

CHAPTER 12

Selection methods

Part 4: Developing open-pollinated varieties using recurrent selection methods

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12.1 INTRODUCTION

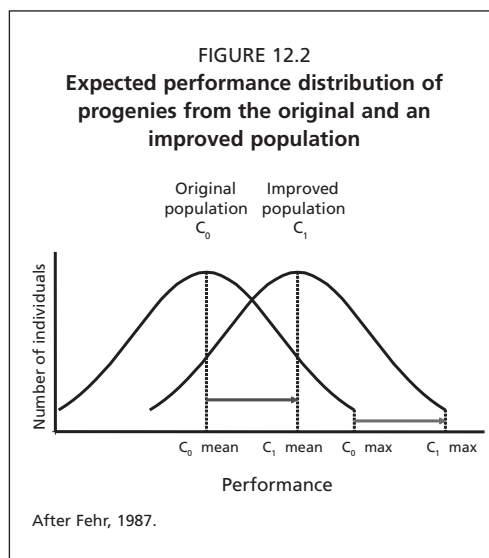
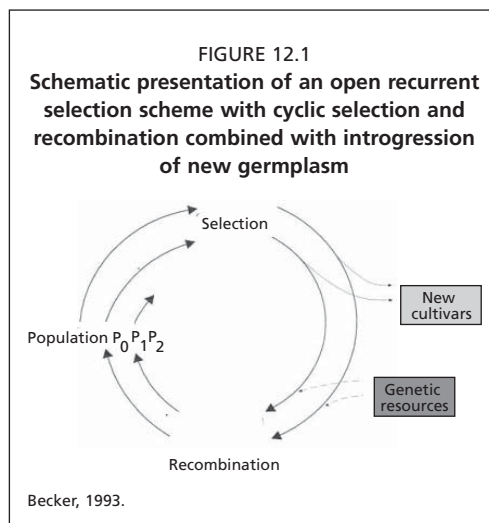
This chapter provides an overview of the use of recurrent population improvement methods in variety development. The major stages of population improvement are addressed, from setting objectives and population creation, through progeny development and selection, to recombination. Factors contributing to successful use of recurrent population improvement methods for participatory variety development are provided, and examples given of farmers' contributions to these efforts.

12.2 RECURRENT SELECTION: WHAT IS IT AND HOW DOES IT CONTRIBUTE TO VARIETY DEVELOPMENT?

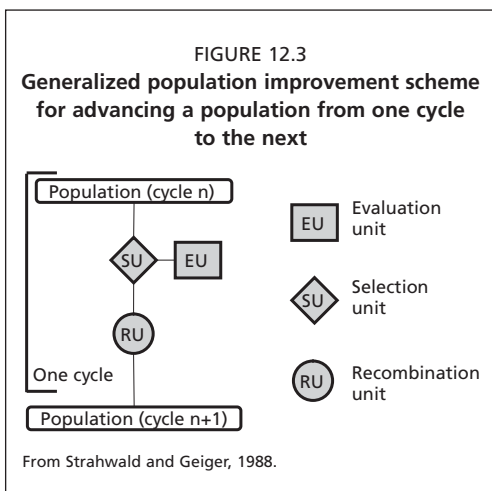
Recurrent selection schemes involve cycles of testing, selection and recombination of breeding 'units', with the possibility of deriving new varieties from each population cycle bulk or from the progenies developed during each cycle (Figure 12.1). Repeated cycles of selection are conducted to increase the frequency of desirable alleles in a population, and obtain progenies that are superior to the best progenies of the previous cycle (Figure 12.2). Ideally, the genetic variability in the population is maintained and thus further genetic gains can be achieved in subsequent cycles.

Recurrent selection methods are readily applied in out-crossing species, where ease of crossing facilitates the frequent and extensive recombinations required in these schemes. The extensive crossing can be more laborious in self-pollinating crops, and requires committed efforts for extensive emasculated crossing or the employment of male-sterility genes or selection for higher out-crossing rates to facilitate recombination.

The basic scheme of recurrent selection is presented in Figure 12.3, with terminology



proposed by Strahwald and Geiger (1988). The plants or progenies that are selected to constitute the next, hopefully improved, population bulk are termed selection units. Selection is based on the performance of individual plants or progenies, named evaluation units, for a single trait or an index of several traits. The next cycle of the population is created by inter-mating the selected plants or progenies which are called the recombination units. These different



units are related to one another or may even be identical, depending on the selection method used. For example, in simple mass selection in a highly cross-pollinating species, the selected S_0 plants are the evaluation and selection units as well as the recombination units, with the half-sib seed of the selected plants used to produce the next cycle bulk. A more complicated example would be an S_2 population improvement scheme where S_2 progeny bulks are used as the evaluation units in order to have sufficient seed for

multi-environment testing. The selection units and recombination units in this case could be the original S_1 progenies, when remnant S_1 seed of the superior S_2 bulks is used for recombination.

A wide range of recurrent selection methods are available, with alternative methods normally identified by the progeny type used as the test unit (Table 12.1), (Hallauer and Miranda, 1981; Gallais, 1981). The choice of selection scheme depends on the type of end-product desired (improved population or pure-line varieties) and the traits to be improved. It also depends on the crop species to be improved (autogamous or allogamous) and the resources and costs (e.g. labour, test site facilities) the breeder can apply for the recurrent selection. For example, the development of pure-line varieties with high grain yield performance could be more successfully pursued by S_1 or S_2 selection methods using multi-location testing of a very large number of test units that more closely resemble the desired end product. In contrast, the development of more genetically heterogeneous varieties of an allogamous species could well be

TABLE 12.1
Alternative recurrent selection methods, required number of generations (or years), and degree of exploitation of the variance of additive (σ_A^2) and dominance (σ_D^2) effects

Selection method	Generations per cycle	Genetic variance σ_G^2	
		σ_A^2	σ_D^2
Phenotypic (mass) ⁽¹⁾ With recombination			
One sex (after flowering)	1	1/2	1
Both sexes (before flowering)	1	1	1
Half-sib			
Selfs recombined	2	1/2	0
Half-sibs recombined	2	1/4	0
Full-sib	2	1/2	1/4
S_1 -line	3	1 ⁽¹⁾	1/4 ⁽²⁾
S_2 -line	4	3/2 ⁽¹⁾	3/16 ⁽²⁾

Notes: ⁽¹⁾ Not equal to σ_A^2 unless $p = q = 0.5$ and dominance decreases to zero with inbreeding.

⁽²⁾ Coefficient difficult to define unless $p = q = 0.5$.

Source: adapted from Schipprack, 1993.

done by applying mass selection for simply inherited traits.

The genetic diversity that is retained in the improved populations enables continued improvement. Several cycles of directional selection should increase the frequency of desirable alleles, resulting in higher probabilities of obtaining superior progenies than in the original population (Figure 12.2). Furthermore, the genetic variability retained in a broad-based population enables selection for different traits or adaptation to new target conditions as the needs emerge. Examples of this are listed below.

- A broad-based population retaining substantial diversity for maturity or other adaptive traits could be given to breeders (researchers or farmers) in differing agro-ecological zones, to develop zone-specific populations.
- A population retaining variability for grain quality traits could be used to derive distinct populations for other quality requirements.
- Rare dwarf segregants in a tall-plant-height population can be selected to develop a new short-plant-height population with potential for increased grain harvest index.

12.3 EXPECTED GENETIC GAIN OR THE RESPONSE TO SELECTION

The response to selection (R), using any type of selection, is a function of the intensity of selection (i), the extent to which observed differences are determined by genetic causes (b = square root of heritability) and the extent of additive genetic variation (σ_A), as indicated by the formula (Falconer, 1981):

$$R = i^* b^* \sigma_A$$

The different recurrent selection methods listed in Table 12.1 vary fundamentally for

the degree to which they can exploit the available additive genetic variance (σ_A). The other two factors (selection intensity and heritability) can be managed by breeders to optimize genetic gains. Options for managing these factors will be discussed in more detail in the sections on mass- and progeny-based selection methods.

It is crucial to consider the time to complete a cycle of selection since the amount of progress is determined both by the gain per cycle and the time per cycle. Table 12.1 indicates the minimum number of generations required for various methods. The time required for one cycle can be reduced significantly if off-season nursery facilities are available.

12.4 BREEDING OPEN-POLLINATED VARIETIES USING RECURRENT SELECTION METHODS

Varieties of cross-pollinated species can be developed by selection in a population bulk *per se*. This approach is appropriate where intra-variety heterogeneity is desirable or necessary. Varieties can be derived from the population bulk *per se* by mass selection for specific highly heritable traits that give the variety a more distinct character; for example, a narrower range of flowering dates or more uniform plant height, or grain or plant colour. The highly successful pearl millet variety ICMV 155 was created by this method, with 59 S_0 plants mass selected during the random mating of the New Elite Composite Cycle 4 bulk used to create a new variety (Singh *et al.*, 1994).

Varieties of cross-pollinated species can also be developed from a set of superior progenies identified during the selection phase of progeny-based recurrent selection. For each variety, a separate set of progenies would be identified based on a

distinct selection criterion or combination of traits, and the progenies in this set would be recombined to create the new variety. Several different varieties can be created in this manner from a given set of population progenies by selecting for different trait combinations or placing different emphasis (weighting) on the targeted traits. Examples of successful pearl millet varieties developed in this manner are ICTP 8203, created by random mating 5 superior S_2 -lines identified by progeny testing a large number of lines derived from a Togolese landrace at Patancheru, India (Rai *et al.*, 1990), and WC-C75, created from 7 full-sib progenies selected out of the World Composite (Andrews, Gupta and Singh, 1985).

Pure-line varieties for predominantly self-pollinating crop species such as sorghum can be effectively derived from the superior partially inbred evaluation units (for example S_1 or S_2 lines) identified in a progeny-based recurrent selection programme. Breeders usually follow the same procedures as for deriving lines from biparental crosses (Chapter 11, this volume).

Use of recurrent selection methods in variety development programmes can be particularly advantageous for enhancing quantitative traits determined by many genes, or simultaneous enhancement of multiple traits. A large number of favourable alleles can be carried forward and concentrated with repeated recombination, breaking undesirable linkages, and selection for favourable recombinants. Allard (1999) notes that the assembly of favourable epistatic combinations of alleles of different loci by means of recurring cycles of selection and intercrossing the superior selections is the single most important genetic mechanism for evolution of adaptation.

12.5 SETTING GOALS AND DEVELOPING BASE POPULATIONS

The success of any plant breeding programme is usually measured by the extent of farmer adoption of the newly produced varieties. As the specific advantages of new varieties determine adoption, breeders must tailor their new varieties to meet priority needs and requirements of the end users. Priority setting for a recurrent selection programme requires good understanding of the environmental conditions under which the newly developed varieties should perform, as well as of the needs of the farmers or end users expected to benefit from the new varieties. Methods and tools for effectively identifying and defining the priority targets for participatory variety development are provided in Weltzien, vom Brocke and Rattunde (2005) and in Chapter 4.

By explicitly defining the goals and expectations of a given population, parents can be selected that best contribute to the creation of the new population/variety with the desired genetic variability. Key questions for choosing parents include:

- What are the target environment(s), zone and group of farmers for whom the population should be of use?
- What is the acceptable range for critical adaptive and quality traits, such as maturity, grain type, biotic challenge resistances, and adaptation to specific soil and water regimes?
- What is the priority trait or combination of traits that are a target for improvement?
- What is the appropriate balance between level of diversity and eliteness?

The balance between level of diversity and eliteness is a critical issue in the choice and number of parents used for developing the population or variety. Maximizing the

diversity of the population through selection of parents with outstanding performance for certain traits but less desirable for others will maximize the potential for long-term genetic gains, but reduce the possibility of deriving agronomically superior end products in the short term. In contrast, greater emphasis on population 'eliteness' through more restrictive inclusion of parents for population creation will maximize opportunities for immediate extraction of distinct finished varieties, but limit long-term potential gains and benefits from intra-varietal diversity.

12.6 MASS SELECTION

Mass selection involves the selection of individual plants or even of individual grains or seeds (Allard, 1999). This type of selection is based on the phenotype only, as a given genotype is neither replicated nor tested in differing environments. Mass selection therefore always has confounding of environmental conditions that can mask genotypic differences. As breeders can only marginally influence the extent to which observed differences are determined by genetic causes (h = square root of heritability), mass selection is only effective for traits with higher heritability and little genotype by environment interaction.

One factor that can be better managed to increase response to selection (R) is the intensity of selection (i) used in mass selection. As the test units are single plants it is relatively easy to increase selection intensity by increasing the area sown with the population bulk, to have a greater number of plants from which to select the minimum number of desirable plants to constitute the next cycle.

The extent of additive genetic variation that can be exploited by mass selection depends on the level of parental control. If

the trait can be evaluated before flowering and undesirable plants culled, full parental control can be imposed and the full extent of additive genetic variance can be exploited. For traits that can only be observed after flowering, only the female parent can be controlled, and thus only 50 percent of σ_A can be exploited (Table 12.1), unless plants are self-pollinated and the selfed progenies are used for recombination.

12.6.1 For which selection objectives and conditions can mass selection be useful?

Mass selection is a very simple method of selection, as selection is based on individual plants. This method thus requires minimal materials and organization for implementation. Mass selection enables maintaining a very large effective population size even with high selection intensity. Several thousand plants can be evaluated and several hundred retained to create the next cycle of the population. An additional advantage of mass selection is that each season results in the recombination among differing gene blocks in the population. This frequent recombination is essential for breaking undesirable linkages and increasing the frequency of desirable trait combinations. This is very important during the initial phases of a recurrent selection programme, when new parental materials are being recombined to form new populations, or when a new variety is formed from partially inbred progenies.

Mass selection will be most effective for traits that are highly heritable, with genetic differences that are observable on individual plants. One study in pearl millet showed quite acceptable heritabilities for single plant expression of plant height (0.58), seed weight (0.52) and flowering date (0.45), but not for grain yield (0.29), based on

parent-offspring regressions conducted in several populations (Rattunde, Witcombe and Singh, 1989). Thus mass selection for traits such as grain colour, grain size or form, plant height or time to flower can be effective, as these traits are expressed in a rather consistent manner, even with moderately heterogeneous soil conditions.

Mild selection with culling of undesirable types can be useful in newly created populations in which the introduction of new diversity or traits is accompanied by introduction of genes (or gene combinations) with undesired effects on quality or adaptation. This was the case in the early stages of the farmer-participatory population breeding work in Burkina Faso (Box 12.1). More intense selection can be applied when trying to concentrate favourable genes, for example with resistance to a pest or adaptation to specific conditions (as described in Box 12.2).

12.6.2 Potential roles and contributions of farmers

Mass selection is the method used by farmers for creating and maintaining the majority of the world's heritage of landrace varieties. Farmers are often skilled at single plant selection, with sophisticated mental indices for weighing several critical traits that are considered during selection, particularly for indigenous crops that they have developed over countless generations of selection. Sorghum farmers in Mali, for example, when choosing each panicle for use as seed consider several aspects of grain type (colour, size), glumes (ease of threshing) and panicle form (optimal density of grains and numbers of panicle branches, but with sufficient spacing to avoid risk of damage from insect feeding). Farmers may observe certain traits more accurately and with more practiced judgment than formal

breeders, particularly for crops in their centres of origin or diversity. Likewise, farmers can weigh the importance of many traits, and set acceptable thresholds for each trait based on the importance of each to meeting their needs. Farmer mass selection also enables selection to be based on plant expression under their own field conditions. Involvement of farmers in mass selection also allows a larger scale of operation than would be possible for individual breeders, with possibilities of several farmers participating, each contributing their time and expertise to observe thousands of plants and select those showing most promise under their field conditions. Weltzien, vom Brocke and Rattunde (2005) propose options for farmer participation in mass selection.

12.6.3 Factors for success

The genetic gains achieved via mass selection can be maximized by attention to factors influencing the three components of the Selection Response Formula (see Chapter 2).

Heritability (h)

The appropriate choice of field and management of the field can help favour expression of genetic differences for the target trait(s). Pre-sowing observations of the terrain can help to choose sites where there is less soil heterogeneity, shading and nutrient effects of trees, piles of animal dung or residues from previous years. Likewise, the planning and uniform application of management practices should help favour expression of genetic differences for the desired target traits. Further, the standards for selection can be adjusted based on the apparent environmental conditions, relaxing standards in patches of poorer growth or raising standards in areas with exceptionally luxuriant growth. Gridded

BOX 12.1

Use of zone-specific sorghum populations as source material for variety development

Zone-specific broad-based sorghum populations were created to serve as sources of genetic diversity for deriving new varieties that combined increased grain productivity with the grain quality and adaptation of the farmer's own varieties for the Central-North (650 mm average annual rainfall), Central-West (800 mm) and Boucle de Mouhoun (900 mm) areas in Burkina Faso (vom Brocke *et al.*, 2008). As the parental materials were of diverse Guinea- and Caudatum-race origins, farmers applied mild selection for grain quality during the back-crossing and recombination cycles to increase the probability of deriving useful segregates for variety development in the resulting populations.

The varietal development process began in each of the three zones by two farmers, one per village, sowing approximately 10 000 plants of the zone-specific population in isolated fields representative of the most important production system in the area. A group of 10 to 25 farmers, both women and men, selected panicles from the population bulk, with each farmer choosing about three of the most desirable panicles for the specific grain or plant type of most interest to them. A total of about 250 panicles were selected per site, and thus 400 to 600 plants per population were selected with a selection intensity of about 2 to 3 percent. Selection by several farmers and in different field environments helped to better sample the plant types to address farmer's different needs and provide a sufficiently large number of progenies for appropriately intense selection in subsequent generations.

The S_1 lines obtained from the selected S_0 panicles were prepared in sets according to the 'variety type' category for which they were selected, and single-replicate nurseries were sown by individual farmers. Selection among and within progenies was applied according to normal pedigree variety development methods.

The fate of progenies selected out of the 2004 Boucle de Mouhoun population for variety development are tabulated below.

Variety type (primary selection criterion)	2004		2005			2006
	S_0 plants selected by farmers	S_0 panicles (S_1 lines) retained by breeder	S_1 lines selected by farmers	Panicles ($S_{2,1}$ lines) selected by farmers in retained S_1 lines	S_2 lines retained by breeder	S_2 lines selected by farmers
Couscous	8	6	3	3	3	2
Malting and beer	34	24	6	12	9	-
Food quality (tô)	40	28	11	16	14	-
Commercial grain	31	24	8	11	7	-
Grain storability	27	19	6	7	3	-
Fodder	50	30	12	15	14	3
New panicle type	46	32	4	4	3	2
Early maturity	55	36	6	12	7	2
Striga resistance	31	22	10	17	12	-
Stems (construction)	39	26	10	10	4	1
Total	361	247	76	107	76	10

(K. vom Brocke, G. Trouches, C. Barro-Kondombo and J. Chantereau)

BOX 12.2

Origin of a flooding-tolerant sorghum population

ICRISAT-Mali conducted several cycles of mass selection in a broad-based random-mating sorghum population with genetic male sterility to recover the special Guinea-race glume and grain characteristics required for free threshing, resistance to grain mould and desirable food quality. The field where this population was grown in 2001 was flooded for three weeks when the river rose due to unusually heavy rains. The more desirable plants that survived that year were selected as probably possessing some tolerance to water logging, as the entire field was flooded. The same year, farmers expressed interest in having a sorghum variety for fields that tend to be inundated in years of heavy rainfall. The following year this 'waterlogged' cycle bulk was given to two farmers in different villages, who sowed it in low-lying fields adjacent to their own sorghum variety. The farmers liked the population very much, and one of them, Diakaridia Dembele, started selecting panicles within it for use as seed the following year. The next year the population performed exceptionally well and he selected panicles for seed for himself, but he also gave away 75 kg of seed in response to demand from many neighbours. Most of the farmers requesting seed were women who grow rice in low-lying areas and used this new sorghum 'variety' on the borders of their fields, where risk of temporary inundation was high. The farmer planned to continue selection in this population for one or two more seasons to obtain an acceptable level of uniformity for glume colour and panicle form, at which time he could consider it to be a finished variety.

(E. Weltzien, D. Dembele, S. Diakite and F. Rattunde)

mass selection offers a systematic approach by dividing the field into grids, and selecting a common number of plants from within each grid.

The effectiveness of selection between plants can be maximized by ensuring that selection is conducted by the most skilled people. For example, the threshability (ease of separating grains and glumes) of sorghums in West Africa can be best observed by farmers who have years of experience and a cultural heritage of selection for this trait. Effectiveness of selection may be further raised by identifying individuals who are the most interested and locally respected for their capabilities as 'seed experts'.

The genetic gains from mass selection in out-crossing species can be increased

through parental control that reduces the extent to which selected plants are pollinated by unselected plants. Self pollination and selection of selfed plants achieves maximum parental control. The same result is achieved with populations of self-pollinating species containing genetic male sterility, through identification and selection of male-ferile plants. Note however that selection of selfed plants would require a separate recombination to constitute the next cycle bulk. If introgression from neighbouring fields is not desired, sufficient isolation distance would need to be maintained. Culling undesired plants prior to flowering also provides parental control and could therefore double gains for traits that can be observed before flowering. Culling out

tall plants in a dwarf population is one such example.

Genetic Variance (σ_A)

The choice of parents for creating the initial population determines the level and usefulness of genetic diversity. The more diverse the parents chosen, the higher will be the expected genetic variance and therefore the potential gain from selection. There is usually an optimal level of diversity beyond which the mean performance of the population would go down, thereby reducing the usefulness of the population in the long-term (Schnell and Utz, 1975).

Maintaining sufficient population size through selection and recombination of a large enough number of plants will help maintain a desirable array of alleles, and assure genetic variation exists for selection in subsequent cycles (Witcombe and Virk, 2001). Likewise, maintaining a sufficiently large effective population size is indispensable to avoid inbreeding, which is of greatest concern in highly outcrossing species. It is exhibited as a loss of vigour of the population and undirected separation into distinctive lines due to random fixation of genes. Effects of inbreeding and strategies for avoidance are summarized by Allard (1999) and Hallauer and Miranda (1981), among others. Using a minimum of 200 plants to create the next cycle bulk will minimize loss of genetic variation and genetic drift that would otherwise arise from mating among a limited number of parents and sampling.

Mass selection, based on single plant selection in a given site, can produce more site-specific responses than would be obtained with multi-environment progeny testing. However, where the objective is to produce an improved population and eventual varieties with wider adaptation,

a population may be grown by several farmers or researchers, with selections from differing sites being pooled by breeders to capture selections that represent a wider sample of conditions or selection criteria. Selections produced by different breeders on differing sites could be simply bulked, or they could be grown out in isolation for recombination, with eventual culling of certain off-type progenies.

Selection Intensity (i)

More intense selection (setting higher thresholds for retaining plants) is expected to increase the genetic gains. The selection intensity coefficient in the genetic gains formula corresponds to the number of standard deviations by which the mean of the selected fraction exceeds the population mean (Falconer, 1981; Becker, 1993), and thus depends on the percentage of selected individuals.

An advantage of mass selection is the possibility of achieving very high selection intensity, by which rare plants possessing the desired combination of several traits or express rare forms of a given trait can be identified. However, to realize this potential it is necessary that a sufficiently large number of plants be available for selection. For example, a population with 10 000 plants could be subjected to selection with a 2 percent selected fraction and still retain 200 plants for reconstituting the next cycle bulk. Observation of farmer selection in sorghum populations in Burkina Faso shows that they frequently retain selected fractions ranging from 0.2 to 5 percent.

12.7 PROGENY-BASED RECURRENT SELECTION METHODS

A range of methods for population improvement rely on testing, selecting and recombining families rather than individual

TABLE 12.2
Selection response per year for pearl millet head yield from alternative recurrent selection procedures using equal level of resources and optimized for allocation of labour

Recurrent selection procedure	Selection response
Mass selection ⁽¹⁾	0.22
Half-sib family ⁽¹⁾	0.34
Full-sib family	0.51
S ₁ line (one stage)	0.27
S ₂ line (one stage)	0.23
S ₁ line (two stage)	0.26
S ₁ line/S ₂ line	0.26
Full-sib/S ₁ line	0.46

Notes: (1) S₁ lines from S₀ single plants used for recombination.

SOURCE: as presented in Schipprack, 1993.

plants. These progeny-based methods may involve a single stage of selection or multi-stage methods that combine evaluation and selection of genetically different evaluation units and selection units in successive seasons or generations (Hallauer and Miranda, 1981; Schipprack, 1993). Superior progenies identified through this testing can be used in a pedigree breeding programme to directly develop new inbred varieties, or to develop parental lines for production of hybrids or synthetics (Box 12.4). For highly outcrossing species, superior progenies of similar agronomic type and maturities could be used to create new open-pollinated varieties by random mating.

The objectives pursued with progeny-based recurrent selection methods tend to be improvement of traits whose expression is unreliable on a single-plant basis, and the development of superior progenies or inbred lines. Increasing yield is a typical objective pursued by progeny-based selection methods, where replicated trials conducted in multiple environments are used to determine the genetic potential of the evaluation units. Modelling of expected

selection responses of alternative recurrent-selection methods for pearl millet grain yield show that certain progeny-based selection schemes may achieve twice the genetic gain for grain yield compared with mass selection (Table 12.2), even with comparable allocation of resources and optimized for labour use (Schipprack, 1993).

Factors for success

Questions to consider for maximizing the response to selection include how many traits are to be improved and when selection for specific traits is conducted during the inbreeding process. Each additional selection criterion will reduce the potential gain for the individual characters. Farmer indications of acceptable thresholds and priorities for specific traits can be helpful to focus selection efforts. Selection for traits with higher heritabilities is recommended when single plant selections are used to generate progenies or in early generations. In contrast, selection for less heritable traits is best conducted in later generations when multiple-environment assessments are feasible and progenies are more homozygous.

Farmer's assistance in single plant selection can be useful to funnel the most promising genetic materials into further stages of testing, and thus use limited testing resources most effectively. Farmers can help create the progenies used to initiate the selection procedure through mass selection of half-sib or S₁ lines from recombined bulks. They can further assist by selection within progenies in on-station or on-farm nurseries. Selection by several farmers helps to retain diversity, especially as cultivar preferences may differ with differing socio-economic backgrounds or production objectives.

Effective population size is also important for progeny-based selection methods. Initial progeny trials should consist of

at least 200 progenies that will allow an appropriate intensity of selection (15 to 30 percent) and still retain a sufficient number of progenies for recombination or a subsequent stage of selection. The initial creation of progenies (S₁, full-sib (FS) or half-sib (HS) for example) can thus be done by selection from thousands of plants. Mass selection by several farmers, each sowing the same bulk in their own fields, has been useful in achieving suitably large numbers of selected progenies.

Progeny evaluations conducted in sufficient test environments is also important to effectively assess genetic potential and to sample the environmental diversity. For example, the wide range of sowing dates, soil and rainfall conditions for sorghum production in even a single agro-ecological zone of West Africa requires a minimum of four to six test environments to provide some measure of representation. Conducting progeny trials on farmers' fields, although logistically challenging, can help achieve the necessary, and appropriate, sampling of test environments.

Progeny-based trials conducted with farmers presents several challenges not encountered with mass selection. The large number of progenies and more complicated trial designs requires researcher assistance, at least during planting and harvesting, or even researcher management of on-farm trials. Trial designs can be modified to make on-farm progeny testing feasible. Individual farmers could, for example, grow a single replication or even a subset (incomplete block) of test entries. Modern statistical procedures and computing power now make analysis of the widest range of incomplete and unbalanced designs possible. Issues of how benefits and costs are shared also need to be considered, since land and labour requirements may be much

higher and direct benefits to participating farmers less than in the case of mass selection.

12.8 EVOLUTION OF POPULATION IMPROVEMENT PROGRAMMES

Although population improvement programmes can follow a single selection methodology for improvement of a given trait or set of traits over many cycles (Rattunde and Witcombe, 1993), this may not often be the case. Population improvement may begin by conducting several cycles of mass selection to narrow and 'clean up' the population to a more acceptable range for critical adaptation or quality traits. Populations may reach appropriate ranges for simply inherited traits after a few cycles of selection and little further progress will be made by selecting for these same traits. Improvement of more complexly-inherited traits, such as yield, would require changing to progeny-based selection methods.

Practical population improvement programmes can also undergo major changes in the breeding objectives in response to evolving needs and opportunities. For example, population improvement by ICRISAT-Mali was initially conducted on a sorghum population of tall plant height as this plant height corresponds to what most farmers grow in the target Sudanian zone of West Africa, and tall parental materials had the required suite of adaptive and quality characteristics. However, the convergence of farmers' priority setting that placed highest value on increased yields, the hypothesis that reducing heights could raise harvest index and thus grain yields, and the identification of novel dwarf segregants in the ongoing population improvement work, led to a major shift to dwarf population and variety development, as described in Box 12.3. Further, this sorghum population

BOX 12.3

The evolving Guinea-race sorghum populations in Mali

A broad-based sorghum population was developed as a source of diversity for breeding sorghum varieties with increased grain yield and the grain, glume and panicle characteristics required for adoption in the Sudanian zone of Senegal, Mali and Burkina Faso in West Africa. BC₁ or BC₂ progenies, created by crossing 13 higher yielding Guinea-landrace varieties to a source population segregating for the *ms3* genetic male-sterility gene locus, with subsequent backcrossing, were bulked together in 1994 (Rattunde *et al.*, 1997). Three cycles of recombination with mild selection and one cycle of more intense mass selection for grain and glume traits followed. Progeny-based selection was then initiated, using S₁ and S₂ progeny testing schemes, for increasing the population's yield level and to derive sorghum varieties with superior grain yield. This population and the varieties derived from it had plant heights of 3 to 5 m, similar to the landrace varieties used to create the population.

A new Dwarf Guinea Population was initiated in 1999 by selecting 50 plants with short stem-internodes (40 male-fertile and 10 male-sterile plants that gave S_{0,1} and half-sib progenies, respectively) out of a total of 15 000 plants of the original tall Guinea Population. These progenies were recombined together, as well as inter-mated with 12 dwarf progenies derived from previous population cycles and five short-statured inter-racial varieties produced by pedigree breeding. This new population was recombined, with the second cycle involving replicated randomized sowings of 240 F₁s to assure thorough recombination. The presence of desirable Guinea-race grain and panicle types on these markedly shorter plants (mean: 2.5 m) was confirmed by farmers, who identified approximately 200 superior S₀ plants.

Two hundred S₁ progenies, derived by selecting the most desirable S₀ male-fertile plants from the Dwarf Guinea Population, were tested in a replicated yield trial and selfed in a separate nursery to advance to the S₂ generation. A total 70 S₂ progenies from the highest yielding S₁ progenies were further evaluated for yield at the ICRISAT-Samanko station (two dates of sowing) and the IER-Kolombada (Mali) station the following year (2003). A total of 20 selected progenies were then recombined to create the cycle 2 bulk of the Dwarf Guinea Population. The recombination was conducted by first making paired crosses among progenies, and the following year random-mating in isolation of all crosses.

(F. Rattunde, E. Weltzien, A. Toure, J. Chantereau and C. Luce)

breeding programme will continue to adjust towards the emerging needs of dual-purpose (grain+fodder) varieties and of new short-statured lines as hybrid parents.

An even more rapid evolution of populations can occur in certain crops, like highly outcrossing pearl millet, where relatively few cycles of improvement are con-

ducted between periodic crossing between populations (Rattunde *et al.*, 1997). This approach would require working with a number of different populations, and possible structured, diallel, population crossing to identify the most promising populations for continued improvement. By periodic inter-population crossing, heterosis could

BOX 12.4

Lata (Bala Berthe): A dwarf Guinea-race sorghum variety and hybrid parent developed through population breeding

S₃ progenies (n = 89) derived from the most promising S₂ progenies (see Box 12.3) were further tested in replicated, multi-environment, on-station trials for variety development. Six of the most promising progenies were included in a 16-entry, 2-replicate, early generation variety trial conducted by 20 farmers in 10 villages in 2005. Each entry was given a name to facilitate discussions by farmers. The progeny 'Lata' showed higher yield, intermediate height (2.5 m), and was appreciated by farmers. This progeny was given to Bala Berthe, a farmer with strong interest and expertise in selection. Bala Berthe conducted two cycles of mass selection for panicle architecture, grain and glume characteristics and shared a portion of his seed lot with ICRISAT. The variety Lata (Bala Berthe), following further testing in larger scale 4-entry 'Variety Test Kits', was submitted for variety registration in Mali. This variety was also used as a male parent to produce a series of experimental hybrids. Analysis of multi-environment hybrid yield trials showed that Lata (Bala Berthe) had the highest combining ability of all male parents in 2007.

be exploited, increasing the mean productivity as well as the genetic variation of the resulting inter-pool populations.

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