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A GENERAL STRATEGY OF PLANT BREEDING FOR VARIETAL DEVELOPMENT

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ABSTRACT

A comprehensive strategy of varietal development appears to have two main axes: population improvement by recurrent selection and varietal development. The aim of population improvement must be to improve the varietal ability of the breeding material, i.e., the expected value of all varieties of a given type which can be derived from it. The aim of varietal development is to extract the best possible varieties from a given generation of the breeding material.

It is thus clear that the system of testing in population improvement must be adapted to the type of variety. The concept of varietal ability of a genotype i.e., the expected value of varieties of a given type which can be derived from the genotype, allows the definition of what the breeder has to improve. Hybrid development requires improved combining ability, synthetic development requires improved synthesising ability, line development improved line value of the material, and clones improved value per se of the breeding material.

In this strategy, the pedigree method for line or hybrid development is considered to be a method of varietal development. When possible it can be advantageously replaced by haplodiploidisation.

Formulae for genetic advance in population improvement and varietal development can be given in terms of genetic effects for varietal abilities. Prediction formulae for varietal values can be used to increase the efficiency of recurrent selection and of varietal development. Both types of formulae must allow the study of the allocation of resources to have maximum genetic advance per unit of resource or time. The use of haplodiploidisation is discussed more specifically.

It is concluded that this overall strategy will remain pertinent as genetic engineering progresses. Tools provided by biotechnology have to be placed within this general strategy.

KEYWORDS

Breeding methods, varietal development, line breeding, hybrid breeding, synthetic breeding, quantitative genetics.

INTRODUCTION

In this introduction, I would like to underline the connection between population improvement and varietal development. Breeding methods will be defined in a broad sense as the total plan to develop improved material and new varieties. I will assume that the type of variety being developed (clones, lines, hybrids, synthetics) has been determined as well as its optimal base for multiparent varieties.

Plant breeding can be considered to be the art or the science of varietal development. From a genetic point of view, it is a combination of operations, selection and systems of mating, applied to a set of individuals to obtain a new reproducible set, the variety, with an agro-economic value better than the first selected sets.

A great number of genes (loci) are involved in such a genetic transformation. Plant breeding is multivariate, and involves very complex characters such as yield. So the aim of the breeder is to accumulate in the same genotype or group of genotypes — the variety — the maximum number of favourable genes or associations of genes, considering only nuclear inheritance. To achieve this goal it is necessary to have a great number of recombinations combined with the selection of segregating units. In the absence of the possibility of direct gene transfer, the tools at the disposal of the plant breeder are selection at the level of the whole plant and mating systems. Recombination will be achieved through meiosis in progenies from the crossing of complementary individuals. Fundamentally, plant breeding is genetic engineering.

In a comprehensive strategy of varietal development it is necessary to combine population improvement and varietal development. Short term efficiency requires high selection intensity with direct varietal development from the breeding material. However, this leads to a loss of variability and to very restricted recombination between loci. Indeed, favourable genes linked to unfavourable genes are eliminated and, if they are present at low frequencies, with the environment having a major effect, the probability of detecting them will be low. So the maximum genetic advance is not achieved.

The maximum genetic advance can only be reached long term by the accumulation of several cycles of selection followed by intercrossing, and with a low selection intensity. Therefore, there is conflict between short term efficiency and long term efficiency. Resolving this conflict, requires a strategy where these two objectives are separated. Long term advance must be preceded by population improvement by recurrent selection to improve the ability of the population to give good varieties. Short term efficiency can be satisfied by the derivation of varieties from the breeding material at any cycle of recurrent selection.

The aim of population improvement is to improve the varietal ability of the population(s), i.e., the expected value of all varieties of a given type which could be derived from the population(s). This will be achieved by increasing the frequencies of favourable genes or associations of genes (favourable in the varietal situation). The aim of varietal development will be to extract the best possible varieties from a given generation of the breeding population(s). Population improvement increases the mean of the population of varieties, and varietal development exploits the variance among varieties of a given type within a generation of the breeding material. In the total genetic advance (ΔG), there are two components: the expected genetic advance due to population improvement (ΔP), and that due to varietal development (ΔV):

$$\Delta G = \Delta P + \Delta V$$

and $$\Delta V = V_m - V = i\, h_{v\,v}\sigma_G$$

where V_m is the expected value of the best varieties with a selection intensity of i, V is the mean of all varieties which can be derived from the breeding population and $h_v = {}_v\sigma_G / {}_v\sigma_p$, where ${}_v\sigma^2_G$ and ${}_v\sigma^2_p$ represent the genetic and phenotypic variances among varieties, respectively.

This strategy is valid whatever the type of variety; clones, hybrids, synthetics, or lines. However, the system of testing in population improvement has to be adapted to the type of variety. To develop hybrids we have to improve combining ability, for synthetics we have to improve synthesising ability, for lines we have to improve the line value of the material, and for development of clones we have to improve the value per se of the material.

We will generally speak of *recurrent selection for varietal ability* to underline that modalities of recurrent selection cannot be independent of the type of varieties to be developed. We recall further the biometrical definition of varietal abilities. Note that in this strategy, line breeding (pedigree selection, single seed descent, bulk, etc) for line or hybrid development, can be considered a method of varietal development because inbreeding plus selection strongly reduces the genetic variability.

It is assumed that genetic variance does not decrease very much in recurrent selection; this has been experimentally proven in maize breeding if the effective number of intercrossed individuals at each cycle is not too low (Hallauer and Miranda, 1981). Moreover it is an open system which accepts new introductions at any cycle of recurrent selection. However, the modalities of introduction of new material have to be studied. After several cycles of recurrent selection, only pre-selected material has to be introduced in recurrent selection for varietal ability. So a new axis must be included in the general strategy for the adaptation of the material before its introduction in the main axis. This strategy has to be completed by the necessary germplasm conservation (Fig. 1).

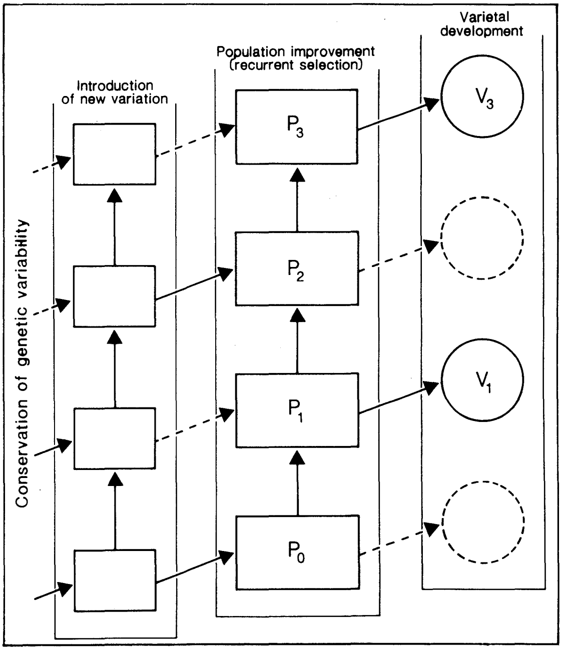

Figure 1. A comprehensive strategy of plant breeding for varietal development.

In practice, population improvement and varietal development are very often more or less confounded. This is due to the preoccupation of the plant breeder with short term efficiency. At the extreme he develops varieties directly from material at his disposal. Recombination is present but only with the best genotypes and with a long cycle. This is the situation with line development in autogamous species. The expected results and the limitation of genetic advance are difficult to deduce from observed genetic advance at the level of varietal development. Very often, there is still progress, but it is impossible to say if genetic advance will have been greater with a more comprehensive strategy of varietal development. However, it is clear that the genetic base of the developed varieties is too narrow, as in wheat and maize. The consequence is considerable uniformity and kinship of developed varieties. The genetic advance which is achieved is due to the introduction of new material. Limitation of genetic advance encountered in several species could come from a poor strategy of varietal development rather than from an absence of genetic variability or from poor selection criteria. The theory of such a strategy has been developed firstly for hybrid development. Recurrent selection was developed first to improve combining ability. It was extended to the case of synthetic development but without specific consideration of this type of variety. To formulate the theory of the presented strategy, for any type of variety, it is necessary to recall the concept of varietal ability developed by Gallais (1978).

THE CONCEPT OF VARIETAL ABILITIES

To define the concept of varietal abilities at the population level, we have to consider the population of all varieties which can be derived from a random mating population.

Varietal abilities of genotypes

For a multiparent variety, synthetics, or hybrids (symmetrical hybrids), the value of a variety can be broken down according to a factorial model. For example for four parents i, j, k, l, taken at random in the population:

$$V_{ijkl} = \mu_V + \Sigma_i a_i + \Sigma_i \Sigma_j d_{ij} + \Sigma_i \Sigma_j \Sigma_k t_{ijk} + q_{ijkl}$$

μ_V is the mean of all varieties which can be derived from the population. It is called the *general varietal ability* (GVA of a genotype, i.e., the expected value of k parent varieties developed with this genotype). Parameters d, t, q are *specific varietal ability* (SVA) of order 1, 2, 3... and are defined as interactions.

In the particular case of crosses between plants we find again the concepts of *general combining ability* (GCA) and of *specific combining ability* (SCA). For synthetics we have, with Wright (1982), introduced the analagous terms of *general synthesising ability* (GSA) and of *specific synthesising ability* (SSA). Then the GSA of a genotype is the expected value of all k parent synthetics which can be developed with this genotype within the population.

Such a parameterisation can be extended to the case where each parent comes from a different population.

In the case of breeding for the development of a line, we have to improve *the line value of a genotype,* i.e., the expected value of all lines which can be derived from this genotype. This value can be approached by single seed descent (SSD) or by haplodiploidisation (HD) techniques. In the case of clones the varietal value of a genotype is its value per se.

General varietal ability (GCA, GSA, line value, clone value) is the property of a genotype; it is equivalent to any one quantitiative character.

Varietal value of offspring from random mating

The aim of recurrent selection is to improve the varietal ability of a population. The varietal ability of a population is the result of the varietal ability of offspring after intercrossing of selected plants. If we consider a large diallel among selected plants, putting the varietal value in place of the cross value of two plants, the varietal value of offspring can be defined as the GCA for varietal value.

Definition of varietal value for genetic effects

Additive, dominance, and epistatic effects can be defined for the value of a variety (Gallais, 1978). The additive effect α_i of an allele A_i is the expected value of all varieties with this allele.

For a clone this is the classical additive effect. For a cross, it is half of the classical additive effect. For the line value, as the line value of a genotype A_iA_j is:

$$L(A_iA_j) = 1/2\,(Y_{ii} + Y_{jj})$$

so $$L(A_iA_j) = \mu_L + \alpha_{i_L} + \alpha_{j_L}$$

α_{i_L} being additive effect for line value:

$$\alpha_{iL} = \alpha_i + 1/2\,[\beta_{ii} - E(\beta_{ii})]$$

β_{ii} is the dominance effect for the homozygous genotype A_iA_i and $E(\beta_{ii})$ is the expectation of such effects.

For synthetics, it is possible to show that the additive effect α_{i_S} of an allele A_i with non inbred parents, is:

$$\alpha_{i_S} = (\alpha_i + 1/4k\,[\beta_{ii} - E(\beta_{ii})])/k$$

A given genotype will transmit to its offspring only half of its additive varietal value.

THE EXPRESSION OF GENETIC ADVANCE

Genetic advance for population improvement

The genetic advance in population improvement for varietal value can be written for diploidy and in the absence of epistasis as:

$$G_p = i\Theta k \text{ cov TM}/\sqrt{\text{var T}}$$

where cov TM is the covariance between T, the value of individuals according to the system of test T and M, the varietal value of the progeny after intercrossing of the selected plants. It is a parent offspring covariance; Var T is the variance of the phenotypic values for the system of test T, Θ is the degree of control of selection on the two sexes, and k is the number of parents.

Table 1 shows some expressions of 2k cov TM for different situations in the absence of epistasis.

Clearly, only additive effects or additive x additive epistasis effects can contribute to genetic advance in population improvement.

In general to have a system of test T more efficient than the direct selection of varietal value (of offspring) it will be necessary to have:

$$\rho^2_{TM}\, h^2_T > h^2_M$$

ρ_{TM} representing the genetic correlation between the value of the parents according T and the varietal value of offspring M, and $h^2{}_T$ the heritability of the system of test. The problem is to find a system of test with high genetic correlation with the varietal value of the progenies and high heritability.

Genetic advance from varietal development

At the level of varietal development, the specific varietal ability can be used. The expression of genetic advance by selection within the population is always of the same form:

$$\Delta G_V = i \operatorname{cov} TV/\sqrt{\operatorname{var} T}$$

where cov TV is the covariance between the predicted value of the variety and its true value V. Expressions of cov TV have been given by Gallais (1979a, b, c,) for various types of varieties and by Wright (1981) for synthetics.

Table 1. Expression of the covariance between a parent evaluated according to T and its offspring evaluated according to M (varietal value), (multiplied by 2k). A are classical additive effects. A_L and A_S are additive effects for line and synthetic values.

Type of variety	System of test T	2k cov TM
Clones	Phenotype	σ^2_A
	GCA	$1/2\ \sigma^2_A$
Crosses	Phenotype	σ^2_A
	GCA	$1/2\ \sigma^2_A$
Lines	Phenotype	σ_{AA_L}
	Line value of parents	$\sigma^2_{A_L}$
	Line value of offspring	$1/2\ \sigma^2_{A_L}$
Synthetics	Phenotype	σ_{AA_S}
	GSA or parents	σ_{A_S}

For hybrids, synthetics, or clones, dominance and epistatic effects for varietal ability will contribute to genetic advance. However, the variance of these effects will have a low coefficient in the equation of expected gain and it will decline with an increasing level of interaction. Furthermore for hybrids and synthetics it quickly decreases with the increase in number of parents. So only first order interactions between genes are expected to contribute significantly to the variance among varieties and only with a small number of parents. To simplify in the case of more than two parents, the general strategy to reduce the number of candidates to study in varietal combination is to select first of GVA and then on SVA.

For multiparent varieties, hybrids, or synthetics, another way to use specific varietal effects is to develop a recurrent selection procedure with several populations bred simultaneously for their value in varietal combinations. In this case, in the development of the variety, one parent will be derived from each population.

Reciprocal recurrent selection is a well known example of developing combining abilities of two populations, i.e., their abilities to give good crosses. Three-way or four-way recurrent selection could be developed for three-way or four-way crosses. This is more justified with autopolyploids. For a synthetic parent we have also proposed to develop k-way recurrent selection. Such k-way recurrent selection will be followed by a k-way pedigree selection to develop varieties. This is another illustration of contention that in a comprehensive strategy of varietal development, variety construction cannot be separated from population improvement, or vice-versa. The variety must be near an end product from any cycle or recurrent selection.

The place of inbreeding or of haplodiploidisation

Inbreeding can be used in recurrent selection and for varietal development. Inbreeding always increases the variance among tests and possible varieties. For varietal development it allows the maximum use of genetic variance. However, in recurrent selection inbreeding increases the length of the cycle and may then decrease the genetic advance per unit time. Moreover if the aim is to develop lines for hybrids or for synthetics, because generally in diploids (in the absence of epistasis), the varietal value of a heterozygous genotype gives the average varietal value of all lines which can be derived from this genotype, there is no problem in having a test of varietal ability.

When the structure of recurrent selection has been adapted to the type of variety everything is settled for varietal devlopment. For example, reciprocal pedigree selection can be branched directly on reciprocal recurrent selection. So there is no discontinuity between recurrent selection and varietal development.

Haplodiploidisation is a particular form of inbreeding. If homozygous plants can be easily derived from any genotype in a short time such a system of inbreeding can be used not only for varietal development (lines, hybrids, synthetics) but also in recurrent selection. A particular case to consider is the development of lines. The theoretical best system of testing will be the HD value of parents (which gives their line value). However, the risk of a longer system of testing exists even if the technique is well controlled. So we may wonder if in recurrent selection Hd will be more efficient than a test on the S_1 value. To answer this correctly it will be necessary to consider time, resources required and precision for each system of testing. With HD the genetic advance in one cycle of recurrent selection will be:

$$\Delta G_{HD} = i_{HD}\, \sigma^2_{A_L}/\sqrt{\operatorname{var} T_{HD}}$$

and with S1: $\Delta G_{S1} = i_{S_1}\ \sigma_{A_{S_1}A_L}/\sqrt{\operatorname{var} T_{S_1}}$

where i_{HD} and i_{S_1} are the respective selection intensities. A_{S_1} are genetic effects in S_1 value. $\alpha j_{S_1} = \alpha j + 1/4\, [\beta_{jj} - E(\beta_{jj})]$. If products from HD are tested separately, i_{HD} will be lower than i_{S_1} and this could counterbalance the positive effect of the gain in precision with the system T_{HD} due to the test of 'pure' families. If after HD, one hetrogeneous offspring is reconstituted for each studied plant, then the variance var T_{HD} and var T_{S_1} would be expected to be similar for a character affected by environment. In this case equal selection intensity can be realised for each method, then we have to compare $\sigma^2_{A_L}$ and $\sigma^2_{A_{S_1}A_L}$. According to the expression of A_L and A_{S_1} we may expect a significant genetic correlation between the two quantities. The S_1 test may be preferred to the HD test if the latter increases the length of the cycle.

The main advantage of HD is the elimination of a long and expensive phase of line breeding. So resources can be concentrated on the more efficient phase, population improvement.

Note that if the additive component in line variance is σ^2_{AL}, the variance of all lines which can be derived from the population is $2\sigma^2_{AL}$. The variance between line values of plants in the random mating population is thus σ^2_{AL} and it is equally important to select between plants and among the lines derived from each plant.

PREDICTION OF THE VARIETAL VALUES

To apply recurrent selection for varietal devleopment, it is necessary to have some predictors of general varietal ability of the plants (or more precisely of the additive varietal ability). Analogously, to 'extract' the best varieties (hybrids, synthetics, or lines) from a given generation of the breeding population, it is necessary to have predictors of the value of the varieties which can be derived from a set of parents.

Hybrids

In recurrent selection, to develop single crosses, GCA can be evaluated directly. In varietal development for diploids, prediction formulae of three-way and four-way cross values from the values of non parental single crosses are well known and are very useful.

For autopolyploids, we have also developed some predictors without epistasis and restricting interactions between alleles to the first order (Gallais, 1975).

Note that, in the absence of epistasis, the GCA of a genotype corresponds to the mean of the lines which could be derived from this genotype. Early tests are therefore possible in varietal development and this justifies the GCA test with S_0 plants in recurrent selection.

Synthetics

In the absence of epistasis, the value k-Syn e of a particular synthetic at equilibrium can be predicted according to the generalisation of Sewall Wright's formula:

$$\text{k-Syn e} = (1\text{-}1/k)\,\overline{C} + 1/k\,\overline{S}$$

$\overline{C}$ represents the mean of all possible crosses among the k parents, $\overline{S}$ means the progenies from one generation of self-fertilisation of the parents.

Analogous predictors have been developed for autopolyploids. For example, a first prediction of the k-Syn e can be approached using mean $\overline{G}$ of GCA inplace of the mean of cross values.

$$\text{k-Syn e} = 2(1 - 1/k)\,\overline{G} + 1/k\,\overline{S}$$

The efficiency of such formulae was tested first by Corkill (1956) for diploids, and for autopolyploids by Busbice (1976) and Gallais (1976).

From such expressions of the value of a variety it is possible to deduce predictors of the GSA of a genotype I.

$$a_I = [2(1 - 1/k)\,g_I + 1/k\,v_I]/k$$

g_I represents the GCA of genotype I, and v_I its S_1 value.

To select for synthesising ability, it will be more efficient to combine GCA and S_1 values if the variance in S_1 values is great in comparison with variance of GCA, and if the number of parents is low (Fig. 2). Such an index is all the more justified because theoretical and experimental results tend to show that maximum genetic advance in varietal development can be reached only with a relatively low number of parents.

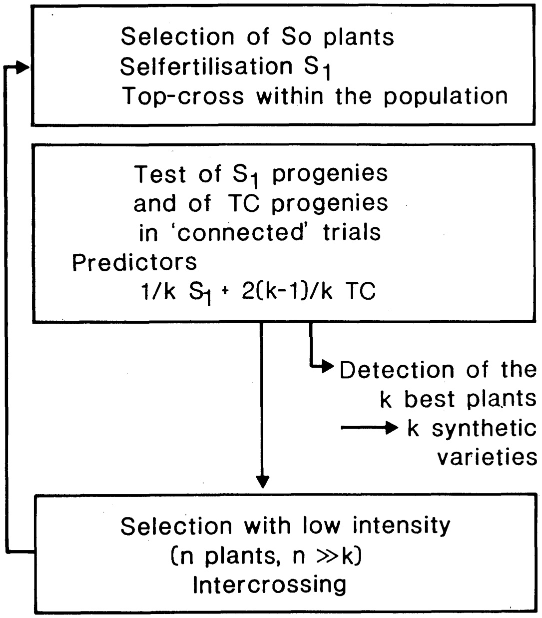

Figure 2. Recurrent selection for general synthesising ability.

Lines

In recurrent selection for line development line value of a genotype can be directly evaluated if it is possible to use HD (Fig. 3). It can also be approximated by the S_1 value.

To predict the best cross of two plants or lines, that is the cross with the best line value, when it is difficult or impossible to use HD, it is possible to use the predictor

$$L = 2F2 - F1$$

which is valid even in the presence of additive x additive epistasis (Gallais, 1979). This is an extension of the results of Jinks and Pooni (1975).

Without the use of HD, to predict the value of the best lines which can be derived from a cross or a plant requires more effort, more generations (at least the F3 generation and perhaps the F4 generation are needed). We may wonder whether it is not better to concentrate efforts on recurrent

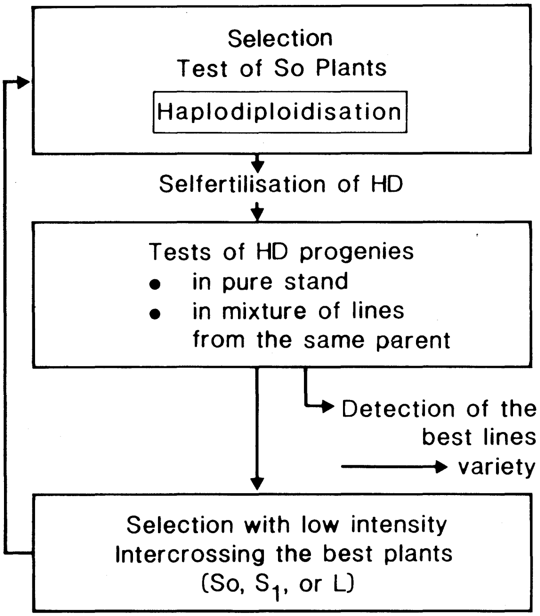

Figure 3. Recurrent selection for line value using HD.

selection for line development. With 'intensive' recurrent selection for line value, selection among plants for their line value will be sufficient to detect plants which give the best line. Indeed, the variance among lines within a genotype is expected to be of about the same magnitude according to genotype. In this situation the value of HD is mainly in shortening the phase of line breeding.

CONCLUSION

The introduction of the concept of varietal ability in a comprehensive strategy of varietal development allows a general approach to the theory of varietal development. The theory can be developed as a whole whatever the type of variety and then specified according to the type of variety. This gives some unity to the breeding methodology. From a plant breeding strategy point of view, there is no fundamental difference between the development of hybrids and the development of lines. This presentation shows how recurrent selection and varietal development are linked. The main problem to solve is the optimum allocation of resources to have maximum genetic advance per unit time at the level of varietal development according to genetic effects and types of varieties. We have also to consider new techniques and new systems of mating such as haplodiploidisation. Due to the possibility of control of hybridisation (e.g. using gametocides or male sterility), the classification of breeding methods according to the natural system of mating — self fertilisation and cross fertilisation — must disappear. Population improvement can be applied to autogamous species to develop lines or hybrids, and it can be used to 'fix' a part of the heterosis when this phenomenon is important as it is in some cross fertilised species.

This general strategy will remain whatever the progress in techniques of genetic engineering or in biotechnology at the molecular or cellular levels. Such techniques are, or will be, powerful tools to be placed within this general strategy.

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SYMPOSIUM DISCUSSION

Dr H.S. Easton, Grassland Division, DSIR

Could you put some numbers, that is percentage elimination, on terms such as low intensity selection for population improvement if we want to get long term development?

Gallais

It depends on the place of the strategy. If it is population improvement we must have low selection intensity, selection intensity is important to the breeder in the number of plants which can be studied and the number of plants it is necessary to keep to intercross to avoid inbreeding depression. So 15-20% can be discarded. But I would also analyse the minimum number of plants to intercross for the next generation; more than 30 plants and not 10-20. A practical plant breeder must cross more than 20 plants.

Dr H. Eagles, Plant Physiology Division, DSIR

In a reciprocal recurrent selection scheme what is your opinion of using an inbred line or a single cross tester from the opposite population rather than a population with itself.

Gallais

For short term efficiency, you must use a line tester related to the population but for long term efficiency it is necessary to develop recurrent selection with outside families using the opposite population as a tester. This is the only way to use maximum genetic effect, maximum specific combining effect.

Dr I.L. Gordon, Massey University

In self pollinating species it is possible to use the inbreeding rate itself to enhance genetic advance even further by selecting amongst lines as well as within lines. How does your genetic advance compare with advances you can get with that combined selection strategy?

Gallais

It is necessary to separate clearly population improvement and line development, so if we discuss population improvement for line development there is no problem. You must not use inbreeding because inbreeding increases the length of the cycle. You can use inbreeding to evaluate the value of the S0 plant. You can test the S1 or S2 plant.

In recurrent selection you have to test the line value of the S0 plant. So you can increase your efficiency by using variance between S2 for example within S1.