Fig. 10. Influence of CO₂ enrichment during stock plant cultivation and during the rooting phase on the subsequent growth of *Saintpaulia ionantha* 'Typ 6' leaf cuttings (mean of two propagation dates—11 Nov. 1985 to 2 Feb. 1986 and 19 Dec. 1985 to 18 Mar. 1986; μl l⁻¹ = microliters per liter.

**Stock Plant Lighting and Adventitious Root Formation**

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Root formation in cuttings is influenced by the light conditions during the growth of stock plants. Exclusion of light from the entire shoot prior to propagation stimulates the formation of roots in some woody species. Localized etiolation of that part of the stem, which will become the cutting base, also can be effective (9, 14, 15).

In many experiments, it has been demonstrated that changes in stock plant irradiance or photoperiod may affect the subsequent rooting process in cuttings (1). The effect, however, differs from species to species. Additionally, it appears that other factors modify the irradiance response. This review summarizes the effects of stock plant irradiance and photoperiod on adventitious root formation and discusses whether the radiant exposure (light integral) could be the factor ultimately controlling the subsequent rooting process.

**IRRADIANCE**

Reduction of natural irradiance by shading has been demonstrated to promote the rooting of cuttings. This was obtained in *Rhododendron* (23) and *Dahlia pinnata* Cav. (5). Biran and Halevy (5) reported that three different cultivars of *Dahlia pinnata* reacted differently. Two cultivars had increased rooting percentages after shading the stock plants. The third cultivar was not significantly affected by the shading treatment.

The effect of different irradiances has been studied in detail in *Pisum sativum* L. by Hansen and Eriksen (17). A decreasing number of roots was found with increasing irradiance from 7 to 68 W m⁻² (400–700 nm). Similar effects have later been observed in several other genera, such as *Hedera* (35), *Hibiscus* (24), *Ligustrum* (26), *Picea* (10), *Pinus* (19, 40), *Populus* (12), and *Rhododendron* (11).

A number of plant species have shown the opposite response. In *Campanula isophylla* Moretti (30) and *Chrysanthemum × morifolium* Ramat. (7, 13), the number of roots was increased with increasing irradiance. The experiment by Weigel et al. (43) with a different *Chrysanthemum × morifolium* cultivar, however, showed a reduction in root number with increasing irradiance. Whether this result is attributable to the different cultivar or other factors is not known. Enhanced root formation was also obtained in *Vigna radiata* (L.) R. Wilcz. when the stock plants had been grown at a high irradiance of 80 W m⁻² (400–750 nm) compared with 18 W m⁻² (22). Furthermore, an increase in root number with increasing irradiance or supplementary lighting has been obtained with *Begonia × elatior* (L. Bertram, personal communication).

A number of investigations that have dealt with the effects of stock plant irradiance on subsequent root formation in cuttings are listed in Table 1. This list comprises only a limited number of plant species, but it indicates that most of the species investigated so far produce fewer roots and/or have a reduced rooting percentage with increasing stock plant irradiance.

**MODE OF IRRADIANCE ACTION**

It is unknown why some species produce more roots with increasing irradiance and why other species produce fewer roots. It is also unknown why different cultivars of the same species react differently. Thus, a general explanation is not possible. Scientists can only speculate of several possible irradiance effects on the stock plant that may subsequently influence the rooting process. Therefore, it may be more valuable to evaluate some of the few experiments that have investigated the modifying effect of different factors on the irradiance response.

In the *Pisum sativum* rooting system, Veierskov et al. (42) demonstrated that the cotyledons played an important role during the first 11 days of stock plant growth (Fig. 1). Removal of cotyledons resulted in a reduction in stock plant growth, and the cuttings, which were excised 11 days after sowing, produced fewer roots than cuttings from intact stock plants. The interesting observation was, however, that the removal of cotyledons strongly affected the type of irradiance response. Whereas no removal or removal a few days before cuttings were excised resulted in cuttings that showed the typical pea-type response (17), opposite irradiance responses were observed with cuttings from stock plants that had their cotyledons removed before the eighth day (Fig. 1).

These results suggest that one or more compounds, which are supplied by the cotyledons, interact with the stock plant irradiance.
Table 1. Effect of increasing stock plant irradiance on root formation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Response</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Begonia x elatior</em></td>
<td>+</td>
<td>Bertram (personal communication)</td>
</tr>
<tr>
<td><em>Berberis thunbergii</em> DC.</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td><em>Campanula isophylla</em> Moretti</td>
<td>+</td>
<td>30</td>
</tr>
<tr>
<td><em>Chrysanthemum x morifolium</em></td>
<td>+</td>
<td>7</td>
</tr>
<tr>
<td><em>Ramat.</em></td>
<td>+</td>
<td>13</td>
</tr>
<tr>
<td><em>Dahlia pinnata</em> Cav.*</td>
<td>0, -</td>
<td>5</td>
</tr>
<tr>
<td><em>Hedera helix</em> L.*</td>
<td>-</td>
<td>35</td>
</tr>
<tr>
<td><em>Hibiscus rosa-sinensis</em> L.*</td>
<td>-</td>
<td>24</td>
</tr>
<tr>
<td><em>Ligustrum obtusifolium</em> Sieb, et Zucc.</td>
<td>-</td>
<td>26</td>
</tr>
<tr>
<td><em>Ligustrum x vicaryi</em> Beckett</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td><em>Malus</em></td>
<td>0, -</td>
<td>8</td>
</tr>
<tr>
<td><em>Picea sitchensis</em> (Bong.) Carr.*</td>
<td>-</td>
<td>10</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em> L.*</td>
<td>-</td>
<td>19</td>
</tr>
<tr>
<td><em>Pisum sativum</em> L.*</td>
<td>-</td>
<td>40</td>
</tr>
<tr>
<td><em>Populus tremula x tremuloides</em></td>
<td>-</td>
<td>17</td>
</tr>
<tr>
<td><em>Rhododendron</em></td>
<td>+, 0, -</td>
<td>42</td>
</tr>
<tr>
<td><em>Vigna radiata</em> (L.) Wilcz.*</td>
<td>+</td>
<td>22</td>
</tr>
</tbody>
</table>

* - , inhibition; 0, no effect; +, stimulation.

that stock plant irradiance affected the transport and accumulation of 14C-labeled auxin in cuttings (3). Accumulation of auxin in the basal 2 mm of the cutting was higher in cuttings from 38 W·m⁻² (400–700 nm) treated stock plants than in cuttings from 16 W·m⁻² plants. Baardsmand and Andersen (3) hypothesized that rooting was favored in the basal 2 mm of cuttings from high-irradiance-treated plants, but that the first initiated roots then could exert a basal dominance. In cuttings from 16 W·m⁻² treated plants, auxin accumulation was smaller and the amount of auxin was more evenly distributed, leading to a more equal stimulation of root formation in a topographically larger part of the stem. In contrast to this investigation, Weigel et al. (43) reported for *Chrysanthemum x morifolium* that the endogenous level of free auxin was higher in cuttings from stock plants grown at 4.5 W·m⁻² than in cuttings from plants grown at 40 W·m⁻².

Another investigation that shows an auxin role was made by Christensen et al. (8). These authors reported for apple rootstocks that the stock plant irradiance (8 to 56 W·m⁻²) did not influence the rooting of cuttings in the absence of applied auxin. When cuttings were treated with auxin, rooting was stimulated but only when the stock plants had been grown at low irradiances. For the moment it is impossible to give any complete explanation to the irradiance effect on rooting. Much more work will have to be done before the mode of irradiance action is understood.

**PHOTOPERIOD**

Photoperiodic effects on rooting have been reported for several species. Moshkov and Kocherzhenko (31) reported that rooting of three different *Salix* spp. was affected by the stock plant photoperiod, but the three species reacted differently. In one species, rooting was stimulated by long-day conditions (18 hr); in the second species, rooting was inhibited by long-day conditions; in the third, the optimum photoperiod was 14 hr. Such a diversity in response is common. However, it is most frequently observed that short-day conditions promote the subsequent formation of roots, whereas long-day conditions suppress root formation. This activity has been shown for *Abelia x grandiflora* (André) Rehd. (39), *Kalanchoe tubiflora* (Harv.) Hamet (33), *Crassula argentea* Thunb. (34), *Ilex crenata* Thunb. (25), and *Pinus sylvestris* L. (18). Opposite responses were reported for *Begonia x cheimantha* T.H. Everett ex C. Web. (21), *Vigna radiata* (22), and *Rhododendron* (4).
An increase in root number on *Ilex crenata* with increasing number of short days (10 hr) was observed as compared with cuttings from stock plants grown at 18 hr (25). Similar observations were reported by Paterson and Root (34) for *Crassula argentea*. The regeneration potential of cuttings increased with increasing duration of stock plant growth under short-day (8 hr) conditions. Precutture under long-day conditions resulted in a low regeneration potential.

It is possible that the diversity in photoperiodic rooting response reflects that different plant species react basically different. It is, however, also possible that there is an optimum photoperiod for a given plant and that this optimum may differ widely among species. More systematic research is required before any general pattern can be established. Furthermore, the photoperiodic rooting response becomes complicated as induction of flowering and dormancy are under photoperiodic control in many plants. Dormant cuttings (38) and cuttings with reproductive buds (6) may be considerably more difficult to root than cuttings from actively growing vegetative shoots.

**RADIANT EXPOSURE**

Seasonal fluctuations in adventitious root formation have been reported for several species, e.g., *Taxus cuspidata* Siebold et Zucc. and *Juniperus horizontalis* Moench (27), *Olea europaea* L. (20), and *Pinus sylvestris* (18). It has been shown, also, in the more herbaceous species *Pisum sativum* (2), that the number of roots per cutting follows a seasonal pattern. The capability of *Pisum sativum* to form roots was reduced during spring, reached the lowest level in July and increased again through autumn (2). A similar pattern was observed for *Pinus sylvestris* (18).

Seasonal changes in light conditions may be the controlling factors. Since the decrease in root number during spring is associated with an increase in irradiance and photoperiod, it is reasonable to assume that the seasonal fluctuation in root formation is related to the natural light conditions. That this actually is the case has been demonstrated for *Pisum sativum* (17) and *Pinus sylvestris* (18).

The most interesting observation, however, is that the formation of adventitious roots in *Pinus sylvestris* is closely related to the radiant exposure (light integral) over the entire stock plant period (18). This relationship implies that neither the irradiance nor the photoperiod is the controlling factor, but that the radiant exposure ultimately determines the number of roots. Until now, this relationship has been established only for *Pisum sylvestris* (18). It would be interesting if such a relationship could be confirmed with other species.

**CONCLUSION**

It is evident that light conditions of stock plants have a considerable influence on adventitious root formation in cuttings. Unfortunately, experimental results for one species are not applicable to all species. Presently available information thus makes a general conclusion difficult. Nevertheless, it is appropriate to conclude that close attention must be directed towards light conditions of stock plants. Most species appear to be able to increase their rooting potential under moderate light conditions.

**Literature Cited**


The discovery and use of auxins in rooting and the development of mist propagation are unequivocal milestones in the history of propagation due to their broad applicability and effectiveness. Stock plant etiolation may prove to be in a similar class with these techniques. The practical use of stock plant etiolation to improve rooting in cuttings has largely been spurred on in the past 10 years by the successes achieved by Howard and others at the East Malling Research Station, United Kingdom (9). For all the renewed interest, however, the practice of withholding light to improve propagation is probably an ancient one, having been employed every time a stool bed or layer was made or even a cutting inserted into opaque media.

What constitutes stock plant etiolation in propagation? Etiolation simply is the growing of plants in the absence of light. However, as the term has come to be used among propagators, it also refers to growing plants in heavy shade. Stock plant etiolation generally refers to the initiation of new stock plant growth in the dark. Typically, a dormant stock plant is covered by a light-tight barrier and the new growth is made in darkness. Shading is gradually reduced after the shoots reach 5–10 cm in length and the shoot allowed to continue growth. An opaque adhesive band often is wrapped around the base of the new shoot (the future cutting base), at the time of shade removal, thereby retaining its etiolated condition while the rest of the shoot turns green in the light. The shoot is removed just below the banded section after several weeks of regreening. The band is removed and the cutting inserted into the rooting bench in the normal manner (12). A related practice called blanching refers to light-grown plants that subsequently are shaded. With this treatment, the shoot accomplishes its initial growth in the light and then has a portion of its stem banded with an opaque material such as black adhesive tape for several weeks before the cutting is made. Shading, which simply refers to any stock-plant growth under reduced light conditions, has also been used as a successful propagation pretreatment in a number of genera. A recent review has revealed more than 28 genera that have successfully been propagated without either etiolation, shading, or blanching as pretreatments to cutting propagation (13).

Despite the often dramatic successes of these various techniques, the mechanism whereby etiolation works is still poorly understood, although several researchers have gathered an impressive amount of correlative and circumstantial evidence. In 1922, Reid (15) successfully rooted cuttings of *Camphora* after stock plant etiolation. She also undertook the first anatomical study of etiolated tissues in the rooting zone and reported findings that were to be repeated many times in the future. Etiolated stem tissue was less lignified than light-grown tissue, had decreased cell wall thickness, and increased protoplasmic content in the cells. She showed that lignification was a developmental process that lagged behind tip growth. Etiolation delayed lignification so that etiolated shoots were lignified to the sixth node while light-grown shoots were lignified to the third node. This decrease in lignification is not caused by stem growth, which causes gaps in normal tissue. Thus, the anatomical explanation of etiolation’s effect began with the idea that a reduction in the mechanical properties of the stem were responsible for the ease of rooting caused by stock plant etiolation. These findings also have been reported by others (5, 8).

Gardner in 1936 (6) was the first to use black adhesive tape to blanch ‘McIntosh’ apple stems, which led to high rooting levels in this difficult-to-root species. He also reported the additive effect of girdling along with etiolation and the observation that blanched shoots contained more undifferentiated tissues, perhaps leading to easier root initiation. He hypothesized that the girdle was increasing some translocated substance in the etiolated zone, which worked with the anatomical changes to increase the ease of rooting.

Not until the 1960s did work on etiolation become popular again. Frolich’s work in 1961 (5) with etiolated avocado shoots showed that roots were produced only in that part of the stem that had been etiolated. Nonetiolated sections above and below that section produced no roots. Again, he cited localized anatomical changes in the stem tissue as the likely reason of this effect, although localized biochemical changes were not ruled out. He also showed that there was a continuum between the total duration of light at a given intensity and the reduction in rooting; the longer a mung bean’s exposure to light of any spectral quality the poorer was its rooting. This was the first evidence that total darkness was not necessary to achieve some level of increased rooting and that the promotional effect was correlated with light intensity.

The work reported by Herman and Hess in 1963 (8) presented both anatomical and biochemical evidence for the etiolation effect. Using *Phaseolus vulgaris* L. and *Hibiscus rosa-sinensis* L., they showed that etiolation greatly increased a tissue’s sensitivity to exogenously applied auxin; however, they also found that endogenous auxin was in no greater supply in etiolated than in light-grown tissue. Anatomically, they cited a reduction in the mechanical strengthening tissues, decreased lignification, and reduced cell differentiation (among other observations) as enhancing potential root primordia formation. In some less-convincing bioassay work, they proposed that there was increased auxin cofactor content in etiolated stems, which increased the efficacy of applied auxin. However, the crude extraction procedure and lack of dilution series made this conclusion doubtful.

### References