

Genetic Variation in Apical Dominance of *Cedrela odorata* Seedlings in Response to Decapitation

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Summary

An assessment was made of genetic variation in apical dominance of *Cedrela odorata* L. using a decapitation test. Nineteen weeks after sowing, pot-grown seedlings belonging to 30 open-pollinated progenies from 5 provenances were decapitated by removal of the shoot apex, leaving shoots of a uniform height of 20 cm. Foliage was reduced to a single leaf with 2 pairs of leaflets on each plant. The length and number of lateral shoots subsequently formed were measured at 2 weeks, 4 weeks and 8 weeks after decapitation to determine the percentage bud activity and dominance ratio of the shoots. Percentage bud activity increased within the first 2 weeks to 4 weeks and declined thereafter as dominance was reimposed. Significant differences between provenances and progenies were recorded both in the timing and extent of peak bud activity ($P < 0.001$, ANOVA). Maximum bud activity ranged from 17.7% to 24.2% in the 5 provenances whereas mean values for the progenies differed by more than a factor of 2, ranging from 13.6% to 32.3%. Pronounced genetic variation in dominance ratio was also recorded; maximum values occurred 4 weeks after decapitation in all progenies. Dominance ratio was negatively correlated with percentage bud activity ($r = 0.65$, $P < 0.001$). These results indicate that significant potential exists for selection of *Cedrela odorata* genotypes with relatively high apical dominance, which may exhibit superior form and pest tolerance.

Key words: Apical dominance, correlative inhibition, genetic variation, branching, screening test, genetic improvement, *Cedrela odorata*.

FDC: 165.53; 161.4; 176.1 *Cedrela odorata*.

Introduction

Cedrela odorata L. ("Spanish Cedar"; Meliaceae) is a valuable timber tree native to Central and South America (LAMB, 1968; PENNINGTON, 1981), often grown in combination with coffee or cacao in agroforestry systems. However, attempts to establish the species in plantations in areas within its natural range have met with repeated failure, largely because of attacks by shoot boring moth larvae (*Hypsipyla* spp.) (NEWTON *et al.*, 1993a). Shoot borers destroy the terminal shoot, resulting in a highly branched or forked tree of little economic worth (GRJFMA, 1976; NEWTON *et al.*, 1993a). Evidence from provenance and progeny tests of *C. odorata* indicate that some genotypes may display tolerance of the pest (GRJFMA, 1976; NEWTON *et al.*, 1993b) by displaying strong apical growth of the leading shoot after attack (CHAPLIN, 1980; VEGA, 1976). Although such a characteristic is clearly of great potential value, the physiological and genetic basis of this pattern of response is not well understood.

Branch formation in trees is controlled by 2 processes: apical dominance (correlative inhibition), involving the regulation of axillary bud development by the terminal bud of a shoot, and apical control, the suppression of growth of existing branches imposed by more apical shoots (BROWN *et al.*, 1967; LEAKEY and LONGMAN, 1986). Although the mechanisms of these processes have not been clearly defined, apical dominance is thought to be controlled by auxins, perhaps in combination with other growth substances (FIELD and JACKSON, 1984). The dominance relationships of shoots have been shown to be particularly sensitive to gibberellin concentration. For example, injection of GA₃ into shoots of *Triplochiton scleroxylon* K. SCHUM. hastened the imposition of dominance by increasing vegetative growth of the dominant shoot (LEAKEY and LONGMAN, 1986). Both apical dominance and apical control are also known to be influenced by a range of environmental factors (LADIPO *et al.*, 1992; MCINTYRE, 1977).

Research into the processes of branch formation in *Triplochiton scleroxylon*, a West African hardwood, has identified pronounced genetic variation in apical dominance, primarily between clones (LEAKEY and LONGMAN, 1986; LEAKEY and LADIPO, 1987; LADIPO *et al.*, 1991b). This variation was identified by the development of a decapitation test, involving the removal of the apical part of the shoot of a young plant, and the subsequent release of axillary buds from correlative inhibition (LEAKEY and LONGMAN, 1986). The expression of apical dominance was found to be influenced by a range of environmental factors, including growth conditions, the height of the plant and the number of leaves (LADIPO *et al.*, 1991b, 1992; LEAKEY and LONGMAN, 1986). On the basis of these results, LADIPO *et al.* (1991b) suggested that decapitation tests could be used to screen genotypes for variation in apical dominance, and could thereby serve as an early selection technique for improved form and yield. This was supported by the strong correlation found between percentage bud activity following decapitation, and the branching frequency of clones at 4 years of age (LEAKEY, 1985).

The development of an early selection criterion for apical dominance would be of particular value in species such as *Cedrela odorata*, where the processes of branch formation appear to be strongly related to tolerance of pest attack. Consequently, this paper describes the first application of a decapitation test to this species. Unlike most previous investigations (LEAKEY and LONGMAN, 1986; LADIPO *et al.*, 1991b), this study was undertaken under operational conditions in the nursery, and involved screening of large numbers of seedlings rather than clones. The main objectives were: (i) to assess whether the decapitation test could be successfully applied to *Cedrela odorata*; (ii) to assess whether the responses of this species to decapitation differed to those observed previously; and (iii) to assess the extent of genetic variation in apical dominance observed using this technique.

Materials, Methods and Experimental Details

The experiment was carried out in the nursery of the Centro Agronómico de Investigación y Enseñanza (CATIE) in Turrial-

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ba, Costa Rica (9° 54' N Lat., 83° 40' W Long.), which lies at an altitude of 600 m.a.s.l., with a mean annual precipitation of approx. 2600 mm and a mean annual temperature of 22 °C. Seed was collected from open-pollinated trees selected from a range of localities in Costa Rica, and sown directly into black polythene bags (2.2 l capacity) containing a 1:1:1 mixture of forest soil, sand and organic compost. After 10 weeks, the plants were repotted into larger polythene bags (5.6 l capacity) filled with the same potting mixture. Plants were grown under full sunlight and received natural rainfall, supplemented by additional watering to field capacity when there was no rain for 2 consecutive days. The pots were hand-weeded at regular intervals.

The experiment included 30 families belonging to 5 provenances (see Table 1), with 6 trees per family per block arranged in a line, and 9 blocks in total, giving a total of 54 seedlings per family. The whole experiment was surrounded by a single-row border of a checklot, and the plants were arranged at a constant spacing of 25 cm x 25 cm. The seedlings were decapitated on 1 October 1990, 19 weeks after sowing, by which time they were 30 cm to 40 cm tall. LEAKEY and LADIPO (1987) recommended that decapitation tests should be carried out under uniformly high irradiance with plants of a uniform age, leaf area and size prior to decapitation. Consequently all plants were cut to a constant height of 20 cm, by removing the apical part of the shoot. All seedlings were partly defoliated, leaving a single leaf which was trimmed to 2 pairs of leaflets in each case. Any lateral shoots that were present at the time of decapitation were removed.

Table 1. – Origins of the *Cedrela odorata* seedlots used in this investigation. All the collection sites were in Costa Rica.

Provenance	Latitude		Longitude		Altitude (m)	Precipitation (mm)
	N	W				
Cañas	10° 25'	85° 6'			70-120	1829-2274
Carmona	9° 60'	85° 15'			60-70	1780
Hojancha	10° 04'	85° 25'			100-350	2232
San Carlos	10° 22'	84° 28'			80-260	2866-3609
Turrialba	9° 54'	83° 40'			600-620	2464-2605

Measurements were made of the proportion of buds that subsequently broke from correlative inhibition and the length of each branch produced after 2 weeks, 4 weeks and 8 weeks. Shoots were considered to be actively growing if they grew by more than 2 mm week⁻¹. Dominance ratio was calculated as the ratio of the length of the longest shoot: mean length of the remaining shoots (following LEAKEY and LONGMAN, 1986). Results were analyzed by ANOVA using SAS (SAS, 1980). Percentages were arcsin transformed prior to analysis, following SNEDECOR and COCHRAN (1980). Correlations were carried out using SigmaPlot v. 5.0 (Jandel Scientific GmbH, Erkrath, Germany).

Results

At the time of decapitation, the number of nodes per seedling varied between 2 to 18, with an overall mean of 9.2. The proportion of buds that were actively growing increased rapidly within the first few weeks after decapitation, reaching a peak at weeks 2 to 4, then declining thereafter. This overall pattern of response was exhibited by all seedlings, although variation

was recorded between provenances and progenies in the timing and maximum value of peak bud activity. For example, peak bud activity in the San Carlos and Turrialba provenances was recorded at week 2, whereas in the other 3 provenances, maximum values were recorded at week 4 (Fig. 1).

Overall, significant differences in maximum bud activity

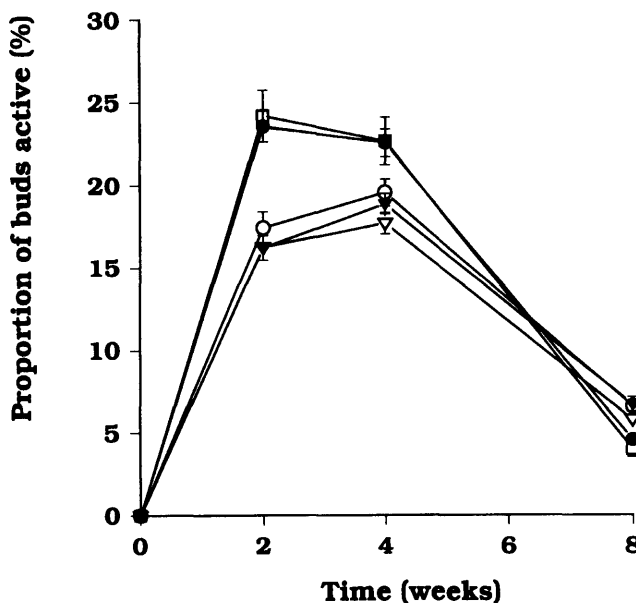


Figure 1. – The percentage bud activity of *Cedrela odorata* seedlings following decapitation in a nursery trial at CATIE, Costa Rica. Values presented are provenance means ($n > 216$); vertical bars represent s.e.m. Symbols: hollow circles, Cañas; filled circles, San Carlos; hollow triangles, Hojancha; filled triangles, Carmona; empty squares, Turrialba.

were recorded between provenances ($P < 0.001$; ANOVA) at weeks 2 and 4. The maximum bud activities recorded in the 5 provenances ranged from 17.7% (Hojancha) to 24.2% (Turrialba) (Fig. 1). The maximum bud activity of the different progenies within each provenance was generally recorded at the same week, although in the case of San Carlos, peak values were recorded in 3 progenies at week 2, and in the other 4 at week 4. Pronounced differences between progenies in percentage bud activity were recorded at both weeks 2 and 4 ($P < 0.001$; ANOVA). Maximum bud activity ranged between 13.6% (progeny 1920) and 32.3% (progeny 1932) at week 4 (Fig. 2). The most striking variation between progenies within a provenance was observed in the Turrialba provenance, where progeny mean values ranged from 14.9% (progeny 1935) to 32.3% (progeny 1932).

Dominance ratio increased rapidly in the first 4 weeks after decapitation, declining gradually thereafter (Fig. 3). The same trends were observed in all provenances, with maximum values recorded in all provenances at week 4. At this time, differences between provenances were not statistically significant ($P > 0.05$; ANOVA), values ranging from 31.7 (San Carlos) to 41.6 (Carmona). However, differences between progenies were highly significant at week 4 ($P < 0.001$; ANOVA); values ranging from 17.8 (progeny 1939) to 69.9 (progeny 1935). Again, pronounced variation between progenies within provenances was recorded, particularly in the case of the Turrialba provenance where values ranged from 19.1 (progeny 1932) to 69.9 (progeny 1935) (Fig. 4). When examined by correlation, dominance ratio was found to be negatively correlated with percentage bud activity at week 4 ($r = 0.65$, $P < 0.001$).

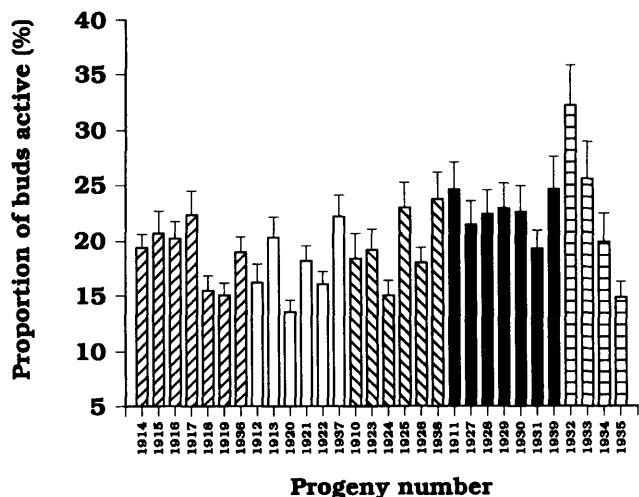


Figure 2. - Variation in percentage bud activity of *Cedrela odorata* seedlings 4 weeks after decapitation in a nursery trial sited at CATIE, Costa Rica. Values presented are progeny means ($n = 54$); vertical bars represent s.e.m. The progenies are arranged by provenance: right hatching, Carmona; hollow bars, Hojancha; left hatching, Cañas; solid bars, San Carlos; horizontal hatching, Turrialba.

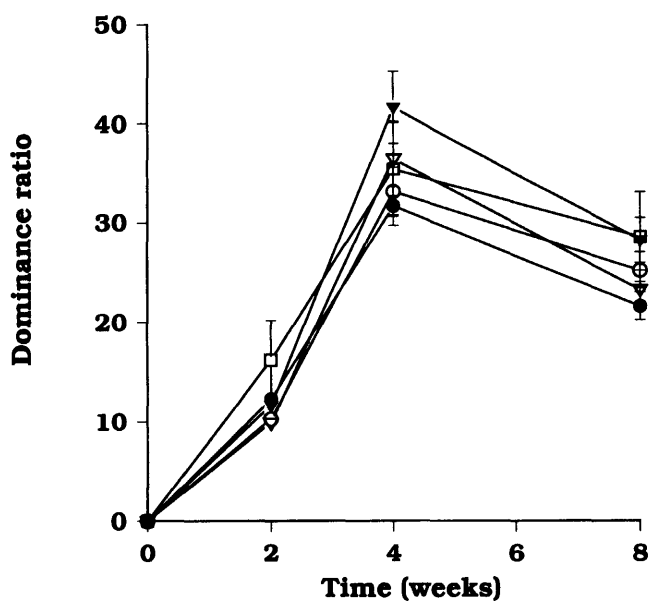


Figure 3. - The dominance ratio of *Cedrela odorata* seedlings following decapitation in a nursery trial at CATIE, Costa Rica. Dominance ratio was calculated as the length of the dominant shoot: the mean length of the sub-dominant shoots (see text). Values presented are provenance means ($n > 216$); vertical bars represent s.e.m. Symbols: hollow circles, Cañas; filled circles, San Carlos; hollow triangles, Hojancha; filled triangles, Carmona; empty squares, Turrialba.

The length of the longest shoot increased continually throughout the period of assessment, with highest rates of increase recorded between weeks 2 and 4 (Fig. 5). A similar trend was recorded in all provenances. Differences between the provenances were highly significant ($P = 0.001$; ANOVA) at week 8, mean values ranging from 56.2 cm (Turrialba) to 66.4 cm (Cañas). Significant variation was also recorded between progenies ($P < 0.001$; ANOVA), mean values ranging from 43.9 cm (progeny 1920) to 94.6 cm (progeny 1938).

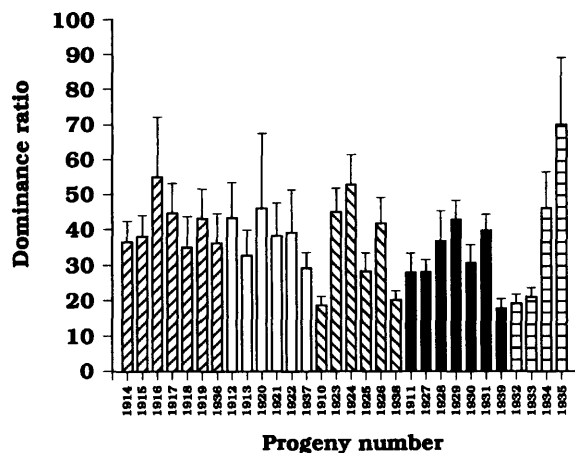


Figure 4. - Variation in dominance ratio of *Cedrela odorata* seedlings 4 weeks after decapitation in a nursery trial sited at CATIE, Costa Rica. Dominance ratio was calculated as the length of the dominant shoot: the mean length of the sub-dominant shoots (see text). Values presented are progeny means ($n = 54$); vertical bars represent s.e.m. The progenies are arranged by provenance: right hatching, Carmona; hollow bars, Hojancha; left hatching, Cañas; solid bars, San Carlos; horizontal hatching, Turrialba.

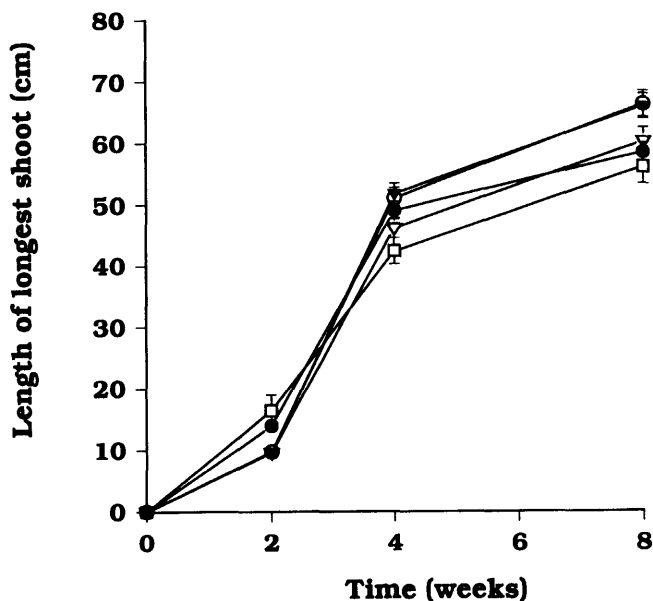


Figure 5. - The maximum shoot length of *Cedrela odorata* seedlings following decapitation in a nursery trial at CATIE, Costa Rica. Values presented are provenance means ($n > 216$); vertical bars represent s.e.m. Symbols: hollow circles, Cañas; filled circles, San Carlos; hollow triangles, Hojancha; filled triangles, Carmona; empty squares, Turrialba.

Discussion

Previous investigations of apical dominance in young plants have identified 2 phases of bud activity following decapitation: the "Sprouting Phase", in which buds are released from correlative inhibition, and the "Dominance Phase", in which the uppermost lateral shoots begin to suppress the growth of lower shoots (LEAKEY and LONGMAN, 1986). Lower bud activities are associated with relatively strong apical dominance (LADIPO *et*

al., 1991b). In *Triplochiton scleroxylon*, the Sprouting Phase generally lasts for the first 3 weeks to 4 weeks after decapitation, when peak values of bud activity are obtained (LADIPO *et al.*, 1991b; LEAKEY and LONGMAN, 1986). This pattern of response seems to be consistent in *T. scleroxylon*, whether the plants are grown under controlled environment conditions or in the nursery (LADIPO *et al.*, 1992). However, the reimposition of dominance in *T. scleroxylon*, indicated by the decline in bud activity after week 4, has not so far been recorded in nursery-grown plants, perhaps reflecting the relatively high nutrient availabilities in such conditions (LADIPO *et al.*, 1992).

The response of *Cedrela odorata* to decapitation was strikingly similar to that reported previously for *T. scleroxylon*, with peak bud activities recorded in weeks 2 to 4, and a subsequent decline in activity recorded at week 8. These results indicate that both the pattern and timing of the response to decapitation are common to more than one species; further investigations are clearly required to define how general these responses are in tropical trees. In comparison with results from *T. scleroxylon*, the values of percentage bud activity recorded here were relatively low, reaching a maximum of 32.3% as a progeny mean. Bud activity values in many of the experiments reported by LEAKEY and LONGMAN (1986) were in a similar range to those recorded here, but those reported by LADIPO *et al.* (1991b, 1992) were generally far higher, reaching maxima of over 80% in some cases. To a large extent this must reflect the conditions under which the plants were grown, as maximum bud activity is sensitive to a range of environmental factors, such as photoperiod (LEAKEY and LONGMAN, 1986), irradiance and humidity (LADIPO *et al.*, 1992). Bud activity is particularly sensitive to nutrient availability: when decapitated plants of *Triplochiton scleroxylon* were treated with 4% or 0.04% nutrient solutions, maximum bud activity in the high nutrient treatment was found to be almost double that in the lower treatment (LADIPO *et al.*, 1991b). In the current investigation, the fact that the seedlings were grown in standard nursery soil with no additional fertilizer may account for the relatively low percentage bud activities recorded. In a preliminary experiment carried out under glasshouse conditions in the UK, with high rates of nutrient addition, a maximum percentage bud activity of over 90% was recorded in *Cedrela odorata* (A. C. NEWTON, unpublished data). Despite the sensitivity of bud activity to environmental conditions, the results of decapitation tests in both controlled environments and nursery conditions appear to be consistent (LADIPO *et al.*, 1992); even though maximum bud activity may vary under different treatments, the ranking of genotypes is maintained (LADIPO *et al.*, 1991a).

The pattern of increase in dominance ratio was also similar to that recorded previously for *Triplochiton scleroxylon* (LEAKEY and LONGMAN, 1986), with a rapid increase during the first 4 weeks after decapitation. However, the subsequent decline in dominance ratio recorded in all provenances at week 8 was at variance with previous results; this may be attributed to the general decline in the rate of shoot growth recorded at the same time, perhaps reflecting the decline in nutrient reserves in the pots. In general, values of dominance ratio were far higher than in *T. scleroxylon*, where a maximum value of 9.6 was recorded previously (LEAKEY and LONGMAN, 1986). Mechanisms of dominance relationships between shoots are not well understood, but appear to be related to rates of shoot growth, which are influenced by gibberellin concentration (PHILLIPS, 1969). LEAKEY and LONGMAN (1986) observed that in *T. scleroxylon*, dominance ratio was increased by application of gibberellin (GA_3), at least within the first 4 weeks after decapitation.

The genetic variation in apical dominance recorded in this investigation highlights the scope for selection of this characteristic in *Cedrela odorata*. Although differences in bud activity between provenances were relatively slight, with the highest value recorded being 36% greater than the lowest, differences between progenies were more pronounced, the highest value being 138% greater than the lowest. This does not take account of the additional variation that exists at the level of individual genotypes: for example, percentage bud activity in 26 clones of *Triplochiton scleroxylon* from a variety of geographical origins varied between 16% to 75% (LEAKEY and LADIPO, 1987). The results presented here suggest that a similar degree of variation may exist within *Cedrela odorata*, particularly if growth conditions were used enabling a wider range of bud activities to be expressed. The differences between provenances recorded here are of particular interest; peak bud activities in the Turrialba and San Carlos provenances were significantly higher than in the other 3. These differences in response correlate with the geographic location of these provenances: while San Carlos and Turrialba are located on the humid Atlantic region of Costa Rica, the other 3 provenances are located in the drier Pacific zone. The apparently higher apical dominance in the Pacific provenances is surprising, given that the mature trees in this area generally appear to be inferior in form to those growing in the Atlantic region (A. C. NEWTON, personal observation).

The value of apical dominance as a selection criterion depends on its relationship to tree form. LEAKEY and LADIPO (1987) found a strong correlation ($r = 0.76$; $P = 0.001$) between percentage bud activity and the total number of branches formed by clones of *T. scleroxylon* after 4 years growth in a clonal plantation. This indicates that decapitation tests could be used as an early predictive test for branching frequency (LEAKEY, 1985; LEAKEY and LADIPO, 1987). Although percentage bud activity has received greatest attention in this context, the potential use of dominance ratio is supported by the significant correlation between these 2 variables recorded in the present investigation. LEAKEY and LADIPO (1987) proposed that decapitation tests could be used to screen a large number of seedlings, which could then be selected and vegetatively propagated for establishment in clonal tests. Following this suggestion, a large-scale screening of *Triplochiton scleroxylon* seedlings has recently been completed in Cameroon (LADIPO *et al.*, 1994). The advantage of screening seedlings in a progeny test design, as in the current investigation, is that genetic values may be estimated for the individual progenies, which may then form the basis of selection.

Decapitation tests may be of particular value in selection for the genetic improvement of *Cedrela odorata* as the removal of the apical portion of the shoot effectively simulates shoot borer attack. The problems with this pest are probably the main constraint to establishment of *Cedrela odorata* in plantations within its natural distribution (NEWTON *et al.*, 1993a). Further information is clearly required on the relationship between decapitation test results and the eventual field performance of *Cedrela odorata* genotypes, particularly with respect to response to shoot borer attack. If genotypes with the ability to recover from attack by strong apical growth could be identified at an early stage, this would greatly accelerate the genetic improvement process. Experiments to relate decapitation test results to eventual field performance of *Cedrela odorata* are currently being planned at CATIE in Costa Rica.

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Rooting *Acacia mangium* Cuttings of Different Physiological Age with Reference to Leaf Morphology as a Phase Change Marker

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Summary

Capacity for adventitious rooting of *Acacia mangium* was assessed for shoot terminal cuttings originating from: (A) the crown and (B) sprouting stumps of 4-year-old trees growing outdoors, (C) 4-year-old hedged stock plants and (D) 1-year-old seedlings kept cultivated in containers. All these cuttings exhibited the mature phyllode morphology. For the stump sprout origin, rootabilities of juvenile-like composed leaf (B1), intermediate leaf (B2) and mature-like phyllode (B3) cuttings were also compared.

Rooting potential was found to be greatly influenced by the cutting source and to lesser extent, although still significantly, by the different types of cutting morphology. In both cases, the highest average rooting rate score of 85% was obtained for the mature-like phyllodes cuttings derived from mature sprouting stumps, whereas the same origin cuttings with juvenile-like leaves were less prone to root. Exogenous auxin treatment was

shown to improve noticeably the number of roots formed per rooted cutting, but had overall no effect on rooting rate with marked differences depending on the date of the experiment.

These results are discussed in terms of ageing influence on the potential for adventitious rooting of *Acacia mangium* cuttings, with reference to leaf morphology as a phase change marker.

Key words: *Acacia mangium*, age, auxin, cutting, maturation, morphological marker, phase change, rootability, vegetative propagation.

FDC: 161.4; 164.3; 164.5; 165.441; 232.11; 232.411.4; 176.1 *Acacia mangium*.

Introduction

Acacia mangium WILLD. has gained an increasing interest for reforestation programmes in the humid tropics over the last 2 decades mainly for pulpwood production. This is due to the