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YIELD EFFICIENCY IN PROGENY TRIALS WITH COCOA

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SUMMARY

Yield efficiency of cocoa, defined as yield over a period of time divided by the increment in trunk cross-sectional area over that period, was estimated in four factorial matings in Sabah, Malaysia, evaluated at a single planting density. The parents were 18 seedlings of Upper Amazon Forastero type, broadly representative of Peruvian Amazon material, and 15 clones of Trinitario type, selected from cultivated cocoa in Ecuador, Trinidad and Papua New Guinea. Both the Upper Amazon and Trinitario parents varied in general combining ability (gca) for yield efficiency, with strong evidence of additive inheritance of the trait. Some of the Upper Amazon parents showed higher yield efficiency than many of the Trinitarios. Correlations between gcas for yield efficiency and yield were inconsistent. This is thought to be because the parents differed markedly in optimal planting density, which is higher for many of the Upper Amazons with high gca for yield efficiency than it is for some of the Trinitarios. At the current stage of cocoa breeding, selection for adaptation to planting density is a higher priority than selection for yield efficiency.

INTRODUCTION

In cocoa, farm yields rarely reach 1t dry beans ha^{-1}, yet Corley (1983) estimated the potential yield as 11 t ha^{-1}. Although yields are limited by pest and disease attack in many cocoa-growing countries, there is great scope for better varieties and agronomic systems, which exploit more of the physiological potential. Yield efficiency, defined as the ratio of the cumulative yield over a period of time to increment in trunk cross-sectional area over the same period (Daymond *et al.*, 2002), is analogous to harvest efficiency in annual crops. In orchard crops, which include cocoa, the combination of small tree size and high yield efficiency provides the potential for higher yield per unit area (Larsen *et al.*, 1992). Although the concept was recognized by Pound (1933) and applied to single tree selection in cocoa by van der Knaap (1953) some fifty years ago, it was not followed through. Recently, Adomako *et al.* (1999) reported variation in 'yield index' (yield divided by the cube of trunk girth) in two trials of seedling cocoa varieties in Ghana, and Daymond *et al.* (2002) observed extensive variation in the partitioning to the yield component in a limited range of cocoa breeding material in Brazil. The latter concluded that there is considerable potential for yield improvement in cocoa by selecting for more efficient partitioning of assimilate to the yield component.

In tree crops, including cocoa, genotypes differ markedly in optimum planting density (e.g. Lockwood and Pang, 1996). Genotypes with low yield efficiency have lower optimum planting densities than those with higher yield efficiency that would not fill

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the space at lower planting density, unless there is variation in assimilate production per unit area. This has influenced cocoa breeding because the origins of formal selection lie in the plantation industries that developed in the West Indies, Central America and Java around the beginning of the twentieth century. In Trinidad, the typical spacing was 14 feet square for Trinitario cocoa (4.27 m, 717 trees ha^{-1}) (Preuss, 1901) with even wider spacing in Java (Van Hall, 1932, p484) and Papua New Guinea (Bridgland, 1960). In Ecuador, it was 'customary to plant very closely, 11 feet being the usual distance' (890 trees ha^{-1}, Van Hall, 1932, p308). By contrast, West African smallholder cocoa was planted at random spacing at higher densities, with the cultivar known as West African Amelonado grown at up to 2700 trees ha^{-1} (Van Hall, 1932, p434). The Trinidad (ICS) and Keravat (K and KA, Papua New Guinea) Trinitario clones, which were represented in the trials discussed here, were taken as single tree selections from wide-spaced plantings. Current recommendations are to plant in the range of 625–1111 trees ha^{-1}, for example in Papua New Guinea and Ghana.

Interest in higher density planting was prompted by Freeman (1975), who planted at up to 6727 seedling trees ha^{-1}. The very high early yields declined rapidly once differential competition set in. The critical follow up was by the Philippines Cocoa Estates Company (unpublished, cited by Lim *et al.*, 1994), where clones were planted at 5000 trees ha^{-1}. Yields were high in the first few years but then declined because the planting density was too high for the clone. At Golden Hope Research Centre, Sabah (formerly Scientific Department, BAL Plantations Sdn Bhd), a wide range of clones was planted at 3333 trees ha^{-1} (Lim *et al.*, 1994). Some, such as the Upper Amazon Forastero clones PA13 and PA300, were high yielding at a high planting density and yielded much the same at the lower planting density of 1096 trees ha^{-1}. Other Upper Amazon Forasteros, such as PA121 and MO81, yielded poorly at both planting densities (Lockwood and Pang, 1996). A 1.32 ha monoclone block of NA33 yielded about 3 t ha^{-1} a^{-1} over 7 years. Several Trinitario clones, including ICS1, K13, K20 and K24-106, yielded very little at high planting density, whereas EET308 from Ecuador, K6-101, KA2-101 and KA5-201 performed around the average for the trial, giving a yield only about half that of the better Upper Amazon clones (J. Thau-Yin Pang, unpublished data).

Many cocoa breeders have measured growth of trunk girth as a proxy for overall growth. The data have been used to predict yields at maturity (e.g. Glendinning, 1960), to measure tree-to-tree variation (e.g. Lockwood, 1976) or to estimate competition between entries in trials (e.g. Bridgland, 1960; Lockwood and Martin, 1976). There is great opportunity for retrospective use of such data to estimate yield efficiency (Daymond *et al.*, 2002) and to investigate if this concept is useful in practical breeding. This was investigated through analysis of the relationship between yield efficiency and general combining ability (gca) for yield in four cocoa experiments in Sabah, Malaysia.

MATERIALS AND METHODS

The field work was undertaken on Table Estate at the Golden Hope Research Centre, Sabah near Tawau (about 4°N,118°E), at an elevation of about 80 m amsl.

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The soils were highly fertile, young volcanic ash derived from basalt. The average rainfall is 2000–2100 mm a^{-1} and well distributed; the driest month averages about 130 mm. The most significant pest and disease problems were cocoa pod borer (*Conopomorpha cramerella*), which was controlled by sanitation and insecticide application, and vascular streak dieback disease, caused by infection with *Oncobasidium theobromae*, which was controlled by sanitation and by fungicide treatment during the nursery and establishment phases.

Upper Amazon clones were used as female parents for four complete factorial mating designs (Tables 1–4). In Trials 1 and 2, the parents used as males were also of Upper Amazon type, and in Trials 3 and 4 they were Trinitarios as indicated in Box 1:

Box 1

AMAZ 2-1, 15-15 (Amazon; Chalmers, 1973)

EET 308 (Trinitario selection from Estaciőn Experimental Tropical, Pichilingue, Ecuador)

ICS1, 6, 8 (Imperial College Trinitario selections; Pound, 1936)

K13, 20, 21, 82, K6-101, KA2-101, KA2-106, KA5-210 (Trinitarios selected in Papua New Guinea; Bridgland, 1960)

IMC14, 23, 47, 53, 67, 85,105 (Iquitos Mixed Calabacillo; Pound, 1938)

MO81 (Morona; Pound, 1938)

NA32, 33 (Nanay; Pound, 1938)

P4 (Nanay type; Pound, 1943).

PA7, 13, 76, 107, 121, 127, 137 and 300 (Parinari; Pound, 1938)

'PA'35 (an unidentified introduced clone with Trinitario affinities)

SCA9 (Scavina; Pound, 1938)

TAP 1-2 (Tapiche; Chalmers, 1973)

UIT1, 2 (Trinitarios introduced to Malaysia as IMC clones, but having close affinities with Pound's [1936] ICS Trinitario selections of Nicaraguan 'Criollo' type).

The clones used as female parents in Trials 1 and 2 were chosen because of previous evidence that they conferred high yield in Sabah or elsewhere; the other Upper Amazon parents were effectively speculative choices. In Trial 3, among the Trinitarios, the three ICS clones had a reputation as being good parents, and 'PA'35 and the two UIT clones had been used previously in Sabah, so only EET308 was entirely speculative. The Keravat parents used in Trial 4 had not been evaluated outside Papua New Guinea. Two crosses (NA33 × UIT1 and PA7 × NA32) were chosen as standards because they were in commercial use when the crossing programmes were done.

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The trials were planted in June 1986 (Trial 1 and 2), January 1989 (Trial 3) and August 1989 (Trial 4). The spacing was 3.8 × 2.4 m (1096 trees ha^{-1}) in all four trials. Plot size was 25 trees (5 × 5) in Trials 1 and 2, 15 trees (5 × 3) in Trial 3 and 18 trees (6 × 3) in Trial 4. There were four, three, five and three replications for Trials 1, 2, 3 and 4 respectively, in randomized block designs. All trials were surrounded by perimeter guard rows or trials of similar planting material, planted at the same spacing and at the same time. Husbandry practices were those of the host plantation. Yield recording ceased in August 1994 in Trials 1 and 2 and in August 1995 in Trials 3 and 4.

Yields were recorded as number of pods per tree and weight of wet cocoa per plot at 10–14 day intervals from the commencement of bearing, 16–18 months after planting. At yield peaks, sample fermentations were made to determine wet to dry weight conversion ratios, up to eight rounds per trial on a plot basis. The number of useable pods at each harvest with a sample fermentation were used to estimate the weighted average wet to dry weight conversion ratios for each genotype. These ratios were applied to the wet weights to estimate the yield of merchantable dry cocoa beans.

Girths were measured annually about 15 cm above ground level, initially using calipers to measure diameters and subsequently tapes to measure circumferences. Yield efficiency was calculated as the annual yield per tree from the commencement of bearing to the conclusion of recording divided by the annual gain in trunk cross-sectional area in cm^2 from July 1990 to July 1994 (Trials 1 and 2) and August 1991 to August 1994 (Trials 3 and 4). All calculations were done using plot means.

RESULTS

Data are presented as gcas for the parents used and absolute values for the trial means and the two standard crosses. In seven of the twelve statistical analyses, over 85% of the genotypic variance was additive, so approximate absolute values for each trait for each cross can be estimated from the gcas and the appropriate trial mean.

Trial 1 was high yielding, averaging 2.72 t dry cocoa ha^{-1} a^{-1} over the period of recording. In this trial, 17 of the test crosses outyielded the mean of the commercial controls. The adjacent Trial 2, which was planted at the same time, averaged 1.65 t ha^{-1}; in this trial of inter-Amazon crosses, all 18 test crosses outyielded the controls. By contrast, in Trial 3, with an average yield of 1.85 t ha^{-1}, none of the Upper Amazon × Trinitario crosses yielded as well as the mean of the controls. In Trial 4, again Upper Amazon × Trinitario crosses, with an average yield of 2.03 t ha^{-1}, 10 test crosses outyielded the mean of the controls, but only three were slightly higher yielding than the better one. The superiority for yield of the better inter-Upper Amazon crosses over Upper Amazon × Trinitario crosses was a general observation at Golden Hope Research Centre.

The two controls yielded about the same as each other in Trial 1 and 2, but in the later planted Trials, PA7 × NA32 was lower yielding. This observation was consistent

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Table 1. Estimates of general combining abilities (gcas) for trunk cross-sectional area, yield and yield efficiency in Trial 1.

Parent	Trunk cross-sectional area July 1994 (cm^2)	Yield Nov 1987–Aug 1994 (kg dry cocoa ha^{-1} a^{-1})	Yield efficiency (g dry cocoa a^{-1} cm^{-2} increment in trunk cross-sectional area a^{-1})
Female gcas			
IMC67	−2.81	−336	−21.4
NA33	0.56	118	10.3
SCA9	2.25	218	11.1
s.e.	1.288	33.6	6.45
Male gcas			
Amaz2-1	3.57	7	−18.4
Amaz15-15	−13.10	−404	−10.9
MO81	−7.65	−3	50.2
PA13	0.92	63	−11.1
PA107	7.31	292	5.1
PA121	1.68	64	5.5
PA127	11.32	34	−40.8
PA300	1.38	160	22.7
Tap1-2	−5.42	−215	−2.3
s.e.	2.232	58.2	11.17
Grand mean	102.51	2735	262.5
Additive component of genotypic variance (%)	64.5	88.9	61.8
Standards (observations)			
UIT1 × NA33	108.92	2597	266.7
PA7 × NA32	102.33	2588	241.4

Table 2. Estimates of general combining abilities for trunk cross-sectional area, yield and yield efficiency in Trial 2.

Parent	Trunk cross-sectional area July 1994 (cm^2)	Yield Nov 1987–Aug 1994 (kg dry cocoa ha^{-1} a^{-1})	Yield efficiency (g dry cocoa a^{-1} cm^{-2} increment in trunk cross-sectional area a^{-1})
Female gcas			
PA7	−11.49	−81	12.8
PA76	28.30	−125	−86.0
SCA9	−16.81	206	73.1
s.e.	1.494	1.7	5.89
Male gcas			
IMC14	4.02	106	7.7
IMC23	4.95	170	−1.5
IMC47	−6.23	−19	16.8
IMC53	−4.80	−111	−7.3
IMC85	6.04	113	16.0
IMC105	−3.98	−258	−31.8
s.e.	2.113	44.8	8.33
Grand mean	96.95	1684	201.6
Additive component of genotypic variance (%)	98.0	86.8	96.2
Standards (observations)			
UIT1 × NA33	96.0	1283	132.9
PA7 × NA32	77.2	1325	193.4

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Table 3. Estimates of general combining abilities for trunk cross-sectional area, yield and yield efficiency in Trial 3.

Parent	Trunk cross-sectional area Aug 1994 (cm^2)	Yield Jul 1990–Aug 1995 (kg dry cocoa ha^{-1} a^{-1})	Yield efficiency (g dry cocoa a^{-1} cm^{-2} increment in trunk cross-sectional area a^{-1})
Female gcas			
IMC14	5.52	127	1.5
IMC53	−9.89	−84	4.6
IMC85	4.37	−43	−6.1
s.e.	1.163	44.3	6.77
Male gcas			
EET308	−9.36	95	38.9
ICS1	4.48	88	2.9
ICS6	3.56	−127	−29.4
ICS8	6.35	293	15.0
'PA'35	10.78	−148	−45.0
UIT1	−9.58	−204	−10.6
UIT2	−6.22	3	28.3
s.e.	1.777	67.7	10.35
Grand mean	97.0	1816	198.5
Additive component of genotypic variance (%)	93.5	68.3	72.3
Standards (observations)			
UIT1 × NA33	80.7	2442	370.5
PA7 × NA32	74.6	1944	297.2

Table 4. Estimates of general combining abilities for trunk cross-sectional area, yield and yield efficiency in Trial 4.

Parent	Trunk cross-sectional area June 1994 (cm^2)	Yield Jan 1991 to Aug 1995 (kg dry cocoa ha^{-1} a^{-1})	Yield efficiency (g dry cocoa a^{-1} cm^{-2} increment in trunk cross-sectional area a^{-1})
Female gcas			
Amaz15-15	−3.77	45	11.4
P4	−3.76	208	31.8
PA137	7.53	−253	−43.2
s.e.	1.540	92.6	4.99
Male gcas			
K13	14.77	−100	−47.6
K20	3.91	−353	−55.3
K21	−1.21	−130	−16.2
K82	−5.25	115	23.9
K6-101	−9.91	153	50.0
KA2-101	1.54	−120	−9.1
KA5-201	−8.86	291	50.0
KA2-106	8.88	292	0.2
UIT1	−3.88	−147	−1.2
s.e.	2.667	92.6	8.64
Grand mean	75.77	2023	162.1
Additive component of genotypic variance (%)	85.6	76.1	92.6
Standards (observations)			
UIT1 × NA33	73.37	2421	224.6
PA7 × NA32	69.04	1938	156.7

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with other trials and reflected the progressive build-up of vascular streak dieback disease on the plantation, with PA7 × NA32 more susceptible than UIT1 × NA33. UIT1 × NA33 was slightly more vigorous than PA7 × NA32 in three of the four trials, with a larger difference in Trial 2. In Trial 2, the trees of PA7 × NA32 grew relatively slower from 1990 to 1994, which accounts for the high yield efficiency, whereas those of UIT1 × NA33 grew at the more usual rate.

There were statistically significant ($p < 0.001$) differences among the entries in all four trials for final trunk cross-sectional area, yield and yield efficiency.

In analyses of combining abilities for yield and yield efficiency, the effect of parents used as males was significant at $p < 0.001$ in all trials except Trial 2 where $p < 0.01$ for yield efficiency. The male parents used in this trial are believed to represent two half-sibling families, so the genetic base was narrow. The effect of parents used as females was significant at $p < 0.001$ in all analyses of Trials 2 and 4. In Trial 1 the effect of females was significant at $p < 0.001$ in the analyses of yield and of yield efficiency, and at $p < 0.05$ in the analysis of trunk cross-sectional area. In Trial 3, where the three IMC parents used as females were closely related, there were significant differences among the estimates of gca for trunk cross-sectional area ($p < 0.001$), and for yield ($p < 0.05$) but not for yield efficiency ($p > 0.05$).

There was no evidence of specific combining ability (sca) in any of the analyses of Trials 2 and 4, and in Trial 3 only for yield ($p < 0.05$). In this analysis, the effect of parents used as females was not significant when tested against interaction ($p > 0.05$), suggesting that there were no effects over and above those due to interaction. The effect of parents used as males was significant at $p = 0.05$ in this test. In Trial 1, there was significant sca in all three analyses. In the yield analysis, the effects of parents used as males and as females were significant when tested against sca ($p < 0.01$ and $p < 0.001$ respectively). In the analysis of trunk cross-sectional area, there was evidence of effects of parents used as males over and above sca ($p < 0.05$) but not for those used as females ($p > 0.05$). In the analyses of yield efficiency, the effects of males and of females were not significant at $p = 0.05$ when tested against sca.

The gca estimates for trunk cross-sectional areas indicate the variability in vigour among the parents used. PA76, which was used as a female parent in Trial 2 and in another trial not discussed here, gave some of the most vigorous crosses seen at Golden Hope Research Centre. As a clone, it is similarly vigorous. PA137, which was used as a female parent in Trial 4, and had a high gca for cross-sectional area, is only slightly less vigorous than PA76 as a clone. At the opposite extreme, AMAZ15-15 showed the smallest gca for vegetative vigour in Trial 1, and in Trial 4 its gca was much smaller than that of PA137. In Trial 1, its crosses did not fill the available space at the planting density of 1096 trees ha^{-1}. As a clone, AMAZ15-15 is characterized by weak vegetative growth, a sparse canopy and apparently prolific yield for its size. When these three clones were tested at the high planting density of 3333 trees ha^{-1}, AMAZ15-15 yielded nearly twice as much per unit area as PA76 (J. Thau-Yin Pang, unpublished observation).

The gca estimates for yield were as variable as those for vegetative growth. In Trial 1, on average the PA107 crosses yielded 130 % of those with AMAZ15-15. In Trial 2, the

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SCA9 crosses yielded 121 % those with PA76, and in Trial 3 the ICS8 crosses yielded 131 % of those with UIT1.

The ranking of the gcas for trunk cross-sectional area and yield were correlated in the two trials of inter-Upper Amazon crosses, Spearman's rank correlation (ρ) = 0.65 ($p = 0.05$) in Trial 1 and $\rho = 0.72$, $p > 0.05$ in Trial 2. There was no evidence of correlations in the two trials of Trinitario crosses, $\rho = 0.39$ in Trial 3 and $\rho = -0.20$ in Trial 4.

The yield efficiency analyses represent the deviations from regression of yield on vegetative growth. In Trial 1, where the differences in gcas among the parents used as males were not significant when tested against sca, MO81 showed the highest yield efficiency, although it was a poor parent for yield. By contrast, AMAZ15-15, which had been thought of as an 'efficient' parent, had the second lowest gca for yield efficiency. The interaction between male and female parents means that there can be no great confidence in these rankings. Among the parents used as females in this trial, SCA9 and NA33 were markedly more 'efficient' than IMC67. In Trial 2 the results for the parents used as females were clear cut: SCA9 had the highest gcas for yield efficiency and yield, and PA76 the lowest. There was significant variation in yield efficiency among the six IMCs used as males, with the weak growing IMC105 crosses giving particularly poor results. However, IMC23, the best parent for yield, was by no means the best for yield efficiency.

In Trial 3, where Trinitario clones were used as pollen parents, the ranking of the three IMCs used as female parents was different to that in Trial 2, but there was little evidence of statistically significant differences among them for yield or yield efficiency. IMC85, which was the second best parent for yield efficiency in Trial 2, was the poorest of the three. IMC53, which showed low yield efficiency in Trial 2, was the best of the three IMCs in Trial 3, although it had the lowest gca for yield. Among the parents used as males, EET308 had the highest gca for yield efficiency and 'PA'35 the lowest. The rank correlation between the gcas for yield and yield efficiency was $\rho = 0.74$, $p > 0.05$.

In Trial 4, the Papua New Guinea Trinitarios were highly variable in yield efficiency. KA5-201 and K6-101, two of the better parents, showed high gca for yield efficiency. UIT1 was about average, as it was in Trial 3. K20, which had a negligible yield when grown at high density, had a strongly negative gca for yield efficiency. The rank correlation between the gcas for yield efficiency and yield was $\rho = 0.75$, $p > 0.05$, indicating good agreement between them.

Yield efficiency was re-calculated for all four trials using the final cross-sectional area rather than the increment. The change made almost no difference to the rankings of the gcas.

DISCUSSION

The results of the four experiments have shown that yield efficiency is inherited additively in cocoa, as are vegetative vigour and yield, from which it is derived. Overall, the results are consistent with the idea that many of the Trinitarios, that were

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selected at low planting density, are less 'efficient' than the better Upper Amazons under the conditions of the trials, especially planting density. It is interesting that EET308, which was selected at an intermediate planting density, has a higher gca for yield efficiency than many of the other Trinitarios. Yield efficiency thus quantifies what cocoa breeders have long known: their breeding material varies in the ratio of vegetative to reproductive growth, and is a useful concept for that reason.

High yielding clones, and presumably good parents, will be those that are adapted to the chosen planting density (and husbandry regime) and have high yield efficiency. In the four trials, the correlations between yield efficiency and yield on a family basis were Trial 1 $\rho = 0.44$ ($p > 0.01$), Trial 2 $\rho = 0.67$ ($p = 0.001$), Trial 3 $\rho = 0.74$ ($p = 0.001$) and Trial 4 $\rho = 0.84$ ($p = 0.001$). In the current state of cocoa breeding, selection for yield efficiency appears to have no advantage over selection for yield and adaptation to planting density. However, the deviations from the regression of yield on a measure of vegetative growth will provide important information on the material under investigation.

The concept of yield efficiency was developed with crops like apples where selection is well advanced. By contrast, in cocoa, the Upper Amazon material that is critically important in breeding, seed production and commercial plantings was taken directly from uncultivated stands in the area of the centre of diversity of the crop or is one or two generations removed from them. There is wide variation in the optimum planting density of this material (Lockwood and Pang, 1996), and it varies too in the plasticity of the response of yield to planting density. For clones like PA13 and PA300 used as parents in the current trials, the yield efficiencies calculated from yield per ha rather than per tree would have been higher at high density than low. Both values would have been higher than the corresponding ones for MO81 and PA121, yet their gcas for yield efficiency were broadly similar. Similarly, at high planting density most Trinitario clones would give low yield efficiencies, but they would be near normal at normal density. The apparent interaction between genotype, optimum planting density and yield will limit the application of yield efficiency to the selection problem until selection is further advanced and adaptation to the planting densities that are agriculturally optimum have been fixed in the breeding material.

The challenge facing cocoa breeders is to identify good parents for yield. In the early days of selection, good clones were usually found to be good parents (Van Hall, 1930) as is expected with an additively inherited trait. However, as a wider genetic base was utilized and especially Upper Amazon material, the relationship appeared to break down, leading Bartley (1967) to conclude that 'the performance of bi-clonal hybrids was not related to the performance of the parents as clones'. It was not for another 25 years that Mooleedlhar and Lauckner (1990) demonstrated the interaction between yield, clone and planting density. Later, Lockwood and Pang (1992) showed that the phenotype is a useful guide to breeding values for yield when clones are grown at appropriate planting densities. Recently, J. Thau-Yin Pang (unpublished observation) suggested that optimum planting density of a set of clones is higher than that of

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the seedlings derived from them and vice-versa, further complicating the selection problem.

Van der Knaap (1953) proposed use of yield efficiency as an aid to selection of seedlings for evaluation of clones. Use of this concept for both family level and individual tree selection in Trial 1 will be discussed in a later paper.

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