

1 OCT 1997

RECIBIDO

# Forest Ecology and Management

---

Forest Ecology and Management 92 (1997) 45–54

## Vegetative propagation of *Cordia alliodora* (Ruiz & Pavon) Oken: the effects of IBA concentration, propagation medium and cutting origin

F. Mesén<sup>a</sup>, A.C. Newton<sup>b,\*</sup>, R.R.B. Leakey<sup>b,1</sup>

<sup>a</sup> Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba 7170, Costa Rica

<sup>b</sup> Institute of Terrestrial Ecology (ITE), Bush Estate, Penicuik EH26 0QB, UK

Accepted 21 October 1996



# Vegetative propagation of *Cordia alliodora* (Ruiz & Pavon) Oken: the effects of IBA concentration, propagation medium and cutting origin

F. Mesén<sup>a</sup>, A.C. Newton<sup>b,\*</sup>, R.R.B. Leakey<sup>b,1</sup>

<sup>a</sup> Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba 7170, Costa Rica

<sup>b</sup> Institute of Terrestrial Ecology (ITE), Bush Estate, Penicuik EH26 0QB, UK

Accepted 21 October 1996

## Abstract

The effects of different concentrations of IBA, rooting media and cutting origins on the rooting of leafy stem cuttings of *Cordia alliodora* (Ruiz & Pavon) Oken were investigated in three experiments using non-mist propagators. During the rooting period, changes in dry mass, photosynthetic rate, stomatal conductance and relative water content (RWC) of the cuttings were assessed. In Experiment 1, cuttings treated with 1.6% IBA achieved 70% rooting after 9 weeks. Bud growth in cuttings was inhibited by increasing concentrations of IBA, which were associated with higher final rooting percentages. No significant treatment differences in RWC or dry mass were found between IBA concentrations, although the dry mass of cuttings in all treatments tended to increase during the rooting period. In Experiment 2, higher rooting percentages were recorded in gravel (89%) and sand (88%) than in sawdust (76%). Although the water content of sawdust was relatively high, cuttings in this treatment displayed significantly lower stomatal conductances ( $g_s$ ), which may be attributed to death of stem tissue resulting from anoxia. In Experiment 3, highly significant differences ( $P < 0.01$ ) were recorded between node positions with respect to rooting percentage, values ranging from 21.3% for Node 2 to 46.3% for Node 5 (basal). Cuttings actively photosynthesized during the rooting period, with photosynthetic rates ( $P_n$ ) of 0.68–6.70  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  recorded. However, no clear relationship between  $P_n$  and rooting ability was apparent. Contrary to previous studies with this species, it was concluded that *C. alliodora* cuttings may be rooted relatively easily using the propagation system described. However, the close relationships recorded between  $P_n$ , irradiance and leaf–air vapour pressure deficit (VPD) suggest that propagator microclimate should be carefully managed if optimal rooting percentages are to be achieved.

**Keywords:** Vegetative propagation; IBA; Rooting medium; Photosynthesis; Water relations

## 1. Introduction

*Cordia alliodora* (Ruiz & Pavon) Oken (Boraginaceae) is a valued timber tree native to tropical America, distributed from central Mexico to northern Argentina and in parts of the Caribbean (Greaves and McCarter, 1990). It has also been

\* Corresponding author. Institute of Ecology and Resource Management, University of Edinburgh, Kings Buildings, Mayfield Road, Edinburgh EH9 3JU, UK.

<sup>1</sup> Present address: International Centre for Research in Agroforestry (ICRAF), P.O. Box 30677, Nairobi, Kenya.

introduced to other tropical countries where, in some cases (e.g. Vanuatu), it has become the major reforestation species (Hudson, 1984; Neil and Jacovelli, 1985). *C. alliodora* is found on a wide range of sites at altitudes from sea-level to 2000 m, and is widely cultivated in agroforestry systems as well as plantations (Greaves and McCarter, 1990). In Central America, it is found in both the Atlantic (0–900 m above sea-level (a.s.l.)) and the Pacific regions (0–1800 m a.s.l.), but is most common in the former, where the tallest and best-formed trees are found (Boshier and Mesén, 1987, Boshier and Mesén, 1988). On these sites, the bole has a monopodial growth habit, essentially straight, cylindrical and clear of branches for 50–60% of the total tree height. However, both in natural and in planted stands, the trees show a high variation both in growth and form, indicating the potential for genetic improvement (Boshier and Mesén, 1987).

A number of tree improvement programmes using traditional techniques are currently in progress with this species (Mesén et al., 1994). It is now widely appreciated that vegetative propagation and clonal selection techniques offer the possibility of rapid genetic gains in such improvement programmes (Zobel and Talbert, 1984). To develop a clonal programme with *C. alliodora*, vegetative propagation techniques need to be developed to allow the multiplication of selected genotypes. The experiments described here investigated the effects of rooting media, IBA concentration and cutting origin on the rooting ability of single-node cuttings of *C. alliodora*, using low-technology, non-mist propagators as described by Leakey et al. (1990). This propagation system is relatively cheap and easy to maintain, and is therefore highly appropriate for use in rural tropical areas.

CATIE  
M572V

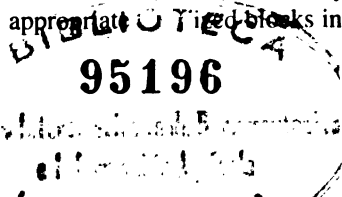
## 2. Materials and methods

Propagators were constructed following the design of Leakey et al. (1990). A wooden frame was enclosed in clear polythene so that the base was water-tight. The base was covered with successive layers of large stones (6–10 cm), small stones (3–6 cm) and gravel, and topped with an appropriate

rooting medium to a total depth of approximately 25 cm. The basal 20 cm was then filled with water. The propagators were placed in the Tree Improvement Project nursery, at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Turrialba, Costa Rica (9°54'N, 83°40'W, 600 m a.s.l.), under a shade screen constructed of nylon netting.

Plants were derived from open-pollinated progeny of plus trees selected by the CATIE Tree Improvement Project (TIP) in Costa Rica. Original seedlings were grown 1 m apart in beds at the CATIE nursery, cut back to maintain a supply of coppice shoots and used as a source of cuttings to build up clonal populations. Rooted cuttings were potted into black polythene bags (600 cm<sup>3</sup>) containing a 1:1:1 mixture of forest soil, sand and organic compost, then weaned under shade and decreasing watering during a 2–3 week period. After this weaning period, cuttings were planted in beds beside the original stockplant, at a spacing of 20 cm × 20 cm. The clonal plants were given fortnightly soil applications of a powdered fertilizer (FERTICA, Puntarenas, Costa Rica) containing 10% N, 30% P and 10% K, at a rate of approximately 30 g per plant. The beds themselves were made up of the potting mixture described above. Mean annual rainfall in Turrialba is 2600 mm, with no month below 50 mm. Consequently, watering was not usually necessary, but the plants were watered to field capacity when there was no rain for two consecutive days (typically in January and February).

In Experiment 1, 250 cuttings of a standard length of 5 cm were collected from each of three clones (Clones 2, 4 and 8), after trimming their leaf area to a single leaf of approximately 30 cm<sup>2</sup>. The tip of each shoot was discarded and cuttings were taken sequentially down the stem, recording node position. Cuttings were then treated immediately with one of five indole-3-butyric acid (IBA) concentrations (0%, 0.2%, 0.4%, 0.8% and 1.6%) dissolved in methanol solution. The IBA was applied to the clean-cut base of the cuttings in 10 µl droplets using a micrometer syringe. The alcohol was evaporated off in a stream of cold air from a fan before inserting the cuttings in sand in the propagators (following Leakey et al. (1982)). The control treatment received 10 µl of methanol only. Cuttings were inserted in ten random-



the course of the experiment, two fine spray waterings were given daily to the cuttings to keep the leaves moist, at 07:00 and 15:00 h.

Each cutting was assessed weekly for number of roots and presence of shoots for 9 weeks in total. In addition, ten cuttings from each clone were harvested for assessments of initial stem and leaf fresh and dry mass at Day 1, and then destructive samples were taken after 14, 28 and 42 days, for measurement of fresh and dry mass of leaves, stems and new shoots. Each clone–treatment combination was represented by five cuttings at each harvest. Foliar relative water content (RWC) was calculated following Beadle et al. (1985), as  $((FM - DM)/(TM - DM)) \times 100\%$ , where FM, TM and DM are fresh mass, turgor mass and dry mass, respectively. Turgor mass was obtained after floating the leaves in distilled water for 24 h. To determine dry mass, the cuttings were oven dried at 80°C for 24 h.

In Experiment 2, a propagator was subdivided into 12 compartments, and each one was assigned randomly to one of three rooting media—fine sand, gravel or sawdust. When the stockplants' shoots had grown to a height of 30–40 cm, 360 cuttings of 5 cm length were taken down the stem as described in Experiment 1, 120 from each of three clones (Clones 19, 22 and 35). Leaves were trimmed to 30 cm<sup>2</sup> using paper templates and the cutting base was treated with IBA in methanol at a concentration of 1.6%, as described above. Cuttings from each clone were assigned randomly to the compartments in the propagator, each receiving 30 cuttings, ten from each clone. Cuttings were assessed weekly as described in Experiment 1 for a total of 6 weeks.

A data logger (21X Micrologger, Campbell Scientific Ltd., Loughborough, UK) was used to characterize propagator microclimate during propagation. Air temperature was measured using thermocouples (Type K chromel–alumel; T.C., Ltd., Uxbridge, UK), humidity using a thermistor probe (MP.100 Rotronic probe, Campbell Scientific Ltd.), substrate temperature using a 107-thermistor probe (Campbell Scientific Ltd.) and irradiance using quantum sensors (Skye Instruments Ltd., Llandrindod Wells, UK, supplied by Campbell Scientific Ltd.). All sensors of each type were cross-calibrated before use. The logger was programmed to record each sensor every 10 s, and to calculate and store mean readings every

15 min. The 107-thermistor probes were inserted in the rooting medium to a depth of 2–3 cm. For measurements of leaf temperature, the thermocouples were attached to the lower leaf surface.

To determine the relative proportion of solids, air and water in the rooting media, three 100 cm<sup>3</sup> samples of each medium were taken. The air volume in each sample was determined by measuring the amount of added water required to saturate the air spaces. The water content was determined by the difference between wet and dry mass. The results were expressed as percentage of each component by volume.

Measurements of net photosynthetic rate ( $P_n$ ) and stomatal conductance ( $g_s$ ) were taken at Week 1, 2 and 3 in a randomly selected sample of six cuttings from each medium. For the assessments of  $P_n$  and  $g_s$ , an IR gas analyser was used (LCA-3, Analytical Development Co. Ltd., Hoddesdon, UK). Measurements were made of cuttings in situ in the respective media.

In Experiment 3, stockplants from Clones 18, 19, 22, 23, 25, 29, 33, 35, 37 and 38 were cut to a height of 20 cm. Three weeks later, stockplants were pruned to the three most vigorous shoots. When the shoots had grown to heights of 30–40 cm, the tip of each shoot was discarded and six single-node, leafy stem cuttings were taken sequentially down the stem, and their leaf areas trimmed to 30 cm<sup>2</sup>. IBA in a 1.6% solution was applied to the base of the cuttings as described in Experiment 1, before inserting the cuttings in sand in non-mist propagators. The cuttings were allocated to eight randomized blocks, each block containing 60 cuttings (ten clones  $\times$  six node positions in the shoot). One week after insertion, the stem length and midpoint diameter of each cutting were measured. Each cutting was assessed for number of roots at weekly intervals for 9 weeks in total. As with the other experiments, rooting percentages were calculated on the basis of these assessments.

Photosynthetic rates and stomatal conductance were measured in situ in six randomly selected cuttings (including all node positions) from Clones 18, 19, 22, 23 and 29 on Days 14, 21 and 28 after insertion. For these measurements, a portable gas exchange system with IR gas analyser (IRGA) attached to a Parkinson leaf chamber was used, as described above. Measurements of propagator micro-

climate were made throughout the rooting period as described for Experiment 2.

In all three experiments, rooting data were subjected to analyses of variance, followed by multiple range tests where appropriate (SAS Institute, Inc., 1980). Percentage data were arcsin transformed before analysis, following Snedecor and Cochran (1980). Interactions between the treatment factors were included in the ANOVA in each experiment. In addition, rooting results were subjected to analysis of deviance for stepwise regression in Genstat 5 (Payne et al., 1987) to determine the influence of different variables on rooting ability. In Experiment 1, estimates of leaf and stem dry mass at Day 1 were obtained by multiplying the total fresh mass of the cuttings at Day 1 by a reduction factor obtained from a sample of 30 cuttings from the three clones, destructively harvested at Day 1.

### 3. Results

#### 3.1. Experiment 1

Nine weeks after insertion, highly significant differences in rooting percentage were found between IBA concentrations ( $P < 0.001$ , ANOVA), with a value of 70% recorded in cuttings treated with 1.6% IBA, compared with only 10% for the control cuttings (Fig. 1(a)). The effect of IBA concentration on number of roots per rooted cutting was also significant ( $P < 0.01$ , ANOVA). This trait showed a similar trend to that of rooting percentage, with higher values recorded with successive increases in IBA concentration (Fig. 1(b)). Stepwise analysis of deviance confirmed that rooting was highly dependent on IBA concentration, but also highlighted a significant effect of the presence of shoots and leaves in the cuttings, cutting diameter and clone, which was positive in the former two cases ( $P < 0.01$  in each case).

Cuttings of Clone 2 displayed significantly higher rooting percentages than Clones 4 and 8 after Week 5, but these differences became non-significant at Week 9 (when rooting percentages of 56%, 47% and 44%, respectively, were recorded). In terms of number of roots per rooted cutting, Clone 2 produced a

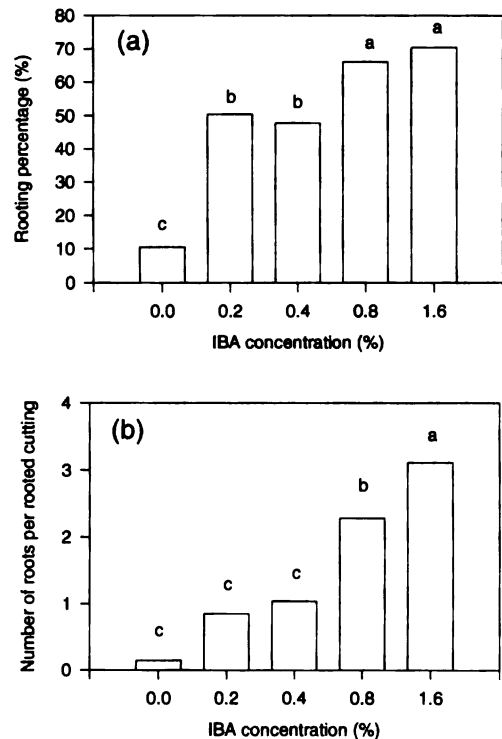


Fig. 1. The effects of five different concentrations of IBA (0, 0.2, 0.4, 0.8 and 1.6%) on (a) the rooting percentage and (b) the number of roots per rooted cuttings of single-node, leafy stem cuttings of *Cordia alliodora*, 9 weeks after insertion in non-mist propagators at Turrialba, Costa Rica. Values are means ( $n = 115$ ) of three clones; values grouped by the same letter are not significantly different at  $P < 0.05$ .

significantly higher number of roots (3.2) than Clones 4 (2.1) and 8 (2.8) at Week 9.

During the first 6 weeks, the percentage of cuttings with growing shoots was higher with successive decreases in IBA concentration. No significant differences were found between clones for this trait. When the percentage of cuttings with growing shoots at Week 3 was correlated with final rooting percentage, a strong negative relationship was found ( $r^2 = 0.63$ ; Fig. 2).

Highly significant differences in RWC were found between clones, with values from Clone 8 being lower than those from the other two clones ( $P < 0.05$ , ANOVA), but no difference between treatments was recorded. At Week 2, the RWC of all the cuttings was close to 100%, but by Week 4, values had

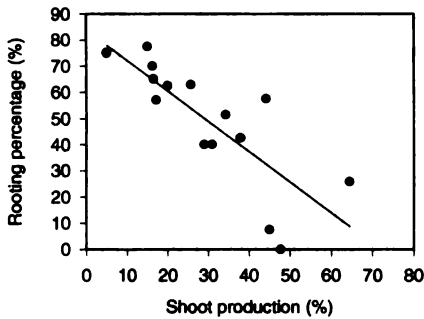


Fig. 2. The relationship between the percentage of *Cordia alliodora* cuttings rooted after 9 weeks and the percentage of cuttings with actively growing shoots at the third week after insertion in non-mist propagators at Turrialba, Costa Rica ( $y = -1.16x + 83.8$ ). Values were calculated for each of 15 clone  $\times$  treatment combinations (3 clones  $\times$  5 treatments), with 40 cuttings per combination.

declined to around 75%, gradually increasing thereafter.

No significant differences in foliar dry mass were found between cuttings subjected to different IBA concentrations during the 6 weeks after insertion. The foliar dry mass of all treatments decreased during the first 2 weeks after insertion, increasing thereafter to reach values similar to those obtained initially, by Week 6. In terms of total cutting dry mass, most IBA treatments showed a steady increase during the 6 weeks in the propagator. Treatment with 0.4% IBA showed a slight decrease during the first 4 weeks, but increased at Week 6 to values similar to those for the other treatments. The estimated dry mass gain over the 6 weeks following insertion was in the range 0.04–0.06 g per cutting.

### 3.2. Experiment 2

A maximum irradiance of  $335 \mu\text{mol m}^{-2} \text{s}^{-1}$  was recorded inside the propagator, with a mean of  $22 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Relative humidity varied between 78 and 100%, with a mean of 97%, and air temperature varied between 20.7 and 37.7°C, with a mean of 24.2°C. Slight differences were found between substrate temperatures; gravel showed the lowest mean temperature (22.9°C), followed by sawdust (23.2°C) and sand (24.3°C). Leaf temperatures also differed between treatments, ranging from 24.3°C (sawdust) to 25.6°C (sand) and 25.8°C (gravel). The largest

differences between treatments were found in leaf-to-air vapour pressure deficits (VPD), with maximum values of 0.61 kPa, 2.21 kPa and 6.58 kPa for sawdust, sand and gravel, respectively. When values of photosynthetically active radiation (PAR) were correlated with VPD, strong positive correlations were recorded ( $r^2 = 0.75, 0.82$  and  $0.63$  in sand, gravel and sawdust, respectively).

The three rooting media showed clear differences in their relative proportions of solids, water and air. The water component was higher in sawdust (53.8%) than in sand (17.6%) and gravel (4.5%). The air content was similar in sawdust (30.3%) and gravel (30.5%), and relatively low (5.5%) in sand.

Rooting percentages were relatively high, with values over 75% in all media. However, highly significant differences ( $P < 0.01$ ) were found between treatments after 6 weeks. Rooting percentages in both gravel and sand were significantly higher than in sawdust (Fig. 3(a)). A similar pattern was

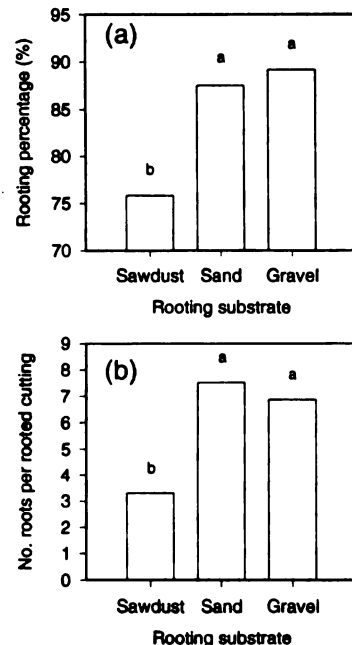


Fig. 3. The effects of rooting substrate on (a) the rooting percentage and (b) the number of roots per rooted cutting of single-node, leafy stem cuttings of *Cordia alliodora*, 6 weeks after insertion in non-mist propagators at Turrialba, Costa Rica. Values are means ( $n = 120$ ) of three clones; values grouped by the same letter are not significantly different at  $P < 0.05$ .

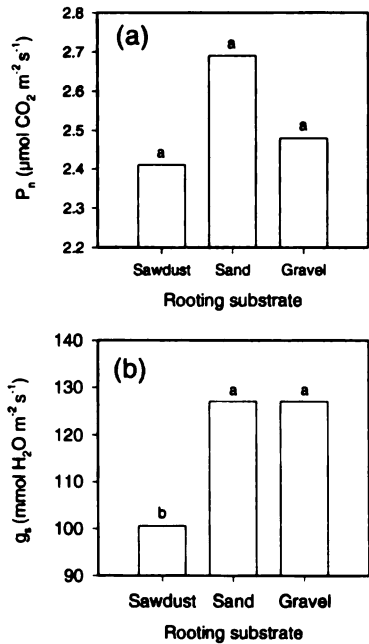


Fig. 4. The effect of rooting substrate on (a) the mean net photosynthetic rate ( $P_n$ ) and (b) the mean stomatal conductance ( $g_s$ ) of single-node, leafy stem cuttings of *Cordia alliodora* during propagation in non-mist propagators at Turrialba, Costa Rica. Values presented are means ( $n = 18$ ); means grouped by the same letter are not significantly different at  $P < 0.05$ .

found for number of roots per rooted cutting (Fig. 3(b)).

Clones also showed significant differences in rooting percentage, with Clone 35 displaying a significantly ( $P < 0.05$ , ANOVA) lower value than Clones 19 and 22 (64.2% vs. 97.5% and 90.8% in Clones 19 and 22, respectively). A similar ranking was found for number of roots per rooted cutting, with means of 5.8, 7.3 and 4.6 recorded for Clones 19, 22 and 35, respectively. The effect of both rooting medium and clone was confirmed by analysis of deviance; the effect of cutting diameter was not significant ( $P > 0.05$ ).

Photosynthetic rates of between 1.67 and 3.41  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  were recorded in the cuttings during the first 3 weeks after insertion. On average, values were higher in sand than in the other media (Fig. 4(a)). Stomatal conductances measured in cuttings in sand and gravel were significantly higher than those in sawdust (Fig. 4(b)). When val-

ues of PAR were correlated with  $P_n$ , positive correlations were found in all rooting media ( $r^2 = 0.54$ , 0.53 and 0.58 for sawdust, sand and gravel, respectively).

### 3.3. Experiment 3

A maximum irradiance of 556  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  was recorded inside the propagator during the course of the experiment. Relative humidity varied between 73.7 and 100%, with a mean of 94.8%. Mean air, substrate and leaf temperatures of 23.9, 21.9 and 25.1°C were recorded, with a maximum leaf temperature of 37.0°C. VPD varied between 0.31 and 2.41 kPa, with a mean of 0.65 kPa. There was a strong positive correlation between PAR and VPD ( $r^2 = 0.71$ ).

Nine weeks after insertion, highly significant differences ( $P < 0.01$ ) in rooting percentage were recorded between node positions. However, rooting percentage did not show a consistent trend with node position, values varying between 21.3% for Node 2 to 46.3% for Node 5 (Fig. 5). No significant differences were obtained for number of roots per rooted cutting, mean values ranging between 2.0 and 3.2. Stepwise regression revealed that rooting percentage was significantly influenced by clone, node position, cutting length and cutting diameter. Mean cutting diameter increased from 3.8 to 5.0 mm from Node 1 to Node 6, but mean cutting length did not show any systematic relation to node position, varying from 35.4 mm for Node 3 to 39.8 mm for Node 6. This

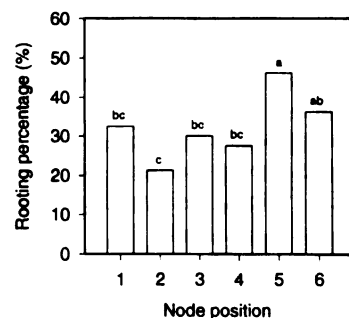


Fig. 5. The effects of node position (1, apical; 6, basal) on the rooting percentage of single-node, leafy stem cuttings of *Cordia alliodora*, 9 weeks after insertion in non-mist propagators at Turrialba, Costa Rica.  $n = 80$ ; values grouped by the same letter are not significantly different at  $P < 0.05$ .

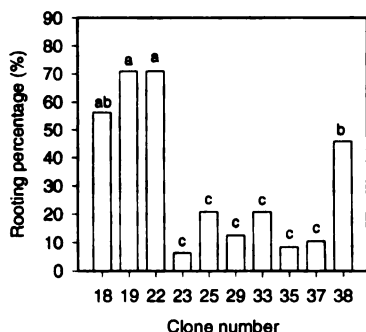


Fig. 6. Clonal variation in rooting of leafy stem cuttings of *Cordia alliodora* during propagation in non-mist propagators at Turrialba, Costa Rica.  $n = 48$ ; values grouped by the same letter are not significantly different at  $P < 0.05$ .

may account for the lack of a systematic relationship between rooting percentage and node position. Large variation in rooting was also observed between clones, values ranging between 6.3% (Clone 23) to 70.8% (Clone 22) (Fig. 6). A significant interaction ( $P < 0.05$ , ANOVA) between clone and node position was also recorded.

Photosynthetic rates of between 0.68 and 6.70  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  were recorded in cuttings during propagation. Stepwise regression showed that PAR and  $g_s$  accounted for the largest proportion of the total variation (58.7% and 14.0%, respectively), whereas clone (2.6%) and node position (1.5%) had a smaller effect. On average, apical (Nodes 1 and 2) and basal (Node 6) nodes displayed higher  $P_n$  val-

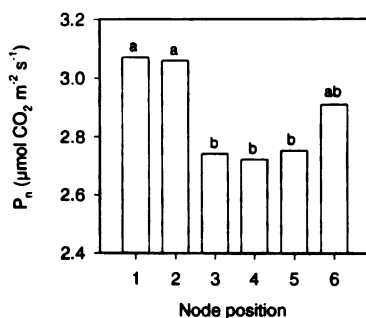


Fig. 7. The effect of node position (1, apical; 6, basal) on the mean net photosynthetic rate ( $P_n$ ) of single-node, leafy stem cuttings of *Cordia alliodora* during propagation in non-mist propagators at Turrialba, Costa Rica. Values presented are means ( $n = 40$ ); means grouped by the same letter are not significantly different at  $P < 0.05$ .

ues, whereas Nodes 3–5 showed the lowest values (Fig. 7). Stomatal conductances varied between 18.0 and 680.0  $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  during propagation; no significant effect of node position was recorded. When values of PAR were correlated with  $P_n$ , a strong positive correlation was recorded ( $r^2 = 0.80$ ).

#### 4. Discussion

The ability of auxins to promote adventitious root development in stem cuttings is well known, and has been attributed to enhanced transport of carbohydrate to the base of the cutting (Hartmann et al., 1990). However, contrasting effects of IBA addition have been recorded with different tree species. For example, the optimum IBA concentration for rooting of *Triplochiton scleroxylon* was found to be 0.4% (Leakey et al., 1982), substantially lower than that recorded here for *C. alliodora*. A particularly striking feature of the present results was the very low rooting in the control treatment, supplied with zero IBA. Successful rooting without applied auxin has been reported in a number of tropical tree species, such as *Shorea macrophylla* (Lo, 1985), *Milicia excelsa* (Ofori et al., 1996) and *Nauclea diderrichii* (Leakey, 1990). Such contrasting results may reflect variation in endogenous auxin contents at time of severance (Hartmann et al., 1990).

The negative relationship found between rooting percentage and shoot development may reflect competition for assimilates between the developing root and shoot during propagation (Davis, 1988), as recorded in *Populus tremula* (Eliasson, 1971). The inhibition of bud growth at increasing IBA concentrations supports results with *Milicia excelsa* (Ofori et al., 1996), and may be attributed to IBA-induced basipetal transport of assimilates. An alternative hypothesis is that applied auxins may inhibit bud growth, as injection of *Nauclea diderrichii* with auxin delayed sprouting of cuttings taken from them (Leakey, 1990).

The importance of propagation medium for the rooting of leafy cuttings is also widely recognized (Hartmann et al., 1990). In general, an appropriate rooting medium is described as one with an optimal volume of gas-filled porespace and an oxygen diffu-



sion rate adequate for the needs of respiration (Andersen, 1986). It is also clear that the provision of sufficient water to prevent wilting is a prime requirement (Loach, 1986). Tree species differ in their response to different media (Leakey et al., 1990). For example, in *Irvingia gabonensis* (Shiembo et al., 1996a), *Ricinodendron heudelotii* (Shiembo et al., 1996b) and *Milicia excelsa* (Ofori et al., 1996), higher rooting percentages were recorded in sawdust than in the other media tested, contrasting with the results obtained here with *C. alliodora*.

In general, media with relatively high water contents, such as sawdust, are associated with higher rates of water uptake in the cutting (Loach, 1986) and consequently higher rooting percentages. However, water can present a major diffusion barrier to oxygen, and excess water may thereby result in anoxia within the cutting base (Loach, 1986). Rotting of the cutting base in sawdust was frequently observed in the present investigation, indicating that *C. alliodora* requires a relatively well-aerated medium for cutting survival. Reduced water absorption through the cutting base resulting from tissue death may also explain the reduced stomatal conductance of cuttings in sawdust observed here (see Grange and Loach (1983)). The fewer roots per rooted cutting recorded in sawdust may also reflect anoxia, as recorded previously with *Chrysanthemum* cuttings (Hartmann et al., 1990) and *Cupressocyparis leylandii* (Loach, 1986).

Photosynthesis during propagation is generally thought to positively influence root formation in leafy cuttings (Davis, 1988), but few studies have actually measured photosynthesis during the rooting period. The photosynthetic rates recorded in Experiments 2 and 3, ranging between 0.68 and 6.70  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , are similar to those reported for *Terminalia spinosa* cuttings (0–6  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) under the same propagation system (Newton et al., 1992). In some cases, increases in the dry mass of the cuttings have been correlated with the rooting ability of cuttings (Leakey and Coutts, 1989), and rooting may also be related to photosynthesis of cuttings on shoots before severance (Leakey and Storeton-West, 1992). The results of the experiments described here, with measurements both of dry mass increment and photosynthetic rate, indicate that cuttings of *C. alliodora* actively photosyn-

thesize during propagation. However, no clear relationship between photosynthetic activity and rooting ability was apparent. It has been suggested that even low photosynthetic rates can contribute significantly to the carbon budget of a cutting (Okoro and Grace, 1976), but further research is required to fully evaluate the importance of photosynthesis during propagation for root development in *C. alliodora*.

Cutting origin has been found to be closely related to rooting ability in a number of other tree species. For example, in *Triplochiton scleroxylon*, rooting percentage of cuttings taken from different node positions was found to decline basipetally (Leakey and Mohammed, 1985). These and other results have led to the suggestion that cutting stem volume, as influenced by basipetal gradients in stem length and diameter, may have a pronounced influence on rooting by determining the storage capacity of carbohydrates produced pre- and post-severance (Leakey et al., 1994). The results recorded here with *C. alliodora* contrast with those obtained with other species: although higher cutting diameters were recorded at lower node positions, no consistent trend in rooting percentage was recorded. This suggests that other factors than stem volume, such as the content of plant growth regulators, may have been influential (Leakey et al., 1994).

One striking feature of these results was the clonal variation in rooting ability. Although no attempt was made to investigate this in any detail, such variation may clearly have profound implications for large-scale multiplication programmes. Genetic effects are among the least studied factors that control or modify rooting by cuttings (Haissig and Riemenschneider, 1988). The clonal variation in rooting ability recorded here was not easily explicable in terms of variation in the morphological or gas exchange characteristics observed.

These results indicate that, contrary to previous reports (Dyson, 1981), *C. alliodora* can be easily rooted, using the techniques described here. IBA should be applied to the cutting base to increase the rooting percentage and the number of roots produced by the cuttings. The highest concentration tested (1.6%) produced the highest rooting percentage and number of roots per rooted cutting, but the nature of the response suggests that the optimal IBA concentration for the rooting of *C. alliodora* may be even

higher than those tested here. Both the rooting percentage and the number of roots per cutting were reduced when sawdust was used, in comparison with sand and gravel, indicating that rooting substrates with relatively low water-holding capacities may be appropriate for propagation of this species.

Previous measurements have indicated that significant water deficits may occur in cuttings of *C. alliodora* during propagation, associated with peaks in VPD and PAR (Newton and Jones, 1993b). The close relationships recorded here between post-severance photosynthetic rate and PAR, and between PAR and VPD, suggest that careful management of the propagator microclimate may be required for optimum rooting of *C. alliodora* to be achieved (Newton and Jones, 1993a). For example, the use of shading may allow relatively low VPDs to be maintained around the cuttings, while providing sufficient irradiance for the cuttings to maintain a positive carbon balance. Further research is required to define more precisely the appropriate microclimate for propagation of this species.

## Acknowledgements

The authors thank the UK Overseas Development Administration and British Council for financial support, the Tropical Agricultural Research and Higher Education Centre (CATIE) for logistic support and the staff of the CATIE Tree Improvement Project for their help during the field work.

## References

- Andersen, A.S., 1986. Stockplant conditions. In: M.B. Jackson (Editor), *New Root Formation in Plants and Cuttings*. Martinus Nijhoff, Dordrecht, pp. 223–255.
- Beadle, C.L., Ludlow, M.M. and Honeysett, J.L., 1985. Water relations. In: J. Coombs, D.O. Hall, S.P. Long and M.O. Scurlock (Editors), *Techniques in Bioproductivity and Photosynthesis*, 2nd edn. Pergamon, Oxford, pp. 50–61.
- Boshier, D.H. and Mesén, J.F., 1987. Proyecto Mejoramiento de Árboles del CATIE: estado de avance y principales resultados. CATIE, Turrialba, 16 pp.
- Boshier, D.H. and Mesén, J.F., 1988. Availability of seed of *Cordia alliodora* for progeny testing. FAO For. Genetic Resource Inf. No. 15. FAO, Rome, pp. 30–35.
- Davis, T., 1988. Photosynthesis during adventitious rooting. In: T.D. Davis, B.E. Haissig and N. Sankhla (Editors), *Adventitious Root Formation in Cuttings*. Dioscorides Press, Portland, OR, pp. 79–87.
- Dyson, W.G., 1981. Report to ODA of the UK Government, London. CATIE, Turrialba, 16 pp.
- Eliasson, L., 1971. Adverse effect of shoot growth in rooted cuttings of aspen. *Physiol. Plant.*, 25: 268–272.
- Grange, R.I. and Loach, K., 1983. The water economy of unrooted cuttings. *J. Hort. Sci.*, 58(1): 9–17.
- Greaves, A. and McCarter, P.S., 1990. *Cordia alliodora*—a promising tree for tropical agroforestry. Tropical Forestry Papers No. 22. Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, 37 pp.
- Haissig, B.E. and Riemenschneider, D.E., 1988. Genetic effects on adventitious rooting. In: T.D. Davis, B.E. Haissig and N. Sankhla (Editors), *Adventitious Root Formation in Cuttings*. Dioscorides Press, Portland, OR, pp. 47–60.
- Hartmann, H.T., Kester, D.E. and Davies, F.T., 1990. *Plant Propagation—Principles and Practices*, 5th edn. Prentice-Hall, Englewood Cliffs, NJ, 647 pp.
- Hudson, J.M., 1984. A note on *Cordia alliodora* in Vanuatu. *Commonw. For. Rev.*, 63(3): 181–183.
- Leakey, R.R.B., 1990. *Nauclea diderrichii*: rooting of stem cuttings, clonal variation in shoot dominance, and branch plagiotropism. *Trees*, 4: 164–169.
- Leakey, R.R.B. and Coutts, M.P., 1989. The dynamics of rooting in *Triplochiton scleroxylon* K. Schum. cuttings: their relation to leaf areas, node position, dry weight accumulation, leaf water potential and carbohydrate composition. *Tree Physiol.*, 5: 135–146.
- Leakey, R.R.B. and Mohammed, H.R.S., 1985. The effects of stem length on root initiation in sequential single-node cuttings of *Triplochiton scleroxylon* K. Schum. *J. Hort. Sci.*, 60(3): 431–437.
- Leakey, R.R.B. and Storeton-West, R., 1992. The rooting ability of *Triplochiton scleroxylon* cuttings: the interactions between stockplant irradiance, light quality and nutrients. *For. Ecol. Manage.*, 49: 133–150.
- Leakey, R.R.B., Chapman, V.R. and Longman, K.A., 1982. Physiological studies for tropical tree improvement and conservation—some factors affecting root initiation in cuttings of *Triplochiton scleroxylon* K. Schum. *For. Ecol. Manage.*, 4: 53–66.
- Leakey, R.R.B., Mesén, J.F., Tchoundjeu, Z., Longman, K.A., Dick, J.McP., Newton, A., Matin, A., Grace, J., Munro, R.C. and Muthoka, P.N., 1990. Low-technology techniques for the vegetative propagation of tropical trees. *Commonw. For. Rev.*, 69(3): 247–257.
- Leakey, R.R.B., Newton, A.C. and Dick, J.McP., 1994. Capture of genetic variation by vegetative propagation: processes determining success. In: R.R.B. Leakey and A.C. Newton (Editors), *Tropical Trees: the Potential for Domestication and the Rebuilding of Forest Resources*. HMSO, London, pp. 72–83.
- Lo, Y.N., 1985. Root initiation of *Shorea macrophylla* cuttings: effects of node position, growth regulators and misting regime. *For. Ecol. Manage.*, 12: 43–52.

- Loach, K., 1986. Rooting of cuttings in relation to the propagation medium. Proc. Int. Plant Propagators' Soc., 35: 472–485.
- Mesén, J.F., Boshier, D.H. and Cornelius, J.P., 1994. Genetic improvement of trees in Central America with particular reference to Costa Rica. In: R.R.B. Leakey and A.C. Newton (Editors), Tropical Trees: the Potential for Domestication and the Rebuilding of Forest Resources. HMSO, London, pp. 249–255.
- Neil, P.E. and Jacovelli, P.A., 1985. Agroforestry as an aid to rational rural development in Vanuatu. Commonw. For. Rev., 64(3): 259–266.
- Newton, A.C. and Jones, A.C., 1993a. Characterization of microclimate in mist and non-mist propagation systems. J. Hort. Sci., 68(3): 421–430.
- Newton, A.C. and Jones, A.C. 1993b. The water status of leafy cuttings of four tropical tree species in mist and non-mist propagation systems. J. Hort. Sci., 68(5): 653–663.
- Newton, A.C., Muthoka, P. and Dick, J.McP., 1992. The influence of leaf area on the rooting physiology of leafy stem cuttings of *Terminalia spinosa* Engl. Trees, 6: 210–215.
- Ofori, D., Newton, A.C., Leakey, R.R.B. and Grace, J., 1996. Vegetative propagation of *Milicia excelsa* Welw. by leafy stem cuttings: effects of auxin concentration, leaf area and rooting medium. For. Ecol. Manage., 84: 39–48.
- Okoro, O.O. and Grace, J., 1976. The physiology of rooting *Populus* cuttings I. Carbohydrates and photosynthesis. Physiol. Plant., 36: 133–138.
- Payne, R.W., Lane, P.W., Ainsley, A.E., Bricknell, K.E., Digby, P.G.N., Harding, S.A., Leech, P.K., Sampson, H.R., Todd, A.D., Verrier, P.J. and White, R.B., 1987. GENSTAT 5: Reference Manual. Clarendon Press, Oxford.
- SAS Institute, Inc., 1980. SAS User's Guide: Statistics, Version 5 edn. Statistical Analysis Systems Institute, Inc., Cary, NC, pp. 113–137.
- Shiembo, P.N., Newton, A.C. and Leakey, R.R.B., 1996a. Vegetative propagation of *Iringia gabonensis*, a West African fruit tree. For. Ecol. Manage., 87: 185–192.
- Shiembo, P.N., Newton, A.C. and Leakey, R.R.B., 1996b. Vegetative propagation of *Ricinodendron heudelotii*, a West African fruit tree. J. Trop. For. Sci., in press.
- Snedecor, G.W. and Cochran, W.G., 1980. Statistical Methods, 7th edn. Iowa State University Press, Ames.
- Zobel, B. and Talbert, J.A., 1984. Applied Forest Tree Improvement. Wiley, New York.