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The need to breed crop varieties suitable for organic farming, using wheat, tomato and broccoli as examples: A review

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ABSTRACT

It is estimated that more than 95% of organic production is based on crop varieties that were bred for the conventional high-input sector. Recent studies have shown that such varieties lack important traits required under organic and low-input production conditions. This is primarily due to selection in conventional breeding programmes being carried out in the background of high inorganic fertilizer and crop protection inputs. Also, some of the traits (e.g., semi-dwarf genes) that were introduced to address problems like lodging in cereals in high-input systems were shown to have negative side-effects (reduced resistance to diseases such as Septoria, lower protein content and poorer nutrient-use efficiency) on the performance of varieties under organic and low-input agronomic conditions. This review paper, using wheat, tomato and broccoli as examples, describes (1) the main traits required under low-input conditions, (2) current breeding programmes for organic, low-input agriculture, (3) currently available breeding and/or selection approaches, and (4) the benefits and potential negative side-effects of different breeding methodologies and their relative acceptability under organic farming principles.

1. Introduction

The characteristics of organic agricultural systems are their biodiversity at soil, crop, field, whole rotation or polyculture, and landscape level and the greater focus on integration of crop and livestock production systems on the farm compared with conventional farming systems [1]. The high biodiversity of organic farms provides many ecological services that enhance farm resilience to a large extent [2]. Integrating biodiversity gains due to agronomic practices with genetic diversity at crop level provides an insurance with respect to the impact of biotic and abiotic stress factors on crop yield and quality [3]. The development of genetic diversity focused crop breeding approaches may therefore be essential to improve yields and quality parameters in foods from organic and low-input farming systems, especially in the context of the challenges expected due to global climate change [2].

To date, there are only few varieties that were specifically bred for organic and low-input systems in developed countries. It is estimated that more than 95% of organic agriculture is based on crop varieties that were bred for the conventional high-input sector with selection in conventional breeding programmes. Recent studies have shown that such varieties lack important traits required under organic and low-input production conditions [4–6].

A range of breeding goals desired for the organic sector, such as yield, resistance to biotic and abiotic stress, baking quality (wheat) and sensory qualities demanded by consumers do not differ from conventional breeding goals, but it is essential that such traits are expressed under low-input conditions, which cannot be guaranteed if selection is done in high-input agronomic backgrounds. However, a range of traits are of primary interest for organic farming, at least on the short term (e.g., increased competitiveness against weeds and resistance to seed-borne diseases such as common bunt in wheat). Also, some traits relevant for conventional high-input farming may have negative side-effects on organic systems. For example, the main focus of most commercial wheat breeding programmes has been on improving yield by increasing the harvest index. This involved the introduction of semi-dwarf genes into cereals and other crops, resulting in short-straw vari-

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eties. In cereals this approach resulted in (1) reduced size and depth of root systems, (2) increased reliance on high inorganic-N inputs to attain satisfactory protein contents, (3) lower nutrient-use efficiency, (4) decreased competitiveness against weeds or decreased robustness against mechanical weed control (and thereby greater reliance on herbicides), (5) greater susceptibility to diseases such as powdery mildew, Septoria [7] and Fusarium, and (6) reduced protein content [8], but (7) improved lodging resistance [9–16].

It often takes 10 years or more from the initial inter-varietal crosses to develop a new crop variety. To realize the varietal improvements needed in organic farming in the coming decades, crosses between appropriate parental varieties have to be made now. It is essential therefore to identify the primary limiting factors of existing varieties for organic production and target them in the breeding programmes for organic farming and subsequently communicate results to public and commercial breeders.

This review describes the main traits required under low-input conditions using three different types of crops as examples: (1) wheat, an arable crop, (2) broccoli, a field-grown vegetable crop, and (3) tomato, a greenhouse-grown vegetable crop. Furthermore, some currently available breeding approaches will be discussed as well as the benefits and potential negative side-effects of different breeding methods and their relative acceptability under organic farming principles.

2. Nutrient-use efficiency

The greatest difference between organic and conventional systems relates to soil management practices used and to processes in the rhizosphere [17]. Organic systems often rely on organic matter based fertilizer inputs and mineralization-driven N and P supplies to crops. Macronutrient availability patterns during the growing period therefore differ significantly from those in conventional systems. Organic crops often experience limited macronutrient (N and P) availability especially during periods when soil temperatures and water availability reduce mineralization capacity by the soil biota [18]. However, regular organic matter inputs have shown to increase soil biological activity and biodiversity and associated mineralization capacity of the soil [19]. Organic matter based fertilization regimes have also shown to suppress diseases [20] and induce biochemical pathways in crops involved in pathogen defence and stress tolerance [21]. In this context it is likely that organic systems require crop genotypes that are able to form active symbiotic relationships with beneficial organisms in the rhizosphere, and thereby establish mechanisms that increase nutrient-use efficiency (e.g., vigorous root systems, ability to form active mycorrhizal associations, reduced root losses due to pathogens, ability to maintain a high mineralization activity in the rhizosphere via root exudates, increased rooting depth and associated ability to recover N leached from the topsoil).

Breeding crops under conventional fertilizer regimes with abundant N may have resulted in varieties that are dependent on readily and consistently available N [22]. For example, older wheat varieties have shown to be superior in N extraction in low-N environments to modern ones [22]. Crop varieties respond to varying systems of fertility management in different ways and mechanisms for the uptake of different nutrients from soil also differ [23]. In addition, varieties have different nutrient requirements and growth capacities. A genotype with high N-use efficiency is able to realize high yields at low soil-N availability. For many crops, significant genetic variation with respect to N-use efficiency has been demonstrated [24], making breeding for resistance to N-deficiency stress feasible and practical [14,25].

Improving the different compounds of nutrient-use efficiency, like maintenance of photosynthesis under nutrient stress, nutrient-uptake capacity, nutrient-utilization capacity and translocation efficiency, will contribute to higher yield and quality under low-input conditions. For organic farming, the adaptation of varieties to efficient nutrient-use derived from slow-nutrient-releasing organic fertilizer is of special importance, which is not addressed in conventional selection programmes with no or less inorganic fertilizer [14].

Nutrient-uptake efficiency of plants can be improved by the capacity of crops to establish and sustain efficient (1) plant-growth-promoting-rhizosphere (PGPR) bacterial communities [26,27] and (2) arbuscular mycorrhizas (AMs), a trait that has been described as “rhizosphere competence”. PGPR-bacteria promote N-uptake efficiency since they (1) protect root systems against attack by soil-borne pathogens [28], (2) maintain efficient mineralization-driven nutrient supplies to plant roots [29,30], and (3) support the establishment of active AM associations [14]. AMs are essential for efficient phosphorus, micronutrient and water uptake in plants grown under organic [26] and low-input conditions [27,31]. Under optimal conditions, especially under high levels of plant available phosphorus (P), AM symbiosis is less relevant for plant nutrition and might even have detrimental effects on plant growth due to carbohydrate costs [32]. Therefore, recent breeding programmes focused on high-input farming might have selected against such rhizosphere competence. For example, Hetrick et al. [33] detected that wheat varieties developed before 1950 were more reliant on mycorrhizal symbiosis than modern ones. Similarly, landraces of mycorrhizal wheat grown in low-P soils produced a higher yield than modern varieties grown under the same conditions [34].

Recently, genes have been identified in tomato [35] and in wheat [36] that control the ability to form mycorrhizal root symbiosis. Moreover, studies have shown that the association of specific micro-organisms on roots can influence gene expression in the plant [21], but breeders have yet to exploit these findings. This area of research is complex and difficult to study because it involves not only the genotype of the plant, but also its influence on and interaction with the soil micro-organism population [37].

The Brassicaceae were once thought not to be able to form mycorrhizal associations, but certain species show low levels of colonization [38,39]. Little work has been done on rhizosphere micro-organism interactions with the growth and development of *Brassica oleracea*, and this may be a productive area to pursue in finding *Brassica* genotypes with enhanced association. Researchers at John Innes Institute studied P-use efficiency in *B. oleracea* [40–42] and showed that there is genetic variation in this trait and that it is under quantitative control [42]. Cauliflower varieties with proportionally more fine roots have been shown to be more N-use efficient [43].

Environmental conditions, especially fertilizer applications, temperature, light intensity and soil moisture also have a significant impact on nutrient-use efficiency (NUE) [44]. Since agronomic practices and climatic conditions significantly affect NUE [45], it is important to quantify genotype × environment interactions of traits contributing to NUE to ensure and/or to select crop plants within the context of different agronomic and climatic environments.

3. Rhizosphere competence for disease suppression

Resistance to soil- and seed-borne diseases and/or mechanisms to maintain disease suppressive organisms (e.g., plant-growth-promoting rhizosphere (PGPR) bacteria, AM-fungi) in the rhizosphere are important traits in organic production because healthy root systems are required for crops to express their genetic potential for nutrient-use efficiency and yield [27,29,46]. Soil microbial populations in the rhizosphere have been shown to have the potential to reduce the severity of both (1) soil-borne root diseases (e.g., *Rhizoctonia*, *Fusarium culmorum*, *Gaeumannomyces graminis* var. *tritici*) and (2) foliar pathogens (e.g., *Septoria tritici* causing blotch and leaf rust) in wheat [47–49]. Bacteria shown to contribute to disease suppressiveness have been classified as PGPR bacteria and root-colonizing Pseudomonads (e.g., *Pseudomonas fluorescens*) [49]. Suppressive effects are provoked by a range of different mechanisms including (1) antibiosis, (2) site and nutrient competition, and (3) induction of resistance in the crop plant [49,50].

Recent research indicates that there is significant interaction between wheat genotypes and soil microbial composition in the rhizosphere [47,51]. Root exudates are an important plant mechanism that affects soil microbial composition [52]. Mazzola et al. [51] demonstrated that the increase in populations of rhizobacteria depended upon the wheat variety that was planted. However, to what extent genetic factors are responsible for the specific associations with beneficial rhizosphere micro-organisms is currently poorly understood. Also, significant efforts are needed to elucidate the potential of improving crop health and nutrition via beneficial plant × soil × microbe interactions before breeding programmes targeting traits associated with such interactions for organic farming can be developed [27].

4. Weed competition

Weed management in row crops grown from transplants, including many *Brassica* and some *Allium* crops, tends to be less problematic than in these crops grown from seed. This is due primarily to a more rapid development and associated competitiveness against weeds as well as the greater suitability of transplanted row crops for inter-row mechanical weeding methods. For example, in the USA, broccoli can be directly sown or transplanted to the field. The decision to sow directly or to transplant depends on several factors, including cost of F_1 hybrid seed vs. open-pollinated seed that could be maintained by the grower, and labour and material costs of transplanting compared with direct sowing. In terms of weed control, broccoli seedlings are small and may take longer than competing weeds to become established (especially true in warmer environments if more rapidly growing C4 weeds may be present). Part of the package of a broccoli variety suitable for direct seeding in organic production systems would be plant types that emerge and grow rapidly and shade neighbouring weeds. Because *B. oleracea* has such a great diversity of cultivated morphological types, sufficient genetic variation should be present in the species to select for more weed competitive varieties.

Weed control also remains a problem in many cereal crops such as wheat. Wheat varieties are genetically variable in their ability to compete with weeds [53,54]. Lemerle et al. [55] found considerable variation in the relative competitive advantage of 12 wheat varieties over annual ryegrass (*Lolium rigidum*). Huel and Hucl [56] showed that spring wheat varieties differed in competitive ability against oriental mustard (*Brassica juncea* cv. Cutlass) and cultivated oats (*Avena sativa* cv. Waldern). Balyan et al. [57] reported that the grain yield of wheat was reduced by 17–62% depending on the variety's ability to compete with wild oats (*Avena ludoviciana*), and Blackshaw [58] found significantly different reductions in yield among wheat varieties due to differential response in competitive ability against downy brome (*Bromus tectorum*). Hucl [59] reported yield gains of 7–9% in 'competitive' compared with 'non-competitive' wheat varieties. Huel and Hucl [56] found statistically significant ($p = 0.001$) weed rate × genotype interactions involving changes in genotype rank for wheat grain yield when tested under weed-free and weedy conditions.

In a study evaluating grain yield and weed suppression ability (WSA) of 63 historical and modern spring wheat varieties, a slight decrease in WSA over the past 150 years corresponded with a large increase in yield [60]. However, no evidence of a causal relation between WSA and grain yield was found, so it is possible that this correspondence may simply reflect the relative emphasis (or lack thereof) these two traits have received during selection. Of these 63 varieties, the top 5 ranked for WSA reduced weed weight per plot by 573% over the bottom 5. This demonstrates the wide range of WSA in wheat varieties, and indicates potential for improvement should this trait become a target for selection. Of the phenotypic traits measured, only plant height was responsible for variation in weed weight, whereas coleoptile length, juvenile growth habit, 1000 kernel weight and leaf area index had no direct effect on WSA in this study [60]. Interestingly, all these traits have been reported previously as weed suppression traits, indicating that traits important for WSA are fluid and often depend on site-specific environmental conditions, and also on the winter or spring growth habit in wheat.

Allelopathy is another potentially important weed suppression trait that has received little attention in recent years. Allelopathy is a chemical process where plants provide themselves with a competitive advantage due to the direct or indirect effect on germination, growth or development of neighbouring plants [61,62]. An initial step towards the development of varieties with allelopathic activity is to evaluate the allelopathic potential of crop germplasm in bioassay-based studies. Using such approaches, different wheat accessions have been shown to strongly inhibit the growth of the weed species *Bromus japonicus* and *Chenopodium album* [63], and a number of allelopathic compounds have been identified in wheat [64,65]. Wheat varieties have also been screened for their allelopathic potential against annual ryegrass (*L. rigidum*). Wu et al. [66] found that the inhibition of root growth of ryegrass ranged from 24 to 91% among 453 wheat varieties. Wu et al. [62] suggested that the identification of varieties with high allelopathic activity and the transfer of such a characteristic into modern varieties could restore an important trait that has inadvertently been lost during the process of selection for higher yields.

In the Brassicaceae, glucosinolate breakdown products have weed- and pathogen-suppressive effects. Myrosinase catalyzes the conversion of glucosinolates to isothiocyanates and related compounds but is not released until plant tissue maceration [67]. The effect has been most clearly demonstrated in crops following ploughing under a cruciferous green manure crop. In the studies that have examined if growing *Brassica* crops have a direct allelopathic effect on weeds, no significant effect was found [68,69]. It is unlikely that weed suppression through allelopathy could be directly used in broccoli, but varieties bred with increased glucosinolate levels in vegetative tissues could be part of a long-term weed control strategy in crop rotations.

5. Tolerance to mechanical weed control

For field crops such as wheat, selection of genotypes with tolerance to mechanical weed control (especially tine weeders) also has the potential of becoming an efficient component of breeding strategies for weed competitiveness. Especially in reduced-tillage systems, which are known to result in higher weed pressure, mechanical weed control is applied more frequently. Tillage systems have a direct effect on soil-carbon balances, soil organic matter, rooting depths, and loss of topsoil by wind and water erosion. Types of tillage systems include no tillage, minimum tillage and deep ploughing. Many no tillage systems are dependent upon herbicides, so that while soil erosion and carbon losses are reduced, herbicide usage is often essential. However, in reduced or minimum tillage systems, herbicide-free protocols are feasible [70,71] and could be further implemented into organic farming if varieties with increased competitiveness and/or resistance to mechanical weed control were available. In many low-rainfall regions of the world (less than 400 mm per year), stand establishment is the most important factor affecting winter wheat grain yield [72]. Early ground cover is one aspect vital to weed suppression [73] and this trait can be introduced into wheat varieties and was shown to provide a competitive advantage over early emerging weeds and increased resistance to mechanical weeding operations [74]. In wheat, emergence is strongly influenced by coleoptile length, a moderately heritable trait that can be effectively incorporated into modern varieties through breeding [72,75,76].

Several studies have demonstrated that the best varieties for reduced tillage and no tillage systems are also the best varieties for conventional tillage systems [77–79]. Results from these studies suggest that tillage system does not need to play a role in varietal selection. Hall and Cholick [80], however, found significant variety × tillage interactions for grain yield over two tillage systems, and suggested that selection under no tillage conditions should be considered to develop spring wheat varieties for no tillage systems. Additionally, in a study on the effect of mechanical harrowing on spring wheat, a genotype × treatment interaction was found with weed weight per plot as a response variable [60]. Six varieties showed improved WSA, three had reduced WSA and ten had reduced yield under the mechanical tillage treatment [60].

Physical damage to wheat plants from mechanical weed control may cause significant yield reduction [81]. Mechanical weed control is usually done with tine weeders early in the season, supplemented in some regions by inter-row cultivation. The ability to tolerate damage and/or a rapid recover following mechanical weed treatments is therefore an important trait for varieties used in organic and low-input systems [60,82].

6. Resistance to major seed-borne diseases

Resistance to seed-borne diseases in organic seed production is an important issue as few seed treatments are permitted for use under organic farming standards. Dwarf bunt (*Tilletia controversa*) and common bunt (*Tilletia tritici* syn. *T. caries*) are major diseases of winter wheat that occur in many areas of the world where winters are relatively mild but regularly have a persistent snow cover. A long period of stable cool temperatures and high humidity provided by the snow cover induces soil-borne teliospores of the fungi to germinate and eventually produce hyphae that infect seedlings during winter. As a rule, infected plants are dwarfed and have an increased number of tillers. The disease replaces the kernel with a fetid sorus filled with teliospores.

Common bunt, the most important disease of wheat in the period early to mid 1900s [83], is now effectively controlled by fungicide seed treatments in conventional farming. However, these treatments are prohibited under organic certification standards. Potential organic seed treatments (e.g., Tillecur) show varying degrees of effectiveness but are additional inputs and increase production costs [84,85]. In organic production it would therefore be a crop health and economical advantage to use varieties with resistance or tolerance to common bunt and dwarf bunt [86]. Common bunt has the potential of becoming an economically devastating disease for organic farmers (especially those using farm-saved seed) unless an effective organic seed treatment is developed or genetic resistance is incorporated into wheat varieties used in organic systems [87].

Valuable breeding achievements have been made in developing wheat varieties with enhanced resistance to common bunt by introgression of major race-specific resistance genes (Bt1–Bt13) [88,89]. However, little research has been done to identify non-race-specific resistance or tolerance to common bunt. In a recent study, Fofana et al. [90] detected three quantitative trait loci associated with common bunt resistance that might be a good source of durable bunt resistance or tolerance.

Seed-borne diseases of tomato include tomato mosaic virus (ToMV), bacterial speck and bacterial spot (caused by *Pseudomonas syringae* pv. *tomato* and *Xanthomonas campesiris* pv. *vesicatoria,* respectively) and fungal pathogens such as *Clavibacter michiganensis*. Whereas ToMV has about the same magnitude of threat to conventional and organic tomato production, bacterial and fungal diseases are a more serious problem in organic systems because the use of fungicides and antibiotics (other than sulphur- and copper-based products) is prohibited. The two basic strategies to control seed-borne diseases in tomato are: (1) the use of seed treatments (e.g., antagonistic micro-organisms, compost extracts, fermentation, acids and acidified nitrite), and hot water treatment, and/or (2) the use of resistant varieties. Resistance to bacterial speck and bacterial spot is available in commercially used tomato germplasm and should be more widely incorporated into tomato varieties bred for organic systems. ToMV can be a major problem in greenhouse-grown tomatoes because the virus is stable and easily spreads through handling. Seed treatment to inactivate the virus does not work well, particularly if the virus is present in the endosperm of the seed. Resistance is the preferred method of control and has been incorporated into a wide range of commercial materials. The most widely used form of resistance (*Tm-2*^{2}) was derived using embryo rescue from *Solanum peruvianum* [91]. Another resistance gene (*Tm-1*) that provides resistance against the predominant strain of ToMV was transferred from *S. habrochaites* without the use of special crossing techniques such as embryo culture [92]. As such, *Tm-1* would be the preferred source of resistance to incorporate into varieties developed for organic production systems.

The major seed-borne disease of broccoli is black rot (caused by *Xanthomonas campestris* pv *campestris*). As in tomato, it can be controlled with antibiotics and copper treatments in conventional production systems. The best option for organic production would be the use of resistance. Incomplete resistance is found in *B. oleracea*, but more complete forms of resistance have been identified in *B. napus* and *B. carinata* [93]. Early attempts to introduce resistance from *B. carinata* into *B. oleracea* were made using somatic hybridization, and recently *in vitro* embryo culture was used to introgress resistance [93].

7. Resistance to other fungal and bacterial diseases

Tolerance to diseases that may cause injuries and are likely to affect plant health and quality is crucial for minimizing the gap between yield potential and actual yield. This applies to conventional high-input as well as to low-input or organic farming.

In Europe, resistance breeding in wheat is focused on the most serious foliar diseases in conventional wheat production systems including Septoria, rusts and to a lesser extent powdery mildew and stem-based pathogens associated with lodging. Duveiller et al. [94] highlighted the effect of changing environmental conditions on the development of foliar disease epidemics in wheat. Climate change is likely to modify the wheat disease spectrum in some regions, and pathogens or pests considered unimportant today may turn out to be potential new threats in future. For example, necrotrophic pathogens (e.g., spot blotch or Septoria) and Fusarium head blight may increase in importance in many areas of northern Europe. While the severity of lodging and powdery mildew was shown to decrease in organic farming systems, the importance of Septoria was reported to increase in UK (e.g., [95]). Resistance to Fusarium head blight is of special importance to minimize the risk of Fusarium toxins in the grain, whereas breeding for root disease resistance has been of minor importance. Fusarium resistance is particularly important in areas where climatic conditions and/or agronomic practices (e.g., where minimum tillage is used and/or maize is grown in rotation with wheat) are favourable for Fusarium development.

Resistance breeding combined with appropriate management approaches (e.g., diverse rotations, timely sowing, and improved irrigation methods) can minimize losses caused by such pathogens. For example, in South Asia it was shown that the effect of spot blotch, a devastating foliar disease of wheat caused by *Cochliobolus sativus*, can be minimized by reducing physiological stress through timely sowing and adequate use of fertilizers [94]. Dordas [96] reviewed the effect of the nutrients N, P, K, Mn, Zn, B, Cl and Si on disease resistance in sustainable agriculture. At high N levels the severity of infection with obligate parasites increases, while infection with facultative parasites decreases. Silicon has been shown to control a number of diseases [97,98]. Dordas [96] concluded that an adjusted nutrient supply can assist to limit disease severity.

Although a number of diseases may affect broccoli regionally, head rot, caused by a complex of soft rot bacteria (*Erwinia* and *Pseudomonas* spp.), can cause problems whenever water accumulates on the developing broccoli head. Genetic variation in head rot resistance exists in broccoli and is associated with smooth, domed heads and small, tight beads [99]. Blackleg (*Leptosphaeria maculans*, formerly *Phoma lingam*), and Alternaria (caused by various *Alternaria* spp., but mainly *A. brassicola*) are two diseases that cause significant economic losses in Europe and eastern USA where pesticide-based control options used by conventional growers are not available to organic growers [4]. Hot water treatment can be used to disinfect seed, but the technique is not completely reliable and may reduce germination [100]. Differences in genetic resistance have been observed among various *Brassica* species, and this resistance needs to be transferred into a *B. oleracea* background.

Tomato diseases such as *Fusarium oxysporum* f.s. *lycopersici* and *Verticillium dahliae* may be of less concern in organic systems compared with their impact on conventional ones due to the suppressive effects of organic matter based fertilization regimes [101]. Other ones, such as various viruses (ToMV, and tomato spotted wilt virus – TSWV) are more universal, or occur regionally (TSWV) independent of production system. Whereas late blight (*Phytophthora infestans*) can occur in conventional and in organic systems, it is of less concern in conventional systems because of the greater choice and efficacy of fungicides available compared with organic systems, where only protective copper-fungicides can be used. This has led to emphasis on breeding for late blight resistance in tomato intended for organic systems [102,103]. Late blight is usually most severe in early spring and late summer or fall when environmental conditions favour disease development. Early-spring infections are generally reported from high-tunnel production systems, whereas fall infections are typically found in the field. Several sources of resistance for late blight are known [104]. Some forms of resistance are qualitative and confer resistance to specific races whereas other ones show quantitative effects. Oregon State University started to combine the *Ph-2* resistance gene with quantitatively inherited genes derived from *S. habrochaites* as well as with *Ph-3* resistance genes [103].

8. Insect resistance

Because insecticides are not permitted under organic farming standards, organic growers apply alternative measures. Examples of cultural management tools are e.g., the establishment of beetle banks to maintain high predator or parasite populations; companion plants to repel or distract pests; mass trapping systems, pheromone-based mating disruption. But also alternative treatments can be applied (e.g., Bt) and barrier-based approaches to control invertebrate pests (most importantly the use of insect-proof netting).

For example, many *Brassica* vegetable growers rely on row covers in early season to prevent cabbage fly infestation (*Erioischia brassicae*), flea beetle (*Phyllotreta* spp.), and lepidopteran pests (*Plutella xylostella*, *Pieris rapae*), and biological control products (Bt and Spinosad) are widely used to control lepidopteran pests (e.g., diamond back moth) and aphids. Aphids (*Brevicoryne brassicae*, *Lipaphis erysimi*, *Myzus persicae*) are often a problem in autumn and on overwintering plants. Epicuticular wax may be positively or negatively associated with insect pest populations. Specifically, glossy (waxless) variants of white head cabbage (*B. oleracea*) showed less damage from lepidopteran pests, reduced whitefly (*Aleyrodes brassicae*, *Bemisia tabaci*) populations and resulted in fewer eggs laid by cabbage maggots [105]. Flea beetle damage was higher on glossy plants, and both an increase and a decrease in aphid populations have been reported. One hypothesis is that insect predator species are able to traverse all leaf surfaces and encounter insect prey [106,107], but other factors such as wax composition and colour may influence insect herbivory and ovipositor behaviour [108]. The glossy phenotype has been associated with reduced tissue damage from thrips [105], but recent research showed a positive correlation between wax layer thickness and cabbage root fly infestation in white head cabbage [109]. Thrips is a major and increasing problem in the Netherlands and is currently studied in a pre-breeding programme of Plant Research International in Wageningen, The Netherlands. Whereas waxless variants have been extensively studied in relation to insect behaviour, over-expressing waxy variants have received little research attention. It may be that both ends of the wax production spectrum have arthropod deterrent properties. The waxless trait would have its best application in glasshouse production environments where only thrips and no other pests are the predominant problem.

9. Tolerance to abiotic stress

Breeding for tolerance to the abiotic stresses is another important issue. Apart from nutrient stress resistance (see above), drought, salinity, aluminium toxicity and heat stress are other important abiotic stress factors that cause yield reductions [110]. With climate change, the importance of drought and the area of irrigated land with saline soils are expected to increase significantly. Breeding for drought and salinity tolerance has proved to be difficult [111] as the mechanisms of tolerance are very complex and poorly understood [110,112,113]. Nevertheless, drought tolerance, water-use efficiency and heat stress tolerance are already considered major breeding goals for wheat production in marginal regions [113]. There are good chances for improving salt and aluminium tolerance in wheat breeding material via introgression of resistance genes identified in wild relatives [114].

Tolerance to abiotic stresses is important not only for organic but also for conventional agriculture. In some cases such as drought stress, organic farmers may give higher priority to such traits as they want to build up a system that is less dependent on inputs.

10. Quality

10.1. Bread-making quality

Only a limited number of studies have focused on quality aspects of organic wheat production [115–118]. This trait is of particular concern to organic farmers and consumers since protein content (an important factor affecting bread-making quality) in organic cereals tends to be lower due to the difficulty and costs of foliar application of inorganic-N fertilizers applied later in the growing season. A higher protein content and/or quality without the need for late season N inputs are therefore major breeding objectives. However, new varieties should be particularly suitable for wholemeal-bread making and artisan baking processes, combining sensory and nutritional qualities (e.g., increased levels of micronutrients) as the consumers of organic bread expect highest organoleptic quality.

The definition of wheat quality differs depending on market class and on the desired baking product. Quality parameters correlated to bread-making quality include protein content, protein quality, single kernel hardness, SDS sedimentation, ash content, Hagberg falling number, flour colour, dough and gluten strength, single kernel size and full baking and milling tests [119]. These tests were designed for the assessment of grain from conventional production and focus on assessing its suitability for white bread produced in large-scale industrial baking processes (e.g., the Campden and Chorleywood process widely used in the UK). More emphasis is needed on the development of tests to assess bread-making quality for wholemeal bread and artisan bread-making processes (including sour dough based bread production) often used by smaller bakeries [118,120].

Grain protein content is one of the most important factors determining overall bread-making quality. Some studies have found no difference in grain protein content between varieties from organic and varieties from conventional systems [121–123]. However, other studies have shown higher levels of protein in conventional compared with organic systems [124,125]. Grain protein content is highly dependent on climatic conditions and available soil-N, especially late in the growing season during grain filling. SDS, a measure of gluten strength, has been shown to be lower in organic than in conventional crops [123] and to increase with increasing N supply [126–128]. Recent studies indicate that organic fertilization regimes, while reducing protein content, will improve other bread-making quality related parameters, such as protein composition, the gliadin to glutenin ratio, acetic acid soluble proteins, starch quality and length of amylopectin chains, diameter of starch granules, pentosan content, α-amylase activity, and water absorption [129,130]. However, according to reports from bakers in several EU countries, this often does not compensate fully for the reduction in protein content. So more research is needed on the exact contribution of these parameters to the overall bread-making qualities before designing selection protocols based on the most important parameters for future organic wheat breeding programmes.

10.2. Nutritional value

The demand for organic products is partially driven by the belief that organically grown products are healthier and more nutritious than conventionally grown products [131]. It is therefore important for a plant breeder developing varieties for the organic sector to also select for nutritional quality parameters. Significant variation in mineral and vitamin contents exists among varieties within crops, and nutritional quality is often dependent on specific management practices [132].

For example, for wheat, differences in mineral content and/or mineral bioavailability among genotypes have been reported for iron, zinc and other micronutrients [133–135]. Grain micronutrient content can also be influenced by environmental and soil conditions, including soil organic matter, pH, and the bioavailability of soil minerals [136–138]. Soils with a low pH have been shown to reduce uptake of the macronutrients Ca and Mg and to increase uptake of the micronutrients zinc, manganese and iron [138]. Genotype × environment interactions should therefore be considered when developing breeding programmes that focus on nutritional quality parameters, since selection under specific soil conditions may allow further optimization of nutritional quality.

Similarly, for broccoli, heterogeneity exists for important nutritional components (e.g., vitamin C, carotenoids, flavonoids, and glucosinolates) [139] and some breeding programmes already select for improved contents of these nutritionally desirable compounds.

The traits associated with tomato fruit quality depend very much on the market type. In general, higher levels of carotenoids (lycopene, beta-carotene), vitamin C, and flavonoids are considered beneficial. Tomatoes are a major source of carotenoids and vitamin C in the diet, but rank fairly low compared with other vegetables for flavonoids. The Oregon State University (OSU) programme has developed tomatoes with anthocyanin levels around 80 mg/100 g fresh weight by combining two genes (*Aft* and *atv*) originally introgressed from wild species [140]. If combined with a third gene (*aw*), anthocyanin but not flavanol accumulation is suppressed, producing tomato fruits with a normal colour but with a greater biological activity associated with flavonoids [141].

Although flavour is one of the most difficult traits to breed for, tomato breeding programmes often include selection steps designed to improve flavour. Growers will state that tomatoes need to have good flavour, but cannot agree on what good flavour implies. It is easier to define bad flavour – soft mealy texture, bland taste with low sugar content or a bad balance of sugar to acid ratio [142,143].

11. Current breeding programmes for organic and low-input wheat production

Wolfe et al. [6] differentiated three different potential approaches to obtain crop varieties suitable for organic agriculture: (1) breeding programmes focused on the needs of conventional agriculture where selection is carried out under conventional farming conditions, an approach requiring farmers to test varieties and select the ones that perform well under organic conditions, (2) varieties derived from conventional breeding programmes where crosses and early selection are focused on traits required in conventional systems, but where later or advanced breeding generations are evaluated and selected under organically managed farming conditions, and (3) varieties derived from breeding programmes where crosses and selection strategies focus on traits demanded by the organic sector and selection is carried out in the background of organic farming conditions. The level of breeder-driven and farmer-driven activities may differ in these three breeding approaches. In addition, there are also farmers who use their own selection programmes, often based on older (regional) varieties or landraces.

11.1. Breeding programmes for organic agriculture (selection under organic farming conditions in advanced generations)

Several commercial wheat breeding companies in Europe have dedicated part of their breeding efforts to breeding programmes for low-input and organic agriculture. For example, Saatzucht Donau GmbH & CoKG in Austria currently uses two different early generation selection methods for wheat: (1) pedigree selection under low-input conditions; and (2) bulk populations with individual ear selection under organic conditions followed by selection under low-input conditions in advanced generations. First, yield trials are conducted parallel under low-input and organic conditions allowing a classification of the breeding material for further selection for organic or conventional agriculture. So far, seven winter wheat varieties have been released in Austria after exclusive organic VCU testing [16].

The private breeding company Saatzucht Schweiger GbR in Germany compared the performance of their varieties under organic and conventional conditions and identified the limited-N availability in organic systems as a specific problem to combine high yield and good baking quality. In these trials one of their varieties showed similar bread-making parameters under organic and conventional farming, but the most relevant parameter, i.e., baking volume, was below the limit under conventional and well above the limit under organic conditions. It was concluded that this variety can produce superior bread qualities under organic conditions only. For future organic breeding programmes, improving baking quality and gluten content are seen as key objectives [144].

In France, some publicly funded wheat breeding programmes started to select under organic and low-input conditions. For example, INRA started an organic farming focused winter wheat breeding programme in 2003 [145,146]. In a variety trial comparing the performance of winter wheat varieties under (1) low-input and (2) organic agricultural regimes in the three main macro-climatic regions (four-year trials) in France that are important for wheat production, INRA showed that some varieties selected under INRA's low-input regime – in contrast to the varieties derived from high-input selection – had similar ground cover, speed of crop establishment (traits correlated to weed suppressiveness) and bread-making quality characteristics (protein content, gluten index, baking tests), but often higher grain yields than varieties selected under and developed specifically for organic production conditions in Switzerland, Germany and Austria [146]. To improve selection of varieties best adapted to organic farming (good response to low levels of nutrients, good competitive ability against weeds, etc.), they proposed a global selection index that takes into account yield, quality (alveograph W and protein content) and weed competition (crop canopy height and wheat ground cover) to optimize results [146].

11.2. *Breeding programmes within organic agriculture (selection under organic farming conditions in all generations)*

Only a few private or publicly funded breeders conduct wheat breeding exclusively under organic conditions. Getreidezüchtung Peter Kunz (GZPK) in Switzerland has been breeding wheat and spelt for 25 years. This company focuses on combining (1) resistance to diseases that remain a problem in organic and low-input systems (i.e., Septoria, Fusarium, rusts, bunt), (2) resistance to abiotic stress factors (drought and low nutrient levels) and (3) quality traits related to high bread-making quality [147]. In order to reach these breeding goals, hundreds of crosses were made between traditional and older long-straw varieties from German and Swiss breeding programmes and modern high performance wheat varieties in order to combine the good characteristics of older and modern varieties. Progenies are selected under organic and low-input conditions in all stages of the breeding process. So far 10 winter wheat varieties have been successfully released.

In Germany, Getreidezüchtungsforschung Darzau, Keyserlingk-Institute and the Getreidezüchtungsforschung Dottenfelder Hof have breeding programmes where crosses are designed to combine traits required by the organic sector and selection is done under organic farming conditions only.

Whereas there are a range of ongoing breeding programmes for organic winter wheat, there is currently limited focus on the development of organic spring wheat breeding programmes, in spite of the fact that in Europe the proportion of spring wheat grown is larger in organic production systems than in conventional farming. This is mainly because breeding companies do not have budgets and facilities (land managed to organic farming standards) to develop separate spring wheat selection programmes under conventional high-input and organically managed conditions, since the overall market potential for 'organic' spring wheat varieties is still too low [10,148]. Due to the absence of specific organic spring wheat selection programmes, no new spring wheat varieties have come onto the market that are suitable for organic farming in many European countries. For example, in the Netherlands organic bread wheat production relies almost entirely on a single spring wheat variety (Lavett) that was developed more than 15 years ago [149].

Washington State University has an extensive ongoing wheat breeding programme (funded by industry, state and federal government sources) focused on the development of varieties for organic and low-input systems [5,150]. A range of existing genotypes, including traditional landraces, modern varieties and wild wheat species are currently being crossed and the progenies selected for optimal grain yield and baking quality, enhanced nutritional value, and improved nutrient-use efficiency and weed competitiveness under organic farming conditions [5,150]. The decision to breed wheat under certified organic conditions in all generations came about from a study in which Murphy et al. [5] demonstrated that the highest yielding soft white winter wheat genotypes in conventional systems are not the highest yielding genotypes in organic systems. As a consequence, breeding for higher yields in organic systems will require direct selection within organic systems rather than indirect selection in conventional systems. In four of the five organic systems direct selection produced yields that were from 5 to 31% higher than the yields resulting from indirect selection [5].

For tomato, Oregon State University breeding programme focuses on varieties suitable for the maritime environments of the Pacific Northwest USA where the challenges are primarily the low growing temperatures. Varieties developed in this programme are early maturing, determinate, and parthenocarpic, i.e., traits that increase productivity under suboptimal growing conditions. In 2005, with funding through the Organic Seed Partnership, tomato breeding for organic systems began with the emphasis on developing open-pollinated varieties with improved late blight resistance. Selection has been based primarily on late blight resistance along with fruit characteristics and was performed under organic growing conditions. Selection for adaptation to organic production has been achieved by selection for productivity without knowing what specific traits provide that adaptation and productivity. In Europe, several small organic tomato breeding programmes are being ran that focus e.g., on late blight [102] and taste [143].

For Brassicas, broccoli is the main example of participatory breeding programmes focused on the organic sector. Such programmes exist in Brittany (France) [151] and at Oregon State University; these will be discussed below.

12. Breeding approaches

Many of the selection approaches that are used in conventional breeding programmes can also be utilized in organic farming focused breeding programmes. For example, for wheat this includes the development of inbred lines using a variety of methods, including pedigree selection, single seed descent, modified pedigree-bulk selection, phenotypic and molecular marker-assisted selection, and participatory breeding.

12.1. *Sources of genetic diversity*

The creation and exploitation of genetic diversity is the main requirement for successful plant breeding. Breeders differentiate between the primary gene pool (elite breeding lines), the secondary gene pool (landraces, lines not adapted to local conditions or gene bank material) and the tertiary gene pool (related species or wild relatives). Wheat breeders have significantly improved wheat performance by exploiting the genetic variability within the primary wheat gene pool. In order to maintain future genetic progress, Trethowan and Mujeeb-Kazi [152] suggested to explore additional sources of genetic variation such as synthetic wheat varieties and landraces, and introgression of genes from related species. For example, synthetic hexaploid wheat, derived by crossings of tetraploid wheat with *Aegilops tauschii*, was shown to provide new genetic variability for resistance to drought, high temperature, salinity, waterlogging, and soil micronutrient imbalances from the secondary wheat gene pool. Synthetically derived materials have performed well in many high stress environments globally. According to Trethowan and Mujeeb-Kazi [152] there is also significant unexploited variation among landraces and modern wheat varieties. The tertiary gene pool, with a few significant exceptions, has been more difficult to exploit due to complex inheritance, meiotic instability, and an associated linkage drag of undesired traits. Nevertheless, related species have proved to be a very valuable source for the introgression of resistance genes in the wheat breeding material [153,154].

12.2. Exploiting genetic variation within varieties

Genetic variation within released wheat varieties is relatively small, because (1) wheat is a self-pollinating species and (2) homogeneity is an essential requirement for variety release. An alternative method employed by Phillips and Wolfe [155], maintaining genetic diversity and evolutionary fitness within varieties, is to create composite cross populations. Composite cross populations are formed by assembling seed stocks with diverse evolutionary origins and characteristics, recombination of these stocks by cross pollination, the bulking of F_1 progenies, and subsequent propagation of the bulked progenies in successive natural cropping environments. Natural selection takes place if more adapted genotypes produce more progenies than less adapted ones. Composite cross populations can provide dynamic gene pools, which in turn provide a means of conserving genetic resources *in situ*. They can also allow selection of heterogeneous crop varieties. According to Phillips and Wolfe [155], composite cross populations may have the potential to allow evolutionary changes based on biotic and abiotic environmental interactions and might be an alternative for selecting superior pure lines especially for low-input systems characterized by unpredictable stress conditions. The effect of natural selection on composite cross populations of wheat was demonstrated by David et al. [156] by analysing the shift in protein patterns after several generations of cultivation in different macro-environments in France. However, further research is needed to verify the superiority of this strategy with respect to tolerance to abiotic and biotic stress under commercial cultivation, considering also the demand of the market for uniform high bread-making quality of wheat and the demand of the farmers for higher yield in organic farming. The development of genetically diverse varieties is strongly prevented by present laws like the Union for the Protection of New Varieties (UPOV) guidelines, EU rules (Regulation 2100/94/EC) or the Plant Varietal Protection Act (PVPA) in the USA, which require that a variety must be phenotypically uniform, stable and distinguishable from other varieties in order to be officially released. Political efforts are undertaken to change this strict legislation.

Multiline varieties and variety mixtures can also provide functional diversity that limits pathogen and pest expansion in cereals and other crops [157]. These approaches also reduce the risk of resistance breakdown, which was due to a range of mechanisms including barrier and frequency effects as well as induced resistance. Also, differential adaptation, i.e., adaptation within races to specific host genotypic backgrounds, may prevent the rapid evolution of complex pathotypes in mixtures [157]. Therefore, yield stability (i.e., consistently high yields over a range of environments) in wheat is commonly greater in mixtures than in pure stands [3]. The wide application of variety mixtures in organic farming is constrained by the concern of farmers and processors about the anticipated negative effect on the homogeneity of the wheat quality. However, if the mixture components are carefully designed and have already been selected for desired traits in the breeding progress, product quality may be equal to or higher than that obtained in pure stands [3]. Nevertheless, there is still a risk that due to genotype × environment interaction unacceptable heterogeneity may occur under different environments.

12.3. Participatory plant breeding

Participatory plant breeding (PPB) programmes originated in developing countries to meet the needs of low-input, small-scale farmers in marginal environments that are not targeted by commercial breeding companies [158]. PPB involves breeders, farmers, as well as consumers, extension specialists, vendors, industry, and rural co-operatives in plant breeding research. It is termed ‘participatory’ because all stakeholders can influence all major stages of the breeding and selection process. These stakeholders become co-researchers as they can help to set overall goals, determine specific breeding priorities, make crosses, screen germplasm entries in the pre-adaptive phases of research, take charge of adaptive testing and lead the subsequent seed multiplication and diffusion process [159]. The fundamental rationale for PPB programmes is that joint efforts can deliver more than when each actor works alone and focuses only on specific objectives.

Due to the special need of farmers for varieties suitable for organic farming and due to the small organic market not always being attractive for commercial plant breeders, this approach gained greater attention in breeding programmes for organic farming systems [149,160]. In conventional systems, inorganic fertilizers and synthetic crop protection chemicals often encourage homogeneity across a diversity of agro-environments. Organic and traditional low-input farms are often more heterogeneous, and experience greater diversity of weed, pest and disease pressure and use more diverse rotational designs and soil management, tillage, fertilization and crop protection protocols. To develop varieties suitable to these diverse agro-environments it is essential to integrate evolutionary breeding [161] with strong participatory selection components [150,160]. This type of breeding strategy utilizes a combination of natural selection (survival and more progenies of the fittest genotype due to adaptation to local conditions) and farmer selection (active selection of genotypes that fit the defined breeding goals) to develop varieties with optimal adaptation to specific organic farming systems. Such integrated breeding approaches are known as evolutionary participatory breeding (EPB) [150], which utilizes the skills and knowledge of both breeders and farmers to develop heterogeneous landrace populations, and has demonstrated to be an effective breeding method for both traditional and modern farmers throughout the world [150].

For example, for broccoli, the Oregon State University (OSU) programme has a breeding project focused on developing open-pollinated (OP) broccoli varieties for organic production using a farmer participatory approach. The rationale for the project is that recently very few OP broccoli varieties have been developed with the productivity and quality traits available in F_1 hybrids. In addition, few of the contemporary varieties have been bred in and for organic systems. Many organic growers would like a broccoli variety that is well adapted to their individual system and environment, and one of which they can save their own seed. After assemblage and random mating of the initial population an EPB programme was initiated. Seed of the OP population was distributed to participating farmers who grew and selected the most productive plants at their location, then allowed them to intercross, and produce seed. A portion of the seed was returned to OSU, where samples received would be combined and then redistributed to farmers in the next growing season. With support from the Organic Seed Partnership, three cycles were completed by 2009. Current efforts are focused on working with specific farmers and institutions to reduce the variability in the population for economically important traits using plant to row half-sib selection with the intention of developing varieties that are specifically adapted to grower's site-specific conditions.

12.4. Indirect phenotypic selection methods

Breeding for biotic stress resistance in wheat still relies mainly on phenotypic selection protocols using natural or artificial infection pressure. However, quantitative resistance to several key diseases in wheat is difficult to assess reliably by phenotypic assessments (especially in early stages of plant development) and requires expensive experimental approaches [162]. Some morphologic traits have been described that correlated with quantitative biotic or abiotic stress resistance. These included leaf tip necrosis as an indicator for leaf rust resistance [163], stem thickness for lodging resistance [164,165], cuticular wax and stem length as indicators for Septoria resistance [166], and vigorous early growth as indicator for weed competitiveness and nutrient-use efficiency. However, indirect selection for such morphological traits has not yet been widely implemented in plant breeding programmes. Further applied research is therefore needed to verify the selection gain in a wider range of wheat germplasm.

12.5. Molecular marker selection

With the advent of molecular markers it became possible to dissect quantitatively inherited traits into single genes. For wheat, the identification of such quantitative trait loci (QTL) using segregating populations of parents with contrasting resistance phenotypes [163], has proved to be difficult, due to the complex hexaploid genetics of wheat [167–169]. However, QTL for resistance to several diseases (e.g., leaf rust, Fusarium head blight, common bunt, Septoria) have been identified in hexaploid wheat. Presently, the implementation of marker-assisted selection into commercial wheat breeding programmes is still limited and restricted to marker-assisted backcross breeding for the introgression of major genes from unadapted material or the pyramidization of resistance genes. However, the rapid development of new, cost-efficient, high-throughput marker systems as well as great improvement of association mapping is expected to allow better coverage of the wheat genome and may improve the ability to identify QTL for oligogenically inherited traits of interest to organic and low-input systems, as well as for the monitoring of the level of genetic diversity present in the wheat germplasm [170–172]. At Oregon State University, breeding for late blight resistance has used pedigree selection under disease pressure. A marker-assisted breeding approach has been used to develop high-flavonoid tomato lines. More than 50% of the sequenced tomato genome has been assembled (http://sgn.cornell.edu/about/tomato_sequencing.pl; accessed 23 March 2010) and as annotated sequence becomes available, it will be possible to identify and directly select candidate genes.

13. Evaluation of breeding methods

Another issue that has to be taken into account with respect to appropriateness of applied breeding methodologies for organic agriculture is their relative acceptability under organic farming principles (e.g., [151,173]). Under current organic farming regulations in the USA and Europe, genetically engineered crops are prohibited from use in organic production. However, it is currently unclear how to deal with techniques that are included in the definition of genetic engineering according to the IFOAM norms [174] but not in the EC directive on genetic engineering, such as cell fusion for introducing cytoplasmic male sterility (CMS) from other species to ease the F_1 hybrid production as applied, e.g., in Brassicas (e.g., [175]). Somatic hybridization has been used to transfer the *B. oleracea* nucleus into radish cytoplasm [176], in order to achieve the most widely used form (Ogura) of CMS. The original Ogura CMS was not economically useful because the CMS lines exhibited low temperature chlorosis. It was not until further *in vitro* manipulation that replaced the radish chloroplast genome with the original parental species that temperature insensitive CMS lines were developed [177]. Many broccoli hybrids currently on the market are produced on male sterile mother plants derived from such cell fusion [178], and it is difficult for growers to obtain information on the breeding history as declaration is not mandatory. In contrast to the cell fusion derived sterility, F_1 hybrid seed of broccoli can also be produced using the natural sporophytic self-incompatibility (SI) system, preventing self-pollination of the mother plants. However, the expression of the SI system depends on the environmental conditions during flowering and does not result in 100% F_1 seeds as obtained by the cell-fusion derived CMS system. Broccoli can be selfed manually using bud pollination or CO_2 treatment. Most modern material for F_1 variety development has been subjected to inbreeding and there are inbred lines that are self-fertile. Breeding programmes use a combination of inbreeding to develop inbred lines, then combining these to produce F_1 hybrids. Broccoli is relatively easy to culture *in vitro* and can be transformed. It is also possible to produce doubled haploids through anther culture. Therefore, genetic engineering, cell fusion and other techniques can be extensively used in conventional breeding programmes of these *Brassica* crops, resulting in varieties that are not in agreement with the organic principles. Without special breeding efforts for the organic sector, there is a great risk that in future the needs of organic farmers will not be met.

In tomato, the seed companies commonly rely on hand labour to produce F_1 hybrid seed. Most contemporary commercial tomato varieties are hybrids, but many organic growers in the USA and some small growers in Europe want to be able to save their own seed. Because tomato is highly self-pollinated, it is possible to develop and release pure lines that can be propagated by seed. There will be a need for both types of varieties, depending on market demands and needs of the grower.

In wheat, natural CMS is available for F_1 hybrid seed production, but hybrid varieties of wheat are of minor importance.

14. Discussion and conclusions

Over the last 40 years, organic farmers have mainly aimed at optimizing their farming systems by agronomic approaches. More and more the sector now also aims at genetic improvements to enhance yield stability under low-input conditions. Most of the available information on the differences in performances and requirements of varieties between organic, low-input and conventional high-input agriculture is concentrated on cereals. In this field already several breeding programmes have been established and several varieties have been released on the market. For the vegetable sector, only a few organic farming focused breeding programmes have been started so far, and farmers still largely depend on varieties bred for the conventional, high-input farming systems.

Although many breeding goals are identical for conventional and organic production, such as yield and disease resistance, the priorities can nevertheless be different. This is mainly due to the fact that conventional agriculture is able to compensate for the lack of certain traits via inputs, including inorganic fertilizers and chemosynthetic crop protection chemicals that are not available for use in organic farming systems. Additionally, some genetic traits that are of high priority in conventional systems are needed mainly because of inputs exclusively used in conventional systems (e.g., powdery mildew and lodging incidence in cereals are increased by inorganic-N inputs) and therefore less important for varieties used in organic systems. Therefore the use of breeding programmes that are focused on conventional farming selection priorities can result in varieties that perform well under high-input but fail under low-input and organic conditions.

Many traits desired for varieties for organic and low-input farming systems are required to provide overall yield stability and include morphological and physiological characteristics, such as plant and root architecture, and vigour. Furthermore, the organic sector demands breeding to focus on optimizing soil processes relevant for plant nutrition, soil fertility and crop disease resistance. The currently available literature (see above) already shows the potential of selection for genotypes that can efficiently establish and exploit associations with beneficial soil micro-organisms especially with respect to positive effects on nutrient and water uptake, but also yield stability via improved disease and pest resistance and competitiveness against weeds.

Performance (yield, yield stability, quality) is also linked to tolerance to abiotic and biotic stress, which are complex inherited traits with high genotype × environment interactions, resulting in the 'masking' of the genotypic value of breeding lines. The improvement of all these traits with the limited resources available in organic farming focused breeding programmes is therefore extremely challenging [6,147]

An important strategy to further improve performance and product quality parameters in organic and low-input production systems is to integrate the development of novel genotypes and agronomic approaches. However, there may be significant genotype × environment × management interactions and the organic sector is known to use more variable management systems. For example, winter wheat may be grown (1) in stockless arable rotations (where often two or more wheat or other cereal crops are grown in succession) or (2) as part of more diverse rotations (e.g., on farms that also produce forages for livestock, vegetables, pulses or potato) [10,179–181]. It is therefore more important to evaluate genotype × management interactions in different agro- and pedo-climatic regions as part of organic farming focused breeding programmes than in conventional breeding programmes.

One of the major points of discussion among breeders is whether separate organic breeding programmes are necessary, or can selection under conventional growing conditions also be effective if more attention is paid to certain desired traits? The efficacy of such approaches may differ for different traits. For example, for wheat, indirect selection under conventional high-input conditions is quite effective for traits with high heritability, including early maturity, plant height, and 1000 kernel weight. However, this is not necessarily the case for quantitative traits characterized by high genotype × environment interactions, like grain yield or end-use quality traits [5,16,182]. Based on a study of a segregating spring wheat population tested under organic and conventional farming conditions, Reid et al. [183] clearly demonstrated the superiority of direct selection (under organic farming) compared with indirect selection (under conventional farming) for grain yield and yield components. Therefore it is necessary to select under organic management at least in the advanced breeding generations [183].

In some cases the size of the organic market is too small to be economically attractive for professional breeding companies. Participatory approaches could represent an efficient alternative to develop new varieties for organic farming and should be further developed to reduce the reliance on commercial conventional farming focused breeding companies. However, more recently developed collaborative strategies involving both breeding companies and farmers and other supply chain stakeholder should also be encouraged to utilize commercial breeding expertise and facilities where this is possible. This is an important opportunity not only to integrate farmers' and breeders' knowledge, but also the farmers' and breeders' eye.

Furthermore, it is encouraging that several breeding companies now consider organic as an interesting market to be involved in. This is often based, at least partially, on the anticipation that their existing conventional farming markets will in the future demand varieties with traits that are currently mainly requested by the organic and low-input sector (e.g., nutrient-use efficiency and specific product quality and resistance traits).

Finally, the introgression of traits urgently needed by the farmers to optimize organic farming systems and improve yield stability will also have a positive influence on conventional production systems that aim to reduce agrochemical input use while improving environmental impacts and long-term agricultural sustainability. Breeding for organic agriculture therefore deserves significantly more attention and support.

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