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Developments in breeding cereals for organic agriculture

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Abstract The need for increased sustainability of performance in cereal varieties, particularly in organic agriculture (OA), is limited by the lack of varieties adapted to organic conditions. Here, the needs for breeding are reviewed in the context of three major marketing types, global, regional, local, in European OA. Currently, the effort is determined, partly, by the outcomes from trials that compare varieties under OA and CA (conventional agriculture) conditions. The differences are sufficiently large and important to warrant an increase in appropriate breeding. The wide range of environments within OA and between years, underlines the need to try to select for specific adaptation in target environments. The difficulty of doing so can be helped by decentralised breeding with farmer participation and the use of crops buffered by variety mixtures or populations. Varieties for OA need efficient nutrient uptake and use and weed competition. These and other characters need to be considered in relation to the OA cropping system over the whole rotation. Positive interactions are needed, such as early crop vigour for nutrient uptake, weed

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competition and disease resistance. Incorporation of all characteristics into the crop can be helped by diversification within the crop, allowing complementation and compensation among plants. Although the problems of breeding cereals for organic farming systems are large, there is encouraging progress. This lies in applications of ecology to organic crop production, innovations in plant sciences, and the realisation that such progress is central to both OA and CA, because of climate change and the increasing costs of fossil fuels.

Keywords Direct and indirect selection · Variety testing · Participatory plant breeding · Wide and specific adaptation · Crop diversity · Organic agriculture

Abbreviations

ABDP	Association of Biodynamic Plant Breeders
AM	Arbuscular Mycorrhizae
BFCA	Breeding programmes For Conventional Agriculture
BFOA	Breeding programmes For Organic Agriculture
CA	Conventional Agriculture
DON	Deoxynivalenol
DUS	Distinctness, Uniformity and Stability
FHB	Fusarium Head Blight
GEI	Genotype × Environment Interaction
GMO	Genetically Modified Organism
GxL	Genotype by Location interaction
HMWGS	High Molecular Weight Glutenin Sub-units
HY	High Yielding
IFOAM	International Federation of Organic Agriculture Movements
IPR	Intellectual Property Rights
LY	Low Yielding
MAS	Marker-Assisted Selection
NUUE	Nutrient Uptake and Use Efficiency
OA	Organic Agriculture
OPB	Organic Plant Breeding (programmes within OA)
PBR	Plant Breeders Rights
PPB	Participatory Plant Breeding
QTL	Quantitative Trait Loci
TKW	Thousand Kernel Weight
VCU	Value for Cultivation or Use

Cereal breeding: needs for organic production

The rapid development of conventional agriculture (CA) over the last 60 years, exemplified by a massive increase in cereal grain production, has been dependent upon a large and continuous investment in plant breeding. Across Europe, breeders have produced hundreds of pedigree line varieties during this time, all adapted to production within CA, and often successful, individually, over relatively large areas. Such performance has been dependent on large-scale, fossil fuel-based inputs that have helped to limit environmental variability. However, climate change coupled with rising oil prices is now beginning to affect developments in conventional breeding.

Over this same time period, organic agriculture (OA) has developed much more slowly, hindered by a lack of breeding investment on the one hand, and by the problems of coping with much greater environmental variability on the other. However, the greater dependence of OA on ecological rather than chemical approaches is opening up many different and novel ways, potentially, of dealing with both increasing variability related to climate change, and the costs of fossil fuel-based control of the environment.

OA relies on measures that stimulate the resilience and self-regulating ability of the farming system, e.g. by enhancing biodiversity (at the farm, crop and genetic level) and soil fertility with a high level of organic matter and wide crop rotation, and by closing the nutrient cycle as much as possible (e.g. Mäder et al. 2002). This approach implies that all parts of the agricultural system including food, water and energy, are regarded as a whole and interactions and feedback among all parts are considered in optimising that whole. The holistic approach attempts to maintain the integrity of all living entities, such as soil, plants, animals, farm, landscape and ecosystem (Verhoog et al. 2003). However, because there are fewer opportunities for immediate compensation or alleviation of abiotic and biotic stress in OA compared to CA, the need for adaptation of varieties to varied environmental conditions is currently more important in OA. Furthermore, because organic farming systems are necessarily adapted to their localities, there is a wide diversity among them, and indeed among individual farms. This requires therefore, a fine-grained adaptation of the crop plants (and animals) used on individual farms. It is also important to consider the relationship between the actual crop, its pre- and post-crop and the overall contribution and impact of the actual crop on the whole rotation, including the livestock element. This need to consider choice of cereal species and variety in the context of the whole farming system should also have an impact on the breeding approach.

These needs for OA cannot be achieved easily by centralised breeding. Although OA is well established in most European countries, breeding specifically for organic farming systems has received little attention. In this paper, we argue that there is a need for different approaches to plant breeding to improve organic farming systems and organic product quality relative to current conventional practice and that this will differ for different markets. We concentrate on cereals, particularly wheat, because it is the most important single crop among, currently, nearly 900,000 ha of organic cereals in Europe. Organic cereals are not only important for feed and food, but also for their contribution to good soil structure and soil fertility in a sound organic farming system. Cereals also deliver straw as a vital component for organic animal housing systems and for composting farmyard manure.

Within this context, we outline the current structure of OA in Europe and the current status of cereal breeding for OA. This leads on to a consideration of appropriate breeding strategies and the characteristics required within those strategies. A brief discussion of breeding techniques is followed by some final comments on the future of cereal breeding for OA.

Organic agriculture defined by three market types that need different solutions

In detail, it is likely that there are almost as many organic farming systems as there are organic farmers. This arises because of the problems that individuals face in adapting the framework of organic farming (Council Regulation (EC) 2007, No 834/2007) to the environmental variables of an individual farm. In this sense, the ideal breeding approach would be a specific programme for each farm. However, to simplify this view, we need to use broader categories, among which the following, based on the market approach for each farm, is helpful for this review (Table 1):

- Global commodity farming, by larger scale farms and farm associations which produce either feed under relatively low-input conditions, or grain for industrialized bakeries requiring high levels of protein for standardized baking procedures. Modern cereal varieties, with relatively high levels of nitrogen input are used to meet the homogeneity and the specific quality standards combined with high productivity. The farm objectives are predominantly oriented to large markets.
- Regional market farming, on both large and small-scale farms, allowing a more variable product, using both modern and older or regional varieties. The farm objectives here are largely ecological, with a major emphasis on minimising inputs.
- Local market farming, mainly by small-scale farmers on mixed farms who regard the crop, farm landscape and society as a whole; they are more likely to use local or conservation varieties. The grain is produced for artisanal bakeries prepared to adjust their baking process according to the variation in flour quality. The farmer's objectives are more social.

In the Table, the kinds of breeding strategy and their application to the three generalised forms of OA relate to the three approaches to naturalness described by Verhoog et al. (2003), see also Lammerts van Bueren and Struik (2004). The scheme indicates a progression based on the form of selection, moving from 'natural' selection in populations (no intervention), to farmer participation (mass selection for specific characters or for site), to farmer plus breeder, to breeder alone. We would expect this progression to be associated with a progression from the local market to the global market production system, although this might easily be upset by unusual success, or failure, at a particular point in the progression. In practice, a wide range of combinations exists and should be promoted in order to enhance interactions among all players. Promoting diversity and increasing the number of breeders will enhance the diversity of genetic material.

Table 1 General characteristics of cereal breeding trends for a continuous range of organic farming systems

Classification of organic farming system/product	Orientation of breeding	Genetic resources	Selection methods	Priority of traits	Characteristic crop structure	Naturalness component in focus
Market: global commodity *Driver*: economics *Product*: uniform	BFCA[a] BFOA OPB	Advanced breeding lines and varieties	Centralized, wide adaptation, special characters	Industrial quality traits, high grain yield, targeted agronomic traits	UPOV approved lines and variety mixtures	Non-chemical approach
Market: regional *Driver*: agroecology *Product*: more variable	BFOA OPB	Advanced breeding lines and former regional varieties	Decentralized, wide and local adaptation	Artisan and regional quality traits, agronomic robustness	UPOV approved lines and variety mixtures, populations	Agroecology approach
Market: local *Driver*: social *Product*: crop, livestock, farm, landscape, society as a whole	OPB including evolutionary-breeding, maintenance of genetic diversity and cultural heritage	Locally adapted genotypes; conservation varieties and landraces	PPB, local adaptation, natural selection	Multifunctional crop/interspecific crop populations integrated with local environmental needs. environmental flexibility and robustness	Populations, farmers own selections	Integrity of life approach

[a] BFCA, breeding for conventional agriculture; BFOA, breeding for organic agriculture (in conventional organisations); OPB, organic plant breeding (in organic organisations); PPB, participatory plant breeding

A large number of cereal varieties is available across Europe from conventional breeding programmes, some of which will fulfil partly the requirements of OA. However, better adapted varieties are needed to optimise OA systems and to comply with the required product quality under low-input, OA conditions, particularly for regional and local marketing (Rastoin 2006). The traits required reflect the fundamental differences between OA and CA in the management of soil fertility, weeds, diseases and pests, together with the different demands on product quality and yield stability under organic conditions (Lammerts van Bueren et al. 2002).

Current status of cereal breeding for organic agriculture

Currently, most organic farmers depend on modern varieties bred for conventional agricultural systems. However, because of the European Organic Seed Regulation (EC 1452/2003), the use of organic seeds is becoming compulsory. Overall, the varieties used in OA originate from three different sources:

(1) Breeding programmes for conventional agriculture (BFCA). Organic farmers select from among the currently available varieties those that perform well enough under organic conditions. BFCA is common in the global marketing model (Table 1).
(2) Breeding programmes for organic agriculture (BFOA). Such breeding programmes often start with specific crosses for OA, but for economic reasons, selection in the first generations (F1-F5) is conducted under regular (conventionally managed) conditions. In later stages of the breeding process, promising lines are tested under organically managed conditions. BFOA is useful across all three organic farming models.
(3) Breeding programmes within organic agriculture (OPB), which means that all breeding steps are executed under organic conditions with selection and propagation techniques that comply with organic principles. These programmes cover a range from breeder-driven to farmer-driven activities. Among the farmers there are those who use their own selections originating from older (regional) varieties or landraces. OPB may be most applicable in the local market model of OA, but also for regional markets.

BFOA takes advantage of the fact that, under specified environmental conditions, the expression of several traits can be highly correlated between CA and OA (Oberforster et al. 2000; Oberforster 2006; Przystalski et al. 2008). This holds true for yield where CA is practised at low-input levels, e.g. with limited nitrogen supply and without the application of fungicides. For highly heritable traits where selection can be imposed in the early stages on a single plant or small plot basis, indirect selection, i.e. selection in an environment different from the target environment, can even lead to higher selection efficiency than direct selection (Hill et al. 1998). Examples for highly heritable traits in wheat in some conditions are: tillering capacity, early vigorous growth, earliness (heading date), disease resistance, culm length, spike-length, other morphological characteristics and grain features such as thousand kernel weight (TKW). A few varieties have already been released from BFOA programmes including Naturastar in Germany (Kempf 2002) and several varieties in Austria (Bundesamt für Ernährungssicherheit 2007; Löschenberger et al. 2008).

The selection strategies for low-input conditions imposed by Hänsel and Fleck (1990) and Spanakakis and Röbbelen (1990) have led to varieties adapted to OA in several European countries together with new conventional varieties that perform best in OA in the US (Carr et al. 2006).

OPB uses exclusively organic conditions and can be referred to as direct selection (see Murphy et al. 2007). Major differences from the CA environment are the limited level and less controlled nitrogen availability to the plant, weed competition, less pressure from several diseases (e.g. powdery mildew, *Septoria tritici* in wheat), but additional diseases (e.g. bunts and smuts). Furthermore, the relative importance of specific traits differs between CA and OA (yield and quality). There is a small number of breeders who are conducting OPB programmes for cereals, mainly in Switzerland, Germany and Hungary. For example, ABDP (Association of Biodynamic Plant Breeders) are developing low-input cereal varieties for organic farming with more regional adaptation. Some 12 varieties have been registered by them (Kunz 2007; Bundessortenamt 2007; Bedő and Kovács 2006) The advantages of these varieties are most pronounced in environments with low N availability (Heyden 2004). Such varieties are mostly taller and have lower harvest indices and higher grain protein content than varieties from BFCA programmes.

New genetic material from other farming systems has to be introduced continuously into OA in order not to lose genetic variability (Carr et al. 2006). The highest possible variability of varieties for OA can be assured by extending the choice to varieties developed within all three breeding strategies, BFCA, BFOA and OPB. After sound testing under organic conditions, organic farmers can then choose either specifically or widely adapted varieties for particular situations. Considering the current multiplication acreage of organic seed in Europe as a reflection of farmer's demand, we can conclude that modern rather than old varieties are the best choice currently for production in OA. Furthermore, the development costs of any variety for the market requires a minimum quantity of seed production, which implies that widely adapted varieties are more likely to be successful.

Breeding strategies for organic cereal varieties and crops

The diversity of agro-ecological and climatic conditions together with different cultural practices in OA represent a considerable challenge for breeders (Murphy et al. 2005). Breeding for OA needs specific strategies that utilise genetic diversity to support or enhance the wide-ranging conditions and farmer practices. These aspects have seldom been investigated in the context of breeding cereals for OA in Europe, but some lessons can be drawn from experiments in various low-input/stressed compared to conventional/non stressed environments.

Breeding for OA must be considered in the context of whole system management, through rotation and other agronomic practices, that can help to buffer the system and its components against abiotic and biotic variability and stress. In this sense, selection of crops for use in OA should be driven by the needs of the whole system as well as the end use. For example, crop nutrition and weed competition can both be helped by the structure of the rotation together with appropriate agronomic interventions. Crop varieties should then be selected according to different priorities in the farming system. Difficult challenges will no doubt arise because of interactions or trade-offs between different selection criteria. For example, a narrow approach focused on weed control may be disadvantageous if it neglected other important criteria such as disease control. A more holistic approach in which there is integration of different system components, perhaps including selective competition among the plant components, is highly desirable.

Diversity is the basis of natural selection and evolution and was the norm in agriculture until the last hundred years or so when modern genetics and plant breeding enabled farmers and end-users to exploit the benefits of uniformity. However, biological sciences continue to reveal the multiple advantages of diversity in all aspects of agricultural production. For example; the work of Tilman's group in the USA illustrates the basic principles for natural systems that are highly relevant to agricultural systems (Tilman et al. 2006). Other reviews include Finckh and Wolfe (2006). Most important is the need for recognition of the urgency and importance of new approaches to breeding based on using diversity – and that space has to be made for these within the current regulatory frameworks.

Considering these and other aspects, we recognise a number of key questions for the development of strategies appropriate to breeding for organic agriculture:

(1) Which genetic resources are appropriate?
(2) Should genotypes be selected for wide or specific adaptation?
(3) Stability of performance over time?
(4) What are the most suitable selection environments?
(5) Can decentralised approaches add to centralised breeding?
(6) Can participatory approaches add to centralised breeding?
(7) What is the most appropriate crop structure?

A further major question, on determining the selection criteria to be used, is dealt with in the following main section.

Genetic resources

In addition to the resources available from modern agriculture, there is a need to identify appropriate genetic resources among the older varieties or landraces either for direct use or as potential parental lines in breeding programmes for better adapted varieties (Hoisington et al. 1999; Hammer and Gladis 2001; Lammerts van Bueren et al. 2005b). Evaluating and exploiting accessions from genebanks can be of use because characteristics required for organic, low-input farming might have disappeared by selection under modern, high-input conditions, such as low-input tolerance and deep or intensive root architecture. Many non-profit organisations dealing with in situ conservation of genetic resources maintain their populations under organic conditions (Negri et al. 2000).

However, despite the availability of large amounts of genetic resources, their real use in organic farming is still limited. More than 140,000 wheat accessions are held in the major genebanks including 95,000 maintained in Europe alone (Faberova and Le Blanc 1996). This includes populations, landraces or local cultivars, varieties and wild relatives, but only 1–2% are used in farming practice overall.

Although the importance and utilization of plant genetic resources is underlined in all strategic papers related to OA, it is difficult to find research related to their practical use, much as in conventional agricultural production and plant breeding. One of the major reasons is the difficulty in evaluating genebank accessions with widely differing phenotypes such as flowering dates, heights and growth morphologies, and quality features. The other main factor is the loss of locally adapted traditional genotypes or landraces, and that most of the ex situ conserved material is not adapted to modern farming conditions. These differences make accurate assessments and comparisons difficult, if not impossible. Even if useful characteristics can be identified, the difficulty of transferring the characteristics to a cultivated species, and the time involved, are considerable. For genetic resources to be a major factor in plant improvement, new methods must be directed to their analysis and transfer into improved varieties. These include physiological measures of plant parameters which are now becoming more exact, rapid, and applicable to large populations, as well as molecular markers (see below). Such advances should allow the more accurate determination of new sources of useful characteristics, or, may, indeed, result in new varieties for organic farming.

The situation is different with old varieties and under-utilised species (Padulosi et al. 2002). Several old varieties have been reintroduced into (organic) breeding and farming practice, and several under-utilized species are succeeding as speciality crops in different regions in Europe. The cultivation of spelt, emmer and einkorn is increasing together with production of, for example, hull-less barley, naked oats and some other “curiosities” (Grausgruber and Arndorfer 2002; Kovács and Szabó 2006; Veisz 2006; Láng 2006). Such developments will be helped further by appropriate pre-breeding of relevant species and their inter-crosses.

Wide or specific adaptation

Target environments can be sub-divided into homogeneous subregions in which genotype by location (GxL) interactions are minimized and within-subregions genetic variances are increased (Comstock and Moll 1963; Ceccarelli 1989; Atlin et al. 2000a). However, the dilemma is that selecting the best genotype over the undivided region may or may not be more efficient than selecting the different genotypes which are best adapted to each subregion. Furthermore, the approach to selection should be considered in relation to the global, regional and local market categories noted above and corresponding to the commercialisation of varieties from widely to specifically adapted.

Atlin et al. (2000b) considered the effect of subdividing environments into sub-regions for the breeding of (sub-)regionally adapted varieties. They showed that subdivision will increase the response to selection only if GxL is large relative to the genetic variance and if a substantial (>30%) part of GxL is due to genotype × sub-region interaction. The efficiency will also depend on the ability to define highly appropriate and meaningful subregions which was not systematically the case in the previous studies. A thorough study of GxL interaction over many environments and many years is necessary to obtain efficient subregions definition as illustrated for sunflower on-farm testing (de la Vega et al. 2001; de la Vega and Chapman 2006).

Genotype × subregion interaction depends on the range of both genetic and environmental variation under study. Increasing the range of environments to severe stress conditions is more likely to result in GxL having a major contribution in the observed variation (Ceccarelli 1989). Reviewing a large set of cereal literature that supports the claim for selection of widely adapted genotypes, Ceccarelli indicated that widely adapted genotypes are the best performers in only a narrow range of environments and usually not including severe stresses. To adapt these results to breeding for OA, it is necessary to identify the range of targeted environments and to carry out experiments in different OA environments assessing heritability, genetic correlations across environments and the different variance components. Moreover, it might be more appropriate to define the sub-regions including farming practices such as livestock on farm or not. It is also important to recognise that climate change is likely to extend environmental variation, increasing the need for adaptation.

Stability over time

Because varieties in OA should have a broad range of adaptability to cope with a large variability in environmental conditions, they need to have various 'buffering capacities' to maintain performance. This means that varieties for OA must not have any severe local weakness in any trait relevant for growth and productivity. Increase and stability of productivity of a wheat variety depend on its individual buffering. In fact, wheat has a high degree of buffering capacity within the genotype (Udall and Wendel 2006), because of its allohexaploid genome, and this can be selected for. There is also likely to be variability among characters that have no detectable effect on features associated with DUS criteria (Distinctness, Uniformity, Stability), VCU (Value for Cultivation and Use) or other easily observable characters. These could also contribute to the buffering capacity of a variety over space and time. There is no doubt, however, that a deliberate approach to introducing genetic variation into the crop (see 'crop structure' below) will have greater value in this direction.

Under CA, individual buffering can also be seen as the varieties' ability to exploit favourable conditions in the environment (Tarakanovas and Ruzgas 2006). Spanakakis and Röbbelen (1990) proposed, therefore, the selection of "combination type" varieties. These varieties are able to react flexibly by adjusting their yield components to the environment, for example, through a high tillering capacity, variable numbers of grains per ear and high grain weight. Also Le Gouis et al. (2000) and Saulescu et al. (2005) proposed simultaneous selection under diverse input regimes in order to favour varieties for low-input management systems. Alternating selection between high and low yielding environments was the most effective way to develop wheat germplasm adapted to environments where intermittent drought occurs (Kirigwi et al. 2004).

Choice of selection environments: organic versus conventional

To develop varieties better adapted for organic farming systems, an important question is the choice of selection environment for organic plant breeding programmes, but little research has been done on this issue. As described above, plant breeders have developed different strategies (Hill et al. 1998), such as choosing an environment with optimal conditions for the crop or choosing the target environment (e.g. an organic environment or a stressed environment) for the crop, or even an alternation of these two. However, it still remains unclear whether the differences between conventional and organic growing systems are large enough to justify, economically, breeding and official variety testing in both environments, rather than the simpler inclusion of additional characteristics of relevance only for organic farming into conventional breeding and tests.

From a theoretical basis, Falconer (1952) established, more than 50 years ago, that direct selection, i.e. in the target environment, is almost always more efficient than indirect selection.

The theoretical framework of quantitative genetics (e.g. Falconer and MacKay 1996) can provide guidelines to optimise the selection strategy. Thereafter, the selection response from indirect selection (e.g. in conventional conditions) can be compared with direct selection (e.g. organic conditions). The relative efficiency of indirect selection is then:

$$\mathrm{RE} = \frac{\mathrm{CR}}{\mathrm{DR}} = r_{\mathrm{A(X,Y)}} \frac{h_{\mathrm{Y}}}{h_{\mathrm{X}}}$$

with CR, the correlated response on a given trait in environment X resulting from selection of the same trait in environment Y, DR the direct response in environment X, $r_{A(X,Y)}$, the additive genetic correlation between environments X and Y and h_X (resp. h_Y) the narrow sense heritability in environment X (resp. environment Y). Using this approach, Murphy et al. (2007) evaluated 35 winter wheat advanced breeding lines in paired organic and conventional plant breeding nurseries. They found significant genotype × farming system interaction at 4 of 5 locations and very low to moderate genetic correlation between organic and conventional systems, leading to the conclusion that indirect selection in conventional systems was less efficient than direct selection in organic systems for identifying the best genotypes for the latter. Important interactions were also found by Legzdina et al. (2007) for yield in barley genotypes grown under organic and conventional conditions. Using the same approach in winter wheat, Brancourt-Hulmel et al. (2005) as well as Sinebo et al. (2002), found that the relative efficiency of indirect selection in conventional high-input conditions over the efficiency of direct selection in different low-input environments ranged from 0.35 to 0.99 in barley. It is also possible to make an a posteriori assessment of indirect versus direct selection: Ceccarelli and Grando (1991) evaluated more than 800 barley breeding lines in 8–10 environments classified as low yielding (LY) or high yielding (HY). The best lines selected in LY always outperformed the best lines selected in HY when evaluated in LY.

Contrary to what is usually acknowledged, all these studies, as well as Ceccarelli (1989) in a review, pointed out that genetic variances or heritabilities were not always lower in stressed environments. This together with the frequent low genetic correlation between a given trait assessed in a stress/low-input/organic environment and the same trait in conventional/high-input environment provide a possible explanation for the poor efficiency of the indirect selection experiments reviewed here.

The question of the importance of genotype by farming system interaction and of the correlation between genotype performance in OA and CA have also been studied using variety testing trials that have recently become available in several European countries. Research projects have been started to gain more insight into this question and results have been analysed by Przystalski et al. (2008). Genetic correlations between the two systems were described for a range of traits observed in variety trials in conventional and organic growing systems that had values in the range 0.8–1.0. However, this does not imply that the top ten varieties would be the same for both systems. They concluded, therefore, that combining information from conventional and organic trials would be the optimal approach for selecting varieties for OA. Additional trials have been reported elsewhere; Schwaerzel et al. (2006) concluded for Swiss VCU tests that winter wheat varieties behaved in a similar way in organic farming and extensive conditions. On the contrary, Baresel and Reents (2006) in a study of a large number of German variety trials under high-input, low-input and organic growing conditions, found substantial differences in ranking of the varieties.

In a Danish study of genotype-environment interactions for grain yield involving conventional and organic farming systems including 72 spring barley varieties and 17 combinations of location, growing system and year, choice of variety was found to be as important a factor for grain yield as other factors in the management (Østergård et al. 2006). Specifically, the genotype × environment interaction contributed about 35% of the total variation among varieties in conventional or well fertilised organic environments but as much as 80% for those growing in the extreme organic environments without application of manure. This supports the idea that genotype-environment interactions are most important in extreme environments.

Thus the likelihood of obtaining significant correlations of variety performance under organic and conventional conditions will depend, partly, on the nature of the systems under consideration, and partly, on the interactions of those systems with the environmental conditions during the period of observation. A compromise would be to include selection under organic conditions in a later stage of the breeding process, e.g. F6, after selecting first under 'regular' conventional conditions (Löschenberger et al. 2008, this issue).

Centralised versus decentralised breeding

The term "decentralised" is synonymous with "in situ" or "on farm" and refers to direct selection within the target environment (see below). Decentralised breeding allows a better fit to the target environment than breeding only under organic conditions in “centralised” or “ex-situ” experiments at a research station. Decentralised selection is a powerful methodology to fit crops to the physical target environment and to the cropping system. However, crop breeding based on decentralised selection can miss its objectives if it does not utilize farmers’ knowledge of the crop and the environment, because it may then fail to fit crops to the specific needs and uses of farmer’s communities. As a consequence, decentralised selection is often associated with participatory selection. These approaches are more appropriate to the specific needs of Regional market farming or Local market farming as defined earlier.

Participatory approaches

Participatory plant breeding (PPB) can be defined as the involvement of several partners (e.g. farmers, traders, consumers, breeders, researchers) in the selection process and is based on the complementarity of skills and knowledge of each partner.

As organic systems are characterized by a wide range of environments and management systems and by a diversity of potential markets (see Table 1), a more direct involvement of larger numbers of actors can raise more issues for crop characterisation than may be considered in conventional breeding (Desclaux et al. 2008). Such issues may include ease of harvest and storage, taste, cooking and nutritional qualities, rate of crop maturity, weed competitiveness, suitability of crop residues as livestock feed and harmony in the plant growing process (Morris and Bellon 2004).

In practice, three kinds of participation are usually distinguished: consultative (information sharing), collaborative (task sharing), and collegial (sharing responsibility, decision making, and accountability) (Sperling et al. 2001; Desclaux and Hedont 2006). The type of participation may determine whether the breeding activity is centralised or decentralised. Although PPB is usually decentralised, it can also be carried out in centralised research stations where farmers are invited to visit, give their opinions and practice selection among plants being grown at the station.

Despite the great diversity of PPB approaches, and of their objectives (improving adaptation, promoting genetic diversity, empowering farmers and rural communities), all have in common the aim of shifting the focus of plant genetic improvement research towards the local level by directly involving the end-user in the breeding process (Morris and Bellon 2004). This interactive approach to breeding may provide the intensity of collaboration which is so crucial to organic agriculture (Lammerts van Bueren et al. 2003). Not only for practical but also for ethical reasons, organic breeding justifies the involvement of farmers and end-users in a PPB programme (Desclaux 2005). Indeed, PPB can provide a relevant fit to the principal aims of organic agriculture for production and processing as prescribed by International Federation of Organic Agriculture Movements (IFOAM 2005b), and especially: “(i) to maintain and conserve genetic diversity through attention to on-farm management of genetic resources, (ii) to recognise the importance of, and protect and learn from, indigenous knowledge and traditional farming systems”.

Though more appropriate, or even essential, in the developing world, there is an increasing number of PPB projects in Europe, especially under organic conditions and they can play a key role in evaluating diversity at different scales (e.g. field, farms, village, production basin) using mixtures, populations or inter-cropping (Desclaux and Hedont 2006). Based on studies conducted in several developing countries (e.g. Almekinders and Hardon 2006), the use of many different genotypes within an area can generate genetic mosaics that may be helpful in delaying the development of epidemics and plagues.

Crop structure

The most common genetic structure of varieties bred in self-pollinating cereals is the pedigree pure line, which means that environmental buffering is dependent on intra-genotypic compensation ability and flexibility, promoted by the allohexaploid genome structure of wheat. It is therefore of interest to consider genetically more diverse structures such as mixtures or populations which allow for complementation and compensation among different plant neighbours. This is particularly important for the more variable environments encountered in OA. Maintaining genetic diversity within a “variety” might allow for more buffering capacity at both the spatial and the temporal levels. For example, variety mixtures can provide functional diversity that limits pathogen and pest expansion thus stabilizing yields under disease pressures (Wolfe 1985; Finckh et al. 2000).

Simple mixtures can be advantageous in OA (Østergård et al. 2005), but they may also be less consistent in OA and low-input systems relative to CA, probably because of the limited genetic variation, but also the need to ensure that component varieties 'nick' together (Phillips et al. 2005). The optimal use of genetic diversity can be obtained by breeding populations derived from composite or more simple crosses or possibly from the consecutive harvest and re-sowing of mixtures of genotypes, because the "variety" in this case may adapt specifically to the local conditions and, if managed appropriately, may also respond continuously to environmental changes over time. Such approaches are based on the founding work that Harlan and Martini (1929), Suneson (1960) and Allard (1988, 1990) developed on barley composite cross populations in California from 1928. The authors showed in particular that the average yield of the different populations increased over time as a result of natural selection and competition among plants. In another long-term experiment, Goldringer et al. (2006) and Paillard et al. (2000a, b) showed that wheat composite cross populations grown for 10 generations in different environments were significantly differentiated for adaptive traits such as earliness components and powdery mildew resistance. Such evolutionary-breeding methods are now being developed in OA associated with participatory approaches allowing, simultaneously, for direct selection in a specific targeted environment, for beneficial farmer involvement and for further adaptation to environmental changes (Murphy et al. 2005; see also Phillips and Wolfe 2005, for a review). Well-designed composite crosses also underpin the concept of "modern landraces", based on the founder effect, which can provide rapid adaptation to local, specialised conditions. At a higher level of diversity, i.e. intercropping, which introduces an even wider range of environmental variables, populations offer the potential for rapid adaptation of the crop to a range of different systems with different crop components.

The logic in favour of the development and use of mixtures and populations is increasing rapidly in a changing world. But there are many questions, such as how many, and which, parents to use (see Witcombe and Virck 2001). However, unlike mixtures, populations with the same numbers of 'parents', provide the potential for more stable performance across variable environments because of their greater genetic variation, plant-to-plant interaction and ability to respond to different environments. The latter will be of high importance given the problems of global climate change. Another question with populations is to determine the spatial and temporal levels at which there may be useful adaptation. There is also a need for more information about the usefulness of the grain from such heterogeneous crops for milling, baking and other processing. It is likely that the uptake of such approaches will be more acceptable and rapid in the local marketing sector followed by the regional and then the global (Table 1).

Required characteristics in breeding for organic agriculture

Physiological and agronomic research, together with field experience, provide insights into the range of characters needed for OA. These include efficient use of a wide range of nutrients and water, weed competition, disease and pest resistance, quality for end use as well as yield and yield stability. The list of potentially important characteristics is enormous and impracticable to consider one by one. As pointed out above, new methods can help in combining traits and their interaction with the environment, but a further four considerations may also be valuable:

(1) to try to identify pleiotropic characters that may have a positive value for a wide range of physiological needs. This could include, for example, vigorous early growth which is valuable in terms of weed competition, uptake of nutrients when they are available and competition particularly against soil-borne disease and pests.
(2) initially at least, to concentrate on major characters that integrate many minor and variable characters, such as yield of grain, yield of protein and yield of straw, or their equivalents in other crops.
(3) to identify characters that can contribute to the crop rotation as a whole rather than only to the cereal crop, for example, root systems that are

adapted to AM (arbuscular mycorrhizas) colonisation, which can help soil structure and nutrition for subsequent crops as well as for the cereal itself.

(4) because the many characteristics needed will be required to be effective under a wide and rapidly changing range of environmental conditions, the question arises whether it would be more valuable to consider heterogeneous crops (mixtures or populations) which can incorporate many more of the required characters and could allow complementation and compensation among the different genotypes

Factors determining nutrient efficiency

Mineralization of organic fertilisers depends on soil life activity which in turn depends on soil temperature and conditions. Thus, climatic or soil characteristics often result in secondary nutritive or biotic stresses, which may become limiting factors for yield and quality. Consequently, nutrient use and uptake efficiency (NUUE) is of particular importance in breeding for OA. We limit our considerations here to nitrogen, the most important single determinant for yield and quality, and phosphorus, which is likely to become more important since there is little or no application currently in OA.

Nitrogen Nitrogen supply in OA depends mainly on symbiotic N-fixation supplemented by organic fertiliser. Particularly towards northern Europe, most N is fixed by fodder legumes in grass-clover mixtures which makes the amount of N introduced into the system often suboptimal, varying greatly in amount between relatively intensified OA systems and more extensive approaches. Its availability is not easily controllable (Mäder et al. 2002) and dependent on the mineralization of crop residues and green or farmyard manure, and possible application times are limited. The results are high mineral N content in the soil immediately after ploughing, when the uptake ability of winter cereals is low, and N-losses during the winter. In the later growth stages of cereals, the demand from the plants is often much greater than the supply from mineralization: matching N need and mineralization is, indeed, one of the major problems in OA (Panga and Leteya 2000).

To compensate for the relatively low N availability in OA systems, the potential for grain protein production has to be higher than in conventional agriculture. This means that total N uptake into the grain has to be improved in order to maintain yield levels, which depends on (1) total uptake from the soil, (2) translocation from the vegetative tissues to the developing grain, (3) direct transfer from the soil to the grain after anthesis, and (4) losses of nitrogen already absorbed (Barbottin et al. 2005; Bertholdsson and Stoy 1995; Pommer 1990; Papakosta 1994). Genetic differences concerning these characteristics have been shown and may be used to improve adaptation to special environmental conditions (Przulj and Momcilovich 2001a, b; Baresel 2008; Kichey et al. 2007). How new varieties are selected will depend on the time course of N-mineralization. If N-mineralization after anthesis is limiting, pre-anthesis uptake and translocation become more important resulting in varieties with more vegetative tissues, lower harvest indexes and higher biomass. More "conventional" types would be better adapted to environments where considerable amounts of N are still available after anthesis (Baresel 2006).

Although nitrogen (as nitrate) is mobile in the soil, an extended root system may enhance nitrate uptake in N-limited conditions (Cox et al. 1985; Laperche et al. 2006), and differences in extension of the root system may explain part of the differences in NUUE as shown from studies in maize (Feil et al. 1990; Wiesler and Horst 1994; Laperche et al. 2006). Root symbiosis and interactions with the soil micro flora may also be of importance for N-uptake. Associations with N-fixing bacteria such as Azospirillum are of limited importance for nitrogen assimilation, but positive effects on root development and thus water uptake have been shown (Kapulnik et al. 1987). A priming effect on soil bacteria of the rhizosphere via exudates, stimulating N-mineralization, is likely (Kuzyakov 2002), but its relevance for plant growth is unknown. There is evidence that associations with bacteria in the rhizosphere are dependent on genotype in wheat (Kapulnik et al. 1987), but direct selection for this trait would be difficult and its effect on NUUE and yield is uncertain.

Phosphorus

At present, *P* availability is rarely an issue because immediately after conversion from conventional to organic agriculture, the content of available *P* in the soil is often high and decreases only slowly over many years (Oehl et al. 2002; Gosling and Shepherd 2005). Nevertheless, *P* recycling and/or better exploitation of the (large) immobile fraction have to be improved in the long-term, so development of more *P*-efficient varieties will become more important. Phosphorus has low mobility in the soil and its uptake efficiency is dependent on soil exploration by roots, root hairs (possible for indirect selection: Gahoonia and Nielsen 2004a, b) and especially arbuscular mycorrhizas (AM), whose absorbing surface is much larger and of low cost to the plant relative to roots and root hairs (Bolan 1991). Numerous studies have shown that AM colonisation and the plant benefit from the symbiosis are dependent on the genotype (Baon et al. 1993; Hetrick et al. 1993; Manske et al. 1995). Breeding for this character could be successful as a long-term objective.

It can be concluded that there is a considerable potential in breeding for improved nutrient efficiency by selecting under conditions which correspond to the target environments. This is particularly important in conditions of low availability of nitrogen or phosphorus.

Competitive ability against weeds in OA

Weed management is essential for successful organic crop production with the aim to suppress undesirable weeds such as aggressive grasses, creeping thistle (*Cirsium arvense*), broad-leaved dock (*Rumex obtusifolius*) and crop volunteers, whilst finding a balance between the plants of crops and other more desirable wild plants. Plant traits that confer a high degree of crop competitive ability, especially against aggressive weeds, are highly beneficial in organic farming (Mason and Spaner 2006). Both plant (e.g. height) and crop characteristics (e.g. ground cover) are important as selection criteria. However, competitive traits are unlikely to have received sufficient attention, or high priority, in conventional plant breeding, except indirectly, for example, through early vigour. This is largely because selection for competitiveness could be at the expense of other important criteria (Brennan et al. 2001) and large genotype × environment × management interactions can mean difficulty in phenotypic selection for competitiveness (Coleman et al. 2001).

Nevertheless, there appears to be sufficient genetic variation in crop competitive ability (Acciaresi et al. 2001; Coleman et al. 2001; Hoad et al. 2006) for such selection to be introduced into breeding programmes (Hoad et al. 2008). Older genotypes are often more competitive than recent introductions (Lemerle et al. 2001a; Bertholdsson 2005). Competitive ability is usually not attributed to a single characteristic, either within or between varieties (Pester et al. 1999; Lemerle et al. 2001b), but the interaction among a series of desirable characteristics is important (Eisele and Köpke 1997; Mason and Spaner 2006).

Early crop vigour is associated with increased competitive ability (Rebetzke and Richards 1999; Pester et al. 1999; Lemerle et al. 2001a, b; Acciaresi et al. 2001; Bertholdsson 2005). Early season crop ground cover confers later competitiveness against weeds (Cousens and Mokhtari 1998; Lemerle et al. 1996; Huel and Hucl 1996). Traits associated with high ground cover include rapid early growth rate (Froud-Williams 1997), high tillering ability (Lemerle et al. 2001a) and planophile leaf habit with high leaf area index (Huel and Hucl 1996; Lemerle et al. 1996). Ground cover is also influenced by agronomic factors such as drilling row width and seed rate (Lemerle et al. 2004).

Plant height is widely reported as an important trait for increasing crop competitiveness (Gooding et al. 1993). Taller varieties are likely to be more competitive than shorter ones as competition for light increases (Cudney et al. 1991). The relative importance of plant height decreases if compensated for by other traits. For example, a short planophile genotype with rapid leaf canopy development and high leaf area index may have higher weed suppression than a tall genotype without these other traits.

Shading ability is a good measure of overall competitive ability of a genotype (Eisele and Köpke 1997). Even small differences in shading ability or the percentage of light intercepted can have a significant affect on weed growth. It would be advantageous if selection for above-ground competitiveness was integrated with improvements in nitrogen use efficiency, root competition and allelopathy (Bertholdsson 2004, 2005). One objective might be to establish if genotypes with enhanced early nitrogen uptake efficiency resulted in further improvements in weed suppression. However, many of the physiological traits for desirable below-ground criteria are less well understood, or less practical for use by plant breeders in their selections. Variation in allelopathic effects on weeds has been identified from in-vitro testing (Wu et al. 2000; Bertholdsson 2004), but little is known about in-vivo behaviour. It is difficult to separate allelopathy from other characteristics of crop competitive ability (Bertholdsson 2005). Consequently there may be as yet unexplored potential for the selection of varieties showing a high allelopathic activity against weeds (Olofsdotter et al. 2002). More promising might be the selection for genotypes with high early nitrogen uptake efficiency amongst those already recognised as having good ground coverage and shading ability.

Breeding for disease resistance

Disease resistance is a major issue in cereal breeding for both conventional and OA. However, plant health in OA is a broader concept involving not only the use of resistant varieties with different morphological traits, but also of agronomic measures that reduce the risk of high disease levels (e.g. tillage, rotation), as well as other features of OA such as lower plant population densities and lower nitrogen levels that may reduce infection and spread of disease.

The most recognized diseases in OA are the bunts and smuts in wheat, barley, and oats, Septoria diseases in wheat, leaf stripe disease (*Drechslera graminea*) in barley, Fusarium head blight (FHB) in wheat, triticale, and rye (Wilbois et al. 2005) and ergot in rye. If deployment of regional cultivars is increased, the number and relevance of critical diseases can be reduced. In dry regions, for example, the bunts and smuts might be the only diseases important for OA.

Generally, diseases that are strongly influenced by sowing time, plant population density and nitrogen nutrition such as powdery mildew, rusts and foot rot are less important in OA. They occur later and with lower incidence, thus producing less damage (Letourneau and Van Bruggen 2006). However, soil-borne diseases, such as *S. tritici* blotch and *Drechslera tritici-repentis* in wheat, FHB in all cereals, and ergot (*Claviceps purpurea*) are of significant economic importance. If control by cultural measures is possible, their damage might be considerably less in OA. A third group of mainly seed-borne diseases, the bunts and smuts, is among the most important because there are hardly any practical and effective seed dressings in OA.

In wheat, most commercial European varieties are highly susceptible to common bunt (*Tilletia tritici* and *Tilletia laevis*) and dwarf bunt (*Tilletia controversa*), because conventional breeders have no interest in breeding for resistance to these diseases. A few fairly resistant varieties have been described (Fischer et al. 2002; Dumalasová and Bartoš 2006; Wächter et al. 2007), but resistance tests are reliable only when several locations and years and a defined bunt inoculum are used. All resistance deployment strategies are possible, but it is not clear which races are prevalent in Europe. In a first attempt to improve bunt resistance, variety tests should be organised at several locations and the bunt races occurring in different regions need to be monitored.

Fusarium head blight (FHB), caused by *Fusarium graminearum*, *Fusarium culmorum* and other *Fusarium* species has gained increasing attention in the temperate wheat producing areas because of yield losses and mycotoxin contamination of grain, especially by deoxynivalenol (DON). As long as maize as a pre-crop and reduced/no tillage is not an option in OA, the disease incidence should be lower than in conventional farming. But in Central Europe, FHB remains problematic in years with frequent rainfall during flowering. FHB resistance is quantitatively inherited; no source with complete resistance is yet known. FHB resistance in wheat can be supported by morphological characters that are, however, mostly unwanted in intensive agricultural systems: tallness, especially through absence of the height-reducing *Rht* genes, large distance between canopy and head, and less dense heads (Mesterhazy 1995; Hilton et al. 1999). Given the high reputation of OA for quality of food and feed, FHB resistance should have a high priority in the choice of varieties.

In conclusion, OA needs resistance breeding, but the overall approach, together with the pattern of diseases and their significance, is somewhat different from conventional farming. OA in general aims at a broader approach to disease resistance combining morphological and physiological traits to ensure overall plant health instead of absolute, specific resistance. More specifically, concerning FHB and Septoria diseases, OA can benefit from the work of conventional breeders in terms of resistance sources for crossing purposes or by growing conventionally bred varieties. For the bunts and smuts, new resistance breeding programmes should be built up to guarantee secure organic seed production through all generations of multiplication from breeding to certified seed. Whether variety mixtures can control bunts and smuts more durably through the deployment of several race-specific resistance genes has yet to be investigated. Additional traits for OA are resistance to other seed-borne diseases (Wilbois et al. 2005).

Quality

Baking quality

Next to yield, the most important basic breeding aim for wheat is quality for milling and baking. The precise needs vary, however, depending on the market use. For the global model, supermarkets usually depend on industrialised milling and baking, using cereals with a constant and high protein content, with relatively hard gluten. Cereals for regional and local markets are often produced for artisanal milling and baking, in which there is more flexibility, for example, to adjust the baking process to the quantity and quality of the proteins, or to mixtures of different types of flour. However, for wholemeal bread products, the process can be complicated because the high fibre content itself can modify the behaviour of the gluten (Rakszegi et al. 2006).

Breeding for baking quality in wheat is determined largely by the common negative correlation between yield and grain protein. Over recent decades, wheat breeding for CA has concentrated on yield, so that newer varieties, generally, have higher yields and lower grain protein. To compensate for this, there has been selection for higher gluten quality, together with improved fertiliser distribution over the season (Canevara et al. 1994; Baresel 2006). This means that in OA, with limited opportunities for improved fertiliser distribution, the same modern varieties have lower yields together with levels of protein that often do not fulfil the requirements of the baking industry. The effect of reduced N input may vary however with the climatic conditions: in continental or Mediterranean climates, where drought occurs often during grain filling, protein contents and consequently baking quality, may be considerably higher than in temperate climates.

The main aim for breeding for OA must therefore be to dissociate yield from grain protein, so that, even at relatively low yield levels, the grain produced can have acceptable baking quality. This goal is being sought currently by OPB breeders in Switzerland and Germany (personal communications). Since there is little GEI for grain protein content and gluten quality, specific selection for the latter for OA (Kempf 2002), may prove difficult.

However, the lack of GEI also means that selection for quality traits can be indirect (Kleijer and Schwaerzel 2006; Baresel 2006), for example, under CA conditions, including also the use of HMWGS (High Molecular Weight Glutenin Subunits) markers. A problem might be that most varieties with high protein content often have softer gluten, which reduces baking quality. A future challenge in breeding for organic farming (or other systems with low nitrogen input) will be, therefore, to develop good lines combining high protein content with high gluten quality.

Malting quality

Organic barley for malting is based predominantly on local supply and use to small, but growing, niche markets, for example micro-breweries. Nevertheless, barley grown for organic malt production should be required to meet the same quality criteria as barley used in conventional malting for brewing, distilling or other food uses. Selection for high malting quality in OA should benefit from advances in breeding for generic (or most essential) malting characteristics. Work by Ogushi et al. (2002) also indicated that selection of high quality malting genotypes could be based on their malting data when grown in another, contrasting, environment. These, and similar, findings suggest a high degree of predictability of malting performance across contrasting environments (Lu et al. 1999; Molina Cano et al. 1997) which is encouraging for OA if improvements in malting quality are based largely within conventional breeding. Specific requirements for OA would need to be introduced later into the selection process. These requirements could include agronomic traits such as disease resistance to reduce contamination of the ears and weed competitiveness to reduce admixture in the bulked grain.

Nutritional quality

Nutritional quality is one of the critical questions in marketing organic food. Although it is hard to find definitive data in the literature, the available information suggests that organically produced, cereal-based foodstuffs can have several advantages. First, they are usually free from pesticides and pesticide residues, resulting in a decrease in allergenic reactions. At the same time, they contain significantly more antioxidants (especially fat soluble antioxidants), probably because of more severe abiotic stress during cultivation (Grinder-Pedersen et al. 2003). Indeed, in organic produce, increased antioxidants and bioactive compounds important in plant defence systems seem to be a general feature (Mitchell and Chassy 2004), making them an excellent source of functional and dietary food (Kovács 2006). Concerning mineral nutrients, Murphy et al. (2008) argue that, from their experience, breeders should be able to increase mineral concentration in modern cultivars without negatively affecting yield.

For the under-utilised hulled wheat species, such as einkorn and emmer, the situation is even more promising, since they contain significantly larger amounts of essential microelements (Cu, Zn, Fe, Ca, Mg) (Bálint et al. 2001), different amino acid profiles, and relatively high amounts of essential fatty acids (Kovács and Szabó 2006). Moreover, there is considerable variation in gluten content relative to modern wheat, especially in einkorn, where extremely high gluten content (over 45% wet gluten) and gluten free genotypes (important for coeliac diseases) sometimes occur together in the same population (Kovács and Szabó 2006). Such species are difficult to grow in CA, because they are often highly sensitive to herbicides, and unproductive at high N levels (Bedő and Kovács 2006).

Breeding techniques

In vitro techniques

Because organic agriculture is a process rather than a product oriented approach, the development of organic breeding is concerned with the values of ‘naturalness’ (Lammerts van Bueren et al. 2003, 2007; Lammerts van Bueren and Struik 2004). As a consequence, the draft standards for organic breeding programmes exclude the use of in-vitro techniques (IFOAM 2005a). If IFOAM does decide in future to exclude in-vitro techniques, this would have consequences, for example, in barley and wheat breeding where embryo or microspore culture is used together with colchicine application for doubling haploids. A potential problem regarding the availability of varieties suitable for OA is that it may be difficult or even impossible to find out which varieties have been subject to embryo culture in their origins. Attempts are being made, therefore, in some countries (e.g. Hungary, Switzerland) to design a certification system for specific organic breeding programmes (OPB) in which no in-vitro techniques are applied to distinguish the varieties produced from those developed in other types of breeding programme (e.g. BFCA, BFOA).

Use of molecular markers

In recent years, the reality of using DNA-based molecular markers in plant breeding has grown rapidly, particularly for maize. Uptake for a cereal such as wheat has been slower because of the relative cost of marker screening against the predicted returns from breeding (Koebner 2004). Further constraints for the organic sector lie in the relatively small size of the market together with possible concerns about some production methods for such markers and their application with respect to the violation of plant integrity (Lammerts van Bueren et al. 2005a).

However, as one early example, Rakszegi at al. (2006) successfully applied the technique to introduce a specific glutenin gene from the old Hungarian variety, Bánkuti 1201, into new lines for organic and conventional production. As screening costs fall, we may expect to see an increasing uptake particularly for rapid introduction of disease resistance genes that are currently unavailable in developed material, for example, resistance to bunt and loose smut (see above). Another example could be in backcross programmes to include certain monogenetic disease resistances from wild relatives so as to avoid undesired linkage drag, as in resistance against the barley mosaic virus complex (Werner et al. 2005).

A further recent application relevant to this review is the use of marker assisted selection (MAS) to help to increase the success rate in selection in participatory plant breeding (Steele et al. 2004). This was achieved in India and Nepal, improving the drought resistance of rain-fed rice by incorporating quantitative trait loci (QTL) for root performance into an older popular variety.

Overall, some promising applications for MAS in organic breeding will be to follow QTLs associated with complex characters, for instance, NUUE and weed competition, under different environmental conditions. Fortunately, methods are emerging that can improve the efficiency of selection for complex characters (Podlich et al. 2004) and provide a better understanding of the genetic architecture of such traits as observed across environments by incorporating QTL by Environment interactions (QxE). Statistical approaches analysing QxE have been proposed in the context of QTL detection (Boer et al. 2007) or association studies that are based on complex population structures but provide the advantage of analysing more diverse QTL alleles (Crossa et al. 2007). In the long-term, such complex statistical approaches derived from animal or human genetics will allow analysis of complex population structures such as multiparental populations that have evolved in different environments. Such methods are likely to be of value in improving our understanding of the genetical changes involved in the responses of populations to different forms and levels of selection, which should be helpful in improving the design of mixtures and populations for particular cropping systems. Such advance will be dependent on decreasing costs for the use of multiple marker assessments and development of the appropriate statistical approaches for inbreeding plants (Jannink et al. 2001; Backes and Østegård 2008), together with an increasing interest in research funding for sustainable crop production.

The future development of organic agriculture and plant breeding

There is no doubt that field trials to compare varietal performance under organic and conventional conditions have provided valuable information, confirming that there can be both differences and similarities, with some varieties showing consistent adaptation to OA or to CA or to both. However, it is also clear that the kinds of difference and their scale are dependent on many factors, the most important being the exact type of OA or CA system. For this reason, it may be important to resist the temptation to continue with trials comparing variety performance in OA and CA, unless there is a highly specific objective. Much more important, in our view, is to recognise that *within* OA and CA there are different sub-systems, such as those described for OA (Table 1), based on the three marketing levels. Similarly, in CA, there are parallels which involve, for example, significantly different levels of inputs. Overall, for the two kinds of agricultural system, it is more important to recognise the structure of the systems and the impacts of the different inputs that are used or not used. Moreover, it is crucial to recognise how these inputs are changing, or how they will change, as climate and resource availability change.

Concerning OA specifically, it is clear that the application of an ecology-based approach to farming implies a primary concern for the interactions among the selected characters, and among those characters and the whole farming system. Furthermore, the inherently more variable conditions of OA needs particular attention to stability of production, which means that adaptation needs to be applied among many different localities rather than over single, large geographical areas. Such an approach can be achieved only by using a range of different approaches to the breeding process (decentralisation, participation etc.) and to the forms of crop populations that are used (variety mixtures, populations, inter-crops). For all of these approaches, there is a need to ensure that more and novel genetic resources are fed into the start of the breeding processes. In other words, success in any form of local selection is dependent on a broad starting array of genetic resources.

Currently, organic farmers are making use of the most appropriate varieties produced in CA programmes, together with a relatively small amount of material bred specifically for organic systems. This amounts to a somewhat small input. However, important changes appear to be on the way, from three sources. The first relates to developments in the applications of ecology to OA, as indicated above. The second relates to other developments in plant science, particularly through a better understanding of selection for efficient use of resources also as discussed above and, for example, by Geiger et al.

(2007). The third change lies in the practical observation that varieties bred under organic conditions may be more efficient in resource terms, and higher yielding, when used in CA (Burger et al. 2008).

If these three changes develop further, together with the other methods discussed above, then we should see significant benefits for both OA and CA. For OA specifically, cooperation among all kinds of breeding efforts and testing in a widely distributed trial network on organic farms would enable organic farmers to choose, more rigorously, the varieties best suited to their local conditions. A combination of all of the strategies indicated above would lead to exploitation of the maximum appropriate genetic diversity for organic farming systems. Furthermore, we would also expect to see stimulation of positive interactions among the different breeding strategies being developed.

Some legal concerns

Legislation for organic varieties varies among European countries. In Austria, Denmark, Germany and Switzerland, for example, VCU tests for organic farming are available and varieties that meet DUS requirements can be evaluated and registered (Donner and Osman 2006). In other European countries such as France and the UK, there is no special VCU testing. Thus, varieties adapted to organic conditions that do not yield sufficiently well under conventional conditions, cannot be registered. And, of course, without registration, the exchange and production of seeds is forbidden. Another current question concerns the potential heterogeneity of, for example, populations, that are not integrated into the legislation. Indeed, varieties that do not comply with DUS cannot be registered. It is urgent that legislation at the European level evolves to take into account the new demands.

In fact, there is no legal problem for marketing seed of variety mixtures as long as all components have passed variety registration and seed certification; indeed, specific mixtures are registered in Denmark. In the case of populations, assuming they prove to be valuable under commercial conditions, the question of IPR/PBR (intellectual property rights/plant breeders rights) arises: how could they be described and protected? How can quality of populations be assured and misuse prevented? One possibility is the regional/limited use on a small-scale that is perhaps in line with the legislation currently being worked on by the EU. A further possibility under discussion is to abandon the current systems of DUS and VCU which are inappropriate for materials that are under continuous dynamic management. The static variety descriptions would need to be replaced by some form of data-logging of the history of the different populations so that they remain fully traceable wherever and whenever they are used.

Summary conclusions

Until recently, interest in breeding for OA has been limited to a handful of small-scale breeders. However, rising input prices, the increasing impact of climate change and the need for sustainability are creating a larger opportunity for the specific breeding objectives needed.

The organic sector itself is differentiating roughly into three scales, Global Commodity, Regional and Local Market. Varietal production overall still tends to be a one-way traffic, with varieties bred for CA being screened for use in OA. In particular, the global commodity market is supplied mainly with such varieties. Smaller scale programmes, including breeding directly for OA, tend to be directed towards regional and local markets.

Though many of the characteristics required in new varieties are common to both CA and OA, there are a number, mostly complex, that have a higher priority in OA. These include characters that are important for the farming system and the crop rotation, for example, weed competition and adaptation to arbuscular mycorrhizas. There is also a need for simultaneous selection of characters such as weed competition, nutrient uptake and disease and pest resistance, which are often helped by positive interactions from early plant vigour.

There is an obvious need for nutrient uptake and use efficiency. For nitrogen, this needs to include improvement of relationships between crop and nitrogen-fixing organisms living either on roots or free-living; a similar conclusion applies to the needs for phosphorus.

Breeding for disease resistance also differs from the CA approach, with the need for plant vigour to encourage general plant health, together with more specific approaches for resistance to seed-borne diseases such as bunt and loose smut.

However well these characteristics may be combined, there will always be a need under the conditions of OA to deal with large genotype-environment interactions. For this reason, the potential for decentralised breeding, to select plants in the places that they will be grown, is particularly important for OPB, combined with PPB at different levels from mostly breeder to mostly farmer.

An important tool to help deal with highly variable environments is the use of genetically diverse crops, including inter-cropping, mixtures and populations, which will all play larger roles in OA. Such approaches can also be valuable in helping to restore or increase biodiversity within the crop.

The use of DNA-based molecular markers has so far played only a minor role in breeding for OA. This is likely to change markedly if, on the one hand, there is a further decline in the cost of the technology and, on the other, interest in breeding for OA and the use of within-crop diversity both increase.

Successful application and dissemination of the outcomes from these different approaches to breeding for organic agriculture and the use of diversity will need modifications to be made to the legislative framework for introduction and use of the material in agriculture.

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