Efficiency of Combined Selection Over Sequential Selection in Forest Tree Progeny Trials

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Summary

A comparison was made between two methods of forest breeding by recurrent selection. Combined selection (CS) based on an index that combines half-sib family and individual merits and sequential selection between and within half-sib families (SS) were considered. Expected efficiency of CS relative to SS was computed as the ratio of the expected gains of each method (CS/SS). For analysis, data from the literature and from a specific open pollinated progeny trial of *Eucalyptus grandis* (Hill) Maiden were taken. An average efficiency of 1.21 (SS = 1.00) was found for the published data, concerning growth characters. For the specific progeny trial efficiency was of 1.27 for H (plant height) and 1.31 for DBH (diameter at breast height) and V (volume). A procedure that allows predicting minimum efficiency for a given trial was worked out. Both methods were also compared under equal effective population sizes (N_e). It became evident that CS is superior to SS, and this superiority is more evident for traits with small narrow sense individual heritabilities or trials with small plot sizes (or both). Efficiency of CS over SS is less evident for traits in general, when effective population size was maintained equal in both schemes. Combined selection is recommendable in selection programs, specially if effective population sizes do not matter.

Key words: Tree breeding, Eucalyptus, selection index.

Introduction

Sequential selection between and within half-sib families (SS) consists in selecting the best trees from each plot of selected families for example to set up clonal seed orchards. This method is common in selection programs of fast growing tree species when the trial itself is expected to be used as a direct source of genetic gains. Combined selection consists in selecting trees based on an index that combines family and phenotypic value. It was originally designed for individual selection in animal breeding, were economic values of individuals are great (Lush, 1947). The literature, in general, points towards a superiority of CS over SS (Cotterill and Jackson, 1985).

This paper makes a comparison of both methods and shows the procedure for obtaining an "a priori" estimate of the minimum efficiency of CS over SS for a given progeny trial, which may help breeders to decide the better way of culling seedling seed orchards. We also express this minimal efficiency by heritabilities and number of trees per plot, for common situations in forest breeding.

Data from *Eucalyptus* sp. progeny trials were taken to illustrate the theoretical developments and to evaluate the relative efficiency of CS under local conditions, prevailing in eucalyptus recurrent selection programs.

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Material and Methods

A- Theoretical Development

Comparisons were made on the basis of an efficiency variable (EF), here taken as the ratio between expected progress under CS and SS. For panmitic species and maternal half-sib families, expected progress under SS is given by

equation (1)

$$Gs_S = i_b \sqrt{\frac{p-1}{p}} \, \theta \frac{\sigma_A^2}{\sigma_b} + i_w \sqrt{\frac{n-1}{n}} \, (1-\theta) \frac{\sigma_A^2}{\sigma_W}$$

where i_b, σ_b, i_w and σ_w, are standardized selection differentials and phenotypic standard deviations among and within families, respectively, for a given trait; σ_A^2 is the additive genetic variance, θ is the genetic intraclass correlation for families; p is the number of tested families and n is the number of individuals per plot. Quantity i_w was computed according to Fisher and Yates (1971).

The combined selection index for the kth individual of the jth replication, belonging to the ith family, can be expressed as

$$I_{ijk} = b_p(\overline{Y}_{i..} - \overline{Y}_{...}) + b_w (Y_{ijk} - \overline{Y}_{ij.}) \qquad \text{equation (2)}$$

b_p and b_w being the family and individual merits, respectively; $\overline{Y}_{...}$ is the overall mean, $\overline{Y}_{i..}$ is the mean of family i, $\overline{Y}_{ij.}$ the mean of the ij^{th} plot, and $\overline{Y}_{ijk}$ the phenotypic value of the given tree. As it can be seen, individual merits were considered in a stratified sense (within plots) such that the deviations between I_{ijk} and the corresponding individual breeding values are given by

$$b_b = \sqrt{\frac{p-1}{p}} \left[\theta + \frac{(1-\theta)}{nr} \right] \frac{\sigma_A^2}{\sigma_b} \qquad \text{equation (3)}$$

and

$$b_w = \sqrt{\frac{n-1}{n}} \, (1-\theta) \frac{\sigma_A^2}{\sigma_W} \qquad \text{equation (4)}$$

where r is the number of replications of the experiment.

Under CS the expected genetic progress is then

equation (5)

$$Gs_C = i_c \sqrt{\left(\frac{p-1}{p}\right)\left[\theta + \frac{(1-\theta)}{nr}\right]^2 \left(\frac{\sigma_A^2}{\sigma_b}\right)^2 + \left(\frac{n-1}{n}\right)(1-\theta)\left(\frac{\sigma_A^2}{\sigma_W}\right)^2}$$

In the present case, assuming half-sib families, $\theta = 0.25$ and $(1-\theta)^2 = 0.5625$; i_c is the standardized selection differential taking I_{ijk} as the selection unit.

Efficiency values, $EF = Gs_C/Gs_S$, were calculated assuming equal selection proportions for both methods (30% among and 10% within families, unless stated otherwise) and alternatively, equal effective population numbers (N_e). The variance effective population number (Crow and Kimura, 1970) was

obtained as given by VENCOVSKY (1976, 1978) and adapted to the particular recurrent selection scheme under consideration. The basic expression of effective size, under HARDY-WEINBERG equilibrium and large parental populations, is

$$Ne = \frac{2N}{\frac{s^2_k}{\overline{k}} + 1} \qquad \text{equation (6)}$$

for N sampled offspring; s^2_k and $\overline{k}$ are the variance and mean of the number of contributed gametes by the parents. Efficiency for equalized N_e is here represented by $EF^* = Gs_c/Gs^*_S$, Gs^*_S, being the expected progress from sequential selection that generates the same N_e value as that found with 3% selection proportion under combined selection. This approach was adopted in analogy with the comparisons of genetic progress under different inbreeding effective number on a seed orchard (KANG and NAMKOONG, 1987).

B- Numerical Evaluations

For evaluations of EF efficiencies two sets of family trials were considered.

B.1. Several Species; Data From the Literature

Special attention was given to growth characters. Estimates of means, phenotypic variances and additive genetic variance were taken from GORGULHO (1990; E. pyrocarpa); IKEMORI (1990; E. grandis); SILVA (1990; E. camaldulensis); KIKUTI (1989; E. grandis); PATIÑO-VALERA (1986; E. saligna); PINTO JR. (1984; E. urophylla); and KAGEYAMA (1980; E. grandis).

B.2. Specific E. grandis Progeny Trial

In this trial 97 open pollinated families, stemming from previously selected E. grandis trees (Coff's Harbour provenance) plus three commercial checks, were evaluated in a 10 x 10 lattice design, with 9 replications, in a single location (Salto, SP, Brazil). Data on diameter at breast height (DBH), plant height (H) and volume (V) were obtained at 7 years (all replications) of age. The method of moments was chosen for estimation of variance components considering the expected values of mean squares of the analysis of variance, under the assumption of a random model. Within plot variances were computed separately as shown by KAGEYAMA (1980).

Results and Discussion

A. Theoretical Analysis and Minimum Efficiency

The efficiency measure $EF = Gs_c/Gs_S$, can be rewritten as

$$\text{equation (7)}$$

$$EF = \frac{i_c \sqrt{\left(\frac{p-1}{p}\right)\left[\theta + \frac{(1-\theta)}{nr}\right]^2 + \left(\frac{n-1}{n}\right)(1-\theta)^2 Z^2}}{\theta \, i_b \sqrt{\frac{p-1}{p}} + (1-\theta)Z \, i_w \sqrt{\frac{n-1}{n}}}$$

for half-sib families.

In equation (7), $Z^2 = \sigma^2_b/\sigma^2_w$ is the ratio between the phenotypic variance among family means and the within families (plots) phenotypic variance. This quantity can be estimated through $\hat{Z}^2 = MSp/[r(MSw)]$, MSp being the among families mean square (adjusted for incomplete block effects), r the number of replications and MSw the within families (plots) mean square.

It can be seen that, with other quantities of equation (7) being fixed for a given experiment, Z^2 will be the sole popula-

tion parameter to determine EF. This opens the possibility of searching for a minimum efficiency of combined selection relative to sequential selection (EF_{min}). In fact, EF reaches its minimum when $Z = Z^*$ and

$$Z^* = \sqrt{\frac{(p-1)n}{p(n-1)}} \left[\theta + \frac{(1-\theta)}{nr}\right]^2 \frac{1}{\theta(1-\theta)} \left(\frac{i_w}{i_b}\right) \qquad \text{equation (8)}$$

for arbitrary intraclass genetic correlation θ.

For large p, n and r values and with $i_b = i_w$, Z^* reduces to $Z^* = \rho/(1-\rho)$, which, for half-sibs is $Z^* = 1/3$. For this specific case efficiency will reach the minimum when $\sigma^2_w = 9 \, \sigma^2_b$, and $EF_{min} = (i_c\sqrt{2})/(i_b + i_w)$. With 20% selection, both between and within families, $i_b = i_w = 1.40$ (i_w here not corrected for finite sample size). This corresponds to 4% overall selections such that $i_c = 2.15$ and $EF_{min} = 1.08$, indicating only a small advantage of CS over SS, at the minimum.

As an additional example, considering $p = 100$ families, $r = 9$ replications, $n = 10$ plants per plot and 30% selection among and 10% within families (plots), $i_b = 1.16$, $i_w = 1.54$ (corrected for finite sample size) and $i_c = 2.27$. Assuming half-sib families, $Z^* = 0.4956$ and $EF_{min} = 1.19$, which indicates an expected advantage of at least 19% of CS over SS.
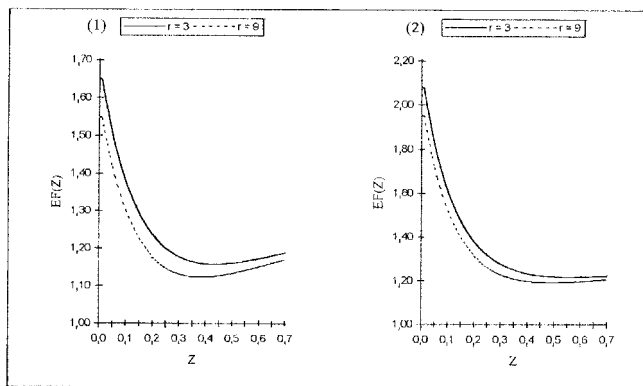

Figure 1. – Relation between efficiency (EF) and $Z^2 = \sigma^2_b/\sigma^2_w$ for r replications in two different situations: (1) $p = 100$ families; $n = 5$ trees per plot and 20% selection among and within families; (2) $p = 50$ families; $n = 10$ trees per plot; 30% selection among families and 10% within families.

This result is very appealing for realistic applications, indicating the minimal superiority of CS over SS expected by a given family test solely by analyzing its dimensions.

Equations (7) and (8) show also that EF, in general, increases as Z^2 becomes small. The CS Method is therefore expected to be more effective when the variance between families is smaller than σ^2_w (Figure 1). Increasing the number of replications, on the other hand, reduces the efficiency of combined selection at a faster rate than increasing the number of families evaluated. Under the conditions of figure 1 it is evident that EF is always larger than one.

Genetic Meaning of Z

Exploring the genetic meaning of Z to put EF as a function of individual heritabilities and number of trees per plot can elucidate previous section for practical purposes.

The plot error variance of the progeny trial is:

$$\sigma^2_e = \frac{\sigma^2_b(1 - dh^2 - h^2)}{\theta h^2 (1+c)} \qquad \text{equation (9)}$$

in which d is the degree of dominance, c is a ratio of environmental variances within and between plots and h^2 is the individual basis heritability.

The within plot variance can now be written as:

$$\sigma_w^2 = \frac{\sigma_b^2 (h^2 - \theta h^2 - c.\theta h^2 + dh^2 + c)}{\theta h^2 (1+c)} \qquad \text{equation (10)}$$

So, Z^2 is then:

$$\text{equation (11)}$$

$$Z^2 = \frac{\sigma_b^2 + \sigma_e^2/r + \sigma_w^2/nr}{\sigma_w^2} =$$

$$Z^2 = \frac{-(\theta nrh^2 + \theta nrch^2 - nh^2 - ndh^2 + n + h^2 - \theta h^2 - c\theta h^2 + dh^2 + c)}{(\theta h^2 - h^2 + c\theta h^2 - dh^2 - c)nr}$$

Letting $r = a/n$ for a trees per family, we get EF as a function of a and h^2, for a fixed family trial (given n trees per plot, p families, c, d, θ, and selection intensities between families and within plots). For example taking $c = 0.5$, $d = 0.5$, $p = 0.25$ (half sibs), $p = 100$, selecting 30% between families and 1 out of 5 trees within plots, we get:

$$\text{equation (12)}$$

$$EF = \frac{\sqrt{226a - 120ah^2 + 24a^2h^2 + 11a^2 + 99}}{1.9361 + 1.6550 \sqrt{\dfrac{3ah^2 - 15h^2 + 20}{a}}}$$

Now we can build response surfaces of EF as functions of heritabilities and numbers of trees per family for different trial specifications. *Figures 2* and *3* show those response surfaces for 12 different combinations of d, n and selection intensities. Many simulations with different p and c values result in the same pattern.
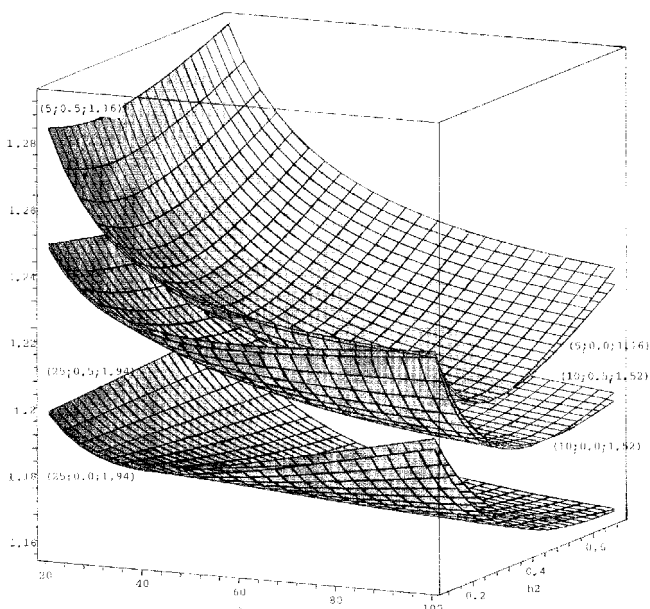

Figure 2. – Response surfaces of EF values for $c = 5$ (ratio of environmental variance within and between plots), $p = 100$ (number of families of the trial), and 30% of families selected by SS, varying a (number of trees per family) and h^2 (narrow sense individual heritabilities). The triplets $(n; d; i)$ describe each of the six ilustrative combinations as follows: the first coordinate is for the number of trees per plot; the second for the average degrees of dominance; the third for the standardized selection differentials.
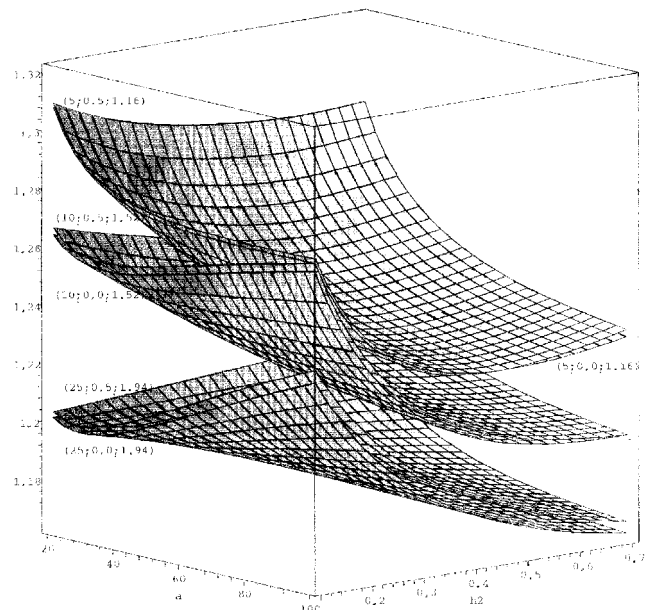

Figure 3. – Response surfaces of EF values for $c = 5$ (ratio of environmental variance within and between plots), $p = 100$ (number of families of the trial), and 20% of families selected by SS, varying a (number of trees per family) and h^2 (narrow sense individual heritabilities). The triplets $(n; d; i)$ describe each of the six ilustrative combinations as follows: the first coordinate is for the number of trees per plot; the second for the average degrees of dominance; the third for the standardized selection differentials.

The small gap between surfaces A to D, B to E, C to F, G to J, H to K and I to L means that the degree of dominance makes little, but positive difference in the superiority of CS over SS. However, dominance effects are mixed with other non-genetical (non-additive) effects in the error term in half-sib family tests: small dominance implies smaller EF.

In the same direction, if the number of trees per family is great the EF values are small (sometimes reaching the limiting value of $EF \approx 1.15$); with fewer trees per family (poor tests) CS is much more effective than SS. This implies that it is not wise to use SS in culling family trials with less than say 50 trees representing each family.

Variation of EF with individual heritabilities shows an interesting and intrincated pattern: in small trials, increasing h^2 does not affect EF too much (sometimes EF even increases). This may be explained by the higher possibility of obtaining poor estimates of genetic values of families compared to individual ones, which increases EF. For higher a values, increasing h^2 in general implies decreasing EF by the correlated increasing of family mean basis heritability (h_m^2), except for small n, i.e. $n = 5$. In this case, the small sample value of the plot makes SS quite inefficient, so EF increases again. This is a sound indication of high EF when plots are small, which is recommended as statistically more efficient for progeny trial designs in forestry.

B.1.- Results From Literature

Considering all eucalyptus species jointly, data from the literature allowed obtaining 50 EF estimates for DBH, 64 for plant height and 6 for volume. *Table 1* gives a summary of estimated EF values and of other pertinent parameters.

All estimated EF values were greater than one. The range of these values (1.15 to 1.31 for DBH; 1.15 to 1.30 for H and 1.17 to 1.25 for V) indicated a very high consistency of the superiority of CS over SS, under equalized selection proportions. Average EF was appreciably greater than EF_{min} only for V.

Table 1. – Average estimates of Efficiency (*EF*), minimum efficiency (*EF*$_{min}$) and of other parameters. Several eucalyptus species. Data from the literatur. Equal selection proportions. Progeny trials with n values varying from 5 to 10 trees per plot and a values varying from 15 to 150 trees per family.

Parameter	DBH	H	V
CV %	11.8	9.8	30.9
h_m^2	0.563	0.521	0.407
Gs$_C$ %	21.58	17.84	19.96
Gs$_S$ %	17.69	14.77	16.51
EF	1.22	1.21	1.21
EF$_{min}$	1.19	1.20	1.16

CV%: experimental coefficient of variation; h_m^2: narrow sense heritability (family mean basis).

Table 2. – *E. grandis* progeny trial. Estimates of parameters for DBH (cm), H (m), V (dm³) at 3 and 7 years of age. *EF* under equal selection proportions for CS and SS.

Parameters	3 years[(+)]			7 years[(++)]		
	DBH	H	V	DBH	H	V
Mean	9.4	16.7	52[(o)]	11.2	20.5	107.2[(o)]
CV %	10.3	10.0	20.1	13.0	11.4	25.4
h_m^2	0.38	0.33	0.40	0.66	0.72	0.67
Gs$_C$ %	8.44	7.25	18.58	12.72	14.03	25.46
Gs$_S$ %	6.64	5.82	14.93	9.69	11.04	19.37
z^2	0.067	0.082	0.083	0.031	0.042	0.031
EF	1.27	1.25	1.24	1.31	1.27	1.31
EF$_{min}$		(1.22)			(1.19)	

(+, ++): based on 3 and 9 replications, respectively. (o): x 10⁻³

B.2- Specific *E. grandis* Trial

Main results of the analyses of the *Eucalyptus grandis* progeny trial, at 3 and 7 years, are given in *table 2*. For this trial (with i_p = 1.159 and i_w = 1.539) CS is, again, expected to be more efficient than SS when effective population size is neglected.

It is obvious that the 3 and 7 years data are not readily comparable due to the inequality in the number of replications considered. However, the reduction of the phenotypic variance among family means at 7 years, relative to σ_w^2, as compared to the 3 years results, was the main factor responsible for the higher efficiencies of CS at that age.

RESENDE (1994) points out that standardized selection differentials for within family (plot) selection in SS (i_w) will be even smaller than those computed according to FISHER and YATES (1971), if the genetic correlation between half-sibs is taken into account. Adjusting results for this effect should enhance the efficiency of CS by a small amount, because the genetic gains from SS are slightly overestimated.

For both schemes a selection of 261 trees was assumed, corresponding to 3% of the total number of trees (8730) in the trial at seven years of age. Under SS the 29 best families and 9 superior trees per family were identified. Since 68 parents were discarded, not contributing any gametes to the offspring, the quantity $s_k^2/\overline{k}$ equals 5.0 and N_c = 87. Under CS, before ranking for selection (previous to trial evaluation), is possible to make projections for resulting N_c supposing known variance components (BURROWS, 1984). Since we works out variance components estimates in the very moment of the selection index calculation, only at this time (the very choice of the trees that mates to new generation) both N_c and N_s may be easily calculated. *Figure 4* enlightens this situation.
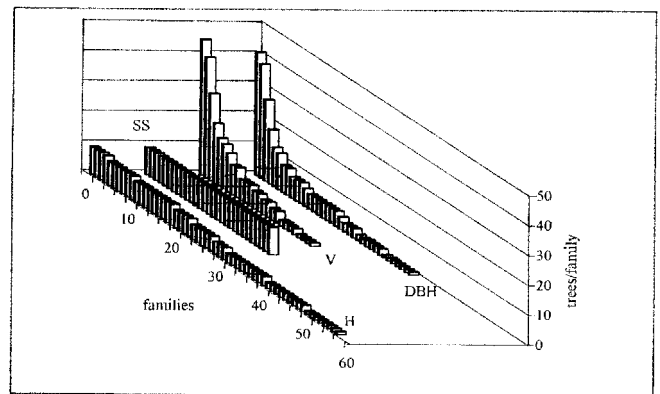

Figure 4. – Numbers of families and trees per family selected by combined selection (CS) for tree height (H), tree volume (V), diameter at breast height (DBH) and for sequential selection (29 families selected from 97 and 9 superior trees identified per family). *Eucalyptus grandis* progeny trial; 9 replications.

For CS results as given in *figure 2*, $s_k^2/\overline{k}$ = 12.3 for DBH, such that N_c = 39.4. For H and V, N_c = 114.4 and 45.7 respectively ($s_k^2/\overline{k}$ being 3.6 and 10.4). For plant height, in this case, the use of the selection index led to a collection of offspring belonging to a much larger number of seed parents (63 as compared to 29 under SS). The result was an increase in N_c, comparing CS with SS, for this trait (114.4 vs. 87.0).

The status numbers (N_s) were calculated as the half inverse of average coancestry, as proposed by LINDGREN et al. (1996), being obtained the following results: 39.5 (D), 114.78 (H) and 46.44 (V). Such results indicate that, when the only information about relatedness comes from pedigree data, N_s and variance N_c are equal.

When effective sizes attained with CS are also used for SS, with selection of 9 individuals per family, this led to new selection proportions among families and, consequently, new expected progresses for SS (Gs_S^*). These new Gs_S^* values are 11.99% for DBH, 10.10% for H and 23.20% for V, which are larger than previous Gss, but smaller than G_{CS} (*Table 2*).

For the 7 years data, analysis led to the following new efficiencies (*EF**) under constant effective population sizes: *EF** = 1.06 for DBH; *EF** = 1.39 for H and *EF** = 1.10 for V. The superiority of CS over SS at a constant N_e, as can be seen, is much smaller than that calculated ignoring N_c. In any case, *EF** values still remained greater than 1.0, when selections CS and SS were confronted under the same genetic basis. It is questionable, however, if small N_e values, such as N_e = 39.4 or N_e = 45.7, as obtained in this example, could be considered adequate for recurrent selection in forest trees.

Conclusions

Combined selection was found to be genetically superior to sequential selection, for improvement of populations. This superiority is more evident for traits with small narrow sense heritabilities or small plot sizes, and less evident when effective population size was maintained equal in both schemes. Combined selection is recommended over sequential selection in selection programs, specially if effective population sizes are not a limitation.

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Appendix

Derivation of Z* point of minimum efficiency for a given progeny trial:

$$\frac{\partial EF(Z)}{\partial Z} = \frac{\partial \left(\frac{i_c \sqrt{\alpha + \beta Z^2}}{\tau + \omega Z} \right)}{\partial Z} \qquad \text{equation (13)}$$

in which:

$$\alpha = \left(\frac{p-1}{p} \right)\left[\theta + \frac{(1-\theta)}{nr} \right]^2$$

$$\beta = \left(\frac{n-1}{n} \right)(1-\theta)^2$$

$$\tau = \theta\, i_b \sqrt{\frac{p-1}{p}} \qquad \text{equation (14)}$$

$$\omega = (1-\theta)\, i_w \sqrt{\frac{n-1}{n}}$$

considering A(Z) and B(Z) as the numerator and denominator of EF(Z), respectively, the minimization condiction is given by:

$$\text{equation (15)}$$

$$\frac{\partial EF(Z)}{\partial Z} = 0 \Rightarrow \frac{\partial A(Z)}{\partial Z} B(Z) = \frac{\partial B(Z)}{\partial Z} A(Z)$$

in which:

$$\frac{\partial A(Z)}{\partial Z} = \frac{i_c\, \beta\, Z}{\sqrt{\alpha + \beta\, Z^2}}$$

$$\frac{\partial B(Z)}{\partial Z} = \omega \qquad \text{equation (16)}$$

The minimal EF(Z) values arise when:

$$\frac{i_c\, \beta\, Z}{\sqrt{\alpha + \beta\, Z^2}} (\tau + \omega Z) = \omega\, i_c \sqrt{\alpha + \beta\, Z^2} \Rightarrow \quad \text{equation (17)}$$

$$\tau \beta\, Z + \omega \beta\, Z^2 = \omega \alpha + \omega \beta\, Z^2 \Rightarrow \qquad \text{equation (18)}$$

$$\text{equation (19)}$$

$$Z^* = \frac{\omega \alpha}{\tau \beta} = \sqrt{\frac{(p-1)n}{p(n-1)}} \left[\theta + \frac{1-\theta}{nr} \right]^2 \frac{1}{\theta(1-\theta)}\left(\frac{i_w}{i_b} \right)$$

which corresponds to equation (8).