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Optimum Design for Seedling Seed Orchards to Maximize Genetic Gain
An Investigation of Seedling Seed Orchards of *Eucalyptus pellita*

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Introduction

Establishing a seedling seed orchard with open pollinated progenies of plus trees is widely employed as a first step towards forest tree improvement for fast growing species in Indonesia (SOESENO, 1988; SUHARTONO, 1991; HASHIMOTO *et al.*, 1996). At present, it might be the most reliable and practical way to meet the immediate demand for genetically improved seed to be used in industrial reforestation programs in Indonesia. This procedure is recommended as an alternative to clonal seed orchards for species with an early flowering habit and where vegetative propagation is difficult (WRIGHT, 1976; ELDRIDGE *et al.*, 2001).

In the seedling seed orchard, genetic gains are captured in three stages: plus-tree selection, half-sib family selection and individual selection (WRIGHT and BULL, 1963). The latter two gains generally depend on the design of the orchard, because this will determine the intensity of family and individual selection. It is already known that there is an optimum allocation of selection intensities for any given set of heritabilities (NAMKOONG *et al.*, 1988). The heritabilities values express the proportion of variation in the population that is attributable to genetic differences among individuals, where, the amount of variation is measured and express as the variance (ZOBEL and TALBERT, 1984; FALCONER and MACKAY, 1996). It is therefore the increasing of number of family and number of trees per plot will increase the variances to both family and within plot as well. However, to maximize genetic gain in a certain design of seedling seed orchard the optimum number of both variables should be found. Studies on the optimum allocation of materials to maximize genetic gains have been reported for seedling seed orchards (NAMKOONG, 1969; KURINOBU, 1993) as well as in clonal tests (SHAW and HOOD, 1985).

In this study, the optimum design for seedling seed orchards originally proposed by Kurinobu (1993) was re-examined using real variance data estimated from trees aged one to five years in seed orchards of *E. pellita* in South Kalimantan and South Sumatra.

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Materials and Methods

Variance components estimation

In this study, the three types of variance components: family variance, plot error variance and within plot variance, were estimated using height data from trees aged one to five years in first-generation seedling seed orchards of *Eucalyptus pellita* in South Kalimantan and South Sumatra. The seed orchard in South Kalimantan was established in January 1994 and those in South Sumatra were established in January 1995. In South Kalimantan, the three provenances (South Kiriwo, North Kiriwo and Serisa Village in Papua New Guinea) were tested at a single site, whereas in South Sumatra they were tested separately at different sites. These orchards were designed in the form of randomized complete blocks (RCBD) with open-pollinated families allocated randomly within each replicates. The numbers of families tested for the South Kiriwo (group A), North Kiriwo (group B) and Serisa Village (group C) provenances were 48, 39 and 34, respectively. Families were usually represented by an initial planting of five trees in a row plot, with 10 replicates a spacing of 4 × 1.5 m. Site characteristics in seedling seed orchards of *E. pellita* at the two locations are presented in Table 1.

Height was measured, at both locations, when the trees were one to five years old. During this period, within family-plot selections were conducted twice: the poorest two trees out of the five per plot were culled in the first step and the poorest individual of the remaining three was removed in the second step. The data prior to this step were used in the analysis. The following linear model was used to estimate the variance components at each age and each orchard (Y_{ijk}):

$$Y_{ijk} = \mu + R_i + F_j + RF_{ij} + \varepsilon_{ijk} \tag{1}$$

where μ is the overall mean, R_i is the i-th replicate effect, F_j is the j-th family effect, RF_{ij} is the plot error and ε_{ijk} is the within plot error.

Table 1. Site characteristics of seedling seed orchards of E. pellita at the two locations

Information	South Kalimantan	South Sumatra
Site	Pelaihari	Pendopo
Latitude (South)	3°58’	4°00’
Longitude (East)	114°38’	104°00’
Altitude (m asl.)	30	80
Rainfall (mm/year)	2,730	2,781
Dry season	May-September	May-September
Soil type	Ferralsols	Acrisols
Temperature (min. – max.)	23° - 33°C	24° - 33°C
Wind	Intermediate	Low
Slope	0%	3%
Vegetation cover	Imperata cylindrica	Imperata cylindrica
Ground cultivation	Plowing 2 ×	Plowing 2 ×
Fertilizer	NPK 2 × /year	NPK 1 × /year

In order to determine any trend in the three types of variance component under the different levels of heritability, they were expressed as percentages, and then a linear regression equation to estimate within plot variance was calculated using family variance as the independent variable. In this study, family variance (σ^2_f) was assumed to be forty percent of the additive genetic variance (σ^2_A), is the chief determinant of the observable genetic properties of the population and of the response of the population to selection (FALCONER and MACKAY, 1996), as shown by the following equation:

$$\sigma^2_A = 2.5\sigma^2_f \qquad (2)$$

This is because the out crossing rate in natural stands of eucalypt is around 0.70, and that 30% selfing gives an average coefficient of relationship among open-pollinated progeny of 1/2.5 (SQUILLACE, 1974; GRIFFIN and COTTERILL, 1988).

Prediction of genetic gain

A formula to predict genetic gain in seed orchards was presented by NAMKOONG *et al.* (1966). In this study, however, our primary concern was the gain obtained as a result of family and individual selection in the seed orchard. Therefore, the gain as a result of plus tree selection and the terms with a genotype-environment interaction variance were omitted from the version used here. The modified formula to predict a local genetic gain (G) is as follows:

$$\begin{aligned} G &= G_2 + G_3 \\ &= i_2 \bullet (1/4)\, \sigma^2_A / \sigma_2 + i_3 \bullet (3/4)\, \sigma^2_A / \sigma_3 \\ &= i_2 \bullet \sigma_2 \bullet (1/4)\, \sigma^2_A / \sigma^2_2 + i_3 \bullet \sigma_3 \bullet (3/4)\, \sigma^2_A / \sigma^2_3 \\ &= i_2 \bullet \sigma_2 \bullet h^2_f + i_3 \bullet \sigma_3 \bullet h^2_w \qquad (3) \end{aligned}$$

where G_2 and G_3 are genetic gain for family and within plot selections, respectively, and σ^2_A is additive genetic variance. σ^2_2 and σ^2_3 are phenotypic variances for family mean and within plots, respectively and they are expressed as $\sigma^2_2 = \sigma^2_w / (n_p \bullet r) + \sigma^2_e / r + \sigma^2_f$ and $\sigma^2_3 = \sigma^2_w$, where n_p, r, σ^2_e and σ^2_w are the number of trees planted per plot, the number of replicates, plot error variance, and within plot variance, respectively. Two types of heritability in equation (3), h^2_f and h^2_w are family heritability and within plot heritability, respectively. The first term on the right-hand side of the equation (3) is the gain due to selection of the best families and the second one corresponds to the selection of the best trees within each plot containing the best families. Thus i_2 and i_3 are the selection intensities for family selection and within plot selection.

In the case of seedling seed orchards, the proportion of selected trees is expressed by n_f / n_i., when the initial density per hectare of seed orchard (n_i) and the final density (n_f) have been determined. When n_p is the number of trees planted per plot, the proportion of within plot selection is $1/ n_p$, and the proportion of family selection is $n_f \bullet n_p / n_i$, because the total proportion of selected trees is the product of the proportion of within plot selection and that of family selection. Therefore, the ratios (P) for i_2 and i_3 are $n_f \bullet n_p / n_i$ and $1/n_p$ respectively. The intensities were calculated by an approximate formula (LINDGREN, 1986):

$$i(P) = (1-P)\,[1.452\sqrt{(\ln(1/P(1-P)))} - 0.45 + 1.122\,(1-P)^{9.0}\,P^{0.84}] \quad (4)$$

where $i(P)$ is an approximation for the selection intensity, and P is the proportion selected (for i_2 and i_3).

The change in genetic gain predicted by equation (3), based on the number of families, was examined under three levels of heritability: low (=0.1), intermediate (=0.2) and high (=0.3). The size of seed orchard, number of replicates and initial density were assumed to be 2.0 ha, 10 replicates and 1,666 trees per hectare (4m × 1.5m spacing); these were the standard figures actually used during the first generation tree improvement program for *E. pellita* (LEKSONO and KURINOBU, 2005). The final density was assumed to be 150 trees per hectare.

The heritability (h^2) is the ratio of additive genetic variance (σ^2_A) to phenotypic variance (σ^2_p), it is of key importance in estimating genetic gains (G) which determined by the heritability of the trait and the selection differential (S) that is used in selection program ($G = h^2S$). Because the selection differential is dependent upon two factors; intensity of selection (i) and phenotypic standard deviation (σ_p), therefore $S = i\sigma_p$, and the expected genetic gain becomes $G = ih^2\sigma_p$ (ZOBEL and TALBERT, 1984; FALCONER and MACKAY, 1996).

Results and Discussion

The relative variance components for height at the two locations are presented in Table 2. Proportions of family variance ranged from 1% up to 15%, whereas the size of within plot variance and those of plot error were much larger than this. During the data collection period, within family-plot selections were undertaken twice, at 2 and 3 years old, however, the effect of

Table 2. Relative size of variance components for tree height in seedling seed orchards of *Eucalyptus pellita* at the two locations

Variance component	South Kalimantan (year)					South Sumatra (year)				
	1	2	3	4	5	1	2	3	4	5
Group A										
Family	0.008	0.047	0.064	0.075	0.048	0.077	0.034	0.041	0.020	0.077
Plot error	0.226	0.574	0.393	0.248	0.447	0.334	0.286	0.326	0.337	0.315
Within plot	0.765	0.379	0.543	0.677	0.505	0.589	0.680	0.633	0.643	0.608
Group B										
Family	0.053	0.035	0.135	0.123	0.138	0.068	0.066	0.037	0.032	0.113
Plot error	0.107	0.108	0.342	0.284	0.266	0.224	0.145	0.213	0.119	0.229
Within plot	0.841	0.857	0.523	0.594	0.596	0.708	0.789	0.750	0.850	0.658
Group C										
Family	0.051	0.038	0.061	0.069	0.152	0.049	0.042	0.027	0.041	0.055
Plot error	0.496	0.483	0.465	0.457	0.408	0.162	0.213	0.164	0.229	0.282
Within plot	0.453	0.479	0.474	0.474	0.440	0.790	0.746	0.809	0.731	0.663

Relative size of variance components was calculated assuming that the sum of family variance, plot error variance and within plot variance accounted for all the variability.

thinning was not obvious at both locations.

A regression of within plot variance against family variance is presented in Fig. 1. The proportion of within plot variance (y) appears to decrease as the proportion of family variance (x) increases; this trend was statistically significant. Thus the regression equation obtained here (y = –1.527x + 0.737) was used in the subsequent analysis to determine the relative size of the three-variance components under different levels of heritability. The plot error variance was calculated as the residual of family variance and the estimate of within plot variance, both of which are calculated from the regression equation. The total of the relative size of the three variances (σ^2_p) was unity (=1.0).

With the variances determined by the above regression equation, genetic gain for each of the number of family, starting from 30 up to 100, were calculated by the formula (3) under three levels of heritability (Fig. 2, a detailed stepwise procedure was presented in Appendix). The size of the seed orchard and the number of replications (r) in this study were assumed as 2.0 ha and 10 replications ($n_i \cdot 2$=3332 trees), therefore the number of trees per plot (n_p) will be decreased with the increase in the number of families tested in the orchard. The optimum number of families in order to maximize gain was around 40 at intermediate and high heritability and 50 at low heritability, although the differences in the gain as a result of larger number of families were small. The optimum number seemed to increase slightly when the heritability was low. This is probably due to the fact that family selection tends to be more effective when the heritability is low (FALCONER and MACKAY, 1996).

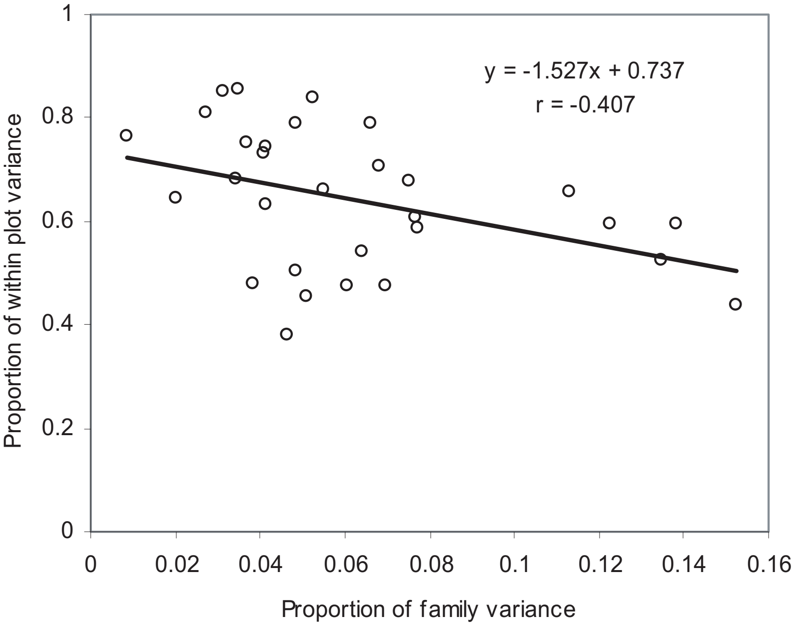

Fig. 1. The regression for within plot variance against family variance.

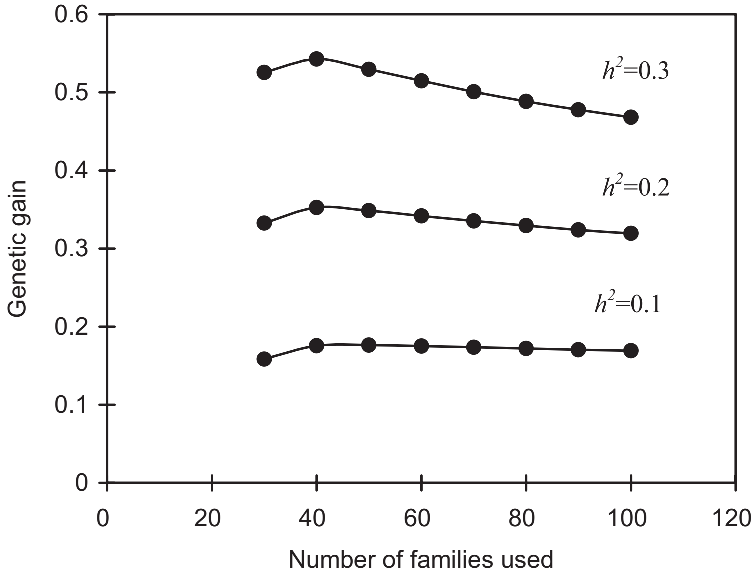

Fig. 2. Changes in genetic gain with an increase in the number of families within the seed orchard and heritability (h^2). The size of the seed orchard was assumed to be 2.0 ha with 10 replicates. Chart was drawn using the data presented in *Appendix*.

The optimum number of trees per plot, assuming the optimum number of families, was 6.7 for low heritability and 8.3 for intermediate to high heritability. This was slightly more than the five trees per plot proposed in the previous study (Kurinobu, 1993). This discrepancy in the number of trees per plot is due to the fact that the size of plot error variance assumed in this study was greater than the one used in the previous study; the proportion of plot error variance in this study was around 30%, compared with less than 20% in the previous study. This larger size of plot variance inevitably reduces the gain by family selection and it consequently emphasizes the gain by within plot selection, hence greater gain as a result of larger plot sizes.

The relative size of plot error variance used in this study, which was based on the results of multiple tests, is more realistic than the size used in the previous study, because that was based on a single test result (Kurinobu, 1993). Therefore the gain might have been increased slightly if the number of trees per plot was around 6 to 8. However, it is well known that the plot error variance can be reduced by careful site selection and blocking when the orchard is being established (Falconer and Mackay, 1996; Williams *et al.*, 2002). Therefore, the design using five trees per plot proposed in the previous study can result in almost the same amount of gain as long as the orchards were established appropriately.

In conclusion, the optimum number of families for intermediate heritability (= 0.20) was found to be around 40 to 50 with six to eight trees per plot in a seed orchard of 2 ha with 10 replicates. This result suggests that the design of the first-generation seedling seed orchards of *E. pellita* was near the optimum to achieve maximum genetic gain through the two stages of selection: within

Appendix. A procedure to calculate genetic gains under 3 levels of heritability

a. h^2 = 0.10

Number of family	Trees per family	Trees per plot (n_p)	Selection rate		Selection intensity		Phenotypic variance		heritability		Genetic gain		
			P_2	P_3	$i_2(P_2)$	$i_3(P_3)$	σ^2_2	σ^2_3	h^2_f	h^2_w	G_2	G_3	G
30	111	11.1	1.00	0.09	0.000	1.738	0.074	0.676	0.34	0.11	0.000	0.159	0.159
40	83	8.3	0.75	0.12	0.357	1.572	0.077	0.676	0.33	0.11	0.032	0.143	0.176
50	67	6.7	0.60	0.15	0.514	1.433	0.079	0.676	0.32	0.11	0.046	0.131	0.177
60	56	5.6	0.50	0.18	0.630	1.314	0.081	0.676	0.31	0.11	0.056	0.120	0.175
70	48	4.8	0.43	0.21	0.729	1.210	0.083	0.676	0.30	0.11	0.063	0.110	0.174
80	42	4.2	0.38	0.24	0.816	1.119	0.085	0.676	0.30	0.11	0.070	0.102	0.172
90	37	3.7	0.33	0.27	0.895	1.038	0.087	0.676	0.29	0.11	0.076	0.095	0.171
100	33	3.3	0.30	0.30	0.966	0.966	0.089	0.676	0.28	0.11	0.081	0.088	0.169

Relative sizes for family, plot error and within plot variances were 0.040, 0.284 and 0.676, respectively.

a. h^2 = 0.20

Number of family	Trees per family	Trees per plot (n_p)	Selection rate		Selection intensity		Phenotypic variance		heritability		Genetic gain		
			P_2	P_3	$i_2(P_2)$	$i_3(P_3)$	σ^2_2	σ^2_3	h^2_f	h^2_w	G_2	G_3	G
30	111	11.1	1.00	0.09	0.000	1.738	0.116	0.615	0.43	0.24	0.000	0.333	0.333
40	83	8.3	0.75	0.12	0.357	1.572	0.118	0.615	0.42	0.24	0.052	0.301	0.353
50	67	6.7	0.60	0.15	0.514	1.433	0.120	0.615	0.42	0.24	0.074	0.274	0.348
60	56	5.6	0.50	0.18	0.630	1.314	0.122	0.615	0.41	0.24	0.090	0.251	0.342
70	48	4.8	0.43	0.21	0.729	1.210	0.123	0.615	0.41	0.24	0.104	0.232	0.335
80	42	4.2	0.38	0.24	0.816	1.119	0.125	0.615	0.40	0.24	0.115	0.214	0.329
90	37	3.7	0.33	0.27	0.895	1.038	0.127	0.615	0.39	0.24	0.125	0.199	0.324
100	33	3.3	0.30	0.30	0.966	0.966	0.129	0.615	0.39	0.24	0.135	0.185	0.319

Relative sizes for family, plot error and within plot variances were 0.080, 0.305 and 0.615, respectively.

a. h^2 = 0.30

Number of family	Trees per family	Trees per plot (n_p)	Selection rate		Selection intensity		Phenotypic variance		heritability		Genetic gain		
			P_2	P_3	$i_2(P_2)$	$i_3(P_3)$	σ^2_2	σ^2_3	h^2_f	h^2_w	G_2	G_3	G
30	111	11.1	1.00	0.09	0.000	1.738	0.158	0.554	0.48	0.41	0.000	0.526	0.526
40	83	8.3	0.75	0.12	0.357	1.572	0.159	0.554	0.47	0.41	0.067	0.475	0.542
50	67	6.7	0.60	0.15	0.514	1.433	0.161	0.554	0.47	0.41	0.096	0.433	0.529
60	56	5.6	0.50	0.18	0.630	1.314	0.163	0.554	0.46	0.41	0.117	0.397	0.515
70	48	4.8	0.43	0.21	0.729	1.210	0.164	0.554	0.46	0.41	0.135	0.366	0.501
80	42	4.2	0.38	0.24	0.816	1.119	0.166	0.554	0.45	0.41	0.150	0.338	0.489
90	37	3.7	0.33	0.27	0.895	1.038	0.168	0.554	0.45	0.41	0.164	0.314	0.478
100	33	3.3	0.30	0.30	0.966	0.966	0.169	0.554	0.44	0.41	0.176	0.292	0.468

Relative sizes for family, plot error and within plot variances were 0.120, 0.326 and 0.554, respectively.

plot selection and family selection. This result also suggest that the current plot size, five trees per plot, will not maximize the gain without a careful choice of site and proper blocking to reduce plot error variance.

Explanation of the calculation

Selection rate and selection intensity: a rate of family selection (P_2) was calculated as given in the text (= $n_f \bullet n_p / n_i$) and that within plot selection (P_3) is an inverse of the trees per plot (= $1/n_p$). Selection intensity at each stage of selection (i_2 and i_3) was calculated with Eq.(4) using the respective rate of selection.

Size of variances: In the gain prediction here, phenotypic variance for individual tree was assumed 1.0, hence the additive genetic variance is equal to the heritability. The family variance was calculated with Eq.(2), then within plot variance (y in relative rate) was estimated with the regression equation in Fig. 1 ($y = -1.527x + 0.737$, where x is a rate of the family variance). The plot error variance was regarded as residuals of the phenotypic variance subtracted by the family variance and the within plot variance ($=1.0 - x - y$).

Phenotypic variances and heritability: the phenotypic variance for family selection (σ^2_2) was a family mean variance as given in the text (= $\sigma^2_f + \sigma^2_e / r + \sigma^2_w / r \bullet n_p$), where the variances were relative rate) and that of within plot selection (σ^2_3) was the estimate with Eq.(2). Heritability at the family selection (h^2_f) was calculated as a rate of a quarter of additive genetic variance [$(1/4)\sigma^2_A$] to the family mean variance (σ^2_2), while the one for within plot selection (h^2_w) was a rate of three quarter of additive genetic variance [$(3/4)\sigma^2_A$] to the within plot variance (σ^2_3).

Prediction of genetic gain: gains at each stage of selection were predicted with Eq.(3).

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Summary

The optimum design of seedling seed orchards was investigated using height data from first-generation seedling seed orchards of *Eucalyptus pellita*, aged one to five years, at two locations in Indonesia (South Kalimantan and South Sumatra). The proportions of family variance ranged from 1% to 15%. Within plot and plot error variances were much larger - 60 to 70% and 30%, respectively. The regression for within plot variance against family variance was statistically significant, so it was used to estimate the relative sizes of the three variances under different levels of heritability. In the case of a seedling seed orchard of 2.0 ha with 10 replicates, the optimum number of families was found to be around 40 with eight trees plot for intermediate to high heritability. This number slightly increased to 50 with six trees plot for low heritability.

These results indicate that the current plot size, five trees per plot, will not maximize the gain without careful site selection and proper blocking to reduce plot error variance.

Key words: *Eucalyptus pellita*, Genetic gain, Optimum design, Plot size, Seedling seed orchard

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遺伝獲得量最大化のための実生採種園の最適設計
− *Eucalyptus pelita* の実生採種園における検討 −

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要　　旨

インドネシアの南カリマンタン，南スマトラの２ヵ所に設定された，*Eucalyptus pelita* の第一世代実生採種園から得られた，1年生から5年生までの樹高データを用いて，実生採種園の最適設計を検討した。家系分散の割合は１％から15％の間を取り，プロット内分散はおよびプロット誤差分散はさらに大きく，それぞれ60～70％および30％であった。家系内分散に対するプロット内分散の回帰は統計的に有意であったため，異なる遺伝率レベルにおける３つの分散の相対的大きさの推定に利用した。中庸から高い遺伝率である場合には，10回反復の2.0haの実生採種園に最適な家系数はほぼ40，プロットあたり8個体の植栽，遺伝率が低い場合には，家系数は若干増加し50，プロットあたり6個体となった。この結果は，現在用いられているプロットあたり5個体の植栽では，プロット誤差を減少させるための慎重な立地選択と適正なブロック配置を行わない限り，遺伝獲得量を最大化できないことを示している。

キーワード： *Eucalyptus pelita*・遺伝獲得量・最適設計・プロットサイズ・実生採種園