Euphytica (2008) 160:143–154
DOI 10.1007/s10681-007-9533-0

REVIEW

Decentralized selection and participatory approaches in plant breeding for low-input systems

Julie C. Dawson · Kevin M. Murphy · Stephen S. Jones

Received: 18 April 2007 / Accepted: 25 July 2007 / Published online: 18 August 2007

Abstract Heterogeneous environments make it difficult to apply consistent selection pressure because often it is difficult to identify a single or a few superior genotypes across all sets of conditions. However, when the target system is characterized by heterogeneity of environmental stress, varieties developed in high-yielding conditions may fail to satisfy farmers' needs. Although this type of system is often found in marginal environments of developing countries, heterogeneous environmental conditions are also a feature of organic and low-external-input systems in developed countries. To meet the needs of these systems, breeding programs must decentralize selection, and although decentralized selection can be done in formal breeding programs, it is more efficient to involve farmers in the selection and testing of early generation materials. Breeding within these target systems is challenging, both genetically and logistically, but can identify varieties that are adapted to farming systems in marginal environments or that use very few external inputs. A great deal has been published in recent years on the need for local adaptation and participatory plant breeding; this article reviews and synthesizes that literature.

Keywords Participatory plant breeding · Organic agriculture · Heterogeneous environments · On-farm selection · Genotype by environment interactions

Abbreviations

PPB	Participatory Plant Breeding
CIMMYT	International Maize and Wheat Improvement Center
G×E	Genotype by Environment Interactions
ICARDA	International Center for Agricultural Research in Dry Areas

Plant breeding for low-input systems

Plant varieties adapted to low-input systems are needed in both developed and developing countries. Organic or low-external-input systems in developed countries may resemble farming systems in marginal environments of developing countries because environmental stress is heterogeneous, there are few varieties that meet the diverse needs of farmers in such systems and there is very little interest from the commercial seed sector (Desclaux 2005). Improving varietal performance in such systems can help improve farmers' livelihoods in all parts of the world. In developing countries, access to inputs is often limited or non-existent, and farmers need varieties that will perform well when grown under severe stress. In developed

J. C. Dawson · K. M. Murphy · S. S. Jones (✉)
Winter Wheat Breeding and Genetics, Department of Crop and Soil Sciences, Washington State University,
201 Johnson Hall, Pullman, WA 99164-6420, USA
e-mail: joness@wsu.edu

countries, inputs are usually available, but many farmers want to reduce there use for economic or environmental reasons. Reducing the need for off-farm inputs increases commercial farmers' profit margin and subsistence farmers' food security. In addition, the total use of agricultural chemicals, particularly nitrogen (N) fertilizer, will need to be significantly lowered if agriculture is to be sustainable.

It is often more difficult to identify superior genotypes or to apply consistent selection pressure under low-input conditions because of environmental heterogeneity (Haugerud and Collinson 1990). When moving from high to low yielding environments, the genetic variance generally decreases while the error variance may increase (Bänziger and Cooper 2001; Bertin and Gallais 2000; Ud-Din et al. 2004; Brancourt-Hulmel et al. 2005). Because the error variance does not usually decrease as much as the genetic variance, experiments in low-yielding conditions may have a lower chance of detecting a statistically significant difference among lines (Bänziger et al. 1999). In cases where soil fertility is low, variability in nutrient supply has a large impact on crop performance. In other cases, low-input systems may have high soil fertility and high-yields due to the use of crop rotations, green manures and animal manures. These systems are often called low-external-input systems, and are much more complex in terms of nutrient cycling than conventional agricultural systems, so there is likely to be a good deal of variability in the nutrient supply over space and time. Variability in soil characteristics or nutrient availability complicates experimental design and analysis, but it is possible to overcome these obstacles and achieve genetic gains when breeding crops for low-input systems.

Heritability and genotype by environment interactions

Because of the decrease in genetic variance in low-input environments, many breeders prefer to conduct selection in relatively high-input environments, assuming the genetic gains will carry over to low-input conditions. Selecting in favorable environments for performance in marginal environments is a type of indirect selection, and is justified if the heritability of traits is significantly higher in high-yielding environments (Ceccarelli 1994). The efficiency of indirect selection depends not only on the heritability, but also on the genetic correlation coefficient between the two environments. High genetic correlation coefficients between two environments makes crossover G×E interactions less likely because the environments are similar, but a low genetic correlation coefficient means that the lines that do best in each environment will probably be different. The efficiency of selecting in environment x for performance in environment y is given by the equation: $CR_x/R_x = r_g*h_y/h_x$ where CR_x is the correlated response in y to selection in x, R_x is the response to selection in x, r_g is the genetic correlation coefficient, h_y and h_x are the square roots of heritability in y and x, respectively (Ceccarelli 1994).

With a low genetic correlation coefficient, heritability in environment x must be several times larger than the heritability in y for indirect selection to be useful. Also, if the genetic correlation coefficient is negative, the heritability is no longer relevant, as indirect selection will be counterproductive (Ceccarelli 1994). Brancourt-Hulmel et al. (2005) showed that indirect selection in maize under high N for performance at low N became increasingly inefficient as the N stress increased. Similarly, a study of European maize lines showed that the genetic correlation coefficient decreased and became negative as N stress increased (Presterl et al. 2003). In ICARDA's barley breeding program Ceccarelli (1994) calculated that it was 28 times more effective to conduct direct selection under farmers conditions with local germplasm than to conduct selection in a high-yielding environment with introduced germplasm.

A review of the experimental evidence shows that heritability is not intrinsically lower in low-input or marginal environments (Ceccarelli 1994). For example, in CIMMYT maize lines, Agrama et al. (1999) found equal heritability estimates at high and low N for traits related to nitrogen use efficiency (NUE). Most studies showing that heritability is lower in low-input environments use genotypes originally selected in favorable environments, which are then tested in low-input environments. In a series of environments with progressively higher stress levels, there will be a point at which two genotypes change rank in performance. At the crossover point, the heritabilities will be lowest, as it is difficult to discriminate between genotypes. At the high and low ends of the spectrum, heritabilities will be higher, so if the target environment is above the crossover point, selection in a high yielding environment will produce the best results.

If the target environment is below the crossover point, selection in a low-yielding stress environment will be best (Ceccarelli 1996a). When crossover interaction occurs, the material from high-input selection will be poorly adapted to the low-input conditions and calculations of heritability will be low (Ceccarelli 1994).

G×E interactions become more important as selection environment and target environment diverge (Ceccarelli and Grando 1999), so selection for specific adaptation becomes more important as yield differences between high- and low-input environments increase (Bänziger and Lafitte 1997). Differences in system management, such as organic or conventional practices, can also result in crossover G×E interactions, and lines selected in one system and grown in another will not be as optimal as lines selected in the target system (Murphy et al. 2007). These crossover G×E interactions can be exploited by breeding for superior adaptation within the target environment instead of looking for high average yields across locations and years. Selection for specific environments involves a positive interpretation of G×E interaction, where top performing lines are selected in each target environment. A negative interpretation is more common, where G×E interaction is seen as a barrier to achieving broad adaptation, and top performing lines in particular environments may be thrown out in favor of those that have the best average performance across environments (Ceccarelli 1996b). Sometimes lines can perform well under both high- and low-input conditions in breeder-managed trials, but do not outperform local varieties in farmers' fields (Berg 1997).

Broad versus specific adaptation and stress tolerance

Varieties that are thought to have broad adaptation across environments may in fact be narrowly adapted to environments that can be modified to be more similar to research station conditions through the use of fertilizers and other inputs. This type of variety has been mostly adopted in favorable environments, while in many marginal areas, there is limited use of modern varieties (Ceccarelli 1994). This could be due to lack of access to seed, but even in regions where modern varieties have been partially adopted, landraces are still grown. There are many cases where landraces still yield better than modern varieties in farmers' fields (Ceccarelli and Grando 1999). Applications of fertilizer may be considered too risky in marginal environments where environmental constraints such as drought severely limit crop yields or cause crop failures in many years (Ceccarelli 1994). Marginal environments include areas where environmental and socio-economic conditions result in complex stresses and high risks to agricultural production. Most of these areas are too different from more favorable production areas to benefit, even indirectly, from breeding in high-input systems (Almekinders and Elings 2001).

Many farmers are most interested in minimizing the amount of variation they observe over years, that is, they prefer yield stability over time rather than high potential yield in favorable years. In terms of meeting social and economic needs, breeding for stability and minimizing crop failures is probably the most important breeding objective (Ceccarelli 1994). This is true in developed as well as developing countries. For example, the wheat breeding programs at Washington State University work with farmers in the driest areas (200–300 mm precipitation) of Eastern Washington who would prefer a variety that yielded 40 bushels per acre (2.7 tons ha^{-1}) every year. They would be willing to give up the few years where they get 60 bushels (4 tons ha^{-1}) to avoid the years with 20 bushels (1.3 tons ha^{-1}) or less.

Temporal variation can be minimized by breeding heterogeneous populations similar to landraces that have specific adaptation to the target environment (Ceccarelli et al. 2001). In a study of barley breeding, groups of genotypes selected in stressful environments generally had lower slopes and coefficients of variation in regression analyses than groups selected in high-input environments, indicating better stability across the range of locations tested (Ceccarelli 1994). Genetic diversity for resistance and stress tolerance buffers against abiotic and biotic stresses which may change from year to year, giving more stability to the population as a whole, even without significant variation for agronomic traits such as quality or maturity (Ceccarelli 1994; Sthapit and Jarvis 1999; Witcombe et al. 1996). Farmer bred varieties often have large amounts of allelic variation within the variety, and farmers may grow multiple varieties within a field, which helps to reduce phenotypic variation under stress (Cleveland et al. 1999). Breeders, however, often try to minimize the amount of variation over space by breeding for broad adaptation (Ceccarelli and Grando 1999). The focus on selecting for broad adaptation has replaced selection for stability over time as modern breeding replaced seed selection on-farms (Riley 2003). Involving farmers in the selection process with breeders in the formal sector tends to maintain more diversity in the region because farmers look for genotypes with good temporal stability while breeders tend to focus on broader adaptation (Ceccarelli et al. 2001).

It is possible that the traits required by farmers in low-input environments are too diverse to be fully addressed by a centralized breeding program, even one focused on agriculture in marginal areas (Smith et al. 2001). Many breeders may not be aware of the wide range of traits farmers working with such systems desire (Desclaux 2005). For example, in observing the characteristics desired by farmers in very dry production environments, breeders learned to select for straw productivity and grain filling ability under multiple stresses. Low-input, drought conditions cause a reduction in plant height, so the best lines in low-input conditions were tall plants with soft straw when grown in high-input conditions. When faced with the stress conditions, these genotypes become short and stiffer, so that lodging is not a problem, but the straw is still palatable to livestock. Superior genotypes in these conditions would be the opposite of what modern breeding programs would look for in a high-potential environment (Ceccarelli 1996a). The fact that some key traits for low-input conditions are not apparent until selection and evaluation is done in those environments is a strong argument for conducting breeding programs in the target environment.

Selection for tolerance to stress may reduce yields when grown in favorable conditions compared with cultivars selected in the favorable environments. High grain yield in very divergent environments appears to be controlled by different sets of alleles across many loci (Bänziger and Lafitte 1997; Ceccarelli 1994). Therefore, varieties with adaptation to severe stress are less likely to be selected when tested in high-input environments (Ceccarelli 1996a). Data on the utility of using both stressful and non-stressful environments for selection is contradictory. Progress made by alternating breeding nurseries between low- and high-input environments may depend on the breeding strategy. It appears that such alternation is successful with pedigree breeding methods but detrimental with a bulk breeding strategy (Van Ginkel et al. 2001). Since environmental conditions in low-input systems rarely approach the conditions on high-input research stations, the potentially lower yields of lines selected in high stress conditions when grown under optimal conditions is unlikely to be a problem (Ceccarelli 1996a).

When stress factors vary over seasons, selecting in different nurseries may help subject breeding lines to the multiple stresses that they could face in farmers' fields. An index of selection that weights performance in multiple environments may be helpful in selecting for stressful conditions. Ud-Din et al. (2004) found that weighting performance in irrigated and drought stressed environments allowed for faster progress under dryland conditions than direct selection under drought stress. This occurred even though the genetic correlation coefficient between the two environments was not significantly different from zero. However, alternating selection in high- and low-yield potential environments could be ineffective because only lines that do well in both are selected, rather than lines that may do very well in one of the environments but not in the other (Ceccarelli 1994).

If certain environmental factors predictably limit yield, but are not always observed in farmers' fields, managed stress nurseries may be useful (Atlin et al. 2001; Wade et al. 1996; Cooper et al. 1995, 1996). An advantage of these nurseries is that thousands of lines can be evaluated at once for their response to a specific stress (Bänziger et al. 1999). Nurseries with human-created stress factors, such as pathogen pressure, are useful for screening for disease resistance, but it is not clear whether they are efficient for abiotic stresses (Basford and Cooper 1998). In an Australian wheat breeding study, there was generally a good correlation between performance in managed stress nurseries and on-farm, but some lines which did well in the managed stress nurseries did poorly when grown on-farm (Cooper et al. 1995, 1996) Because low-input environments generally have multiple interacting environmental stress factors, designing managed stress environments that capture the key elements limiting yield may be difficult. It is challenging for both farmers and breeders to predict the likelihood of certain types of interactions (Bänziger et al. 1999), so the best way to guarantee breeding progress is to consistently work in the target environment. This means decentralizing the selection environments of a breeding program to include nurseries in all target environments.

Decentralized selection and participatory plant breeding

Decentralization of selection environments is critical to achieve good adaptation to marginal agricultural environments. Although decentralized selection and participatory plant breeding (PPB) are separate ideas, in practice it is difficult to separate the two (Ceccarelli et al. 2001). Having broadly adapted varieties justifies salaries and research expenses in a centralized system (Smith and Weltzien 2000). If breeding is to be decentralized, the same amount of resources are not available for each location. By enlisting the support and expertise of farmers, decentralized selection becomes possible. PPB is usually focused on making productivity gains in marginal areas and non-commercial crops, enhancing biodiversity and the conservation of genetic resources, developing germplasm for socially or economically disadvantaged groups and making breeding programs more cost effective through decentralization (Sperling et al. 2001). This is because of the contribution of farmers in terms of management and because their expertise helps ensure that breeding effort is not wasted on lines that are never adopted.

Farmers involved in PPB are researchers alongside the plant breeders. They set priorities for the breeding process, make crosses, screen germplasm, test selections in multiple environments and lead the seed multiplication and distribution process (Sperling et al. 2001). Certain farmers are known for their skill in seed selection and saving and are especially good to have on a participatory breeding team (Smith and Weltzien 2000). Working with a few enthusiastic and well trained farmers may improve the efficiency of a participatory breeding program as farmer experts can make selections for their entire community and spread the benefits of participatory plant breeding through seed exchanges or community plots (Gyawali et al. 2007; Sperling et al. 1993).

While the skill of farmers in selection and their ability to handle distinct populations is often questioned, in many projects farmers have proved to be extremely competent. In Syria, farmers were more effective than breeders at selecting superior barley genotypes in their own fields, and farmers were able to handle large numbers of entries, including segregating materials in early generations (Ceccarelli et al. 2001). Selection on-farm, using germplasm from local landraces, produced pure lines that out-yielded the landraces by 20% in farmers' fields (Ceccarelli 1996a). This was a productive short term strategy for improving yields in stressed environments, and these superior genotypes may eventually be used in crosses or blended to form heterogeneous improved landraces. It is important to consider the impact of selecting homogeneous lines from landraces on genetic diversity, and to have a long-term breeding strategy that maintains genetic diversity since this diversity is one of the primary reasons that landraces have yield stability (Ceccarelli 1996a). In the PPB program at ICARDA, farmer skills increased over several seasons, and they became active participants in suggesting new crosses and selection criteria. Farmers were enthusiastic about the potential of making selections from landraces and demanded that the program be extended to other crops in addition to barley (Ceccarelli et al. 2001).

Similarly, in a participatory rice breeding program in Nepal, farmers increased the effort and time they invested in breeding as the project started showing results (Sthapit et al. 1996). Joint selection by farmers and breeders have produced most of the successful lines from this program. A simple bulk breeding strategy is used, with bulk populations created by breeders and then grown in large populations by interested farmers. Lines selected by farmers have become popular and are spreading to other villages in the area (Gyawali et al. 2007).

In Rwanda, farmers identified as bean experts helped make selections on-station by ranking breeding lines for traits of interest and then taking 2–3 of these lines to grow in home gardens alongside their traditional mixtures. The lines identified by local farmers out-yielded the local mixtures 64–89% of the time, with an average increase in yield of 38%. In contrast, breeder selections out-yielded local mixtures 41–51% of the time on a national scale, with an average 8% increase in yield (Sperling et al. 1993). Six seasons later, 71% of the farmer selected varieties were still being grown; 32% were used to create new mixtures and 35% were incorporated into existing mixtures of farmer varieties. One of the most popular varieties from the formal sector had a 61% chance of still being grown six seasons later (Sperling et al. 1993). The farmers were aware of G×E interactions and were fairly accurate at predicting how certain lines would perform based on their observations on the research station. Sperling et al. (1993) found that by working with farmers, promising lines were selected earlier, more lines were selected and these varieties were better adapted to local conditions as shown by higher yields on-farm.

On-farm selection

Atlin et al. (2001) proposed three main strategies to improve on-farm selection: increasing selection intensity by using larger populations, increasing the genetic correlation between the target and selection environment by making sure the selection environment is highly representative of the target population of environments, and increasing the heritability of the traits of interest by improving the precision with which genotypes are evaluated. Further work is still needed to improve the precision of on-farm trials in highly variable environments (Ceccarelli et al. 2001).

Farmers often make selections after harvest, which excludes selection on plant traits such as decreased barrenness and improved stay-green characteristics under drought stress. For example, in a survey of Ecuadorian farmers, over 90% selected seeds for the next season after harvest based on ear and kernel appearance, without considering plant traits in the field (Almekinders et al. 2007). Field stratification and gridded selection where farmers select a certain percentage of plants and ears from each part of the field avoids this problem and increases gains from selection (Smith et al. 2001). Improved experimental designs, appropriate for farmer's conditions, can make it possible for farmers to achieve greater response to selection. These designs increase the ability of farmers to make selections based on genotypic differences without using complex statistical models (Bänziger et al. 1999; Cleveland et al. 1999). This includes training in methods of selection for correlated traits such as index selection (Riley 2003).

It is often difficult to get enough seed to distribute to several farmers for participatory selection from early segregating generations. Farmers can help to select promising line on-station in early generations, then selection can move to farmers' fields when enough seed is available (Witcombe et al. 1996). Networks of farmers evaluating the same lines could serve as replicates in a multilocational trial. With more locations, it is possible to identify promising entries in earlier generations when seed supplies are still limited (Witcombe et al. 2005b). Genotype by year by location interactions are often the largest component of variation, and this is best dealt with by replicating over locations and years (Atlin et al. 2001). Because of large genotype by year by location interactions, programs that combine the results of several farmers are more likely to be effective than selections by individual farmers (Bänziger et al. 1999). As the genes desired occur with greater frequency in the population, the phenotypic variance decreases, so visual selection is less effective and more replications are necessary. Products that come from programs with adequate replication and selection intensity tend to perform well across areas with similar environmental conditions (Atlin et al. 2001).

Formal breeding programs usually make many crosses, and only advance a small population of progeny from each cross for selection in later generations. In PPB, a more efficient strategy may be to carefully choose parents based on important characteristics, make a few crosses with these parents, and then increase the progeny population size for on-farm selection (Witcombe and Virk 2001). An unadapted parent might be used from a breeding program in another region or in a high-input system which has good disease and pest resistance, good quality or high-yield potential, but most of the parental germplasm should posses good adaptation to the target environment. In this way PPB can benefit from existing formal breeding programs and the potential wide adaptation of their products (Witcombe and Virk 2001), as well as the specific adaptation of landraces or varieties popular with local farmers.

Suneson (1956) proposed an evolutionary breeding method where diverse parent material was crossed and the resulting population was allowed to evolve through natural selection in cropping environments. Although initial yields were very low, 15 cycles of natural selection produced a population that was fairly high-yielding, with excellent yield stability and disease resistance. Improvements in yield related traits were most apparent in populations that were always grown either in favorable environments or in unfavorable environments so that directional natural selection was consistent (Allard 1999). Suneson stated that this method would produce new varieties at minimum cost with assurance of adaptability, and could be used to develop either superior populations or pure lines, through selection of individuals out of the population. The primary drawbacks to this method are the length of time required due to low selection intensity, and the inability to select for quality traits that do not confer a fitness advantage. Combined natural and artificial selection within a local environment may be a highly effective selection method, combining evolutionary and directional selection strategies (Murphy et al. 2005).

High selection intensity can be achieved through mass selection with large populations (Atlin et al. 2001). Farmers can use mass selection by walking through a population and removing plants they do not like, and/or selecting superior individuals and bulking the seed from these for the next generation. In a self-pollinated population, using multiple parents with diverse genetic backgrounds would increase the amount of genetic variation within the population. After several generations, individual plants in a bulk population would reach homozygosity, but the population would still be heterogeneous. Farmers could then select individual plants and produce pure lines of superior genotypes. The most successful pure lines could be bulked and grown as a blend, which would meet end-use marketing standards but still be capable of adaptation (Murphy et al. 2005). The choice of high end-use quality parents is particularly important for this method, as quality is difficult for farmers to asses if they grow a crop for the commercial market, and is not necessarily improved by natural selection (Murphy et al. 2005).

Some breeders claim that participatory breeding projects involve too much risk for farmers, however, farmers often have sophisticated risk management systems. Farmers use genetic variation to reduce their risks, planting both multiple varieties of the same crop and several different crops. They usually try new material on their worst land, thus any new variety first must grow in the poorest conditions. If a variety does well in the most marginal spot, it may be planted on more productive land. This contrasts with the tendency of researchers to put experimental plots on the best and most uniform ground (Sthapit et al. 1996). There is a greater risk that, through breeding for high-input systems, formal breeding programs will produce varieties that are seldom adopted because they do not work in marginal farming areas (Witcombe 1996). This has occurred in many areas because landraces either out-yield or have greater stability than modern varieties released by formal breeding programs. However, because farmers may exchange seeds frequently, and often do not have consistent strategies for selection, landrace germplasm may not have been subjected to continuous directional selection. A more conscious effort is needed to make full use of local knowledge and germplasm (Berg 1997).

An integrated system of plant breeding could use aspects of both formal and participatory breeding. Plant breeders would enhance useful germplasm, both from local landraces and promising introductions. Local communities do not always have access to the resources preserved in germplasm collections and genebanks, especially in developing countries. Establishing partnerships with plant breeders at public institutions is a potential mechanism for returning this germplasm to farm communities, and for making use of germplasm that has useful traits but is not local (Berg 1997). It would be more useful if this germplasm was first crossed to local materials, making enhanced populations which would then be released to farmers and selected on-farm (Berg 1997). Selection and evaluation would be done with or by farmers, with continued exchange of information and ideas (Riley 2003). On-station screening is still important in participatory projects, particularly for disease resistance and for traits which are difficult for farmers to assess (Smith and Weltzien 2000; Witcombe 1996). Breeders contribute their knowledge of genetics and statistics and farmers contribute their knowledge of the specific challenges of their farming system and of plant traits needed to overcome these challenges. When landraces are used as parents along with more modern varieties and there is maximal farmer input, the breeding strategy can complement in situ conservation by conserving favorable alleles in landraces that have been selected in that particular environment. PPB conserves and creates genetic resources in farmers' fields (Witcombe et al. 1996). It also increases the efficiency of selection by raising farmer's awareness and knowledge of genetic processes.

Participatory plant breeding in high-input environments

The relevance of participatory plant breeding to developed agricultural systems is often questioned. In such systems, the use of high-yielding modern varieties is the norm, and little if any of the farm output is for the farmers' own consumption. The use of off-farm inputs such as fertilizer and pesticides makes the growing conditions similar from farm to farm and region to region, so a few varieties may perform well over a wide spectrum of environmental conditions. However, there is concern over the increasing cost of inputs and growing interest in precision farming and sustainable agriculture. Organic and low-external-input farmers choose to limit their inputs and rely on biological processes for many reasons, including economic and environmental concerns. A growing number of these farmers are interested in participatory approaches to plant breeding (Desclaux and Hédont 2006). Highly productive areas have the potential for greater diversity in crop species and varietal diversity within species (Witcombe 1999). Breeding crops adapted to specific farming systems and ecological zones is important for these systems, and will require decentralized breeding programs that can address the needs of a diverse landscape.

For this to be successful, it is essential to have farmers actively participating in the research process. Farmer participation can take many forms, from helping to set research priorities and breeding goals, to selecting from diverse plant populations on their farms, to evaluating nearly finished varieties and giving feedback on varieties that have been released. Farmers in developed countries are as diverse in their interests and needs as farmers in developing countries, and there should be options for involvement at all stages of the breeding process. Many PPB projects are initiated in intermediate stress zones, and there are also examples of projects in low-stress environments where end-user preferences are fairly well defined. This is often to help farmers gain greater control of their seed supply, or to expand varietal diversity in areas which are predominantly monocultures (Sperling et al. 2001)

Farmers in industrialized agriculture rely largely on the private sector for the seed they plant each year, and to a lesser extent on public plant breeding programs. Wheat is one of the few species where the public sector is still the major source of new varieties. The process of relinquishing control of the seed supply began in the early twentieth century with the advent of hybrid corn. The process of creating hybrid corn is relatively simple, but the vast number of crosses and the record keeping required to keep track of them shut most farmers out of the process. After the professional field of plant breeding began to develop, breeders only worked with farmers if they needed more land for nurseries, and questioned whether farmers were capable of making crosses and keeping track of progeny lines (Fitzgerald 1993). Seed companies also pressured the USDA to stop encouraging farmers to save seed, claiming that farmers did not have the knowledge to save high quality seed or to work on breeding their own varieties (Fitzgerald 1993). Both traditional agricultural practices and modern participatory plant breeding projects have shown otherwise.

The assumption is that formal plant breeding programs serve high-yielding environments well, because many of the environmental risks and constraints of marginal environments are absent in more favorable environments or can be overcome with the application of agrochemicals such as fertilizers (Witcombe 1999). Many modern agricultural systems in high-yielding areas have adopted a monoculture of one or a few crops. This is often to simplify management and to increase profitability, both for farmers and breeding companies. Larger breeding programs can invest in larger testing nurseries and small-scale programs have limited ability to compete. Smaller testing networks have lower power to detect superior lines, so small-scale breeding programs have difficulty staying in business. This results in the consolidation of breeding programs and an economic incentive to release fewer, broadly adapted lines (Atlin et al. 2001). However, because of economic forces such as increased costs of inputs, including seeds, and stagnant or falling crop prices, many farmers are looking for alternatives to the commodity system. Diversity can provide buffering capacity for the system and for farm incomes, so many farmers are now looking to re-diversify and grow a range of higher-value products. For farmers growing for the commercial market, it is important to also involve processors and end-users in the process, and the development and distribution of varieties through PPB should be linked with market opportunities (Almekinders et al. 2007).

Some public sector programs are already highly participatory because they are funded by commodity commissions where farmers fund the research projects they feel are most relevant (Witcombe et al. 2005b). Breeders usually use varieties that have been widely adopted by farmers as parents in formal breeding programs, which is an established feedback mechanism where the popularity of a variety indicates farmer preference for that combination of traits (Witcombe et al. 2005b). However, in under-served environments, farmers may not have access to varieties that truly meet their needs and therefore they grow varieties that are not ideal. Using these varieties as parents might not address the true needs of the farmers growing them. In general, participatory plant breeding is most useful where meeting end-user quality concerns is challenging. In high productivity environments, the risk of a mismatch between environmental conditions on the breeding station and those in farmers field is less, but still exists when breeders use the recommended "best agronomic practices" which may not be feasible for farmers due to economic cost or other constraints (Witcombe et al. 2005b).

Distribution of varieties from participatory plant breeding

Even though most PPB projects are based on single farms or small communities of farmers, the resulting varieties may be useful to a much larger group of farmers who have similar environmental conditions on their farms. Although the varieties developed through PPB will have specific adaptation to certain environmental conditions, it is likely that they will also perform well on-farms that share similar climates and soil types. It is unlikely that they will spread as far as varieties specifically targeted to have wide adaptation in higher input systems (Morris and Bellon 2004), but it is possible that they will benefit many farmers in neighboring areas. Genetically variable materials such as multilines, mixtures, open pollinated varieties and synthetics make it more likely that they will be useful to farmers in environments that differ from the original selection environment (Smith et al. 2001). This is because the existing genetic diversity in these materials buffers performance when exposed to new environmental conditions and in the case of outcrossing they can continue to evolve. Farmers may distribute heterogeneous materials through the informal seed sector and these can continue to diversify and evolve (Berg 1997).

Local germplasm is still the primary, and sometimes the only, source of seed in developing countries (Almekinders and Elings 2001). Strengthening the seed exchange system and helping farmers distribute disease and weed-free seeds helps to make the products of plant breeding more widely available (Riley 2003). Establishing links with local NGOs or farm groups that know how best to distribute seed can help with more widespread distribution of a promising variety to farmers who have similar environmental constraints and production systems (Witcombe 1996). Using the informal seed sector and PPB instead of a formal approach to variety testing and release may put the products of plant breeding into farmers fields 5–6 years earlier. The informal seed sector can work equally well in high-input environments, as there is usually extra seed farmers can distribute (Witcombe 1999).

Formally releasing a variety can make the results of PPB available to many farmers outside the immediate area in which it was developed. If it were possible to release heterogeneous varieties, i.e., modern landraces, through the formal seed sector, the benefits of PPB could have an even greater impact. Unfortunately, many developing countries have variety release requirements similar to those in developed countries, which are designed to release a few widely adapted cultivars for intensive agricultural systems that can be made uniform through management practices (Witcombe 1996). This is often not appropriate for the diverse cropping systems and environmental stresses found in low-input agriculture, in either developed or developing countries. Genetic uniformity is usually not demanded by farmers, although the variety release process may require it.

For the formal varietal release process to work for participatory plant breeding, data on farmer perceptions and demand for seed need to be considered by varietal release committees, rather than almost total reliance on yield data from scientifically managed trials (Witcombe et al. 1996). Authorities may not feel that data based on farmer-managed trials is as precise or relevant as data produced on research stations, however, projects involving farmer assessment of varieties shows remarkable consistency in farmer rankings. In an example of participatory selection of rice in India, farmers ranked varieties similarly, even for traits such as tillering and panicle length that are harder to measure than yield, maturity and height.

This information was more relevant than the multi-locational trial data which was primarily measuring yield and had significant G×E interaction (Joshi and Witcombe 1996). Farmers agreed with each other and breeders on superior varieties, probably because farmers selected to participate had good seed selection skills, and breeders were aware of what traits were important to farmers (Sthapit et al. 1996).

If superior varieties are identified through PPB that are suitable for similar low-input farming systems and environments across a broader geographic range, intellectual property rights (IPR) may become an issue (Smith et al. 2001). The exchange of varieties between countries is often restricted because of the belief that IPR must be defended, but in most cases there are no plant breeders' rights in the countries involved (Joshi and Witcombe 1996). Farmers do not receive any royalties, although they do receive an indirect benefit through investment in further research and breeding and by recognition of the role of farmers in germplasm conservation and improvement (Sthapit and Jarvis 1999). The improved varieties themselves are generally the most useful compensation to the farmers. In some cases, it is possible to compensate farmers for their time, and to purchase the seed grown for the breeding program if the farmer does not want to keep it. Most public sector plant breeders do not get royalties or any financial gains from the development of their varieties, so there are no profits to be shared. PPB schemes would be problematic for private companies, because profits would need to be divided, and companies might worry about competitors taking varieties from fields if they were freely distributed. This is a major reason why public sector plant breeding programs are vitally important in underserved and marginal areas (Witcombe 1996).

Scientific relevance of participatory plant breeding

The perception exists that farmer participation in research interferes with objectivity, precision, control and repeatability of experiments so participatory methods may not generate predictive theories (Van de Fliert and Braun 2002). This perception discourages researchers from using participatory methods, even if examples of successful participatory projects exist (Morris and Bellon 2004). Reasons for not including farmers are often based on the assumptions that breeders have training that gives them an advantage in conducting selection and that complex systems of selection and thousands of entries are needed, which farmers are not equipped to handle (Witcombe et al. 2005b). Breeders may also feel that they require special training in participatory breeding methods, and such training is not usually part of a plant breeding training program (Morris and Bellon 2004). Using farmers' practices may complicate the experimental design and analysis (Haugerud and Collinson 1990).

However, breeders and farmers have complementary skills that can contribute equally to successful varietal development in complex environments. Breeders have training in selection theory and experimental design; farmers have valuable knowledge about environmental conditions, the performance of varieties on different parts of their farm and the characteristics that make a variety successful in their region. Participatory research does not have to compromise the scientific contribution of research when appropriate experimental designs and selection strategies are used. The choice of strategy depends on the logistical capabilities and end goals of both the breeding programs and the farmers. Many farmers already do their own kind of research in testing and adapting new ideas and technologies (Conroy et al. 1999). Involving farmers in the selection phase of plant breeding is not always essential, but in certain situations it becomes critical to have farmer input during selection. These situations include those where farmers trade-off multiple traits against each other and if desirable end-user qualities cannot easily be assessed with laboratory methods (Witcombe et al. 2005a).

Conclusion

The need to reduce external inputs in agricultural systems throughout the world is a challenge for both plant breeders and farmers. Including farmers in the research and breeding process will help to meet this challenge by developing varieties that are well suited to particular cropping systems and environments. Participatory plant breeding can benefit farmers in marginal environments in both developed and developing countries, and also those farmers who are seeking to lower their synthetic inputs for environmental or economic reasons. Because low-input systems are highly heterogeneous, there will need to be decentralization of the breeding process for it to be successful. The most efficient way to decentralize selection is to have breeding nurseries or populations on-farms in the target environment, and to recruit interested farmers to help set priorities, evaluate breeding lines or select promising types in early generations. While these methods do not compromise scientific integrity, it will take a shift in priorities and perspectives at many institutions. Many researchers in developing countries are already doing participatory research, but much more can be done to reach the full potential for this research in developed agricultural systems.

Acknowledgments The authors would like to thank two anonymous reviewers for their comments. This material is based upon work supported by the National Science Foundation under a Graduate Research Fellowship. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

References

Agrama HAS, Zakaria AG, Said FB et al (1999) Identification of quantitative trait loci for nitrogen use efficiency in maize. Mol Breed 5:187–195

Allard RW (1999) Principles of plant breeding, 2nd edn. Wiley, New York

Almekinders CJM, Elings A (2001) Collaboration of farmers and breeders: participatory crop improvement in perspective. Euphytica 122:425–438

Almekinders CJM, Thiele G, Danial DL (2007) Can cultivars from participatory plant breeding improve seed provision to small-scale farmers? Euphytica 153:363–372

Atlin GN, Cooper M, Bjørnstad Å (2001) A comparison of formal and participatory breeding approaches using selection theory. Euphytica 122(3):463–475

Bänziger M, Cooper M (2001) Breeding for low-input conditions and consequences for participatory plant breeding: examples from tropical maize and wheat. Euphytica 122(3):503–519

Bänziger M, Lafitte HR (1997) Efficiency of secondary traits for improving maize for low-nitrogen target environments. Crop Sci 37:1110–1117

Bänziger M, Edmeades GO, Lafitte HR (1999) Selection for drought tolerance increases maize yields across a range of nitrogen levels. Crop Sci 39:1035–1040

Basford KE, Cooper M (1998) Genotype × environment interactions and some considerations for wheat breeding in Australia. Aust J Agric Res 49:153–174

Berg T (1997) Devolution of plant breeding. http://www.idrc.ca/books/focus/833/berg.html

Bertin P, Gallais A (2000) Genetic variation for nitrogen use efficiency in a set of recombinant maize inbred lines I. Agrophysiological results. Maydica 45:55–66

Brancourt-Hulmel M, Heumez E, Pluchard P, et al (2005) Indirect vs. direct selection of winter wheat for low-input or high-input levels. Crop Sci 45:1427–1431

Ceccarelli S (1996) Adaptation to low/high-input cultivation. Euphytica 92:203–214

Ceccarelli S (1996b) Positive interpretation of genotype by environment interactions in relation to sustainability and biodiversity. In: Cooper M, Hammer GL (eds) Plant adaptation and crop improvement. CAB International, pp 467–486

Ceccarelli S, Grando S (1999) Decentralized participatory plant breeding. Ileia Newsletter December:36–37

Ceccarelli S, Grando S, Bailey E et al (2001) Farmer participation in barley breeding in Syria, Morocco and Tunisia. Euphytica 122(3):521–536

Ceccarelli SS (1994) Specific adaptation and breeding for marginal conditions. Euphytica 77:205–219

Cleveland DA, Soleri D, Smith SE (1999) Farmer plant breeding from a biological perspective: implications for collaborative plant breeding. CIMMYT, economics working paper no 10

Conroy C, Sutherland A, Martin A (1999) Conducting farmer participatory research: what, when and how. In I.F. Grant and C. Sear (eds.). Decision Tools for Sustainable Development. Natural Resources Institute, Chatham, U.K. p. 12–45

Cooper M, Woodruff DR, Eisemann RL et al (1995) A selection strategy to accommodate genotype-by-environment interaction for grain yield of wheat: managed-environments for selection among genotypes. Theor Appl Genet 90:492–502

Cooper M, Brennan PS, Sheppard JA (1996) Positive interpretation of genotype by environment interactions in relation to sustainability and biodiversity. In: Cooper M, Hammer GL (eds) Plant adaptation and crop improvement. CAB International, pp 487–511

Desclaux D (2005) Participatory plant breeding methods for organic cereals. In: Lammerts Van Bueren ET, Ostergard H (eds), Proceedings of the COST SUSVAR/ECO-PB workshop on organic plant breeding strategies and the use of molecular markers, Driebergen (NK), 17–19 January 2005, pp 17–23

Desclaux D, Hédont M (eds) (2006) Proceedings of the ECO-PB workshop on participatory plant breeding: relevance for organic agriculture? Workshop held in Domaine de la Besse, France, 11–13 June 2006, European Consortium for Organic Plant Breeding, Institut Technique de L'Agriculture Biologique, Paris, France

Fitzgerald D (1993) Farmers deskilled: hybrid corn and farmers' work. Technol Cult 34(2):324–343

Gyawali S, Sunwar S, Subedi M et al (2007) Collaborative breeding with farmers can be effective. Field Crops Res 101:88–95

Haugerud A, Collinson MP (1990) Plants, genes and people: improving the relevance of plant breeding in Africa. Expl Agric 26:341–362

Joshi A, Witcombe JR (1996) Farmer participatory crop improvement II. Participatory varietal selection, a case study in India. Expl Agric 32:461–477

Morris ML, Bellon MR (2004) Participatory plant breeding research: opportunities and challenges for the international crop improvement system. Euphytica 136:21–35

Murphy KM, Lammer D, Lyon SR et al (2005) Breeding for organic and low-input farming systems: an evolutionary-participatory breeding method for inbred cereal grains. Renewable Agric Food Syst 20(1):48–55

Murphy KM, Campbell KG, Lyon SR et al (2007) Evidence of varietal adaptation to organic farming systems. Field Crops Res 102:172–177

Presterl T, Seitz G, Landbeck M et al (2003) Improving nitrogen-use efficiency in European maize: estimation of quantitative genetic parameters. Crop Sci 43(4):1259–1265

Riley KW (2003) Decentralized breeding and selection: tool to link diversity and development. http://www.idrc.ca/library/document/104582/riley.html

Smith M, Weltzien E (2000) Scaling-up in participatory plant breeding. In: Almekinders C, De Boef W (eds) Encouraging diversity. Intermediate Technology Publications, pp 208–213

Smith ME, Castillo GF, Gomez F (2001) Participatory plant breeding with maize in Mexico and Honduras. Euphytica 122(3):551–565

Sperling L, Loevinsohn ME, Ntabomvura B (1993) Rethinking the farmer's role in plant breeding: local bean experts and on-station selection in Rwanda. Expl Agric 29:509–519

Sperling L, Ashby JA, Smith ME et al (2001) A framework for analyzing participatory plant breeding approaches and results. Euphytica 122:439–450

Sthapit B, Joshi KD, Witcombe JR (1996) Farmer participatory crop improvement. III. Participatory plant breeding, a case study for Nepal. Expl Agric 32:479–496

Sthapit BR, Jarvis D (1999) Participatory plant breeding for on-farm conservation. Ileia Newsletter December:40–41

Suneson CA (1956) An evolutionary plant breeding method. Agron J 48:188–191

Ud-Din N, Carver BF, Clutter AC (2004) Genetic analysis and selection for wheat yield in drought-stressed and irrigated environments. Euphytica 62(2):89–96

van de Fliert E, Braun AR (2002) Conceptualizing integrative, farmer participatory research for sustainable agriculture: from opportunities to impact. Agric Human Values 19:25–38

van Ginkel M, Ortiz-Monasterio I, Trethowan R et al (2001) Methodology for selecting segregating populations for improved N-use efficiency in bread wheat. Euphytica 119(1):223–230

Wade LJ, McLaren CG, Samson BK et al (1996) The importance of environmental characterization for understanding genotype by environment interactions. In: Cooper M, Hammer GL (eds) Plant adaptation and crop improvement. CAB International, pp 549–562

Witcombe JR (1996) Participatory approaches to plant breeding and selection. Biotechnol Dev Monit 29:26–32

Witcombe JR (1999) Do farmer participatory methods apply more to high potential areas than to marginal ones? Outlook Agric 28(1):43–49

Witcombe JR, Virk DS (2001) Number of crosses and population size for participatory and classical plant breeding. Euphytica 122(3):451–462

Witcombe JR, Joshi A, Joshi KD et al (1996) Farmer participatory crop improvement. I. Varietal selection and breeding methods and their impact on biodiversity. Expl Agric 32:445–460

Witcombe JR, Gyawali S et al (2005a) Participatory plant breeding is better described as highly client-oriented plant breeding. II. Optional farmer collaboration in the segregating generations. Expl Agric 42:79–90

Witcombe JR, Joshi KD, Gyawali S et al (2005b) Participatory plant breeding is better described as highly client-oriented plant breeding. I. Four indicators of client-orientation in plant breeding. Expl Agric 41:299–319