Journal of Tropical Forest Science 12(1):77–91 (2000)

VEGETATIVE PROPAGATION OF *KHAYA IVORENSIS* (AFRICAN MAHOGANY): EFFECTS OF STOCKPLANT FLUSHING CYCLE, AUXIN AND LEAF AREA ON CARBOHYDRATE AND NUTRIENT DYNAMICS OF CUTTINGS

Z. Tchoundjeu* & R. R. B. Leakey

Institute of Terrestrial Ecology†*, Bush Estate Penicuik, Midlothian, EH26 0QB, Scotland, United Kingdom*

Received November 1997

TCHOUNDJEU, Z. & LEAKEY, R. R. B. 2000. Vegetative propagation of *Khaya ivorensis* (African mahogany): effects of stockplant flushing cycle, auxin and leaf area on carbohydrate and nutrient dynamics of cuttings. Four clones of *Khaya ivorensis* were grown in tropical glasshouses in Edinburgh. Single-node cuttings were treated with IBA and set under mist. Duplicate batches of cuttings were dried and analysed for their soluble carbohydrate and starch contents after 0,10, 20 and 30 days in the propagator. The first experiment tested the factorial combination of two levels of IBA (0 and 200 µg) and two leaf areas (50 and 100 cm^2). The primary effect was the enhanced rooting of auxin-treated cuttings. In the reducing sugar and starch contents (mg/cutting) of both leaf and stem, there was a decline up to day 10, with subsequent increase to day 20, especially in the larger-leaved, auxin-treated cuttings. In the second experiment, cuttings from dormant and flushing shoots were trimmed to 50 cm^2 leaf area and treated with 200 µg IBA. Cuttings from dormant shoots tended to root better than those from flushing shoots, this effect being significant in clone 8002. Flushing shoots had a greater concentration (% of dry mass) of soluble carbohydrates than dormant shoots throughout the 30-day propagation period. N, P, K concentrations were not significantly different in dormant or flushing shoots. Cuttings from basal nodes had greater NPK, soluble carbohydrate and starch contents, especially in dormant shoots. Rooting in dormant shoots peaked at node 7, but fluctuated between node positions in flushing shoots. It is concluded that there is no evidence of carbohydrates being a major factor affecting the rooting ability of *K. ivorensis* cuttings.

Keywords: Rooting - mist propagation - node position - *Khaya ivorensis* - carbohydrates

TCHOUNDJEU, Z. & LEAKEY, R. R. B. 2000. Pembiakan tampang pokok *Khaya ivorensis* (mahogany Afrika): kesan kitaran pengeluaran pucuk baru tanaman stok, auksin dan luas daun terhadap dinamik karbohidrat dan nutrien bagi keratannya. Empat klon *Khaya ivorensis* ditanam di dalam rumah kaca tropika di Edinburgh. Keratan buku tunggal dirawat dengan IBA dan diletakkan di bawah kabus. Kumpulan keratan secara ulangan dikeringkan dan kandungan karbohidrat terlarut dan

---

**Current address: IRAD/ICRAF Programme, PO Box 2123, Yaoundé, Cameroon.*

†*A component of the Edinburgh Centre for Tropical Forests.*

kandungan kayu dianalisis selepas 0, 10, 20 dan 30 hari di tempat pembiakan. Ujian pertama menguji gabungan faktor bagi dua tahap IBA (0 dan 200 μg) dan dua luas daun (50 dan 100 cm^2). Kesan awal ialah peningkatan pengakaran dalam keratan yang dirawat dengan auksin. Bagi pengurangan kandungan gula dan kanji (mg/keratan) dalam kedua-dua daun dan batang, terdapat kekurangan sehingga hari kesepuluh, dengan pertambahan secara berturutan hingga hari kedua puluh, terutama dalam keratan yang berdaun lebih besar dan dirawat dengan auksin. Dalam ujian kedua, keratan daripada pucuk dorman dan pucuk muda dipotong kepada 50 cm^2 luas daun dan dirawat dengan IBA 200 μg. Keratan daripada pucuk dorman didapati mengakar dengan lebih baik daripada pucuk muda. Kesan ini bererti dalam klon 8002. Pucuk muda mempunyai lebih kepekatan (% daripada jisim kering) dalam karbohidrat terlarut berbanding dengan pucuk dorman pada keseluruhan tempoh pembiakan selama 30 hari. Kepekatan N, P, K berbeza dengan tidak bererti dalam pucuk dorman atau pucuk muda. Keratan dari buku pangkal mempunyai kandungan NPK, karbohidrat terlarut dan kanji yang lebih tinggi, terutama dalam pucuk dorman. Pengeluaran dalam pucuk dorman memuncak pada buku 7, tetapi turun naik antara posisi buku dalam pucuk muda. Kesimpulannya tiada bukti yang menunjukkan karbohidrat menjadi faktor utama yang mempengaruhi keupayaan pengakaran keratan *K. ivorensis*.

Introduction

African mahogany (*Khaya ivorensis* A. Chev.) has been cultured and rooted *in vitro*, using meristem proliferation (Mathias 1988), and rooted as leafy stem cuttings under intermittent mist (Tchoundjeu 1989, Tchoundjeu & Leakey 1996). From the earlier study of rooting in leafy stem cuttings, it was clear that in this shade-tolerant, late succession, emergent species (Okali & Ola-Adams 1987), the optimal requirements for rooting differ in a number of respects from those of the early succession, light-demanding, shorter rotation *Triplochiton scleroxylon* (see Leakey 1983, Leakey *et al.* 1982, Leakey & Mohammed 1985). In *T. scleroxylon*, detailed studies have shown that the production of soluble carbohydrates by cuttings during the rooting process is of prime importance for successful propagation (Leakey & Coutts 1989, Leakey & Storeton-West 1992). However, for root initiation in cuttings from plants in general, the role of carbohydrates is unclear; some workers finding them to be important (Okoro & Grace 1976, Eliasson 1978, Jarvis & Booth 1981), while others report that there are no clear relationships between carbohydrates and rooting (Veierskov *et al.* 1982). The role of carbohydrates in rooting has been reviewed by Veierskov (1988).

Little is known about light and the photosynthetic process in cuttings (Davis 1988) and especially whether adaptations to different light environments are important. Like in many shade-tolerant trees in the tropics, shoot elongation in *K. ivorensis* is by short periods of recurrent flushing, separated by periods of bud rest or dormancy. This mode of growth is distinct from the free-growth of *T. scleroxylon*. The present study is part of a programme (Tchoundjeu 1989) to investigate the hypothesis that carbohydrates play a minor role in the rooting of *K. ivorensis*, a shade-adapted species (different from that already reported in a light demanding species like *T. scleroxylon*) and, in particular, considers this relative to the effects of its leaf area and flushing cycle. A study of the micropropagation of

K. ivorensis also examined the effects of the flushing cycle on the success of propagation *in vitro* (Mathias 1988, Newton *et al.* 1994) and found that explants from dormant shoots yielded more shoots per culture than flushing shoots, especially in shoots decapitated 2–3 days before taking the explants.

Materials and methods

Plants of three out of four clones of *K. ivorensis* were used in different combinations in two experiments. Clonal material was used to reduce the variability associated with the genetic differences between seedlings. These clones were propagated vegetatively by rooting leafy stem cuttings, as described by Tchoundjeu and Leakey (1996). These clones were derived from juvenile, hedged stockplants less than two years old, originating from seeds collected in Oyo State, Nigeria, by the Forestry Research Institute of Nigeria. The stockplants were grown in pots in automatically-controlled glasshouses at the Institute of Terrestrial Ecology (28 °C ± 2 °C with natural daylight supplemented by 400 W mercury vapour lamps to give a daylength of 19.5 h with a minimum irradiance of 150 μmol $m^{-2} s^{-1}$ PAR). The potting compost was a 7:3:1 mixture of peat:sand:loam with 4.2 g kg^{-1} "Enmag" (ICI, Haslemere, UK), 2.6 g kg^{-1} John Innes Base (Bentleys, Humberside, UK) and 0.3 g kg^{-1} fritted trace elements (ICI Haslemere, UK). Plants received weekly applications of 1% Sangral (L and K Fertiliser Ltd., Lincoln, UK) liquid fertiliser (NPK = 20:20:20) in place of the daily watering. White fly, red spider mite and scale insects were controlled by Diazinon (Murphy), Plictran (ICI Midox) and Vydate (Dupont) respectively.

Single-node leafy cuttings with, unless otherwise stated, a lamina area trimmed to 50 cm^2 using a template were taken from regularly hedged 2-shoot stockplants. Cutting length was determined by the length of each internode and varied from 12 to 98 mm. Except in untreated controls, 200 μg indole-3-butyric acid (IBA) dissolved in 10 μl industrial methylated spirit (IMS: 98% alcohol) was applied to the cutting base, using a micropipette (Eppendorf Comforpette 4700). IMS was evaporated off in a stream of cold air, prior to inserting the cuttings into a medium of coarse sand (2–4 mm) under intermittent mist (40 psi from Evenproducts No. 14, size 2, jets arranged 0.9 m apart and 0.65 m above the surface of the medium). Misting frequency was controlled by a timeclock giving 2 or 4 second bursts at 2 or 16 minute intervals day or night respectively. The beds were heated to *c.* 30 °C by 100 W m^{-2} insulated electric heating cables (Camplex Ltd.) arranged in successive layers of gravel as described by Leakey *et al.* (1982). The air temperature of the propagation area was 20 ± 3 °C, regulated by automatic venting and supplemented by extraction fans. The irradiance was that of the natural light.

Weekly assessments were made of rooting between weeks 2 and 11 by lifting the cuttings from the rooting medium. A cutting was said to be rooted when it had one or more roots in excess of 2 mm, but only cuttings with one or more roots exceeding 1 cm were potted. The compost used was the same as described above for stockplants and removed from the experiment. Cutting length was measured to the nearest mm at the first rooting assessment.

Analysis of variance was done on data with continuous variation (e.g. dry mass, cutting length, etc.) using Statview 512 computer packages (Abacus Concepts Inc., 24009 Venture Blvd., Calabasas, California, USA), and unless otherwise stated, statistical significance was at 5% level ($p = 0.05$). For data with binomial distribution, standard errors for percentages of cuttings rooted were transformed using the procedures of Snedecor and Cochrane (1980):-

$$\sqrt{\frac{\frac{a}{n}\left(1-\frac{a}{n}\right)}{n}}$$

where n = number of observational units (i.e. cuttings)
a = number with specific property (i.e. rooted cuttings).

Effects of leaf area and auxin (Experiment 1)

Eight stockplants of clones 8002 and 8012 and sixteen plants of clone 8013 were used in a factorial design to test two levels of IBA (0 and 200 μg/cutting) by two leaf areas (50 and 100 cm^2). Eight cuttings were taken per stockplant from dormant (quiescent) (i.e. non-flushing) shoots. Equal numbers of single-node cuttings of each clone were used for each treatment ($n = 16$ [8 × 2 plants] per treatment for clones 8002 and 8012, $n = 32$ [8 × 4 plants] per treatment for clone 8013). Because of the low numbers of cuttings of each clone per treatment, no attempt was made to analyse clonal variation in response to treatment. The cuttings were inserted in node order in equal numbers in 16 randomised blocks, according to the recommendations of Leakey *et al.* (1994). Half of the cuttings of each treatment were selected at random and used to assess rooting ability (n=32), while the other half were used for destructive harvests after 0, 10, 20 and 30 days ($n = 8$ per harvest per treatment) under intermittent mist. The latter cuttings were divided into stem and leaf portions for chemical analysis. These samples were dried at 80 °C for 48 h and ground, using a Glencreston Stanmore mill, to produce a powder which would pass through a 0.5 mm sieve. Reducing sugar content, as glucose equivalent, was determined after perchloric acid digestion, boiled at 100 °C for 10 minutes, by the Somogyi method (Allen *et al.* 1974). Starch content was determined by the same method after incubation with amyloglucosidase for a further hour at 55 °C. Non-reducing sugars were assayed by paper chromatography.

Effects of stage of flushing cycle (Experiment 2)

Eight plants each of clones 8002, 8013 and 8017 were selected for uniformity and twelve cuttings taken from the top shoot of each plant. The terminal buds of half of these plants were in a dormant state, while those of the other half were flushing and making rapid growth ($n = 144$ per treatment: $n = 48$ per clone ×

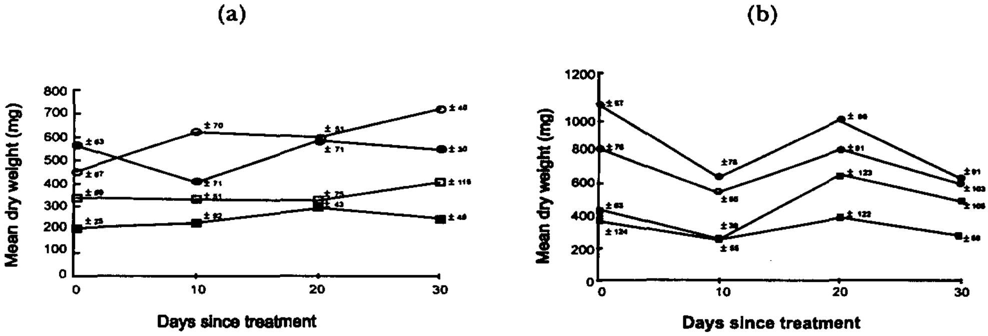
treatment). Single-node cuttings were taken and set in node order (1 = apical end) within 12 randomised blocks, each containing equal numbers of cuttings from dormant and flushing plants. Half the replicates of each treatment (i.e. dormant or flushing) were used to assess rooting ability (n=72), while the other half were allocated at random to destructive harvests after 0, 10, 20 and 30 days under intermittent mist (n = 18 per treatment). Leaf and stem portions were dried and ground, as in Experiment 1, for chemical analysis. Soluble carbohydrate content (mg per cutting) was determined by reflux boiling in distilled water for two hours (Deriaz 1961) and then assessed using Anthrone reagent. Starch was extracted using perchloric acid and glucose equivalent determined by thiosulfate titration, using the Somogyi method (Allen *et al.* 1974). Nitrogen and phosphorus contents were determined by auto-analyser using the salicylate-nitroprusside and molybdenum blue methods respectively. Potassium determination was by a gravimetric method using cobaltinitrite (Allen *et al.* 1974).

Results

Effects of leaf area and auxin

In cuttings with leaves trimmed to 50 cm^2, stem and leaf dry weights were virtually unchanged throughout the period of propagation, regardless of whether treated with auxin or not (Figure 1a). However, in auxin-treated cuttings with leaves trimmed to 100 cm^2, there was a significant loss of dry matter from days 0 to 10, in both leaf and stem. This was followed by an increase in dry matter, which was significant in both leaf and stem of auxin-treated cuttings, between days 10 and 20 (Figure 1b). Similar, but non-significant patterns of change were seen for cuttings that did not receive auxin (Figures 1a and b). The treatments had no significant effects on the dry weights of cuttings from different node positions, although overall basal node cuttings had greater dry weight than those from apical nodes, with the relative difference between them increasing with time in the propagator (Figure 2).

As a percentage of dry matter, the reducing sugar concentrations of both leaves and stems of cuttings were not significantly affected by leaf area, auxin application, or by time in the propagator. By contrast, the starch concentration (% dry matter) of auxin-treated, 100 cm^2-leaved cuttings declined significantly between days 0 and 10, with this trend continuing to day 20. On a dry matter per cutting (mg cutting^{-1}) basis there were significant fluctuations in both starch and reducing sugar contents between days 0 and 10, 10 and 20, and 20 and 30 in the leaf of 100 cm^2-leaved cuttings (Figures 3a and b), which were less pronounced, but still significant, in the auxin-treated stem portions. In the 50 cm^2 - leaves, there was a peak in starch content of non-auxin-treated cuttings at day 10 and a steady increase over time in their reducing sugar content (Figures 3 c, d), while leaves of auxin-treated cuttings increased in both starch and reducing sugar contents from days 10 to 30.


(a)

(b)

Figure 1. Effects of leaf area (a = 50 cm², b = 100 cm²) and auxin (□,○ = without IBA; = ■,● with 200 μg IBA per cutting) on the mean dry weights of stem (■, □) and leaf (●,○) portions (± s.e. of mean) of *K. ivorensis* cuttings during thirty days under intermittent mist

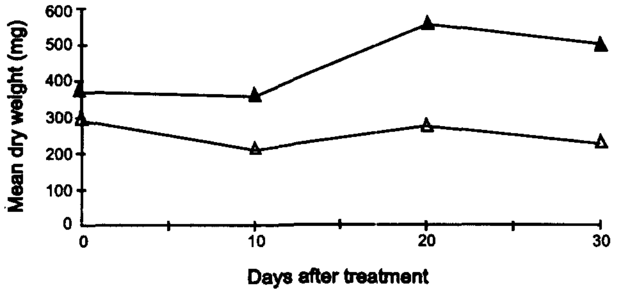


Figure 2. Effects of cutting position within a shoot (Δ = 6 apical nodes, ▲ = 6 basal nodes) on the mean dry weight of the stem portions of *K. ivorensis* cuttings during 30 days under intermittent mist (mean of 2 leaf areas + 2 auxin treatments) (n = 64)

Rooting in these cuttings was overridingly affected by auxin application. IBA-treated cuttings had high rooting percentages (70–80%). Untreated cuttings rooted at less than 5%, while those with leaves trimmed to 100 cm² failed to root at all (Figure 4). No auxin by leaf area interaction was observed.

Effects of stage of flushing cycle

Cuttings from dormant and flushing shoots rooted equally well up to week 4. Thereafter there was a non-significant tendency for cuttings from dormant shoots to have higher rooting percentages (Figure 5). This difference between dormant and flushing shoots was, however, significant in one of the clones tested (clone 8002), suggesting a clone x flushing cycle interaction.

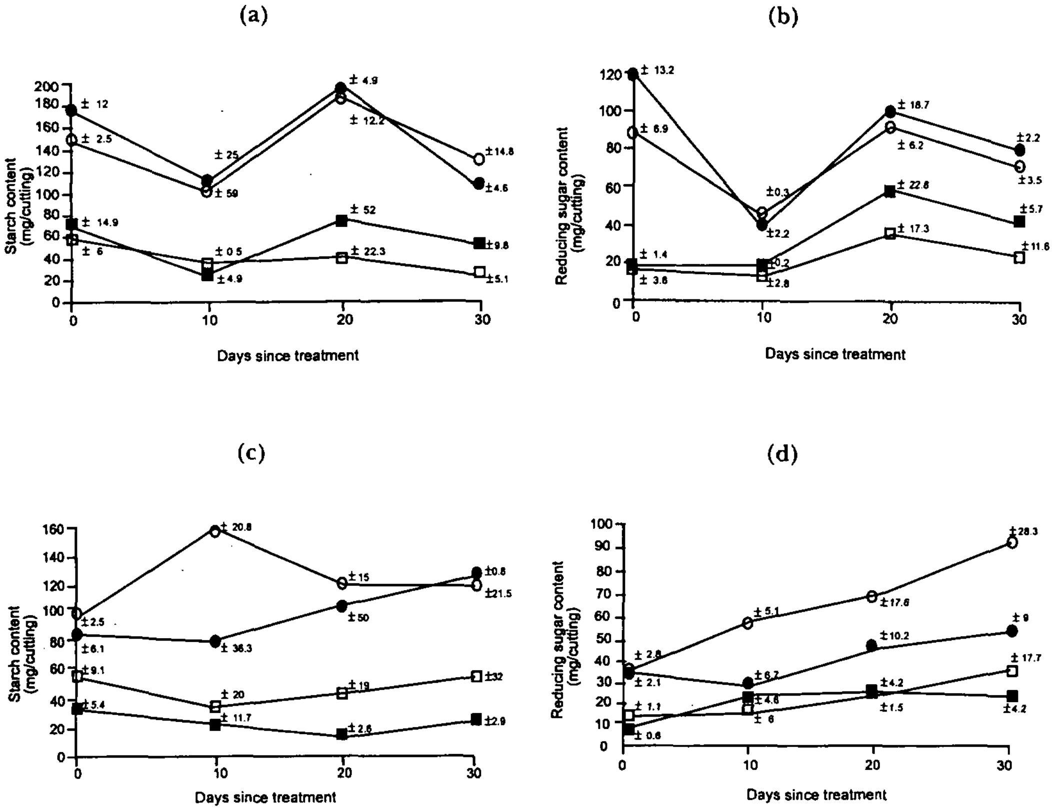


Figure 3. Effects of leaf area (a and b = 100 cm^2, c and d = 50 cm^2) and auxin (□,○ = without auxin; = ■,● with 200 μg IBA per cutting) on the starch (a & c) and reducing sugar (b & d) contents of stem (□,■) and leaf (○,●) portions (± s.e. of mean) of *K. ivorensis* cuttings during 30 days of intermittent mist

The mean dry weights of leaves and stems of cuttings from dormant and flushing shoots were not significantly different (Figure 6). In both leaves and stems, dry weight declined significantly over the first 10 days after severance, increasing again by day 30 (Figure 6). This decline in dry matter over the first 10 days after severance was associated with a significant increase in the concentration (% dry matter) of soluble carbohydrates in both flushing and dormant shoots. Flushing shoots had a greater concentration of soluble carbohydrates than dormant shoots throughout the 30 days period of propagation. This difference between flushing and dormant shoots in their soluble carbohydrate contents (mg per cutting) was significant at days 10 and 20 (Figure 7a). The starch contents of dormant and flushing shoots were similar and increased significantly from day 10 to day 30 (Figure 7b).

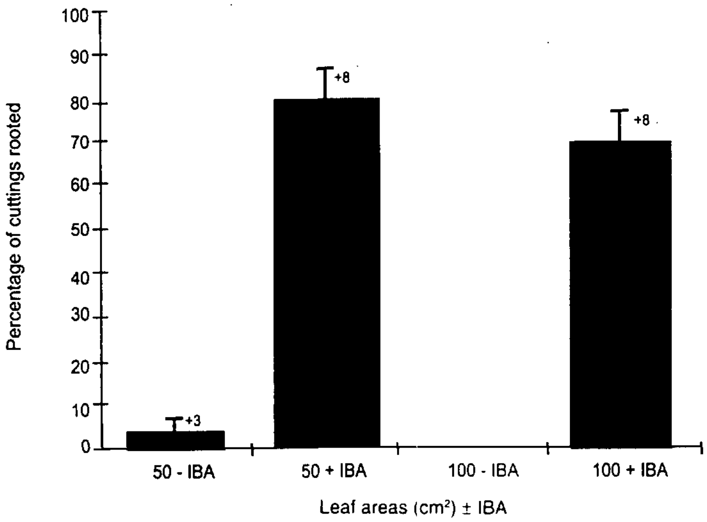


Figure 4. Effects of leaf area (50, 100 cm^2) and IBA (0, 200 μg per cutting) on the rooting of single-node *K. ivorensis* cuttings (± s.e. of mean) under intermittent mist (week 11)

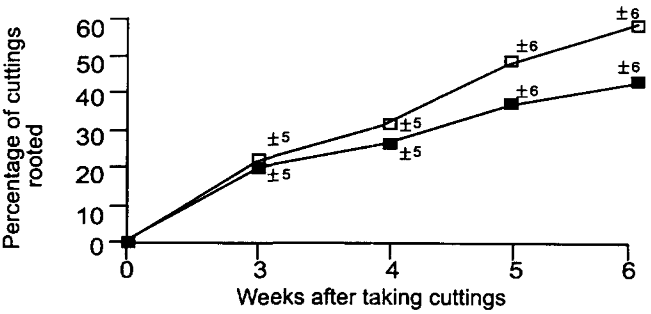


Figure 5. Effects of the stage of the flushing cycle (dormant (☐) and flushing (■)) on the cumulative rooting of *K. ivorensis* leafy (50 cm^2) cuttings treated with 200 μg IBA during propagation under intermittent mist (± s.e. of mean)

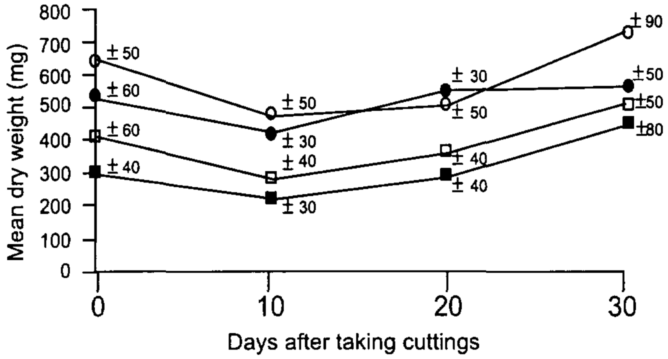


Figure 6. Effects of the stage of the flushing cycle [dormant (○,□) and flushing (●,■)] on the mean dry weights of leaf (○,●) and stem (□, ■) portions of *K. ivorensis* leafy (50 cm²) cuttings treated with 200 μg IBA during propagation under intermittent mist (± s.e. of mean)

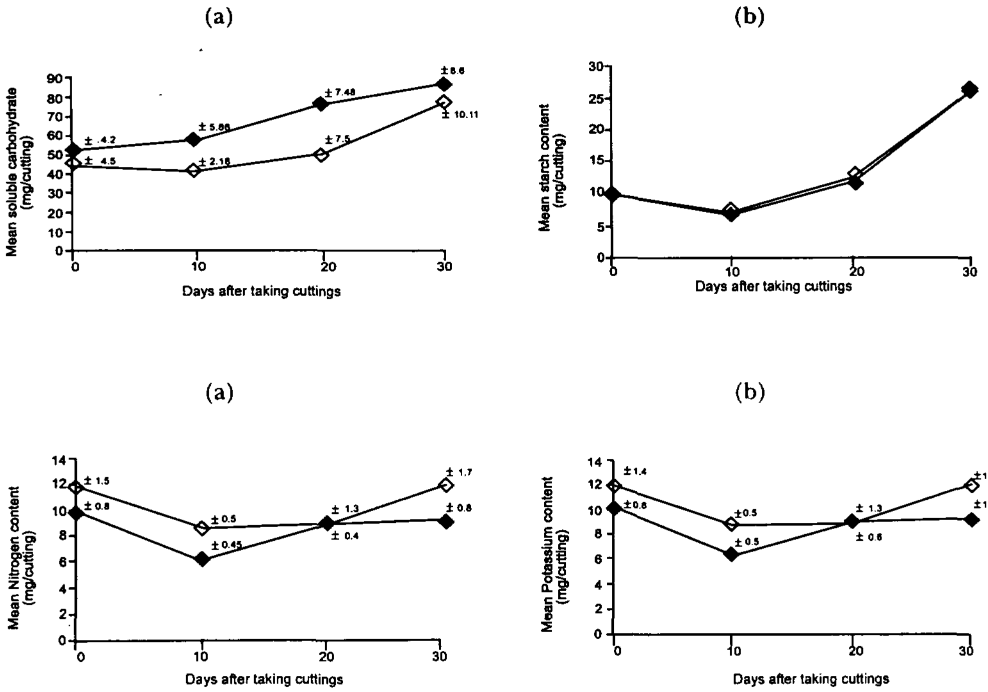


Figure 7. Effects of the flushing cycle (flushing ◆, dormant ◇) on mean contents (mg/cutting) of a) soluble carbohydrate, b) starch, c) nitrogen, and d) potassium of auxin-treated *K. ivorensis* cuttings after 0, 10, 20 and 30 days propagation under intermittent mist (± s.e. of mean)

Nitrogen, phosphorus and potassium concentrations (% dry matter) were not significantly different in dormant or flushing shoots. While the phosphorus contents (mg per cutting) were the same in dormant and flushing shoots and were unchanged with time, the contents of nitrogen and potassium between the two shoot types did differ significantly at different dates after severance (Figures 7c, d). Higher levels of NPK, soluble carbohydrates and starch were found at basal nodes than at the next nodal positions, more so at day 0 in dormant than in flushing shoots (Figure 8, Table 1). There was a relationship between nitrogen content of cuttings and their soluble carbohydrate and starch contents; the relationship between nitrogen and soluble carbohydrate contents was particularly strong ($r^2 = 0.96$) in flushing shoots (Figure 9), across the different node positions.

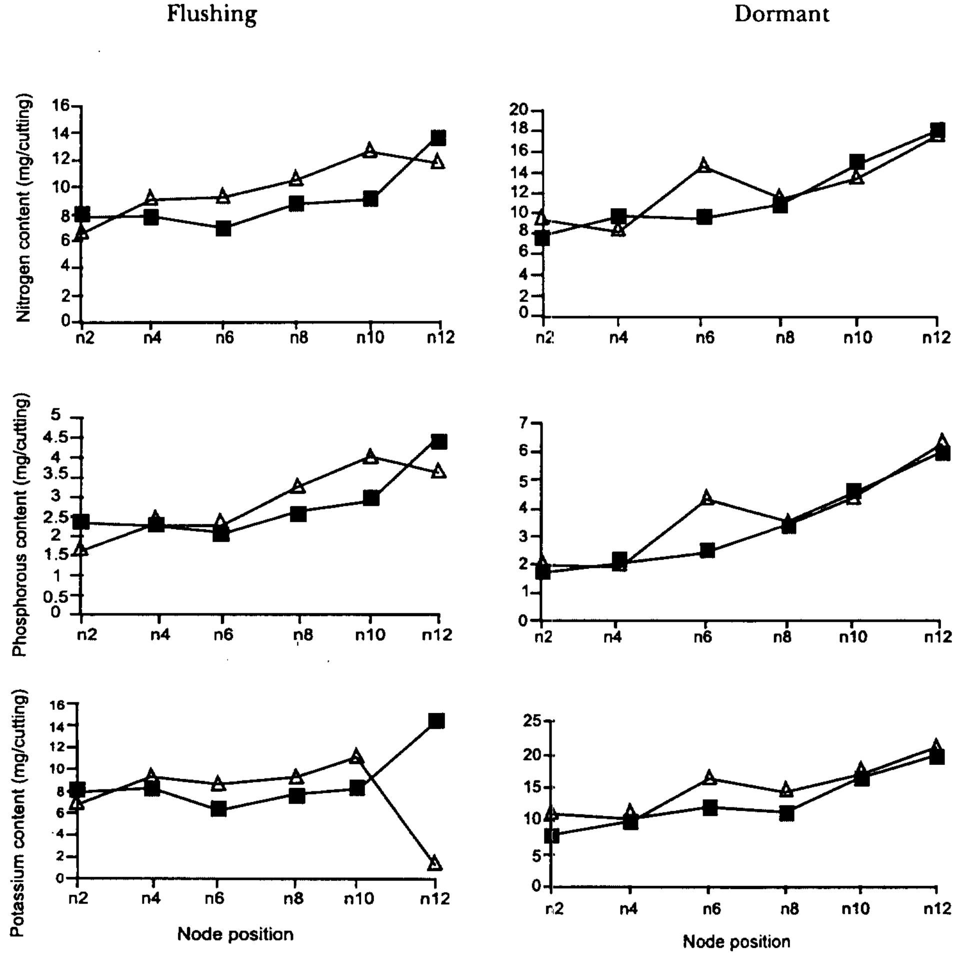


Figure 8. Effects of the stage of the flushing cycle (flushing, dormant) on the nitrogen, phosphorous and potassium contents (mg/cutting) of auxin treated *K. ivorensis* cuttings from different node positions, during 0 (Δ) and 30 (■) days propagation under intermittent mist

Table 1. Effects of node position on soluble carbohydrate and starch contents (mg per cutting) of single-node, leafy (50 cm^2) stem cutting from dormant and flushing shoots of *K. ivorensis*, and the percentage of cuttings rooted. Data for carbohydrates and rooting are from alternate node positions on the same plants.

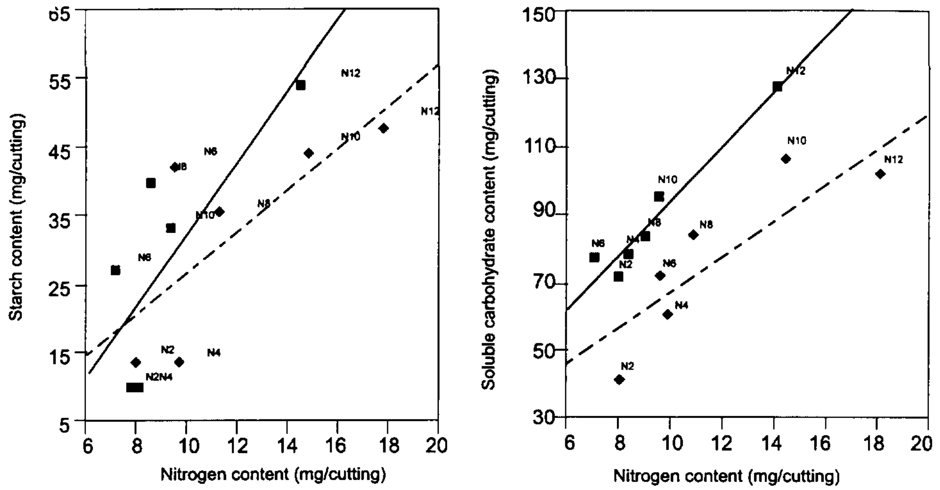
		Node position					
		2	4	6	8	10	12
Soluble carbohydrate							
Dormant	Day 0	34.7	28.9	52.3	44.5	48.1	58.0
Flushing	Day 0	38.7	50.8	48.1	69.6	56.8	53.6
Dormant	Day 30	40.0	61.2	75.3	83.3	109.6	96.5
Flushing	Day 30	71.3	78.1	76.1	83.6	92.9	128.8
Starch							
Dormant	Day 0	5.0	3.0	12.0	10.0	11.0	23.0
Flushing	Day 0	5.0	8.0	14.0	12.0	12.0	11.0
Dormant	Day 30	14.0	14.0	42.0	13.0	44.0	48.0
Flushing	Day 30	9.0	9.0	27.0	41.0	32.0	54.0

		Node position					
		1	3	5	7	9	1
Rooting percentage							
Dormant	Day 42	42	75	67	83.3	50	33.3
Flushing	Day 42	42	33.3	67	33.3	18.2	33.3

Regression analysis of carbohydrate content (starch or solubles) of cuttings and their rooting percentages (Table 1) showed that they were not strongly related in either of the two experiments of the present study.

Discussion

High rooting percentages of *K. ivorensis* cuttings can be obtained by optimising leaf area, cutting length and auxin application (Tchoundjeu & Leakey, in press). This result conforms with previous experience in *T. scleroxylon,* another West African hardwood which has an optimum leaf area of 50 cm^2 for rooting (Leakey *et al.* 1982, Leakey & Mohammed 1985, Leakey & Coutts 1989). However, a similarity between these species was not apparent in the present study. The rooting of *T. scleroxylon* cuttings, as in *Eucalyptus grandis* (Hoad & Leakey 1992, 1996), depends on the production of current assimilates during the rooting process. In the light demanding species, rates of net photosynthesis post severance are conditioned prior to severance by the predetermining effects of stockplant light quality, irradiance and nutrients (Leakey & Coutts 1989, Leakey & Storeton-West 1992, Leakey *et al.* 1994).



Regression results, fitting the model y= a + bN

	a	b	r^2
Flushing, Carbohydrate	14.2	0.98	0.96
Dormant, Carbohydrate	13.8	0.83	0.68
Flushing, Starch	-20.2	0.77	0.59
Dormant, Starch	-3.3	0.76	0.58

Figure 9. Relationships in single node cuttings from flushing (■, —) and dormant (◆, - -) shoots of *K. ivorensis* between (a) nitrogen and starch contents, and (b) nitrogen and soluble carbohydrate contents. Cuttings are identified by node positions (N2 - N12)

In contrast, the rooting of *K. ivorensis* cuttings does not seem to be influenced by carbohydrate content, as no relationships were found at any stage of the rooting process between the carbohydrate content of cuttings and their rooting. The small optimum leaf area reported for rooting (Tchoundjeu & Leakey 1996) also suggests that the production of current assimilates is not crucial for rooting. The difference in independence on carbohydrates between these species is perhaps explained by the greater shade tolerance of *K. ivorensis*, which occurs later in the forest succession of West Africa than *T. scleroxylon*. It is perhaps possible that *K. ivorensis* cuttings would be carbohydrate limited if grown in deep shade, but in these experiments stockplants of both *K. ivorensis* and *T. scleroxylon* were grown in environmentally-controlled glasshouses in which natural daylight was supplemented by artificial lights. This glasshouse environment equates approximately with nursery conditions in the tropics (Ladipo *et al.* 1992).

Khaya ivorensis grows by recurrent flushing, as opposed to the free growth of *T. scleroxylon*. In cocoa (*Theobroma cacao*), recurrent flushing is reported to be regulated by cyclical fluctuations in the production of and demand for carbohydrates (Machado & Hardwick 1987). Thus, because of their very different carbohydrate contents, cuttings from flushing and dormant shoots might be expected to have different rooting abilities. However, despite the difference in the carbohydrate and NPK contents of cuttings from dormant and flushing shoots of *K. ivorensis,* there was only limited variation in their rooting abilities. While generally carbohydrates are necessary for rooting (see reference in the Introduction), the result here suggests that they are not the key factor determining success in this species.

In the present study, the dynamics of the carbohydrate content of cuttings were followed throughout the rooting period. It was clear that although there were minor fluctuations in carbohydrate reserves, the minor losses soon after severance were subsequently replenished. Indeed, especially at the more basal nodes, these levels increased and a higher proportion of cuttings rooted. In the present study, cutting leaf area had less effect on rooting than in that of Tchoundjeu and Leakey (1996). It is possible that the size range was insufficient to obtain a difference. This may also explain the lack of any effects of leaf area on the carbohydrate dynamics of these cuttings, especially since these leaf area effects have been reported to be greater in short stemmed cuttings (Tchoundjeu & Leakey 1996).

The application of IBA to the base of these mahogany cuttings had a major promotive effect on rooting without any apparent effect on the carbohydrate contents of the stems. This was despite a temporary post-severance decline in the reducing sugar, starch content and dry weight of the leaves. This concurs with the suggestion that one of the effects of applying auxin is to increase the supply of carbohydrates at the cutting base for root formation (Dick & Dewar 1992). The magnitude of these responses to IBA in *K. ivorensis,* however, suggests that the effect of exogenous auxin on carbohydrate supply to the cutting base may be important, even in a species in which carbohydrates are not limiting overall.

Although not found in this study, cuttings from basal nodes of *K. ivorensis* have been reported to have the greatest rooting percentages (Tchoundjeu & Leakey 1996). The results of the present study suggest that the relationships between nutrient and carbohydrate contents and rooting may warrant further study especially as (i) C:N ratio is reported in some species to be an important influence on rooting (see review by Veierskov 1988), and (ii) there is consistently a relationship between nitrogen content and carbohydrates (soluble and starch) in *K. ivorensis* at the different node positions (Figure 9).

In conclusion, this study found no relationship between carbohydrate content and rooting in *K. ivorensis* cuttings. This is in marked contrast to cuttings of light demanding species like *T. scleroxylon* (Leakey & Coutts 1989, Leakey & Storeton-West 1992) or *E. grandis* (Hoad & Leakey 1994, 1996). Further studies are required to determine whether species from different ecological niches have different relationships between their rooting abilities and carbohydrate requirements from reserves or current photosynthesis.

Acknowledgements

The Commission of European Communities (CEC) DGXII and the Overseas Development Administration (ODA) are gratefully acknowledged for provision of research funds.

References

Allen, S. E., Grimshaw, H. M., Parkinson, J. A. & Quarmby, C. 1974. *Chemical Analysis of Ecological Materials.* Blackwell Scientific Publications, Oxford. 565 pp.

Davis, T. D. 1988. Photosynthesis during adventitious rooting. Pp. 79–87 in Davis, T. D., Haissig, B. E. & Sankhla, N. (Eds.) *Adventitious Root Formation in Cuttings.* Dioscorides Press, Portland, USA.

Deriaz, R. E. 1961. Routine analysis of carbohydrates and lignin in herbage. *Journal of the Science of Food and Agriculture* 12:152–160.

Dick, J. McP. & Dewar, R. 1992. A mechanistic model of carbohydrates dynamics during adventitious root development in leafy cuttings. *Annals of Botany* 70:371–377.

Eliasson, L. 1978. Effects of nutrients and light on growth and root formation in *Pisum sativum* cuttings. *Physiologia Plantarum* 43:13–18.

Hoad, S. P. & Leakey, R. R. B. 1992. Morphological and physiological factors induced by light quality and affecting rooting in *Eucalyptus grandis.* Pp. 51–58 in *Mass Production Technology for Genetically Improved Fast Growing Forest Tree Species.* Volume 1. AFOCEL, Nangis, France.

Hoad, S. P. & Leakey, R. R. B. 1994. Effects of light quality on gas exchange and dry matter partitioning in *Eucalyptus grandis* W. Hill ex Maiden. *Forest Ecology and Management* 70:265–273.

Hoad, S. P. & Leakey, R. R. B. 1996. Effects of preseverance light quality on the vegetative propagation of *Eucalyptus grandis* W. Hill ex Maiden: cutting morphology, gas exchange and carbohydrate status during rooting. *Trees* 10:317–324.

Jarvis, B. C. & Booth, A. B. 1981. Influence of indole-butyric acid, boron, myoinositol, vitamin D2 and seedling age on adventitious root development in cuttings of *Phaseolus aureus. Physiologia Plantarum* 53:213–218.

Ladipo, D. O., Leakey, R. R. B. & Grace, J. 1992. Bud activity of decapitated nursery-grown plants of *Triplochiton scleroxylon* in Nigeria: effects of light, temperature and humidity. *Forest Ecology and Management* 50:287–298.

Leakey, R. R. B. 1983. Stockplant factors affecting root initiation in cuttings of *Triplochiton scleroxylon* K. Schum., an indigenous hardwood of West Africa, *Journal of Horticultural Science* 58:277–290.

Leakey, R. R. B., Chapman, V. R. & Longman, K. A. 1982. Physiological studies for tropical tree improvement and conservation. Some factors affecting root initiation in cuttings of *Triplochiton scleroxylon* K. Schum. *Forest Ecology and Management* 4:53–66.

Leakey, R. R. B. & Coutts, M. P. 1989. The dynamics of rooting in *Triplochiton scleroxylon* cuttings: their relation to leaf area, node position, dry weight accumulation, leaf water potential and carbohydrate composition. *Tree Physiology* 5:135–146.

Leakey, R. R. B. & Mohammed, H. R. S. 1985. Effects of stem length on root initiation in sequential single-node cuttings of *Triplochiton scleroxylon* K. Schum. *Journal of Horticultural Science* 60: 431–437.

Leakey, R. R. B., Newton, A. C. & Dick, J. McP. 1994. Capture of genetic variation by vegetative propagation: processes determining success. Pp. 72–83 in Leakey, R. R. B. & Newton, A. C. (Eds.) *Tropical Trees: The Potential for Domestication and the Rebuilding of Forest Resources.* HMSO, London.

Leakey, R. R. B. & Storeton-West, R. 1992. The rooting ability of *Triplochiton scleroxylon* K. Schum cuttings: the interactions between stockplant irradiance, light quality and nutrients. *Forest Ecology and Management* 49:133–150.

Machado, R. C. R. & Hardwick, K. 1987. Does carbohydrate availability control flush growth in cocoa? Pp. 143–149 in *Proceedings 10th International Cocoa Research Conference.* Santa Domingo.

Mathias, P. 1988. Micropropagation of the Tropical Hardwoods *Khaya ivorensis* A. Chev. and *Nauclea diderrichii* (De Wild and Th. Dur.) Merril. Ph.D. thesis, University of Nottingham. 312 pp.

Newton, A. C., Leakey, R. R. B., Powell, W., Chalmers, K., Waugh, R., Tchoundjeu, Z., Mathias, P. J., Alderson, P. G., Mesén, J. F., Baker, P. & Ramnarine, S. 1994. Domestication of mahoganies. Pp. 256–266 in Leakey, R. R. B. & Newton, A. C. (Eds.) *Tropical Trees: The Potential for Domestication and the Rebuilding of Forest Resources.* HMSO, London.

Okali, D. U. U. & Ola-Adams, B. A. 1987. Tree population changes in treated rainforest at Omo Forest Reserve, south-western Nigeria. *Journal of Tropical Ecology* 3:291–313.

OKORO, O. O. & GRACE, J. 1976. The physiology of rooting *Populus* cuttings. I. Carbohydrates and photosynthesis. *Physiologia Plantarum* 36:133–138.

SNEDECOR, G. W. & COCHRANE, W. G. 1980. *Statistical Methods.* 7th edition. The Iowa State University Press, Iowa, USA.

TCHOUNDJEU, Z. 1989. Vegetative Propagation of the Tropical Hardwoods *Khaya ivorensis* A. Chev. and *Lovoa trichilioides* Harms. Ph.D. thesis, University of Edinburgh. 270 pp.

TCHOUNDJEU, Z. & LEAKEY, R. R. B. 1996. Vegetative propagation of African mahogany: effects of auxin, node position, leaf area and cutting length. *New Forests* 11:125–136.

VEIERSKOV, B. 1988. Relations between carbohydrates and adventitious root formation.Pp. 70–78 in Davis, T. D., Haissig, B. E. & Sankhla, N. (Eds.) *Adventitious Root Formation in Cuttings.* Dioscorides Press, Portland, U.S.A.

VEIERSKOV, B., ANDERSEN, A. S. & ERIKSEN, E. N. 1982. Dynamics of extractable carbohydrates in *Pisum sativum.* I. Carbohydrate and nitrogen content in plants and cuttings grown at two different irradiances. *Physiologia Plantarum* 55:167–173.