% and 77% for hardwood and softwood shoots respectively), while mature cuttings rooted poorly (4% and 7% for mature hardwood and softwood shoots respectively). Physiologically (*i.e.*, in carbon assimilation, leaf transpiration and stomatal conductance and leaf retention), the four cutting types were not significantly different early in the post-severance period (day-4); but, by day-22, stomatal conductance was lowest in mature hardwood cuttings that still had leaves. It seems that inter-shoot competition and the morphological and light environment differences attributable to location in the tree crown severely affected the physiological activity of severed cuttings during propagation.

(j) Attempt to induce physiological youth in the ontogenetically mature crowns

To induce physiological youth the upper branches in the crown of three fruiting *Barringtonia procera* trees in Vovohe village, Solomon Islands were first pollarded at 5 and 10m. Seven months later when new shoots had formed, large pots filled with soil were fixed to the cut ends of the branches (**Figure 3**), with 3 shoots passing through the pot, and 2 other shoots passing outside the pot (Control treatment). The internal shoots were ring-barked about 10cm above the base of the pot and treated with 0.8% IBA to form roots (air-layering) in the pots [22]. The ringed and unringed shoots were then pruned to the height of the top of the pot, so that they would resprout. Cuttings were taken from these new shoots after five months growth). While overall there was no significant difference in the rooting ability between air-layered and control cuttings, the cuttings from a few air-layered shoots did root better (60% versus 40%) than the cuttings taken from untreated shoots. It is clear that pollarding *per se* is not a sufficient stimulus to physiological rejuvenation. However, while far from conclusive, this study does suggest that some shoots have been physiologically rejuvenated by the roots now in the tree crown. Unfortunately, the amount of root on each air-layered stock shoot was not assessed to determine any relationship with rooting ability of the cuttings. Interestingly, however, cuttings from the air-layered shoots did produce more roots (5.5) than control shoots (2.5). Further studies are therefore required to determine whether rooted shoots within the tree crown can be fully rejuvenated physiologically.

Figure 3. Establishing a root system on lateral shoots in the crown of *B. procera* trees in Solomon Islands as a source of stem cuttings.

This study suggested that to resolve the debate about factors that affect the rooting ability of juvenile and mature cuttings it is necessary to achieve morphological and physiological comparability in the tissues.

3. Induction of ontogenetic ageing in juvenile plants

At the other end of the ontogenetic spectrum there is evidence that precocious flowering (ontogenetic maturity) in the tropical tree *Triplochiton scleroxylon* (Obeche) can be induced by extreme environmental stress in the roots (chilling 8, 12, 16, 20 ℃ *versus* 28 ℃ in aerial environment—**Figure 4**) in ontogenetically juvenile cuttings [23,24]. This also suggests that the relationships between ontogenetic ageing and physiological ageing are not mutually exclusive. In the field *T. scleroxylon* trees would not normally flower for 15–20 years and then in mast years apparently related to severe ‘short dry’ season. In this study between 10–100 flowers/plant formed in root-chilled plants with the most from plants with roots at 16 ℃. Many of these flowers were then successfully cross pollinated and former viable seeds (**Figure 4**). Assessment of leaf, stem and root soluble carbohydrate contents (greatest in leaves of chilled plants, but they accumulated in stems and roots at 16 ℃). A similar pattern was found in total nitrogen content. These findings indicate that severe environments can induce ontogenetic maturity in juvenile plants through the interference of translocation of carbohydrates and nitrogen within the plants. Further work is required.

Figure 4. Induction of flowering in young plants of *T. scleroxylon* by chilling the root systems.

4. Plagiotropism

Relating to the above aspects of ageing in plants, there are also questions about the epigenetic regulation of changes from orthotropic to plagiotropic branching and in phyllotaxis associated with proleptic and sylleptic branching. A study of responses to shoot decapitation in another tropical tree *Nauclea diderichii* [25] found that the transition from orthotropic growth to plagiotropic growth in lateral shoots occurred over a period of only 2–3 days as lateral buds emerged from the apical bud [25]. In *T. scleroxylon*, plagiotropism in distal shoots was induced by growing stockplants at either 45^{o} or 90^{o} from vertical [25]. The effects of gravitational fields on plant growth and orientation are known as gravitropisms.

5. Discussion

These studies have identified that in juvenile, managed stockplants of the tropical trees *T. scleroxylon* and *E. grandis* the critical factors for the determination of rooting ability in leafy stem cuttings with one or two leaves include: (i) variations in internode length/diameter/storage capacity (sinks) for current assimilates; (ii) nutrients for growth; (iii) inter-shoot competition for available resources (N, C, H_20) due to shoot number/position/micro-environment; light (irradiance and quality) and its interactions with nutrients. Interestingly, small differences in these factors seem to have substantial impacts, even at the level of a single leafy node. This suggests that the environment at the time of mitosis/meristematic activity within the terminal bud affects the development of the morphology/anatomy of leaves and shoots determining the presence or absence of constraints to subsequent (pre- and post-severance) physiology critical for the rooting of cuttings.

Interestingly, the same set of environmental factors are also important for correlative inhibition by the terminal bud (apical dominance). This is relevant as stockplant management involves decapitation and pruning/hedging. Successful rooting is both a function of rooting ability (% cuttings rooted) and process of re-establishing dominance among the new lateral shoots usually by the uppermost shoot. Delaying this re-imposition of dominance increases the length of the non-dominant shoots (i.e. lowers the dominance ratio) allowing more internodes to grow and become a source of easily rooted cuttings from shaded shoots. The percentage bud activity during the sprouting phase following shoot decapitation is characteristic of different clones [26] presumably determined within the terminal bud and so unaffected by decapitation. However, this clonal ‘fingerprint’ is affected by environmental variables (e.g. nutrients and light) prior to decapitation [27,28]. After the three-week sprouting phase there is a phase of reimposition of dominance by the uppermost shoot. This second phase in which lateral shoot growth is not predetermined, dominance ratio is strongly affected by nutrient application, irradiance, temperature etc. [29]. Importantly for rooting ability in cuttings, light quality affected dominance ratio, being greatest at low R:FR ratios [10]. All these variables affecting correlative inhibition also have important impact on branching patterns [29,30], source/sink relationships and the complexity of the tree crown. Consequently, dominance relationships are an additional facet affecting the level of inter-shoot competition [26], the rooting ability of cuttings and the number of cuttings rooted per stockplant.

Intertwined with all this there are impacts on physiological processes, especially gas exchange for photosynthesis, and the avoidance of end product inhibition due to starch accumulation in the internode (**Figure 2**). Furthermore, consistent with the role of competition between shoots, some mitigation of these effects arises from increased access to soil nutrient pools, and from the proximity of the root system. Thus, as in seedlings and coppice shoots, post-severance rooting ability is probably greatest when cuttings can actively photosynthesise and mobilize sugars without the imposition of pre-severance constraints such as very short internodes and accumulated starch. The role of phytochrome is implicated in the effects of light quality on shoot and leaf anatomy affecting photosynthesis and the storage capacity of the internode. A mechanistic model of rooting in leafy stem cuttings based on the processes of photosynthesis and the use and mobilization of assimilates has illustrated the high importance of leaf area, internode length and carbohydrate dynamics in root development [31].

In contrast, the very low rooting ability of shoots harvested from the periphery of the mature tree crown may arise because irradiance, light quality, and inter-shoot competition for nutrients, are all expressed in their least favourable state (perhaps similar to T4 in **Figure 2**). Interestingly, in *T. scleroxylon* the induction of root system dormancy by chilling, led to the accumulation of carbohydrate and nutrient, in the leaves and stems of upper shoots. This seems to have had led to positive effects on the initiation of flowering. In this experiment, root dormancy due to chilling may be replicating the effect a severe short dry season in the field - the trigger for mast flowering. Thus, floral initiation seems to be induced by the accumulation of carbohydrates and nutrients in the shoots due to the loss of a sink for current assimilates. Other well-known flower induction treatments like the removal of bark in a ring around a shoot [32] also interfere with the distribution of assimilates.

These two outcomes imply that physiological ageing and ontogenetic ageing may occur at opposite ends of a phase change/topophytic continuum driven by environmental factors (especially light quality and irradiance and nutrients) experienced by the developing apical bud. These affect both inter-shoot competition for nutrients, water and other root-based factors (e.g. giberellins and cytokinins) and source/sink relationships in ways that interfere with the dependence on an uninhibited current assimilate source. It seems clear that, in managed stockplants, micro factors at the level of a single node, determine rooting ability through perseverance morphological and physiological changes in the subsequently harvested cuttings (**Figure 1**). The reversibility of these effects by environmental manipulation implies no association with ontogenetic maturation.

Interestingly, the report of micro-RNA in the regulation of phase change [16] seems to be compatible with the above suggestion of a chrono-sequence of adaptive morphological and physiological growth and development at the shoot apex. This may additionally be associated with the absence or presence of certain bioactive metabolites.

The long-running and unresolved mystery about phase change in vegetative propagation has hindered progress in horticulture. Its resolution has practical importance for the application of robust vegetative propagation techniques in the domestication of new tree crops in the tropics [33], and the future of tropical agriculture [34].

6. Conclusion

Typically, most vegetative propagation research has focussed on post-severance treatments and the rooting environment. The emphasis of this review on the crucial importance of pre-severance stockplant management, and associated treatments, suggests that the impacts of environmental factors on physiology and morphology explain the loss of rooting ability. Thus, this review suggests that there are legitimate reasons to question the importance of ontogenetic maturation as a factor in rooting ability. Instead, it suggests that rooting ability is driven by a chrono-sequence of adaptive morphological/physiological growth and development. It is therefore proposed that the concepts of ageing and ontogenetic maturation should be ~~juvenility is~~ omitted from discussion of variables affecting vegetative propagation and should be replaced by physiological and morphological 'fitness'.

Conflict of interest: The author declares no conflict of interest.

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