# Detection of non-additive gene Action with nested polycross Designs. I. Procedure assuming epistasis negligible

By M. J. J. Janssens

Institut pour les Sciences Agronomiques au Rwanda
(ISAR), Rubona, BP 138 Butare, Rwanda

(Received January / April 1980)

**Summary**

It is proposed to use nested polycross designs with an increasing number of testers (in the pollen-mix) across nests, in order to modify gradually the sib relationship within the polycross progenies. Regression analysis, using the least-squares method, will estimate the additive and dominance variance components under the assumption of no epistasis. This "progressive" nested polycross design is believed to be superior to the half disconnected diallel mating design both from the genetic as from the experimental point of view.

*Key words:* gene action, progressive nested polycross design, half disconnected diallel design

**Zusammenfassung**

Es wird vorgeschlagen, Sätze von Polycross-Plänen mit einer zunehmenden Anzahl von Testern im Pollengemisch über die Sätze hinweg zu verwenden, um die Verwandtschaft zwischen Geschwistern innerhalb der Polycross-Nachkommenschaften Schritt für Schritt zu modifizieren. Unter der Annahme, daß keine Epistasie vorliegt, werden mittels Regressionsanalyse, unter Verwendung der Methode der kleinsten Quadrate, die Varianzkomponenten für die additive und die Dominanzvarianz geschätzt. Von diesem Polycross-Plan mit „progressiven" Sätzen wird angenommen, daß er sowohl vom genetischen als auch vom experimentellen Standpunkt aus, besser ist als das nicht zusammenhängende Halb-Diallel.

## 1. Introduction

Burdon and Shelbourne (1971) proposed different forms of nested polycross designs (NPD). In the "tester" NPD, each set of female parents is tested against a different pollenmix. They regretted that the NPDs are unable to detect non-additive gene action while on the other hand being advantageous in the following aspects: simplicity, high number of parents can be involved, possibility of advanced generation selection. They recommended nests of at least 20 female select parents such that the assumption could be made that each nest would approach the average genotypic value of the selected population. Barnes (1973) pointed out that the half-sib relationship of a polycross progeny holds strictly only in so far the number of pollen parents in the pollen-mix can be considered to be infinite. The variance component of the polycross progeny effects ($s^2_P$) will have a variable genetic content depending on the number of testers in the pollen-mix, according to the following formula (all parents having their inbreeding coefficient F = 0):

$$s^2_P = (1/4 + 1/4m)\, s^2_A + (1/4m)\, s^2_D \quad \text{.....(1)}$$

(Barnes, 1973)

where

m = number of parents included in pollen-mix

$s^2_A$, $s^2_D$ = additive and dominance variance components repectively

Above formula applies only onto polycross progenies containing more than one sibling per tester parent.

In the half disconnected diallel mating design the number of parents within each diallel nest is restricted because of experimental limitations and is generally comprised between four and six parents. This small number of parents leads towards a lack of genotypic homogeneity across diallel nests and finally towards biased estimates of general combining ability (GCA) effects as the sib relationship cannot be considered as a pure half-sib relationship owing to the small number of non-recurrent parents (Formula 1).

## 2. Procedure to detect non-additive gene action with NPDs

### *(a) Principle*

The sib relationship within a given "tester" NPD will be modified gradually by allocating to each nest, through controlled pollination, a pollen-mix with an increasing number of pollen parents. The pollen-mixes will be unrelated to each other and the female parents will be randomly distributed over the different nests. From formula (1) it follows that each nest will have an estimate of the variance component of the polycross progeny effects ($s^2_P$) with a different genetic content. Regression analysis (least-squares method) will determine the respective additive and dominance variance components. For simplicity, a same number (20 if possible) of polycross progenies will be used within each nest. The size of the polycross progenies will be proportional to the number of parents involved in the pollen-mix such as to sample the gametes of each pollen parent in a realistic way.

Parents of different inbreeding coefficient could possibly be used in a same experiment, in which case nests of parents with same inbreeding coefficient ought to be constituted, while using a generalized form of formula (1) i. e.

$$s^2_P = \left[\left(\frac{1+F}{4}\right) + \left(\frac{1+F}{4m}\right)\right] s^2_A + \frac{1}{4m}(1+F)^2\, s^2_D \quad \text{.....(1-bis)}$$

where F = inbreeding coefficient

Epistasis and F will be considered to be equal to zero.

### *(b) Genetic model*

The effect of the j-th polycross progeny within the i-th nest will be equal to

$$PC_{j(i)} = g_i + g_{j(i)} + s_{ij(i)} \quad \text{.....(2)}$$

where

$$g_i = \frac{\sum_{t=1}^{m} g_{t(i)}}{m(i)}$$ = average of the general combining ability effects (GCA) of the testers of the pollen-mix for the i-th nest and where $g_t$ = the GCA effect of the t-th tester

m = number of testers in pollen-mix

$g_{j(i)}$ = GCA effect of the j-th female parent within the i-th nest

$s_{ij(i)}$ = specific combining ability effect (SCA) between the j-th female parent and the i-th pollen-mix

$= \frac{\sum_{t=1}^{m} s_{jt\,(i)}}{m\,(i)}$ = average of the SCA effects between the j-th female parent and each of the t pollen testers within the i-th nest

Hence formula (2) can be rewritten as

$$PC_{j\,(i)} = \frac{\sum_{t=1}^{m} g_{t\,(i)}}{m\,(i)} + g_{j\,(i)} + \frac{\sum_{t=1}^{m} s_{jt\,(i)}}{m\,(i)} \quad \text{.....(2-bis)}$$

Note that for large values of m both $g_i$ and $s_{ij\,(i)}$ will become negligible so that $PC_{j\,(i)} = g_{j\,(i)}$ i.e. a pure half-sib effect.

When modifying the sib relationship, the only term of formula (2) to remain genetically unaltered, whatsoever the number of testers, is $g_{j\,(i)}$ i.e. the GCA effect of the j-th female parent. In a normal (single nest) polycross design the average GCA effect of the pollen-mix is confounded with the grand mean. In a NPD the $g_i$ effect corresponds approximately to the deviation of the nest mean w.r.t. the grand mean. Hence, the actual measured polycross progeny effect in a normal (singular) polycross design corresponds in fact to

$CPC_{j\,(i)} = g_{j\,(i)} + s_{ij\,(i)}$ .....(3)

where

$CPC_{j\,(i)}$ = corrected polycross progeny effect i.e. the polycross progeny effect from which the pollen-mix "pooled" GCA effect ($g_i$) has been removed

i = 1 for a singular polycross design

In a factorial mating design, which is close to the "tester" NPD, the full-sib variance component, $s^2_{FS} = {}^1/_2\, s^2_A + {}^1/_4\, s^2_D$ can be partitioned into a variance component attributable to SCA, $s^2_{SCA} = {}^1/_4\, s^2_D$, and two variance components attributable to GCA, one for the male parents, $s^2_{g_i} = {}^1/_4\, s^2_A$ and one for the female parents, $s^2_{g_j} = {}^1/_4\, s^2_A$. From (3), whereby the GCA effect of the pollen-mix ($g_i$) has been removed, and from the fact that the GCA effect of a female parent ($g_{j\,(i)}$) remains an unaltered half-sib effect, it follows that formula (1) ought to be changed into

$s^2_c = {}^1/_4\, s^2_A + (1/4m)\, s^2_D$ .....(4)

where

$s^2_c$ = variance component of the corrected polycross progeny effects $CPC_{j\,(i)}$

Moreover, from (1) and (4) it follows that

$s^2_{g_i} = (1/4m)\, s^2_A$ .....(5)

where

$s^2_{g_i}$ = the variance component corresponding to the pooled GCA effects of a given pollen-mix

*(c) Biometrical analysis*

(I) Model

The observation on the j-th polycross progeny in the k-th replication within the i-th nest is

$y_{ijk} = \mu + N_i + CPC_{j\,(i)} + R_{k\,(i)} + e_{jik}$ .....(6)

where

$\mu$ = grand mean

$N_i$ = deviation of the i-th nest mean from the grand mean, approximately equal to $g_i$, for i = 1.....n

$CPC_{j\,(i)}$ = effect of the j-th polycross progeny within the i.-th nest corrected for $g_i$, for $_j$ = 1.....c

$R_{k\,(i)}$ = k-th replication effect within the i-th nest for k = 1.....r

$e_{ijk}$ = error effect due to the interaction between $CPC_{j\,(i)}$ and $R_{k\,(i)}$

From (2) and (3) it follows that equation (6) could be written out as

$y_{ijk} = \mu + PC_{j\,(i)} + R_{k(i)} + e_{ijk}$ .....(7)

The effects are either random or fixed according to the adopted model *(Table 1)*. In the mixed model, only the $N_i$ and $CPC_{j\,(i)}$ effects are considered to be fixed.

(II) Analysis of variance

The complete analysis of variance with degrees of freedom and expected mean squares, for both a random and a mixed model, is given in *Table 1*. The following restriction are to be satisfied:

(1) $\sum_{i}^{n} g_i = 0$ across nests

(2) $\sum_{j}^{c} g_{j\,(i)} = 0$ within each nest

(3) $\sum_{j}^{c} s_{ij\,(i)} = 0$ within each nest

The estimate of the variance component of the corrected polycross progeny effects ($s^2_c$) can be easely partitioned in n estimates of $s^2_{c_i}$ i.e. one estimate for each nest, as there are n times (c — 1) degree of freedom available. The error variance ($s^2_e$) can be partitioned in a similar way as there are n times (r — 1) (c — 1) degrees of freedom avail-

*Table 1.* — Analysis of variance of a "progressive" NPD: random and mixed models.

| Source | Degrees of freedom | Expected Mean Squares (a) | |
|---|---|---|---|
| | | Random model | Mixed model (b) |
| Replications w/n nest | n(r - 1) | $s^2_e + c\, s^2_r$ | $s^2_e + c\, s^2_r$ |
| (PC-progen.) | (nc - 1) | $(s^2_e + r\, s^2_p)$ | $\left(s^2_e + r\, \frac{\sum\sum P^2_{ij\,j(i)}}{nc - 1}\right)$ |
| Nests | n - 1 | $s^2_e + r\, s^2_c + rc\, s^2_n$ | $s^2_e + rc\, \frac{\sum_i N^2_i}{n - 1}$ |
| CPC-prog. | n(c - 1) | $s^2_e + r\, s^2_c$ | $s^2_e + r\, \frac{\sum\sum C^2_{ij\,j(i)}}{n(c - 1)}$ |
| Error | n(r-1)( c-1) | $s^2_e$ | $s^2_e$ |
| Total | ncr - 1 | | |

(a) $s^2_e$, $s^2_c$, $s^2_n$, $s^2_p$, $s^2_r$: variance components for error, corrected polycross progenies, nests, polycross progenies, and replications, respectively P, N, C: fixed effects for polycross progenies, nests, and corrected polycross progenies

(b) Polycross progeny effects (and hence both the nest and corrected polycross progeny effects as well) considered fixed, all other effects assumed to be random

able. Hence within each nest the expected mean squares for the CPC $_{j\,(i)}$ effects will be

$$s^2_{e_i} + r\, s^2_{c_i} \quad \text{.....(8)}$$

(III) Regression analysis

From (8) n estimates of $s^2_{c_i}$ are obtained whose genetic content will be given by formula (4). A matrix can be constituted with n linear equations of the form

$$s^2_{c_i} = {}^1/_4\, s^2_A + (1/4m)\, s^2_D + d_i \quad \text{.....(9)}$$

where

$d_i$ = deviation from linearity

Above equation is analogous to the linear equation

$$y_i = a + bx_i + d_i$$

The solution equation $y = a + bx$ will be given by least-squares regression analysis, whereby $s^2_{c_i}$ is the dependent and m the independent variate, and where $s^2_A$ and $s^2_D$ are considered as constant across nests. This assumption is acceptable in the case of nests of similar average genotypic value as preconised by Burdon and Shelbourne (1971). Genotypic homogeneity is approximated by randomly allocating a large number (say 20) of female parents to each nest. The deviations from genotypic homogeneity could be estimated from the importance of the error estimates $d_i$ e.g. by calculating the coefficient of variation (%)

$$CV = \frac{s_d}{\bar{x}_d}\, 100 \quad \text{.....(10)}$$

where

$\bar{x}_d$ = mean of the estimates of $d_i$

$s_d$ = square root of the variance of the estimates of $d_i$

## 3. Conclusions

(I) Non-additive gene action, assuming epistasis negligible, can be estimated with a "progressive" NPD using a simple and practical procedure of varying the number of testers within the pollen-mixes across nests. Hence, the greatest objection against the use of NPDs, i. e. no estimate of non-additive gene action, is herewith eliminated.

(II) Formula (1) has been corrected into (4) by removing the pooled GCA effect of the pollen-mix from the polycross progeny effect. In a more general form, formula (4) becomes

$$s^2_c = \left(\frac{1 + F}{4}\right) s^2_A + (1/4m)\,(1 + F)^2\, s^2_D \quad \text{.....(4-bis)}$$

(III) With progressive NPDs the estimates of the genetic variance components are less biased than for the half disconnected diallel mating design, because of greater genotypic homogeneity across nests and because of a precisely known sib relationship which is taken into account.


## Acknowledgements

I wish to thank B. Louant, University of Louvain, Belgium, and A. Nanson, Station de Recherches des Eaux et Forêts, Groenendaal-Hoeilaart, Belgium, for their critical and helpful comments on the typescript.


## References


Barnes, R. D.: The genetic improvement of *Pinus patula* Schiede and Deppe in Rhodesia. Ph. D. Thesis, Univ. London (1973). — Burdon, R. D. and Shelbourne, C. J. A.: Breeding populations for recurrent selection: conflicts and possible solutions. N. Z. J. Forestry Sc. 1 (2): 174—193 (1971).