

Review

Effects of Light on Adventitious Rooting In Vitro

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Abstract

Vegetative propagation through stem cuttings and in vitro microcuttings enables large-scale multiplication of superior genotypes in various crop species. This approach is widely used both to propagate and select trees with desirable genetic traits as well as to preserve a significant proportion of genetic diversity. However, successful plant regeneration using this technique requires the development of an adventitious root (AR) system at the base of cuttings or microcuttings. Reduced root formation and functionality strongly limit the application of vegetative propagation, both in vivo and in vitro. The complex process of AR development is greatly influenced by the physiological state of the donor plant, as well as by genetic and environmental factors. Among the environmental factors involved, light quality and intensity have been mainly studied empirically. This review summarizes advances in understanding how light quantity and quality influence in vitro rooting of micropropagated plants, emphasizing species-specific responses. Furthermore, medium components such as sugars and growth regulators, which interact significantly with light, are also considered. Based on existing studies across different plant species, particularly in the absence of growth regulators, the most effective spectrum for root induction is a temporary enrichment of red light, either alone or combined with small amounts of blue or green light. An efficient root growth occurs when the explants are re-exposed to white light, typically at intensities of 40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$. After root development, exposing the microcuttings to higher intensities could help acclimatization. Finally, considering its capacity to precisely regulate light quality and intensity, LED technology offers a valuable tool for optimizing the rooting process and reducing production costs.

Keywords: in vitro propagation; LED; light quality and intensity; microcutting; root development; difficult-to-root species



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1. Introduction

Horticulturists and breeders use agamic propagation through stem cuttings for commercial propagation of elite genotypes and in breeding programs, respectively. Currently, the nursery industry employs diverse tissue and cell culture methods of in vitro technology. Among these, micropropagation represents the most commercially efficient and practically oriented plant biotechnology to propagate clonal plant (true-to-type) and overcome many technical limitations encountered in the traditional in vivo propagation.

However, for many recalcitrant species, some specific micropropagation steps need to be improved at practical and basic levels, to increase the efficiency of plantlets production.

One of challenges faced is the induction of de novo regeneration of adventitious roots (ARs) in microcutting and the development of an efficient root system. Root quality also affects the survival rate and acclimatization of young plantlets.

The event of AR regeneration must undergo many steps of de novo regeneration processes (Figure 1) regulated by a plethora of internal and environmental signals and physiological interactive nodes. The adventitious rooting capacity differs among species, individuals within species, populations, or even clones, since it is controlled by quantitative characters [1]. Moreover, wounding, light, temperature, nutrient state, and acquired internal competence (window of competence) are some of the main factors involved [2,3].

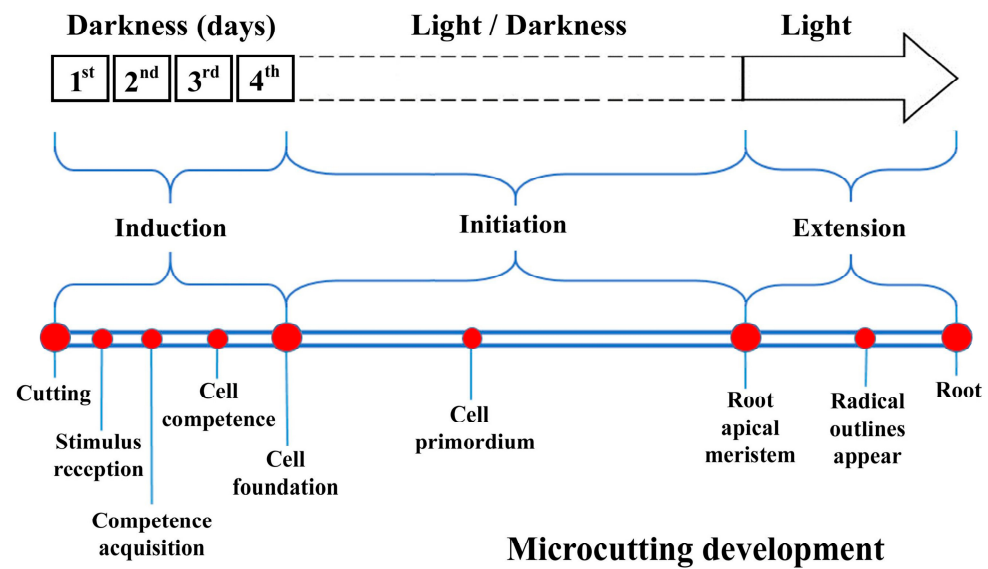


Figure 1. Schematic representation of adventitious root formation in microcuttings of woody fruit crops grown in vitro. Large red circles indicate the main time points of the three key events, while small red circles represent internal time points.

A harmonic plant development involves both shoots (the aerial part) and roots (the underground part), with continuous communication and cross-talking between them. This interaction is influenced by various external factors, including light, water, nutrients, temperature, applied exogenous hormones, pathogens, and anthropic activities, etc. [4–8]. Phytohormones act as major internal factors regulating the growth and developmental adaptive response to ambient in a coordinated manner; this action is also carried out in cuttings in vivo, in vitro, and in undifferentiated tissue explants to generate adventitious roots (ARs) [9,10].

AR formation in excised plant parts is a critical biological process necessary for the constitution of de novo plants from cutting. In in vivo and in vitro cuttings, the ARs originate post-embryonically from cells of non-root tissues like cambium, cortex, pericycle, or vascular bundles and require cell re-differentiation (direct formation); in the difficult-to-root species, the AR mostly occurs from callus tissue (indirect formation), formed upon mechanical cut determined by explant preparation [11]. A few discrete biological phases occur in plant tissues as they acquire the competence to form AR. Porfirio et al. [12] indicated three main biological stages, induction, initiation, and extension, distinguishable on occurrence of the histological events involving the tissues in which the AR evocation occurred, from the cell foundation to the developed root in the competent tissues (Figure 1).

The spatial and spectral properties of the light environment underpin many aspects of plant behavior, ecology, and evolution, and the information carried on is crucial in many fields of agriculture, plant sciences, food science, and final human wellness. Signals gener-

ated by light are the most constant and influential among the environmental signals; they regulate many growth and developmental processes in *in vivo* plants. The increasing use of specialized artificial light presents challenges for controlling plant growth and development, both in horticulture and nursery farms *in vivo*, and particularly in micropropagation technology [13,14]. Plant hormonal pathways are often triggered and regulated by light to mediate developmental changes [15]. Even under *in vitro* conditions, light quality can modulate auxin synthesis, degradation, and distribution, thereby influencing plant growth and development in response to changing light environments [16–18]. Among the light spectrum, red and blue wavelengths are the most effective for both photosynthesis and plant morphogenesis [19–22]. Genetic and photobiological studies performed in many plant species have ascertained that plants possess a plethora of photoreceptors capable of detecting even very low-fluence variations in light quality and intensity. The molecular characteristics of photoreceptors determine which wavelengths they detect. UV-B radiation is sensed by the protein UVR8. UV-A/blue light (UV-A/BL) is perceived by three protein families: cryptochromes (cry1 and cry2 in the cytoplasm, cry3 in chloroplasts and mitochondria), phototropins (phot1 and phot2), and Zeitzlupe family proteins (ZTL, FKF1, and LKP2). Red (RL) and far-red light (FRL) are detected by phytochromes (phyA–phyE).

Photoreceptors are functionally specialized to intercept light quality and translate it into biological information. The acquired information regulates numerous adaptive responses, from shade avoidance response and phototropism to external factors like temperature and pathogens, and developmental transitions, from germination to flowering. Many physiological responses are specifically triggered by a single photoreceptor; however, in some cases, multiple light sensors ensure a coordinated response [14,23,24].

In recent years, light-emitting diodes (LEDs) have been attracting increasing attention as potential light sources for various applications of plant tissue culture and the best choice in a controlled environment [25–27]. In fact, compared to fluorescent lamps (FL), LEDs require less energy and have a longer operating lifetime, low heat emissions, and a more robust plastic body. LEDs also possess also a wide range of systems capable of generating various typologies of white, red and blue (monochromatic light), and purple light spectra.

In a previous review [14], the effects of light on shoot proliferation, the other main process of *in vitro* propagation, were discussed. The current review focuses on understanding and summarizing the literature concerning the effects of light signaling on the *in vitro* rooting process.

2. Light and In Vitro Rooting Process

The relationship between light and the *in vitro* rooting process is complex and influenced by multiple factors, particularly the species-specific responses of the plants and the composition of the culture medium. Different plant species have varying light requirements during each developmental phase, depending on their evolutionary adaptation to natural habitats. In only a few cases are the light conditions optimal for plantlet growth also suitable for rooting [28]. Regarding the culture medium, both the hormonal composition and the availability of nutrients, especially carbohydrates, significantly affect *in vitro* rooting. The main results obtained on *in vitro* adventitious rooting across different species, in relation to growth medium, light wavelength, and intensity, are summarized in Table S1.

The data summarized in Table S1 clearly demonstrate that light quality has a substantial influence on *in vitro* adventitious rooting. Certain light conditions tend to promote root initiation and increase root number, while others often enhance root elongation and root fresh and dry weight. Some conditions show species-specific effects. Overall, these patterns indicate that rooting responses depend not only on light wavelengths but also on

intensity, photoperiod, and plant genotype. These findings emphasize the importance of different light conditions to improve root characteristics in plant tissue culture.

In recent years, there has been increasing interest in the molecular bases of AR [29–33]. Although many of the physiological and biochemical events underlying the initiation of AR development are understood reasonably well, the molecular processes underlying AR development, particularly during the early stages, are still largely unknown [32], and research into their mechanisms is still ongoing. Numerous studies have identified a large number of genes directly involved in the induction and initiation of ARs in different plant species. In a recent review [32] focusing on genes involved in the AR generation process, the author concluded that the critical genes involved in adventitious rooting are the auxin-signaling-responsive genes, including the *Auxin Response Factor* (ARF) and the *Lateral Organ Boundaries-Domain* (LOB) gene families, and genes associated with auxin transport and homeostasis, the quiescent center (QC) maintenance, and the root apical meristem (RAM) initiation. Several genes involved in cell wall modulation are also known to be involved in the regulation of adventitious rooting.

Furthermore, the molecular processes that involved ethylene, cytokinin, and jasmonic acid signaling pathways and their interaction modulate the generation of ARs [32]. Thus, at the molecular level, complex networks are involved in the AR generation in plants. Additional information on the transcription factors involved in root regeneration is reviewed by Bidabadi and Jain (2020) [29].

In *Arnebia euchroma*, Devi et al. (2021) [31], using transcriptomic analysis, observed a similar pattern of genes, but their level of expression varied across subsequent phases of in vitro AR formation. In detail, their data exhibited a predominant role of auxin-responsive (*Auxin Response Factor8*, *IAA13*, *Gretchen Hagen 3.1*) and sucrose translocation (*Beta-31 Fructuranosidase and Monosaccaaride-Sensing protein1*) genes during the induction phase. In the initiation phase, the expressions of *Lateral Organ Boundaries Domain16*, *Expansin-B15*, *Eendoglucanase25* and *Leucine-rich repeat Extension-like proteins* increased. During the expression phase, the same transcripts, with exception of *Lateral Organ Boundaries Domain16* were identified. Thus, molecular studies confirm that the main molecular processes involved in the formation of ARs are linked to the auxin regulation. For this reason, a synthesis of information on the influence of light, even at the molecular level, on the auxin modulation, has been presented in Section 2.1.

2.1. Light and Hormonal Component

Auxins are considered the main phytohormones regulating the rhizogenic process. The formation of ARs can be divided into three phases: induction, differentiation, and extension (Figure 1). Under auxin signaling, specific chromatin and epigenetic modifications occur. These changes are essential for reprogramming cells, forming root founder cells, and initiating cell division, ultimately leading to the formation of the AR primordium [34].

Although auxin is mainly synthesized in aboveground tissues, like shoot apices and young leaves [35], it is redistributed across the plant through the interaction of auxin influx carriers and auxin efflux carriers that determines polar direction transport of auxin flux [36–38] in all plant organs. In the roots, the auxin flux is controlled by the PIN efflux carrier proteins that are located at the plasma membrane [39]. In cuttings and microcuttings, the gradient of auxin and its polar transport from apex to the base promotes activation of root founder cells, for initiating ARs, and regulates the later stages of development of lateral roots (LRs) [40–43]. The polar transport and different distribution of auxin, which are essential for AR organogenesis, are regulated by the plant's endogenous state and environmental factors. These interacting signals modify auxin distribution by altering the hormone's polar transport, thereby regulating root formation [44,45].

There is evidence that specific regions of the light spectrum play an active role in the induction and growth of ARs [46]. However, the mechanisms underlying AR induction and growth remain partially unclear, and obscure physiological behaviors under in vitro conditions require further investigation. In a recent review, Yun et al. [47] summarized the role of light-regulated auxin signaling in root growth and development, reporting that various photoreceptors including phytochromes (PHYs), cryptochromes (CRYs), phototropins (PHOTs), and UVR8 are involved. Notably, even roots, which are normally not exposed to light, can synthesize photoreceptors. In plants engineered to overexpress the UVR8 protein, primary root length and lateral LR density were reduced, indicating a negative role of UVR8 in root development [48]. However, it remains unknown whether UVR8 also affects the development of root hairs or ARs.

In addition to photoreceptors, other components, including phytochrome-interacting factors (PIFs), constitutive photomorphogenic 1 (COP1), HY5, and MYB73/77, also play key roles in light responses mediated by the auxin, under interactive action to regulate root growth and development. Light quality modifies and the RL regulates the expression of genes involved in auxin synthesis and genes involved in the interaction between rhizogenic hormones and those responsible for the development of root tissues through PIF proteins [49,50]. Phytochrome A (phyA) and phytochrome B (phyB), together with phototropin (PHOT) receptors, mediate phototropism and, consequently, local levels of endogenous auxin in different plant tissues. The BL receptor PHOT1/PHOT2 might be involved in the induction of AR under BL by increasing the transcript level of the auxin-signaling gene *PIN3*. Some auxin-related target genes, such as *PIN1*, *PIN2*, *PIN3*, *LAX3*, *ARF19*, *HAT2*, *SUAR23*, *SAUR28*, and *IAA29*, have also been involved in root development. Notwithstanding all the research so far conducted, Yun et al. [47] concluded that the molecular mechanism underlying light-regulated auxin signaling during rooting still needs to be further explained and completed.

In most cases, endogenous auxin is not sufficient to induce ARs, so exogenous formulations are used to enrich the concentration of auxin in the basal portion of the microcuttings. The most used are indole-3-butyric acid (IBA), indole-3-acetic acid (IAA) and an exogenous analog of auxin, 1-naphthaleneacetic acid (NAA) [51] (Table S1). Prolonged exposure under different light regimes determines changes in the levels of endogenous auxin, influencing its homeostasis [52], especially during the inductive phase of AR, and this is attributable to the photolability of the endogenous auxin, reducing the IAA amount in the tissue.

In fact, the predominant use of the exogenous molecule IBA is often more efficient than IAA, although the latter is involved in the natural rooting processes [53,54]. Therefore, it is now known that IBA in the culture medium is a more stable form of auxin and, when assimilated by the tissues, is readily converted into IAA [55]. The slow absorption of IBA from the medium determines a continuous auxin supply, thus maintaining appropriate auxin concentrations for rooting [54]. Low concentration of IBA used in in vivo cuttings (500 ppm) was more effective for root initiation, while increasing the concentration of this hormone above the optimal level has shown an inhibitory effect on further AR development [56]. Similarly, low IBA concentrations, ranging from 0.1 to 2.0 mg L⁻¹, have been successfully used in the medium of different species in the in vitro trials (Table S1). Higher amounts, in fact, can induce a greater synthesis and accumulation of secondary metabolites, which would act as inhibitors of AR. In a *Jatropha curcas* culture, high levels of IBA caused the accumulation of ethylene in the growth container, which acted as an inhibitor of rooting induction [54]. A synergistic action with auxins could be induced by the addition, in the culture medium, of some phenolic metabolites such as Phloroglucinol (PG), a benzenetriol, which is effective in promoting rooting in some species such as apple [57,58], *Prunus avium* [59], and *Jatropha curcas* [54]. It acts as an auxin synergist

during the auxin-sensitive phase of root initiation [58]. De Klerk et al. [60] reported that PG, as well as other phenolics, protects the auxin IAA from decarboxylation during in vitro rooting, and a similar action was also reported on the exogenous auxin IBA by Daud et al. [54]. Moreover, they observed that PG is effective in WPM medium but not in MS, and they suggest that decarboxylation seems to be more pronounced in WPM medium. In *Pyrus communis*, the addition of *trans*-cinnamic acid alone significantly improved rooting (78% rooting of explants) [61]. *Cis*-cinnamic acid (c-CA) is the photo-isomerization product of the phenylpropanoid pathway, intermediate *trans*-CA (*t*-CA), and acts as an inhibitor of auxin efflux [62]. Lotfi et al. [61] hypothesized that endogenous auxin, synthesized in the shoot meristems and transported downwards, is trapped at the shoot base by the c-CA mediated inhibition of auxin efflux. Once the auxin concentration passes a critical threshold, cambium cells will be activated to develop ARs. Simultaneous exposure to RL increased the rooting rate up to 100%, while exposure to BL did not modify the rooting rate, and an inhibitory action was carried out by far-red light (FRL) and by combinations of this light with the others. In the absence of *trans*-cinnamic acid, only the exposure of *Pyrus* microcuttings to BL + RL and RL lights induced adventitious rooting, although to a reduced extent (33 and 40%, respectively). Light effects, influencing the level of endogenous auxins, may permit a reduction in the addition of exogenous auxins in the rooting phase, positively influencing the following phase of acclimatization and growth in greenhouse [53].

2.2. Light and Carbohydrates

Glucose plays an important role in auxin signaling and transport mechanisms, thus controlling the induction and development of ARs. In Table S1, some information about the sucrose content used in medium composition is shown. In *Doritaenopsis* and *Anthurium andreanum*, Shin et al. [63] demonstrated that the most effective light spectrum, RL + BL, determined a greater growth of shoots and an accumulation of carbohydrates with consequent better root development. Gu et al. [64] suggested that the optimal growth of shoots influences root formation by supplying them with carbohydrates to support their growth, as demonstrated by the high correlation between the total dry weight of shoots and number of roots. Therefore, the effect of adopting a more effective light spectrum in promoting shoot development can determine, in some cases, greater root development. Furthermore, well-rooted plantlets are suggested to cope better with in vivo acclimatization process. However, it seems that this theory is acceptable for what concerns root growth but not their induction. In fact, it seems that, for the induction of the rooting process, high levels of carbohydrates are inhibitory, and auxins play the main role.

2.3. Light and Antioxidants

Light can cause oxidative stress on in vitro plantlets stimulating the induction of phenols and antioxidant enzymes to prevent oxidative damage and remove or neutralize toxic substances [65]. Soon after the cutting of plantlets, wounding determines an increase in extracellular peroxidase activity which results in a strong process of IAA decarboxylation. In the light, IAA is also greatly oxidized [66]. As seen in Section 2.1, the addition to the medium of some exogenous phenolics (such as PG) may reduce this process [60]. Exogenous auxin NAA is not decarboxylated and is inactivated only by conjugation. So, in the presence of NAA, the addition of phenolics is almost ineffective [60]. Moreover, phenolic compounds are not only associated with auxins through their protective role against oxidation. Flavonoids can also act as inhibitors of auxin transport [67], interacting with PIN2 or influencing the distribution of PIN proteins [68]. As concerns the specific effects of the light spectra on the phenolic acid synthesis during AR development, BL dramatically increased some phenolic compounds such as ferulic acid, p-coumaric acid,

sinapic acid, vanillic acid, and syringic acid as compared to Fluorescent light (FL); the exposition to RL further decreased these phenols and p-hydroxybenzoic acid as compared to FL in *Panax ginseng* [69]. The lowest concentrations of 3,4-dihydroxybenzoic acid and ferulic acid were also reported in *Protea cynaroides* irradiated with RL [70].

It has also been suggested that UVL and BL trigger the biosynthesis of flavonol quercetin, a compound with antioxidant properties [71]. It is likely that the reduction in p-hydroxybenzoic acid and ferulic acid under RL could be responsible for higher fresh weight and dry weight of ARs compared to BL and FL. The BL and RL treatments increased the total phenol and flavonoid levels in the leaf and root of *Rehmannia glutinosa* [72]. However, in this species, unlike what was observed in *Protea* and in *Panax* under BL, positive effects on ARs were observed. Even in this case, BL significantly promoted antioxidant enzyme activities in the leaf and root, followed by RL. Mucciarelli et al. [73] argued that an inverse relation could exist between 3,4-dihydroxybenzoic acid concentration and growth of roots, since the lowest concentration (0.1 μM) showed an auxin-like activity by stimulating cell dedifferentiation, callus induction, and rooting of leaf tissues; the highest (1000 μM) inhibited the proliferation of leaf tissues, callus growth, shoot regeneration and root growth in micropropagated plants of *Nicotiana tabacum*. Similarly, an inverse correlation was ascertained between 3,4-dihydroxybenzoic acid concentration, rooting percentage, and number of roots as well as between ferulic acid and number of roots per plantlet in *Protea cynaroides* [70]. The authors also concluded that the best results obtained under RL on root formation are the result of the low endogenous concentrations of 3,4-dihydroxybenzoic acid and ferulic acid. Thus, the species-specific response to light stress and to the related amounts of endogenous phenols affects rooting characteristics differently and requires further study.

2.4. Light Quality and Adventitious Rooting

Previous studies have shown that light wavelengths affect AR's formation of leaf explants and cuttings (Table S1), even though, according to plant species and experimental conditions, the results are contradictory [74–78].

2.4.1. Effects of Red (RL) and Far-Red Light (FRL)

RL positively influences the induction of AR, and the number of roots emitted in at least one third of the examined articles. In some species, RL induces adventitious rooting independently of the presence of rhizogenic hormones in *Tripterospermum japonicum* [79], *Dianthus caryophyllus* [80], *Prunus insititia* [81], and *Pyrus communis* [82]. Significant improvements in rooting in the presence of RL and the main rhizogenic hormones have been observed in *Ficus benjamina* [76], gerbera [83], bromelia [84], *Vitis vinifera* [21], *Morinda citrifolia* [85], the zygotic embryos of *Castanea crenata* [86], *Gossypium hirsutum* [87], *Anthurium andraeanum* [88], *Protea cynariodes* [70], *Jatropha curcas* L. [54], *Panax ginseng* [69], *Plectranthus scutellarioides* [89], *Chrysanthemum morifolium* [90], and in the plum rootstock Saint Julien [91].

In *Dieffenbachia 'Compacta'*, positive effects on rooting were found under both RL and green light (GL) [92] and in *Gardenia* under both RL and yellow light (YL) [93]. In rare cases, an inhibitory effect on rooting was noted under RL [63,94,95]. Salisbury et al. [96] found that light qualities supplied to aboveground organs of plants during the development of belowground roots (generally exposed to darkness) regulate via phyA and phyB the emergence of LR. In *Arabidopsis* PHYA and PHYB null mutants, a reduced rate of LR formation and decreased polar auxin transport from shoot to root have been observed, demonstrating that phytochromes in aerial organs respond to aboveground light signals and regulate root growth through a long-distance signaling mechanism.

The regulation of auxin transport may represent a signaling mechanism for cryptochrome, as the auxin transport inhibitor (NPA: 1-N-naphthylphthalamic acid) greatly reduces the stimulation of root growth by BL [97]. Moreover, cryptochromes play a regulatory role, via modulations of auxin transport, in root growth. However, roots also contain photoreceptors able to capture light through the soil or by transmission downward through the vascular cylinder, as demonstrated by Galen et al. [98], which highlighted the association between the photoreceptor PHOT-1, synthesized in the root, and root growth efficiency and drought tolerance. In tobacco seedlings, the growth of LR was tightly related to the acceleration of endogenous auxin transport from the leaves to roots, which occurred when seedlings were cultivated under RL (9 days of treatment), in comparison with those cultivated under white light (WL) and BL [99]. The RL light promoted *PIN3* expression in tissues of shoot/root junction and root, promoting auxin transport; on the contrary, in the same tissues, the BL reduced the expression level of *PIN1,3–4* and auxin transport. In fact, under RL, higher IAA concentrations in roots and lower concentrations in leaves were detected, simultaneously with an elevated number of primary and secondary LR density. The authors interpreted their findings by suggesting that different light qualities regulate auxin polar transport, which in turn differentially controls LR formation in tobacco seedlings. However, light perceived by photoreceptors in aerial organs is not the only source of signaling; root-localized photoreceptors also regulate root development and growth by responding to light signals transmitted over long distances from other organs [96]. Light quality differentially regulates the transcriptional levels of *PIN* genes, and LR formation is associated with changes in auxin transport mediated by *PIN* expression [100,101]. Thus, auxin polar transport appears to play a key role in light-quality-regulated root growth. For example, in cherry microcuttings, RL is more effective than BL in promoting AR elongation but less effective in AR formation [53], whereas in bean explants, RL induces approximately twice as many ARs as BL [74]. Moreover, under RL conditions, the addition of PG significantly improved the acclimatization of *Jatropha curcas* [54]. In *Protea cynaroides*, Wu and Lin [70] demonstrated that the clear improvement in the emission of ARs under RL compared to fluorescence (+60 percentage points) was due to the reduction in endogenous phenols determined by light. Other authors stated that RL promoted adventitious rooting by repressing the accumulation of the phytohormones (Jasmonic acid and cytokinins) induced by cutting [50]. Jasmonic acid is a stress-related hormone that inhibits adventitious rooting and influences the IAA pathway [102].

As concerns FRL, at low intensities, it is reported to improve rooting in combination with both RL or the combination of RL:BL in *Oncidium* [103], *Chrysanthemum* [90] and *Castanea crenata* [86], while at higher intensities it is inhibiting. FRL alone exerts an inhibitory effect on rooting [53,61]. FRL could act as an antagonist to RL by inducing the reversibility of phytochromes (P_r) in vivo; however, the combination of RL and FRL emitted by LED induced early rooting in microcuttings of lavender (*Lavandula angustifolia* Mill.), and the most substantial increase in root number and length were detected compared to BL and FI [104]. Under RL:FRL under in vitro condition, plantlets could have perceived the combination of light qualities as shaded conditions, and it could support an increased development of adventitious roots and their dimension. What appears to be recurrent in all the search works is that light and its photoreceptors act directly on the transport and distribution of the auxin hormone in the tissues that are subject to acquire the competence to reprogram cell fate. Ruedell et al. [78], in *Eucalyptus globulus*, reported positive effects on ARs because of the FRL exposition of donor plantlets growing in a medium devoid of sucrose, even in the absence of exogenous auxin. The presence of sucrose in the donor plant medium abolished the positive effect of FRL. Moreover, the addition of *trans*-cinnamic acid into the

culture medium in combination with RL-FRL produced the most favorable overall results, with a further increase in number of LRs compared to RL or FRL alone [104].

2.4.2. Combined Effects of Red Light (RL) and Blue Light (BL)

Several authors confirmed the effectiveness, on in vitro rooting, of the addition of BL in lighting systems that already included RL. In most cases, these systems proved to be more effective than RL used alone. In particular, root development and growth showed significant improvements by a moderate addition of BL to RL, in *Anthurium* (RL:BL, 75:25) [88], the orchid *Oncidium* (RL:BL, 70:30) [95], *Musa paradisiaca* (RL:BL, 80:20) [105], *Solanum tuberosum* (RL:BL, 80:20) [106], *Saccharum* (RL:BL, 82:18) [107], in *Fragaria × ananassa* (RL:BL, 70:30) [108], and in the apple rootstock JM7 (RL:BL, 60:40) [109].

Some papers reported positive effects on the rhizogenic induction and/or on the number of roots of equal proportions (1:1) of RL and BL, in *Pyrus communis* [61] even without growth regulators, *Lilium* [110], *Anthurium andraeanum* [64], *Elegia capensis* [111], and *Rosa canina* [112]. Finally, Li et al. [113] observed longer roots on *Brassica napus* plantlets cultured under a light mixture where BL is preponderant (BL:RL, 3:1). Kwon et al. [114], in *Populus euramericana*, reported that the combined effect of RL:BL (1:1) or RL:BL:GL (7:1:2) light had positive effects on the fresh weight of plantlets, while the highest number of roots was obtained with BL. In *Doritaenopsis* hort. [63], the highest levels of starch and carbohydrates were recorded in correspondence with the RL:BL (1:1) light combination.

2.4.3. Effects of Blue Light (BL)

In one of the first studies on the role of light on microcuttings cultured in vitro, Chée [115] found that BL was more effective than RL at inducing ARs in the grape genotype Remailly Seedless. However, Poudel et al. [21] observed that in the other two grape genotypes, Hybrid Franc and Kadainou, RL induced a higher rooting percentage and higher root number.

The effects of BL on root induction appear to be species- and genotype-dependent. In *Arabidopsis*, it is reported that BL acts via the photoreceptor PHOT1, via the downstream BL transducer NPH3, on the activation of the auxin transporter PIN3 [116], thus assisting the action performed by RL on the lateral transport and accumulation of auxin in cortical tissues, where the signal for cellular reprogramming begins.

The BL is generally thought to be partially or totally inhibiting root formation and/or growth as reported in *Castanea crenata* [86], *Plectranthus scutellarioides* [89], *Chrysanthemum* [90], *Cymbidium* [117], *Prunus serotina* [75], *Fragaria vesca* [118], and in *Vitis vinifera* [119] and the effect seems to be strongly dependent on the intensity. However, in some cases, BL would favor some rooting in *Pyrus communis*, in the absence of hormones [61], *Prunus avium* L. x *Prunus cerasus* hybrid [53], *Doritaenopsis* hort. [63], *Abeliophyllum distichum* [94], *Achillea millefolium* [120], *Rehmannia glutinosa* [72], and in *Populus euramericana* [114]. Finally, since this light induces a higher stress to in vitro plantlets, increasing some phenolic compounds which are inversely correlated to rooting (see Section 2.3), the different species response to BL stress may be linked to the specific amounts of endogenous phenols.

In *Tillandsia ionantha*, cultured in a hydroponic system, Lee et al. [27] found that BL and RL resulted in significantly longer roots compared to other light wavelengths. In addition, BL led to the highest rate of shooting success (69.42%) and was close to achieving a 100% rooting success rate in different *Pachyphytum* species, suggesting its effectiveness for enhancing shoot and root development [26].

2.4.4. Effects of Green Light (GL)

Significant improvements in AR as a result of the addition of GL at high RL intensities and low BL intensities were observed in *Cunninghamia lanceolata* [121]. In single-node

cuttings of the grape cultivar Manicure Finger, the exposition to GL induced significantly greater root length, root surface area, root volume, and root dry mass than those observed in explants exposed to BL or WL and were similar to those obtained for plantlets exposed to RL [119]. Cho et al. [89] showed, in *Plectranthus scutellarioides*, that the combination of RL:GL (80:20) increased root number and dry biomass more than twice as much as WL. The combination of WL and GL was effective in promoting adventitious rooting in *Chrysanthemum* (*Dendranthema* × *grandiflorum*) [122]. Exposure of microcuttings to GL resulted in an increase in root number equal to that determined by RL in *Dieffenbachia* ‘Compacta’ [92]. However, in *Tillandsia ionantha*, GL resulted in the lowest root count, highlighting its relatively inhibitory effect on root development [27].

2.4.5. Effects of White Light (WL)

As compared to RL, WL promoted better root development in the peach rootstock GF677 [123] and in *Musa paradisiaca* [124], improved root fresh weight in *Gerbera jamesonii* [83], *Gardenia* [93], and *Vanilla* [125], and improved root number in *Dendranthema grandiflora* [126]. The highest rooting percentage under WL or BL or RL was recorded in *Pyrus* [82], *Hyacinthus orientalis* [127], *Chrysanthemum* [122], and *Bambusa vulgaris* [128]. A higher root dry weight was obtained by Gu et al. [64] in *Anthurium* under WL or RL plus BL.

2.4.6. Effects of YL

Few works reported significant improvements with YL when used alone, for example, in *Prunus serotina* [75], or in combination with RL in *Gardenia* [93].

2.4.7. Effects of Ultraviolet Light (UVL)

Very few studies have examined the effects of UVL on rooting and root characteristics. Negative effects on root fresh weight under UVL + WL were observed in *Gerbera jamesonii* [83]. In contrast, WL + UVL in the presence of 2iP increased both root length and fresh weight in *Dieffenbachia* cv. *Compacta* [92]. The UV-B photoreceptor UVR8 inhibits *Arabidopsis* LR development in vivo. In fact, this photoreceptor physically interacts in the nucleus with MYB73/MYB77, hampers the DNA-binding activities of MYBs, and directly represses the transcription of their target auxin-responsive genes [129].

2.5. Effects of Light Intensity

Very few studies have investigated the effects of light intensity during the rooting phase [130–132]. Most research has been conducted under WL; however, the results are not consistent, likely due to species-specific responses. Most authors agree on the positive effects of low light intensity or even darkness on rooting. In *Achillea millefolium*, the best rooting results were obtained at a light intensity of $27 \mu\text{mol m}^{-2} \text{s}^{-1}$ [120]. The interaction between light and auxins suggests that different stages of the rooting process may require distinct light intensities, as higher auxin levels during the induction phase and lower levels in subsequent stages are necessary [46]. The literature survey (Figure 2) indicates that most studies (approximately 78%) employed light intensities between 30 and $70 \mu\text{mol m}^{-2} \text{s}^{-1}$, with 40, 45, and particularly $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ being the most frequently used.

As shown in Figure 2, few authors reported the positive effects of exposure to intensities $> 70 \mu\text{mol m}^{-2} \text{s}^{-1}$. In *Vaccinium corymbosum*, Noè and Eccher [132] reported that short exposures (7 days) to high intensities ($210 \mu\text{mol m}^{-2} \text{s}^{-1}$) applied at the end of the proliferation phase increased the growth and rooting of plantlets ex vitro. In the peach rootstock GF677 [123], the intensity used was $90 \mu\text{mol m}^{-2} \text{s}^{-1}$. In *Acacia melanoxylon*, during ex vitro rooting, the mean root number and rooting rate increased, raising the light intensity; the optimal intensity was $135 \mu\text{mol m}^{-2} \text{s}^{-1}$ [133]. In a difficult-to-root clone of

Sequoia sempervirens, the high intensity of light resulted in improved rooting percentage, root number, and acclimatization [130]. In the same species, at low and medium irradiance, however, a 16 h photoperiod increased rooting percentage.

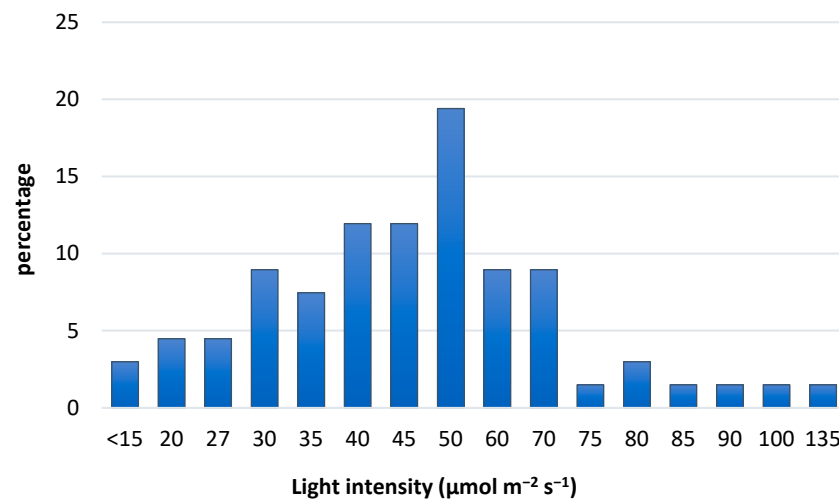


Figure 2. Light intensity used for the rooting process by different investigations ($n = 70$) in diverse species during the rooting phase.

2.6. Effects of Darkness (D)

Positive effects of continuous D were not observed in the different species examined except in the presence of exogenous hormones (Table S1).

In addition, a dark environment at the base of cuttings can enhance the accumulation of photosensitive auxins improving rooting, as observed in many species. For this reason, black dye [134] or activated charcoal [135] are frequently added to the rooting medium.

Short expositions (from 5 to 14 days) to D (Figure 1), prior to incubation under white (W) radiation, are recommended to improve rooting performance, in some species such as *Prunus cerasifera* Ehrh [136], an almond/peach hybrid rootstock [137], *Olea europaea* [138], and *Saccharum* spp. [107]. Radiation exclusion protects auxin from photodegradation [139] and reduces the activity of peroxidase, an enzyme that contributes to auxin degradation [140].

2.7. Effects of Light During In Vitro Rooting on Acclimatization

As concerns the effects of light supplied during in vitro rooting on the subsequent acclimatization, Ramírez-Mosqueda et al. [125] affirmed that explant survival during acclimatization mainly depends on the proper development of the root system during in vitro rooting. An efficient root system favors acclimatization because it increases the plant potential to absorb water and nutrients. However, due to the stress imposed on the plantlets during the transition to acclimatization environment, which can generate ROS stress, the fast acquisition of photosynthetic competence plays a vital role in ensuring their ex-vitro survival [141]. According to Iacona and Muleo [53], the greatest root induction occurred with BL but the highest level of plant survival occurred during acclimatization occurred under RL and BL:RL (1:1). The light quality effect was also retained under the following growth under greenhouse culture conditions, as shown by growth parameters at the end of six months. The use of LEDs during in vitro plantlet development and subsequent acclimatization to increase the rate of plant survival has been overviewed by Dutta Gupta and Agarwal [28]. The regulation of antioxidant metabolism during the acclimatization stage also contributes to improving plantlet survival [142]. In sugarcane, during the first five days of acclimatization, the plants grown under LED did not change

the activities of the antioxidant enzymes, superoxide dismutase (SOD) and catalase (CAT), suggesting that no acclimatization stress occurred [107].

Moreover, there was better development, lower water loss, and a higher survival rate in plants from in vitro culture under R + B LED conditions when compared to FI in sugarcane [107] and in *Fragaria* [108]. BL improved the quality and the survival during acclimatization in *Heliconia champneiana* [143]. However, it seems that higher irradiances are useful to improve the subsequent acclimatization, more than in root induction. In strawberry, $75 \mu\text{mol m}^{-2} \text{s}^{-1}$ was found to be the suitable intensity for acclimatization [118].

The acclimatization of an easy-to-root clone of *Sequoia sempervirens* was suggested to be affected by the phytochrome system, since night breaks by FR during rooting hastens acclimatization and this effect is reversed by RL [130].

3. Concluding Remarks

In vitro adventitious rooting strongly differs from in vivo AR. The physiology and biology of plantlets grown in vitro during the multiplication phase cannot be considered equivalent to those of donor plants grown in vivo from which cuttings are taken. Numerous biological signals active in plant organs are absent in the in vitro plantlets due to the absence of a root system, interruption of vascular transport, and likely changes in hormone synthesis. Moreover, photoperiod perception by plant photoreceptors involved in daily rhythms and annual systems, which play a role in the formation of competence states such as those of adventitious rooting, may be differently activated in vitro. Therefore, cuttings taken from donor plants grown in vivo may exhibit physiological, ontogenetic, and phenological states that differ completely from those of microcuttings derived from in vitro grown plantlets, regardless of whether the donor cuttings are taken during the shoot elongation stage or directly from the shoot multiplication stage. Environmental factors differ markedly between in vitro and in vivo conditions, including constant light intensity and spectral quality, constant photoperiod, stable temperature, constant temperature oscillation between darkness and lighting time, higher relative humidity, etc. The effects of these environmental differences require further investigation, as no systematic studies have addressed them from physiological and ontogenetic perspectives. However, the examination of a substantial portion of existing research indicates that light plays a critical role in in vitro rooting. Therefore, due to their direct or indirect influences on root induction, development, and architecture, careful optimization of light conditions can be an important tool to promote in vitro AR formation. At the same time, the challenges of providing a clear, univocal recommendation regarding light quantity and quality have also been highlighted.

The optimal light conditions for rooting are, in fact, species-specific. Several studies have shown that the effects of darkness or specific light wavelengths vary depending on the presence or absence of auxins. Thus, to better understand the effects of light quality, it is recommended to use substrates with little or no growth regulators. Furthermore, components of the culture medium, such as growth regulators, carbohydrates, or other substances, interact significantly with light, and inside the plantlet, interactively regulate the gene expression in the auxin biosynthetic pathway, consequently influencing the development of root tissues.

Endogenous auxin levels are often insufficient and supplying exogenous auxins is, in most cases, beneficial to obtain higher and homogeneous rooting.

The indole-3-butyric acid (IBA) is the most commonly used synthetic auxin in laboratories due to its stability and slow absorption by plant, providing a continuous auxin supply with appropriate concentrations for rooting. Low IBA concentrations are more effective for root initiation, whereas higher concentrations can stimulate increased synthesis and accumulation of secondary metabolites that may inhibit AR formation. The addition of

certain phenolic metabolites, such as Phloroglucinol (PG) and *trans*-cinnamic acid, to the culture medium can enhance rooting, as they act synergistically with auxins.

Similarly to the proliferation phase, several studies have demonstrated a positive effect of a temporary exposure to RL on root induction, either alone or combined with modest amounts of BL or GL, particularly in the absence of growth regulators. In some species, darkening the substrate or short exposures to darkness (5 to 14 days) are used to enhance rooting performance. Subsequently, re-exposing microcuttings to WL or a combination of RL + BL appears to promote root growth and *ex vitro* acclimatization.

Regarding light intensity, few studies have focused on establishing a threshold intensity for the different species. However, a useful indication from the literature suggests that the most commonly used intensities are around 40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$. After root development has occurred, the exposition of microcuttings to higher intensities could help acclimatization.

LEDs can emit narrow wavelength bands of specific light quality, making them an efficient light source for activating targeted photoreceptor and/or physiological pathways. This feature can contribute to optimizing the rooting process and reducing production costs. Moreover, further research is still needed to clarify the role of light in improving the rooting process of recalcitrant species. In this context, particular attention should be given to elucidating the molecular mechanisms underlying light-regulated auxin signaling during rooting, as well as the species-specific responses in terms of phenol synthesis in response to light-induced stress.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy15112597/s1>, Table S1: Effects of light on rooting characteristics of different species in relation to medium composition, light wavelength and intensity.

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