Revised Heritability Estimates for Cupressus lusitanica in East Africa

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Introduction

Cupressus lusitanica MILLER is the most important exotic softwood in East Africa, where it is grown as an ornamental tree, for hedges, for Christmas trees and in forestry plantations for timber production. The species is a hardy one and individual trees will survive on sites in East Africa from sea level to 3000 m elevation, provided annual rainfall exceeds 800 mm. For profitable timber production, however, C. lusitanica should be planted on sites between 1500 and 2,900 m elevation with deep soils and annual rainfall exceeding 1000 mm. Timber crops are grown on rotations of 30—35 years and yield about 480 m^3/ha at clear felling. Extensive planting began about 1930 in Kenya and Tanzania and ten years later in Uganda. By 1968, the volume of timber cut from the older Cypress plantations was about 4 times that cut from the small reserves of indigenous conifers (Juniperus procera ENDL. and Podocarpus spp) and represented about 45% of all sawn timber produced in the region. Current planting programmes are about 3000, 1000 and 450 ha/yr in Kenya, Tanzania and Uganda respectively (ANON. 1968, 1971).

Plantations established before World War 11 varied greatly in growth and form and in the amount of damage they suffered from Cypress canker (RUDD-JONES, 1954). There was also evidence of hybridization with other species of Cupressus (GRIFFITH, 1953). In an attempt to improve crop uniformity, instructions were issued in 1936 restricting seed collection to selected, registered, good quality stands. The Registered Seed Area Programme did not become fully effective until 1957, but has resulted in the development of a preferred East African strain of Cupressus lusitanica, which shows greatly improved crop uniformity and resistance to Cypress canker (DYSON, 1969; OLEMBO, 1969; RAUNIO, 1973). A regional programme to establish clonal seed orchards from intensively selected plus parents was begun in 1963 and most seed now used for cornmercial planting is collected from these orchards. Estimates of the celection gain achieved have been published by PATERSON together with preliminary astimates of heritability. This article describes progeny trials of plus trees used in the orchards and heritabilities calculated from measurements of them (PATERSON, 1966; DYSON 1969 (b).

Materials and Methods

Open-pollinated seed was collected from Cypress plus-trees selected in commercial plantations and registered seed stands. Seedlings from each tree were raised separately in undercut., Swaziland beds by routine nursery practice and planted out as barerooted stock into fully cultivated ground when about nine months old from seed. The trial plots were parts of larger taungya plantations and the young seedlings were tended together with agricultusal food crops for the first two years from transplanting.

In April 1965, 10 families were planted out at Muguga, Kenya in 9-tree plots at 2.4 m spacing, replicated seven times in randomized block design. The planting was repeated in March 1966 but using 16-tree plots in four replications.

Each of these two trials was accompanied by an adjacent Nelder design, radial spacing plot (design la, NELDER, 1962) with families entered as spokes and replicated four times in 1965 and three times in 1966.

In April 1967, a larger trial was established in Tanzania and comprised 31 open-pollinated families planted in four replicates of 16-tree plots on each of two sites; at Hambalawei in the Usambara mountains and Olmotonyi on the slopes of Mt Meru.

In each trial a "control" batch of the best seed stand seed available, and in current commecial use, was included as an additional treatment. For the random block trials, a general prescription was issued that the plots should be grown and tended in the same way as commercial coypress timber plantations are grown at that locality. This prescription has resulted in some differences in the ages at which silvicultural treatments have been carried out but, in general, all trees have been green-pruned to about half total height at 3-year intervals and were thinned to half the original stocking when dominant height reached 10 m, (except, of course, the Nelder spacing plots).

Periodic measurements of survival, height, breast height diameter and crown width have been taken. Stem volumes have been derived by entering height and diameter measurements in a standard volume table equation (ACKHURST and MICSKI, 1971): — $\text{Log}_{10} V_{(m3)} = 4.3146 + 1.7486 \log D_{(cm)} + 1.177 \log H_{(m)}$. Losses from cypress canker, except in very young trees when it may be lethal, are chiefly due to deformations of the stem which reduce its value as a saw log. Damage from this disease and stem straightness were assessed on five-point scales as follows: —

score	stem straightness	canker damage
1	= Perfectly straight & erect.	1 = No canker observed.
2	= Slight bend-usually butt-sweep	2 = Canker on branches only.
3	= Moderate bend.	3 = Stem cankers present; distortion negligible.
4	= Severely crooked, butt-log would require crass-cutting before sawing.	4 = Stem distortion such that value of saw-logs impaired
5	= Stem so crooked that saw-logs cannot be cut from it.	5 = Stem not utilizable for saw timber, or tree dying or dead from canker.

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Data from these assessments has been summarised and published in local technical notes (PERSSON, 1972; RAUNIO, 1976) but the latest assessment before thinning the trial plots is the last opportunity to make unbiased estimates of family variation and heritability calculations based on them, which may be of wider interest. Plot mean values were used as entries in analyses of variance to estimate variance components for among-family variation and residual error variation following KUNGS's Model 11 (KUNG, 1972). These values were entered in the general formula:

$$h^2 \text{ (families)} = \frac{\sigma^2_f}{\sigma^2_f + \frac{\sigma^2_e}{r}}$$

where r = number of plots per family, to calculate the heritability estimates shown in the following tables. The standard errors of heritability estimates shown in *table 1* was calculated as 4 σ^2_t from the interclass correlation equation: —

$$\sigma^2_t = \frac{2\,(1 + (n-1)\,t)^2\,(1-t)^2}{n\,(n-1)\,(N-1)} \quad \text{(FALCONER, 1962)}$$

Where $t = \frac{1}{4}h^2$ for half-sib families, N = number of families and n is the number of plots per family.

Results

The larger trial, established in 1967 in Tanzania, provides more reliable estimates of family heritabilities by the variance partitioning method. The estimates obtained before and after thinning, are shown in *Table 1* below.

Survivals in this trial were extremely good, 93 per cent overall, but losses were concentrated in one block at the Olmotonyi site, and stem form and canker assessments from this block were discarded as being atypical. There were no significant differences between family survivals.

Height and Diameter growth and stem straightness of the 31 families were found to be closely correlated between the two sites and with previous 3-year old measurements. The derived parameter, stem volume, was similarly correlated at the P = 0.001 level of significance. Crown width did not differ significantly among families nor were the data from the two sites correlated. Canker damage scores differed significantly at Hambalawei but not at Olmotonyi: results at the two sites were not significantly correlated. Thinning the stands had very little effect on the correlations observed (PERSSON, 1972; RAUNIO, 1976).

Effects of thinning on heritability estimates

Inspection of *Table 1* shows a tendency for h^2 values to be lower after thinning than before. This would be expected because foresters thin with the aim of producing a more uniform crop, thus curtailing the variation both within and between plots and the variance ratios, h^2, would also be expected to decrease. This hypothesis was more fully examined on the smaller, 1966 planted, trial at Muguga, which was thinned at age 6.2 years when dominant height reached 10 m.

Table 2 shows family mean values for four traits measured before and after thinning, together with their coefficients of variation. Heritability estimates calculated from analyses of variance before and after thinning are also given.

Table 2 shows that within-faimly variation has been greatly reduced (except in two families in respect of stem defect score and one family in respect of canker damage). Between family variation has also been reduced (except for stem form) and, as expected, the heritability estimates also fell.

Effect of Age on heritability estimates

The Nelder circle design plots, which are un-thinned, provide opportunity to examine the effect of age of crop on the heritability estimates made at successive measurement uncomplicated by the effect of thinning. *Table 3* presents heritabilities calculated from the two Nelder trials at Muguga.

It might be expected that the heritability estimates for

Table 1. — Heritabilities of various traits of *Cupressus lusitanica* on two sites in Tanzania, — Age 7 Years from field planting.

Character Examined	Site 1 Hambalawei Sign. level of Fam. diffs.	h^2	SE	Site 2 Olmotonyi Sign. level of Fam. diffs.	h^2	SE	Site 1 & 2 Combined Sign. level of Fam. diffs.	h^2	SE	Trial overall Means (units)
Before Thinning	(3)			(3)			(3)			
Survival (2)	NS	—	—	*	0.44	± 0.35	NS	—	—	93.4%
Mean Height	***	0.72	± 0.38	**	0.57	± 0.36	*	0.63	± 0.24	11.3 (m)
Mean Diameter	***	0.82	± 0.38	***	0.80	± 0.38	***	0.86	± 0.27	15.9 (cm)
Stem Volume	***	0.83	± 0.38	***	0.76	± 0.38	**	0.82	± 0.27	0.169 (m^3)
Crown Width (2)	NS	—	—	NS	—	—	NS	—	—	3.3 (m)
Stem Straightness	**	0.53	± 0.36	**	0.86	± 0.47	***	0.73	± 0.27	3.04 (score)
Canker damage (2)	**	0.55	± 0.36	NS	—	—	NS	—	—	1.56 (score)
After Thinning										
Mean Height	***	0.67	± 0.37	***	0.61	± 0.37	*	0.60	± 0.24	11.5 (m)
Mean Diameter	***	0.74	± 0.38	***	0.77	± 0.38	**	0.81	± 0.27	16.4 (cm)
Stem Volume	***	0.74	± 0.38	***	0.77	± 0.38	**	0.79	± 0.26	0.182 (m^3)
Stem Straightness	**	0.51	± 0.36	**	0.87	± 0.47	**	0.16	± 0.19	2.91 (score)

Notes: — (1) This column included to indicate the sizes of trees measured.
(2) Heritability estimates not shown because meaningless where significant difference between families were not detectable.
(3) Familiy differences significant at: — *** p = 0.001; ***p = 0.01; * p = 0.05.

Table 2. — Cypress progeny trial Muguga, Kenya Age 6.2 years Coefficients of variation (COV.) and Heritability Estimates (h^2) before and after Thinning:

Family No.	Mean ht. (m)	COV. %	Mean dbh. (cm)	COV. %	Stem form (score)	COV. %	Canker damage (score)	COV. %
			Before Thinning					
K 9	9.7	16.2	14.2	20.9	2.85	23.9	2.70	27.4
K 150	8.0	34.7	12.2	41.0	3.06	28.9	3.20	24.4
K 153	7.8	26.3	12.9	22.6	3.09	21.3	2.77	22.2
K 155	8.5	16.5	12.1	25.3	2.85	19.2	2.86	23.1
K 157	10.0	18.1	14.5	15.2	2.88	18.1	2.62	25.7
K 158	9.5	13.9	13.2	18.2	2.86	15.2	2.57	19.5
K 159	9.4	17.1	12.9	24.1	2.63	29.0	2.75	22.4
K 160	9.4	16.4	12.4	25.3	2.57	29.5	2.59	26.5
T 6	7.8	22.6	12.2	28.7	3.30	22.0	3.41	24.8
T 71	9.2	20.2	12.8	28.6	2.90	35.1	3.08	30.1
K.N (control)	9.1	24.0	12.0	31.5	2.92	32.9	3.02	30.8
C.O.V. family means	8.8%		6.5%		7.0%		9.5%	
h^2 Est.	0.87		0.73		0.70		0.81	
			After Thinning					
K 9	10.3	11.6	15.5	12.0	2.70	25.3	2.53	21.0
K 150	9.2	20.7	14.3	24.2	2.80	26.0	2.91	19.5
K 153	8.7	20.8	14.0	17.0	2.97	16.2	2.67	18.7
K 155	9.2	12.9	13.9	14.2	2.85	14.7	2.63	17.3
K 157	10.2	11.2	15.1	11.7	2.78	16.6	2.53	20.4
K 158	9.8	11.2	14.6	11.3	2.85	7.0	2.50	20.4
K 159	10.1	8.9	14.4	13.6	2.43	28.9	2.63	18.8
K 160	10.2	11.1	14.0	16.6	2.33	28.6	2.41	19.2
T 6	9.1	11.8	14.2	14.7	2.90	12.7	3.00	18.2
T 71	9.6	15.4	13.5	23.6	2.68	38.7	2.89	26.5
K.N (control)	10.0	15.4	13.9	19.6	2.58	27.8	2.66	19.0
C.O.V. family means	5.7%		4.0%		7.3%		7.1%	
h^2 Est.	0.57		0.61		0.68		0.55	

Table 3. — Cypress Heritability Estimates calculated at seven ages from un-thinned Nelder design plots.

Age from Field Planting	1965 planting Mean ht.	Mean dbh.	Stem form	Canker damage	1966 planting Mean ht.	Mean dbh.	Stem form	Canker damage
years								
3	.59	.84	.58	.71	—	—	—	—
4	—	—	—	—	.58	0	.11	.44
5	.79	.78	.48	.93	—	—	—	—
6	—	—	—	—	.26	.15	.63	.67
7	.73	—*	—*	.91	—	—	—	—
9	—	—	—	—	.30	.51	.69	.51
10	.72	.93	.49	.90	—	—	—	—

(—* not measured 1972)

growth characters would slowly fall with increasing age, as environmental factors progressively restricted the trees to the optimum size for the site. Similarly for canker damage, as stem distortions slowly heal over, differences between families should become more difficult to detect and the heritability estimates gradually fall. *Table 3,* shows no clear trends in this direction and it is concluded that these plots will need to be retained for many more years before definite trends are established.

Discussion

Cupressus lusitanica as grown in East Africa is a variable species, which has responded well to selection, and heritability estimates derived from young progeny trials have have usually been disconcertingly high, whether based on vegetative, open-pollinated or control-pollinated families. Paterson (1966) expected that heritabilities would decrease with age and used much lower values when predicting gains from the Cypress breeding programme.

Heritability values shown in this paper show no convincing change with age up to 10 years from field planting, but do show a marked fall as a result of thinning the trial plots. In these trials, in order to thin as evenly as possible, each family was reduced to the same number of stems per plot, but more selective "silvicultural" thinning would have produced more uniform crops and depressed the heritabilities calculated even more than shown here.

Selective thinning reduces the phenotypic variance both within and between families and will probably, but not necessarily, also reduce the heritability values calculated by variance partition. It will also, except in the case of vegetative progeny, alter the genotypic make-up of the families, and alter the environment in which they grow subsequently. It is thus necessary to recalculate heritabilities, whenever a thinning of the trial plots is made. Heritabilities should not be thought of as a "property" of a particular measured trait, like, say, the boiling point of a liquid which is constant under set environmental conditions.

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Summary

Cupressus lusitanica Miller is an important re-afforestation tree in the highland area of East Africa, where it produces valuable softwood timber. Seed improvement work at first through registered seed stands and later by clonal seed orchards has been carried out since 1957 on a regional basis.

Estimates of heritabiliy calculated from measurements of several open-pollinated progeny trials range from .87 to .26 for height growth, from .93 to NIL for stem diameter, from .70 to .11 for stem form and from .90 to NIL for damage caused by Cypress canker disease. Thinning the trial plots reduced within-family variances and between-family variances and resulted in reduced heritability values. No consistent change of heritability values with age of crop upto 10 years from field planting (11 m height) was detected.

The interpretationn of heritability estimates from thinned trial plot data is briefly discussed.

Key words: Cupressus lusitanica, Progeny Trials, Heritability.

Zusammenfassung

Cupressus lusitanica Miller ist eine wichtige Waldbaumart für Wiederaufforstungen in Hochlagen Ostafrikas. Seit 1957 werden Erntebestände dieser Baumart registriert Dazu wurden Samenplantagen angelegt. An den Nachkommenschaften von Beständen und Einzelbäumen wurden Untersuchungen zur Schätzung der Heritabilität bezüglich der Merkmale: Höhenwachstum, Dickenwachstum, Stammform und Krebsbefall, durchgeführt.

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