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Clonal Variation in a Four-Year-Old Plantation of Triplochiton scleroxylon K. Schum. and its Relation to the Predictive Test for Branching Habit

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Summary

Considerable clonal variation is reported in the size and form of the West African tree *Triplochiton scleroxylon* K. SCHUM. after four years of growth in plantations near Ibadan, Nigeria. At normal spacing (2.4 m) mean heights ranged from 5.9 m to 8.1 m, whilst at wide spacing (4.9 m) the range was 5.1 m to 7.8 m, although the trunks had a greater diameter. Form varied considerably, some clones having straight monopodial stems while others were multi-stemmed, much-forked or heavily branched. The relationship between these characteristics and the result of a Predicitive Test for Branching Habit is reported. This test is based on genetic variation in apical dominance following decapitation and is made on very young plants in the nursery, 3 to 4 weeks after removal of the terminal bud. There were correlations between field characters (extent of branching, the incidence of heavy branching, and the diameter of the stem) and indices obtained from the test. The possibility is discussed of using the test to screen young seedlings for those which, following vegetative propagation, are likely to give clones with a low branching frequency and high harvest index.

Key words: apical dominance, correlative inhibition, clonal variation, branching, decapitation, screening test, tree improvement, Triplochiton scleroxylon.

Introduction

Triplochiton scleroxylon K. SCHUM. (Sterculiacase) is an important forest tree of West Africa. For much of this century it has accounted for more of the timber extracted annually from the region than any other species (HALL and BADA, 1979). In the early 1960s it was realised that the quality and quantity of the remaining resource had been diminished by over-exploitation, and so a programme of tree improvement began at Ibadan, Nigeria, known as the West African Hardwoods Improvement Project (HOWLAND and BOWEN, 1977). Methods of vegetative propagation of *T. scleroxylon* were rapidly developed and clonal trial plantations were established in 1975 and 1976.

The first purpose of the present paper is to describe the clonal variation in some of the main morphometric attributes of 4-year-old trees and to relate these to a physiological characteristic measured in very young plants. It is possible that undesirable traits, like forking, multiple stem growth and heavy branching, may be related to inherent features of apical dominance which persist throughout the life of the tree. Earlier studies have demonstrated that decapitation of young plants breaks apical dominance and reveals clonal variation in bud outgrowth (LEAKEY and LONGMAN, 1986; LADIPO, LEAKEY and GRACE, 1991 and in press b). It is hypothesised that this phenomenon provides a prediction of the branching habit inherent to each clone. We have therefore called this assessment of asical dominance and branching frequency the Predictive Test for Branching Habit.

The second aim of the present work is to search for relationships between the result of the Predictive Test in young clonal plants at the nursery stage and the size and form of the same clones after several years' growth in plantation. If such relationships exist, it should be pos-

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Table 1. — Origin of clones and their distribution (0 = tested) between experiments.

Clone Number	Nigerian Provenance			Rainfall (mm)	Spacing (2.4m)	Spacing (4.8m)	Tested by Decapitation
137/9	Olokomeji	7.35°N	3.52°E	1300–1500	0		0
139/6	"			"	0		0
139/9	"			"	0	0	0
142/10	Omerelu	5.28°N	6.92°E	2000–2500	0	0	
144/1	Igbo-ora	7.45°N	5.62°E	1000–1300	0	0	0
144/4	"			"	0		
144/5	"			"	0		0
144/7	"			"	0		0
144/9	"			"	0		0
161/3	Owo	7.03°N	5.72°E	1300–1500	0		
161/5	"			"	0		0
166/1	Azukala	7.03°N	6.45°E	"	0		0
166/3	"			"	0		0
116/8	"			"		0	
175/1	Igbado	6.82°N	4.87°E	1500–2000	0	0	0
175/2	"						
175/5	"			"	0	0	0
175/6	"			"	0		0
175/7	"			"	0		0
175/8	"			"	0		0
175/9	"			"	0		0
175/10	"			"	0	0	
177/10	Ilugun	7.35°N	3.65°E	1300–1500	0	0	0
224/1	Ede			"		0	
224/7	"	7.70°N	4.43°E	"	0		0
225/8	"			"			

sible to make selections from juvenile material and thus speed up the process of forest tree improvement by screening large populations of seedlings to detect genotypes worthy of subsequent vegetative propagation and more detailed field testing.

Materials and Methods

The clones all originated in Nigeria (*Table 1*), and had been both maintained in the nursery as clonal stockplants, and established in 1975 in three experimental plantations using rooted cuttings (Howland and Bowen, 1977). These plantations were at Onigambari Forest Reserve, near Ibadan (7.12 ^{0}N, 3.75 ^{0}E; rainfall exceeding 1500 mm y^{-1}).

The plantations contained replications, single-tree plots at two spacings. (i) Expt 7/75 at (2.4 m x 2.4 m) normal spacing which included 15 reps of 7 clones of each of 14 different half-sib seed sources and (ii) Expts 3/75 and 5/75 at wide spacing (4.9 m x 4.9 m) which included 23 to 42 reps of 9 clones from 7 different half-sib sources (Howland and Bowen, 1977). These experimental plots had been weeded to prevent competition at the early stages of tree growth.

The following parameters were recorded: —

i) number of stems per tree
ii) height to the tip of the tallest shoot
iii) diameter of the longest stem at 1.3 m
iv) total number of branches, including dead but not abscinded ones
v) number of heavy branches (ie diameter exceeding 25% that of the mainstem)
vi) number of forks (including multiple stems), forming a Y shaped mainstem
vii) number of branch scars formed by branch abscission
viii) abscission index (ie no. of scars as a percentage of scars plus branches).

Branches on the main stem arise in two ways (Tomlinson and Gill, 1973): those formed on the current season's growth (sylleptic branches), growing out without a period of correlative inhibition, whilst those on the previous season's growth (proleptic branches) grow out only when released from correlative inhibition by, for example, a period of terminal bud rest or decapitation. In *Triplochiton*, the two types may be distinguished on the basis of their distribution on the stem segment of each year's growth, with sylleptic branches forming between the annual proleptic whorls. Sylleptity was assessed on a scale 1 to 5 as a proportion of the total number of branches that were of the sylleptic type.

The decapitation test was performed as described in Ladipo *et al.*, (in press *a*) on 3 to 6 month old plants both in the tropical glasshouses at Edinburgh and at the nursery of the Forestry Research Institute of Nigeria (FRIN), Ibadan (Ladipo *et al.*, in press *b*). Most clones growing in the plantations were also available in the nursery as recently rooted cuttings for the Predictive Test (*Table 1*). Two important parameters were obtained from the test:

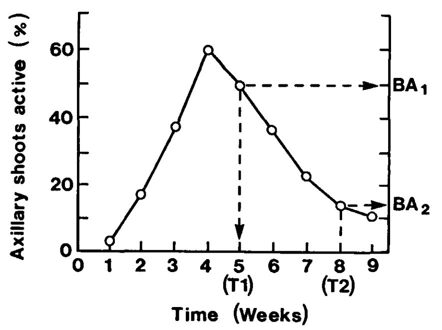

Figure 1. — Bud activity (BA) applies throughout the experiment and is defined as the percentage of axillary shoots that are actively growing (by more than 2 mm/week) following decapitation. The curve is experimentally determined. The Rate of Re-establishing Dominance (RRD) applies only after the peak of bud activity (ie usually week 4 and is determined from logarithms and has units of time^{-1}. RRD = $(\ln BA_1 - \ln BA_2)/(T_1 - T_2)$, were T denotes time. For the example shown RRD = 0.45 week^{-1}.

the peak bud activity usually at four weeks (BA) and the rate of reasserting dominance (RRD). These terms are defined in *Figure 1.*

Results

At 2.4 m spacing, the mean height after four years ranged from 5.9 m to 8.1 m. Clones differed significantly in all attributes assessed, but most notably in the height and diameter of the main stem, the number of stems plant^{-1} and the number of branches m^{-1} (*Table 2*). Mean height and stem diameter were positively correlated with each other ($r = 0.76$, $p = <0.001$) and both were correlated with the total number of branches ($r = 0.71$ and 0.66 respectively $p = <0.001$).

At 4.9 m spacing, clones ranged in height from 5.1 m to 7.8 m and again showed clear differences (*Table 3*). In addition to the correlations mentioned in the case of normal spacing, height was positively correlated with the incidence of heavy branching ($r = 0.75$, $p = <0.02$. Clones from lower latitudes (*Table 1*) often tended to be less heavily branched. One clone (244/1) was exceptionally large, with approximately three times the mean volume and numerous heavy branches and a single unforked monopodial stem.

The response to spacing may be assessed in the six clones which were present in both 4.9 m and 2.4 m spacing by examination of the gains and losses in the measured parameter (*Figure 2*). Height, stem diameter incidence of heavy branching, and branch abscission were the characteristics that were most sensitive to spacing. At wide spacing all clones were shorter but most had greater stem diameters. Monopodial, forked and multi-stemmed individuals occurred at about the same frequency in the two spacings indicating strong genetic control, but the wide-spaced trees did have more heavy branches. At wide spacing, branching frequency (number of branches and scars per unit height) was greater in some clones and less in others, suggesting that this is a trait subjected to site/clone interaction. Sylleptic branching was relatively unaffected by wide spacing, except in clone 139/9. Branch abscission which was always at the base of the canopy, was greatly reduced by wide spacing. This retention of branches gave trees with a deeper crown.

An important practical question is the extent to which clonal variation may be exploited by selecting top-ranked clones. Estimates can be made by calculating the mean timber volume that would have resulted from selecting any given percentile from the ranked clones (*Figure 3*).

Table 2. — Mean Morphometric characters of 23 clones of *Triplochiton scleroxylon* after four years of growth at normal spacing (2.4 m), arranged in ascending order of stemvolume. Standard errors of means are in parentheses (n = 8).

Clone	Height (m)		Diameter (mm)		Stems plant^{-1}		Branches m^{-1}		Scars m^{-1}		Heavy branches plant^{-1}		Forks plant^{-1}		Sylleptcity (1-5)	
166/1	5.9	(0.6)	73	(6)	2.1	(0.2)	2.2	(0.1)	6.0	(0.6)	1.2	(0.3)	2.4	(0.4)	2.1	(0.3)
144/5	6.1	(0.3)	75	(5)	1.0	(0.0)	2.2	(0.1)	6.6	(0.5)	0.9	(0.3)	0.9	(0.03)	2.1	(0.3)
225/8	6.1	(0.3)	85	(3)	1.0	(0.0)	3.2	(0.1)	3.7	(0.6)	2.0	(0.3)	2.0	(0.3)	3.0	(0.2)
144/4	6.4	(0.4)	84	(5)	1.2	(0.0)	2.6	(0.2)	6.2	(1.3)	1.8	(0.5)	0.8	(0.04)	3.2	(0.2)
144/1	6.3	(0.3)	86	(7)	1.0	(0.0)	4.4	(0.9)	8.7	(1.3)	1.6	(0.7)	0.5	(0.1)	2.4	(0.4)
175/9	7.1	(0.4)	84	(3)	1.0	(0.1)	4.4	(0.9)	3.3	(0.9)	1.6	(0.8)	0.0	(0.0)	2.1	(0.3)
144/7	6.6	(0.3)	88	(5)	1.0	(0.0)	2.5	(0.5)	5.5	(0.8)	2.2	(0.6)	0.5	(0.04)	2.6	(0.3)
175/10	7.0	(0.4)	87	(9)	1.1	(0.1)	2.7	(0.1)	4.9	(1.3)	2.3	(0.3)	0.8	(0.3)	1.7	(0.3)
139/9	7.8	(0.3)	93	(3)	1.1	(0.2)	3.7	(0.5)	3.8	(0.8)	1.3	(0.3)	2.1	(0.8)	2.0	(0.2)
139/6	6.8	(0.3)	93	(2)	1.0	(0.0)	3.5	(0.6)	6.4	(1.6)	1.6	(0.5)	1.1	(0.03)	1.6	(0.3)
177/10	7.0	(0.3)	93	(5)	1.0	(0.0)	3.1	(0.1)	4.8	(1.0)	2.1	(0.6)	1.1	(0.4)	2.6	(0.4)
166/3	6.9	(0.3)	97	(6)	1.5	(0.3)	3.7	(0.3)	5.8	(1.4)	1.8	(0.4)	0.5	(0.03)	1.5	(0.1)
137/9	6.9	(0.4)	100	(6)	1.0	(0.0)	4.4	(0.6)	5.7	(0.5)	3.3	(0.4)	0.91	(0.05)	2.3	(0.2)
144/9	7.7	(0.3)	95	(9)	1.1	(0.1)	3.8	(0.4)	5.4	(0.8)	2.3	(0.4)	0.6	(0.04)	2.5	(0.4)
161/5	7.3	(0.4)	101	(6)	1.0	(0.1)	2.9	(0.4)	3.7	(0.2)	2.0	(0.6)	0.8	(0.1)	2.3	(0.3)
224/7	7.0	(0.3)	110	(7)	1.0	(0.1)	4.3	(0.2)	4.1	(0.3)	1.3	(0.3)	1.1	(0.2)	1.6	(0.2)
175/7	7.8	(0.5)	105	(10)	1.0	(0.0)	3.5	(0.3)	5.6	(1.1)	1.2	(0.4)	0.8	(0.03)	2.3	(0.3)
161/3	6.9	(0.3)	115	(4)	1.0	(0.1)	4.2	(0.2)	6.6	(0.5)	0.0	(0.0)	0.0	(0.0)	1.0	(0.1)
175/5	8.1	(0.4)	109	(6)	1.3	(0.2)	3.9	(0.2)	6.8	(1.2)	1.6	(0.4)	0.8	(0.07)	2.5	(0.3)
175/1	7.6	(0.5)	115	(6)	1.0	(0.0)	3.9	(0.2)	5.3	(1.4)	3.1	(0.4)	0.6	(0.06)	3.4	(0.3)
175/8	7.4	(0.3)	118	(6)	1.0	(0.1)	4.1	(0.4)	5.1	(1.0)	3.6	(0.4)	0.4	(0.2)	1.5	(0.2)
175/6	7.8	(0.6)	115	(6)	1.3	(0.2)	3.4	(0.2)	4.7	(1.4)	1.6	(0.4)	0.8	(0.03)	2.7	(0.3)
175/2	7.4	(0.6)	123	(6)	1.0	(0.0)	3.5	(0.1)	7.4	(0.9)	3.1	(0.4)	0.6	(0.2)	2.0	(0.3)

Table 3. — Mean Morphometric characters of nine clones of *Triplochiton scleroxylon* after four years of growth at wide spacing (4.8 m), arranged in ascending order of stem volume. Standard errors of means are in parentheses (n = 8).

Clone	175/10	144/1	175/5	166/8	142/10	139/9	177/10	175/1	244/1	Overall Mean
Height (m)	5.8 (0.2)	5.1 (0.3)	5.8 (0.3)	6.5 (0.4)	6.3 (0.4)	6.1 (0.3)	6.2 (0.4)	6.7 (0.3)	7.8 (0.3)	
Diameter (mm)	95 (3)	102 (6)	107 (6)	106 (5)	110 (10)	117 (7)	121 (7)	131 (9)	173 (3)	
Stems plant^{-1}	2.0 (0.0)	1.0 (0.0)	1.0 (0.1)	1.2 (0.1)	1.0 (0.1)	1.0 (0.0)	1.2 (0.2)	1.1 (0.1)	1.0 (0.0)	
Branches m^{-1}	5.6 (0.5)	5.5 (0.2)	6.1 (0.7)	5.5 (0.4)	6.5 (0.9)	5.7 (0.8)	5.0 (0.7)	7.2 (0.5)	7.4 (1.3)	
Scars m^{-1}	1.8 (0.1)	4.4 (0.2)	2.3 (0.3)	2.8 (0.3)	2.4 (0.5)	3.6 (0.1)	2.5 (0.2)	3.6 (0.6)	2.3 (0.3)	
Heavy branches plant^{-1}	1.0 (0.2)	3.7 (0.6)	1.3 (0.4)	1.5 (0.3)	2.6 (0.4)	4.8 (0.8)	2.4 (0.4)	2.0 (0.4)	13.3 (1.8)	
Forks plant^{-1}	2.0 (0.0)	0.5 (0.0)	0.5 (0.1)	1.0 (0.2)	0.5 (0.1)	0.5 (0.0)	1.2 (0.3)	0.5 (0.1)	0.0 (0.0)	
Sylleptycity (1-5)	3.0 (0.2)	2.7 (0.2)	2.6 (0.4)	2.5 (0.3)	3.8 (0.2)	3.1 (0.2)	2.8 (0.3)	3.0 (0.4)	4.6 (0.4)	

This exercise suggests that taking the top 20% of clones would have increased the mean yield of timber by about 50% and 75% at 2.4 m and 4.9 m spacings respectively. At higher selection intensities the numbers of clones involved becomes small and thus the predicted gains are very sensitive to the presence of particular individuals like the apparently very productive clone 244/1 in the wide spacing experiment.

This exercise does, however, indicate that the genetic gains are greater at wide spacing, such as might occur in an agroforestry situation, on a per tree basis. This may not be the case on a per hectare basis. but to test this requires experimental designs different from those used here. The data were then examined for relationships between clonal performance in the Predictive Test and the growth in experimental plantations. At 2.4 m spacing, there was a strong relationship between bud activity at four weeks and the number of branches and branch scars at four years (*Figure 4a*, $r = 0.71$, $p = < 0.001$), showing that the tendency to release buds from the effect of apical dominance is a persistent attribute. There was also a positive relationship between RRD and the mean frequency of heavy branches (*Figure 4b*, $r = 0.54$, $p = 0.02$).

Only five of the clones planted at wide spacing were subjected to the Predictive Test, and relationships were not statistically significant. A correlation matrix for all the measured parameters is presented elsewhere (Ladipo, 1981).

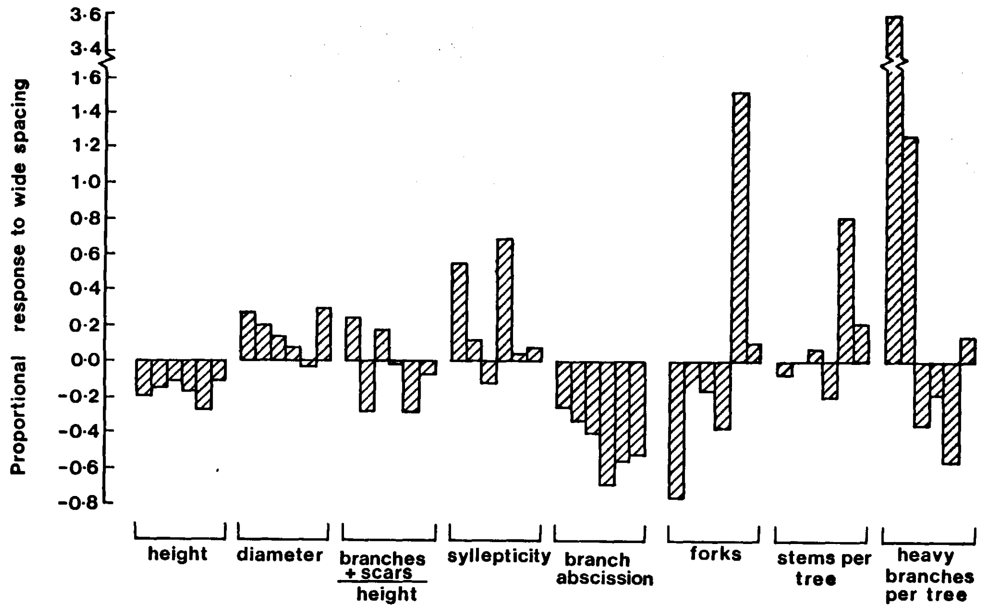

Figure 2. — Response of six clones to growth at different spacings. The measurements or scores for height, diameter etc. obtained at 4.9 spacing are expressed as a fraction of the score at 2.4 m spacing. Each histogram contains six bars, representing clones 139/9, 144/1, 175/1, 175/5, 175/10 and 177/10 respectively.

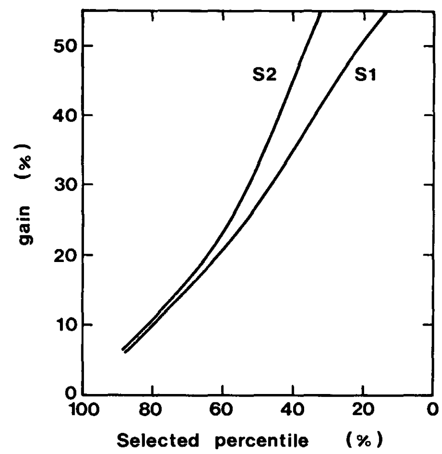

Figure 3. — The estimated gain in mean timber volume that would have resulted from selecting the best clones. Selection intensity is expressed as the percentile of best clones based on their timber volume (calculated from the diameter and height, assuming a cone). Two curves are for 2.4 m (S1) and 4.9m (S2) spacing ,and were hand-drawn through the data (for S1, n = 23; for S2, n = 9).

Discussion

In seeking to account for clonal differences in timber production it is useful to consider the carbon balance of the tree. The photosynthetic rate of a shoot depends on both the quantity of leaf as well as the rate of photosynthesis. The quantity of leaf to a large degree depends on the strength of apical dominance, as this determines the release of axillary shoots from correlative inhibition. We may suppose that this tendency to release primary axillary shoots and thus generate more leaf area, will bear some relationship to the result of the Predictive Test. This relationship is, however, unlikely to be true for secondary branching ,as many large trees with weak apical dominance in their mainstem, have strong apical dominance in their branches (Hallé et al., 1978).

At the same time, the area-specific and weight-specific rates of photosynthesis and respiration are known to differ between clones of *T. scleroxylon,* and it has been shown statistically that a simple expression involving these parameters is significantly correlated with yield (Ladipo et al., 1984). Also ,the partition of the shoot's photosynthate betwen different plant parts is likely to vary clonally (Cannell *et al.,* 1984). Thus, the characteristics of apical dominance are only one of the parameters which can be expected to influence the performance of the tree.

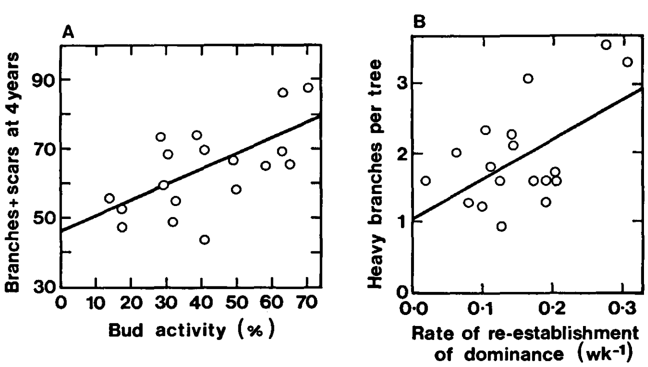

Figure 4. — Correlation between the result of the decapitation test (expressed as BA at 4 weeks or RRD) and characteristics assessed on 4-year old trees in plantations at 2.4 m spacing.

It is thus not surprising that the results of the Predictive Test do not always bear strong correlation to growth in the plantation, especially as spacing affects the level of competition between trees, and, as we have seen, branch retention.

It was, therefore, encouraging to find a good relationship between bud activity following decapitation and the production of branches over the course of four years. At 4.9 m spacing, the clones producing the greatest frequency of branching (branches per m) also tended to be those with the greatest height and diameter (*Table 3*).

At 2.4 m spacing, the light regime is greatly modified and different relationships apply. Shade strengthens apical dominance in this species (Ladipo *et al.,* in press *b*), and the overall lower sylleplicity score may be interpreted as the result of a stronger apical dominance. Branching intensity was lower and a smaller fraction of the branches fell into the heavy category. Moreover, lower branches abscinded, leaving a bole which was relatively free from knots and consequently more desirable as timber. The correlation between RRD and heavy branching is not difficult to account for. RRD is a measure of the rate at which the number of extending lateral shoots diminishes as one of them (normally the tompost) becomes dominant (Leakey and Longman, 1986).

The prospects of establishing improved plantations based on clonal selections with a high harvest index seem good. In the four-year-old plantation the highly significant between-clone variation was considerable compared with the within-clone variation. The data revealed that qualitative characters like forking and multi-stemming are under strong genetic control and less influenced by spacing than the quantitative and continously varying characters like height and girth. Consequently the qualitative characters are easily selected against. Forking and multi-stemming were highly correlated, and as multi-stemming is an early trait, it might be useful as a predictor of forking. However, while the quantitative characteristics are also genetic traits some clones perform best at one spacing and do not necessarily perform well at another. Clone 175/5, for example, grew well at 2.4 m spacing but poorly at 4.9 m spacing. Neither its performance on the Predictive Test nor its morphometric characters give any indication of why this may be so. It is also known that clones that yield the most in the phase of growth before canopy closure may not continue to do so after canopy closure, as by then, attributes such as canopy depth (which determines the interception of radiation) become of prime importance.

It is therefore prudent to consider a number of selection criteria in any tree improvement programme. As the first of these, the Predictive Test seems to be appropriate as a preliminary screening process for large seedling populations. This would allow those with strong apical dominance to be selected for vegetative propagation and retesting as clonal material. Those clones which are then confirmed as sparsely-branched genotypes can be established in clonal field trials for further testing and selection. In this way, very large populations can be sampled without the need for a massive field testing programme.

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Clonal Variation in Apical Dominance of Triplochiton scleroxylon K. Schum. in Response to Decapitation

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Summary

Clonal trials with the West African hardwood *Triplochiton scleroxylon,* K. Schum. have indicated a positive relationship between stem size (height and diameter) and branching frequency (mean no. of branches per m of mainstem). As part of a programme of vegetative propagation and clonal selection, the present study with young plants examined clonal variation in apical dominance, the process which determines branching frequency. Young potted plants of five clones were decapitated by removing the apex and uppermost node. The plants were partially defoliated, leaving 4 to 6 leaves at the apical nodes. These plants were grown in a glasshouse at 25 °C to 30 °C under experimental conditions testing:- (i) two rates of fertilizer application (4.0% and 0.04% liquid feed, NPK = 23:19.5:16); (ii) three rates of water application, ranging from field capacity to severe water stress (watering with 250 ml either every day, every three days or every 12 days); and (iii) two daylengths (10 h and 19.5 h). The length and number of lateral shoots formed on these decapitated plants were measured weekly to determine the percentage bud activity. In the first four weeks after decapitation, percentage bud activity increased (Sprouting Phase) and, thereafter, it declined as dominance was re-imposed (Dominance Phase). Peak bud activity at week 4 was greatest with the higher rate of nutrient application under the daily and 3-day watering regimes, but was unaffected by daylength. During the Dominance Phase, bud activity remained high at the higher rate of nutrient application, under the 3 and 12-day watering regimes and under long days. The relative performance of different clones was consistent in all treatments. Of the three clones used in all experiments, clones 8038 and 8049 had similarly high activity (rank one or two) and clone 8053 displayed less activity. However, inconsistencies in clonal ranking occurred under the lowest rate of watering. Responses to decapitation can thus be used as a robust indicator of genetic variation in apical dominance, provided care is taken: (i) to avoid extreme environmental conditions; and (ii) to maintain uniformity in the morphological (height, no. of leaves etc.) and physiological state (eg water and nutrient status) of the plants and their growing environment (especially light).

Key words: apical dominance, correlative inhibition, clonal variation, branching, decapitation, screening test, tree improvement, *Triplochiton scleroxylon.*

Introduction

The development of techniques for clonal propagation of several West African hardwoods has been the basis of a tree improvement programme involving the selection of superior genotypes (Leakey *et al.*, 1982; Leakey, 1986). The gene pool of many species in West Africa is dysgenic, as a result of selective logging. The approach taken has been to vegetatively propagate young trees and to make selections based on their field performance in clonal trials (Howland and Bowen, 1977). Although genetic gains are made faster by this approach than by traditional forms of tree improvement, it is still laborious, expensive and slow. It would be desirable therefore to find a clonal trait in young plants that could be correlated with later yield in replicated trials.

What are suitable physiological criteria for this purpose and to what extent can any juvenile trait be used to predict adult performance? In a previous paper (Ladipo et al., 1984), we have shown that the CO_2 exchange rates of young plants can be used to predict the rank order of timber yield of *Triplochiton scleroxilon* K. Schum. clones in a trial plantation. The commercial quality of a tree,

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