

Review

Evolutionary Plant
Breeding as a Response
to the Complexity of Climate ChangeSalvatore Ceccarelli^{1,*} and Stefania Grando¹

SUMMARY

Climate change is one of the processes that have already overstepped the safe planetary boundaries, together with the rate of biodiversity loss and human interference with the nitrogen and phosphorus cycles. The three processes are related to agriculture and, as such, to both food safety and food security, and ultimately to human health. Adaptation to climate change is a difficult breeding objective because of its complexity, its unpredictability, and its location specificity. However, one strategy exists, which is based on a more dynamic use of agrobiodiversity in agriculture through the cultivation of evolutionary populations. In this review, we show how the translation into agricultural practice of nearly 100 years of research on evolutionary populations and mixtures is able to address the complexity of climate change while stabilizing yield, decreasing the use of most agrochemicals, thus reducing emissions and producing healthy food.

THE COMPLEXITY OF CLIMATE CHANGE

The concept of “planetary boundaries” was proposed in 2009 to define a “safe operating space for humanity” (Rockström et al., 2009). The boundaries include climate change, rate of biodiversity loss, ozone depletion, acidification of the oceans, human interference with nitrogen and phosphorus cycles, global freshwater use, change in land use, chemical pollution, and atmospheric aerosol loading. Three of the nine boundaries, namely, climate change, rate of biodiversity loss, and human interference with nitrogen and phosphorus cycles, have been already crossed (Steffen et al., 2015), together with the use of fresh water (Jaramillo and Destouni, 2015).

The three processes affect agricultural productivity, and in fact there has been already a decline in crop resilience as recently shown in the case of wheat in Europe (Kahiluoto et al., 2019). However, the argument of resilience is still debated as Piepho (2019) disputed the previous claim and a new methodology to estimate resilience has been recently proposed (Zampieri et al., 2020).

In the case of climate change, it is recognized that projections of future climate change and its impacts are uncertain (IPCC, 2018), which makes crop adaptation to climate change a difficult breeding objective. The difficulty is made even greater because changes in temperature and rainfall influence the spread, growth, and survival of crop pathogens (Rosenzweig et al., 2001). There are several examples of interactions between climate change, crop development, and both pests and their natural enemies (Heeb et al., 2019). Zavala et al. (2008) showed how elevated CO₂ increases the susceptibility of soybean to an invasive insect, whereas Deutsch et al. (2018) estimated 10%–25% global yield losses per degree of global mean surface warming of three staple grains, rice, maize, and wheat: this is because individual insect’s metabolic rate accelerates with the increase of temperature and an insect’s rate of food consumption must rise accordingly. Furthermore, the number of insects will change because population growth of insects also varies with temperature. Pollinators such as bumblebees are also affected by climate change as it is shown by the range shift in bumblebee species (Kerr et al., 2015). Newton et al. (2011) and Pautasso et al. (2012) reviewed several studies showing the complexity of the interactions of each component of the host-pathogen relation, and how these interactions are affected by climate change, thus representing another area of uncertainty in predicting the effects of climate change. Climate change affects the adaptation and the spreading of weeds as well as an increased risk for the evolution of herbicide-resistant weeds (Ziska and Dukes, 2010; Colautti and Barrett, 2013; Matzrafi et al., 2016). The expansion of the geographical ranges

¹Independent Consultant,
Corso Mazzini 256, 63100
Ascoli Piceno, Italy

*Correspondence:
ceccarelli.salvatore83@gmail.
com

<https://doi.org/10.1016/j.isci.2020.101815>



of several important insects, weeds, and pathogens has been documented in the United States (Rosenzweig et al., 2000).

In addition to affecting diseases, insects, and weeds in a largely unpredictable and continuously evolving way, a further aspect of climate change is represented by the frequency of extreme climatic events such as spells of very high temperatures, torrential rains, and droughts, which, besides affecting crop yields directly, may affect the transmission dynamics of insect pests and plant diseases (Rosenzweig et al., 2001). Tropical storms are additional events, which may contribute to the spreading of diseases (Campbell and Madden, 1990; Lehmann et al., 2020).

The challenge posed by climate change has led terms such as “climate-smart agriculture” (Lipper et al., 2018), “climate-smart crops” (Kole, 2020), or “climate-resilient crops” (Kole et al., 2015) to become popular. However, most of the strategies suggested are based on the identification and incorporation of traits conferring tolerance or resistance to specific biotic or abiotic stresses, failing to recognize the evolving nature of the challenge. This applies also to the attempts to stack tolerance to more than one stress, particularly when this is done in controlled conditions (Menkir et al., 2020). Most of these solutions are “within the capacity for micro-evolutionary change of the parasite” (Robinson, 2009), and several examples of accelerated evolutionary changes in disease organisms, agricultural pests, and weeds have been reported (Palumbi, 2001; McDonald and Stukenbrock, 2016; Böhn and Millstone, 2019). In contrast, spatial and temporal crop diversity can reduce the need to breed for new resistance or to discover new pesticides, given that “each defense sows the evolutionary seed to its own demise” (Tilman and Clark, 2014).

Setting objectives for a breeding program that aims at adapting a crop to climate change becomes therefore a daunting exercise. In fact, it is a case of breeding for multiple objectives. On the one hand, we have abiotic stresses such as high temperature and drought, and on the other we have biotic stresses affected by those abiotic stresses: each of these stresses is a separate breeding objective, which in the real world have to be tackled together. For a situation like this, breeders have standard multi-trait breeding schemes such as tandem selection, independent culling, and index selection (Falconer, 1960), but whose efficiency depends on the correlations between the traits involved, which can change in space and in time. In fact, correlation coefficients have both a genetic and environmental component and their relative strength affects selection efficiency. Multi-objective optimized breeding strategies are being considered as a promising alternative, although based on unrealistic assumptions such as constant heritability (Akdemir et al., 2019). In addition, as we have seen, those multiple objectives are largely unpredictable. By the time one breeding cycle is completed, the objectives set at its inception may have already changed.

Climate change also affects human health both directly owing to the occurrence of heat waves, floods, and fires and indirectly owing to its effects on agriculture, food supply, and diets (Springmann et al., 2016; Cécilelli, 2019). One of the paths connecting climate change with human health is through biodiversity loss (Watts et al., 2018).

Two strategies to cope with climate change are usually discussed in the literature: a mitigation strategy, which relies on the reduction of greenhouse gas emissions and an adaptation strategy based on adapting crops to climate change. D’Amato et al. (2011) and IPCC (2014) suggested ways in which the two strategies can be combined. In this paper, we propose that it is possible to combine the two strategies in crop management by cultivating diversity.

BIODIVERSITY AND HUMAN HEALTH

Biodiversity, and in particular agrobiodiversity, is a key to food security making production systems more resilient (FAO, 2019) and is an essential resource for crop improvement to adapt agriculture to a changing climate and consumer preferences (Hufford et al., 2019). Yet, the very same science, which is based on this resource, namely, plant breeding, is considered to be one of the causes of its decline (van der Wouw et al., 2010). The reduction of diversity associated with plant breeding is somewhat controversial: for example, Landjeva et al. (2006) found that genetic diversity did not decline in Bulgarian winter wheat, whereas Bonnin et al. (2014), using an integrative indicator of genetic diversity developed by Bonneuil et al. (2012), found a decline in the genetic diversity of wheat during the 20th century. Reiss and Drinkwater (2018) reached similar conclusions.

Already in 1950 there was a warning that the “concept of purity has not only been carried to unnecessary length but that it may be inimical to the attainment of highest production” (Frankel, 1950).

At farm level, agrobiodiversity can be in the form of different crops, of different varieties within the same crop, and of heterogeneous (genetically not uniform) varieties. Of 7,000 plant species used for food through the millennia, over the past 50 years, only six crops, wheat, soybeans, maize, rice, barley, and rapeseed, have covered 50% of the arable land (Jacobsen et al., 2015).

The decline in agrobiodiversity that contributes to our food is even more striking: rice, wheat, and maize contribute about 60% of our plant-based calories and 56% of our plant-based proteins (Thrupp, 2000; FAO, 2013) and use nearly 50% of all the water used for irrigation. The most widely grown varieties of these crops are genetically uniform, being pure lines or hybrids, making the reduction of agrobiodiversity even greater.

The decline of agrobiodiversity has two major consequences. First, it makes our crops more vulnerable because their genetic uniformity makes them unable to respond to both short- and long-term climate changes (Keneni et al., 2012) and provides an ideal breeding ground for the rapid emergence of fungicide-resistant variants (Fisher et al., 2018). A recent study shows that, globally, climate variability accounts for roughly a third (32%–39%) of the observed yield variability (Ray et al., 2015). Second, in the last 10 years, medicine has recognized the association of agrobiodiversity with diet diversity and human health (Heiman and Greenway, 2016; Ceccarelli, 2019). In fact, the composition and diversity of the microbiota affects both our physical and mental health (Khamsi, 2015; Hoban et al., 2016), and the diet affects the composition and diversity of the microbiota (Singh et al., 2017). Nutritionists recommend a diet as diverse as possible for having a healthy microbiota (Heiman and Greenway, 2016), but a diversified diet remains a challenge, given the decline in agrobiodiversity described earlier.

Food production is the largest cause of global environmental change being responsible for up to 30% of global greenhouse gas emission and 70% of freshwater use (Willett et al., 2019). Our present food system leaves almost 1 billion people hungry; on the other side, almost 2 billion are eating too much of the wrong food while unhealthy diets account for up to 11 million avoidable premature deaths per year (Lucas and Horton, 2019).

Despite global efforts and after years of decline, the number of people who suffer from hunger has been on the rise again since 2015 (FAO, IFAD, UNICEF, WFP and WHO, 2019).

CULTIVATING DIVERSITY MAY OFFER THE SOLUTION

To cope with the complexity of climate change combined with the need to address heightened demand due to human population increase, food security, food safety, and human health, there is a need to reconsider plant breeding strategies in a way that generates diversity rather than eroding it. One strategy, which is able to maximize genetic gains and crop genetic diversity is decentralized selection, defined as selection in the target environment (TE) (Ceccarelli, 2015). Such a strategy emphasizes specific adaptation and therefore leads to selecting different varieties, each adapted to a specific TE. In terms of selection theory, this allows elimination of genotype $\times$ location (GL) interactions keeping only genotype $\times$ year within location (GY_L) interactions (Allard and Hansche, 1964; Singh et al., 2006). This is important because GY_L interactions are largely unpredictable, and even more so because of climate change, whereas GL interactions can be, to some extent, repeatable and therefore predictable: decentralized selection makes a positive use of GL interactions by selecting different, locally adapted varieties. However, although this is the solution to GL interactions, the solution to GY_L interactions, namely, building the resilience to the unpredictable year-to-year variations can be achieved by growing heterogeneous populations. In fact, heterogeneous populations have the advantage of exploiting both individual and population buffering (Allard and Hansche, 1964). Such a solution responds to the natural selection theory because the fitness of an individual is the result of the interaction of the phenotype with the environment and not an intrinsic feature of either one (Wade and Kalisz, 1991).

There are two types of heterogeneous materials: those known as composite crosses (CC) or evolutionary populations (EP), or bulk populations, are obtained by mixing the F₁ or the F₂ seed obtained by crossing in all or several combinations a number of varieties. We will use the term EP throughout the paper. Those known as mixtures are obtained by mixing the seed of different varieties. Mixtures, in turn, can be either

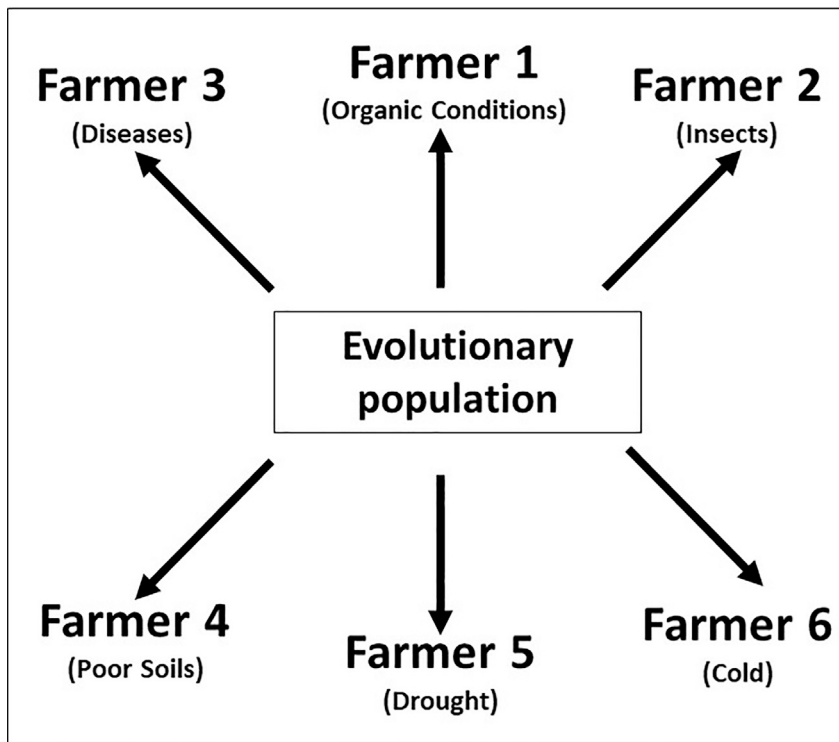


Figure 1. An Evolutionary Population Is Distributed to Different Farmers (Six Farmers Are Shown as an Example) Representing Different Target Environments

Each farmer can, independently, plant and harvest the evolutionary population using part of the seed harvested in the same farm. Each farmer can also use the evolutionary population to start a program of selection as shown in Figure 2. The same would apply to a dynamic mixture.

static or dynamic (Wolfe and Ceccarelli, 2020). Static mixtures are mixtures that are re-constituted from their original component varieties at the beginning of each growing season and therefore cannot evolve. Some farmers, however, prefer to grow mixtures from the seed harvested at the end of the previous cropping season, thus converting them to dynamic mixtures, namely, mixtures that evolve. Because of natural inter-crossing between plants within the dynamic mixtures, in a few seasons, following segregation, recombination, and natural selection, they become populations. Therefore, some of the literature on mixtures is relevant to the issues discussed in this paper.

Decentralized selection can make use of evolutionary populations and of dynamic mixtures as shown in Figure 1, where the evolutionary population or dynamic mixture is distributed to several farmers in different target environments. This is the first step of an evolutionary breeding program that will be implemented as shown below and that has to be based on evolution and decentralized selection in the target environment to express its full potential.

THE SCIENCE OF EVOLUTIONARY POPULATIONS AND MIXTURES

Research on heterogeneous populations started with the original paper of Harlan and Martini (1929) who proposed the composite cross method of plant breeding that they implemented by pooling an equal number of F_2 seeds obtained from 378 crosses among 28 superior barley cultivars representing all the major barley growing areas of the world. They called CCII this first EP. Harlan and Martini (1938) were also the first to demonstrate evolution by natural selection in dynamic mixtures, with few varieties becoming dominant in specific locations, while almost disappearing in others; they also showed how rapidly poorly adapted varieties disappeared everywhere.

It was only in 1956 that the method was called evolutionary plant breeding and was suggested as a plant breeding method by Suneson (1956).

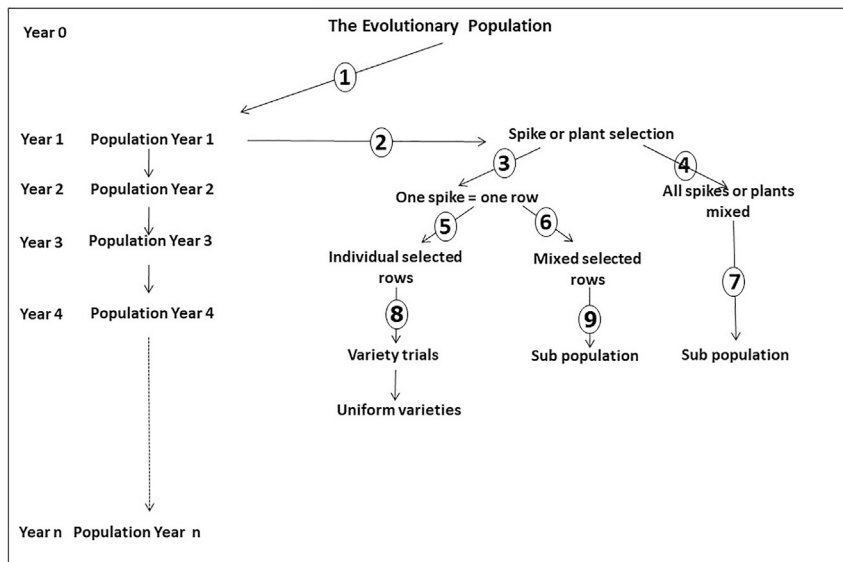


Figure 2. Steps, in a Single Farm, that Follow the Distribution of the Evolutionary Population Shown in Figure 1

The evolutionary population in each target environment is left evolving under natural selection pressure (path 1). It can also be subjected to different modes of artificial selection (path 2) leading to either improved sub-populations (steps 4–7 or 3–6–9) or uniform varieties (steps 3–5–8).

Suneson (1956) suggested a “prolonged subjection [of the population] to competitive natural selection in the area of intended use.” This is what is represented as path 1 in Figure 2, which summarizes the main steps of an evolutionary plant breeding program in one of the environments shown in Figure 1. Like any breeding program, in Figure 2 it is possible to identify the three main stages typical of a plant breeding program (Schnell, 1982), namely, generation of genetic variability, selection, and testing to identify superior recombinants, and release, distribution, and adoption of new cultivars. As indicated in Figure 2, the population is planted and harvested year after year using a portion of the seed harvested the previous year and hence let evolve under the sole force of natural selection, thus generating new genetic variability. As the population evolves, it is subjected to natural selection on one side, and like in any breeding program can be subjected to human selection. In this case, as the population evolves in farmers’ fields, farmers, alone or in partnership with scientists, can use the population as a source to impose artificial selection leading to either improved sub-populations or uniform varieties as shown in the various paths, which include the testing phase of newly selected material.

The third stage (release, distribution, and adoption) is not represented explicitly as it may assume the connotation of an informal adoption, or of a formal release following the regulations of the country, therefore being similar to a more traditional plant breeding program.

In the figure we refer to spikes, but the scheme can be applied to pods (in the case of legumes) or to berries (in the case, for example, of tomatoes).

One possible drawback is represented by correlations due to genetic linkages that may limit the development of new genetic combinations. However, as demonstrated by Allard and Hansche (1964), this can be overcome using large population size. Indeed, evolutionary plant breeding allows working with much larger population size than conventional breeding. For example, Raggi et al. (2017) used a population size of 30,000 individuals to propagate a barley EP to rule out genetic drift and sampling effects. However, EPs often evolve in farmers’ fields while grown as production crops and, therefore, most often as even larger populations. The issue of population size has been discussed also by Brumlop et al. (2019) but with regards to the need of avoiding genetic drift.

One additional concern is selection for competitive ability, which, for example, in the case of cereals, translated into selection for tall plants (Goldringer et al., 2001; Knapp et al., 2020), thus shifting the population in

a direction opposite to the reduction of plant height, which has been one of the main objectives of modern plant breeding (Denison et al., 2003). Indeed, under organic no-herbicide conditions, a relatively tall crop may be of advantage (Knapp et al., 2020) because of its ability to suppress the development of weeds as often informally reported by the several Italian farmers currently growing these EPs as commercial crops.

When artificial selection is applied, molecular tools ranging from marker-assisted selection to high-throughput phenotyping and to genomic selection can be incorporated in the process. Goldringer et al. (2001), Rhoné et al. (2010), and Raggi et al. (2016) are examples of the potential of EPs to generate interdisciplinary research ranging from climatology to evolutionary science, plant protection, genetics, seed quality, etc.

So far, there has been a large body of research demonstrating that natural selection in EPs and mixtures is effective in changing phenology, improving yield, yield stability, and host plant resistance to pathogens.

Most of this research has been reviewed during the past 15 years. Phillips and Wolfe (2005) reviewed the evidence that EPs may provide useful genetic material in agricultural systems with dynamic selection pressures between and within years, with advantages particularly in low-input systems. Dawson et al. (2008) suggested merging participatory and evolutionary plant breeding to maximize the efficiency of decentralized selection as a way to address the need of farmers in heterogeneous environments.

A more recent review (Döring et al., 2011) underlines the importance of the resilience of EPs as one of their most important attributes to cope with the environmental unpredictability. Interestingly, in this review the authors call for a change in legislation to allow the practical use of EPs, anticipating the “Commission Implementing Decision” that the EU Commission issued on March 18, 2014, that we will discuss later in the paper.

Most research on EPs and mixtures has been conducted on small grains, notably the self-pollinated wheat and barley, and to a less extent rice, likely because these were the crops of interest to those scientists addressing the issue of diversity in plant breeding. However, there are good reasons to believe that if a technique that relies on recombination and selection works on a self-pollinated crop, it should work even better on cross-pollinated crops. Although we are not aware of specific studies on evolutionary populations of cross-pollinated crops, because of the mating system of these crops, we may extrapolate from studies conducted on mixtures, such as one of the most recent meta-analysis (Reiss and Drinkwater, 2018), in which the largest positive effect on relative yield was found in the 125 studies of corn.

Evolutionary Populations and Phenology

One of the first demonstrations that EPs can evolve adapting their phenology has been obtained with rice. A random sample of the F_2 deriving from a cross between a late and an early heading rice variety was sent to 20 rice research stations scattered all over Japan and was grown as a bulk from F_2 to F_5 generations. The average heading time of the populations grown in northern locations shifted gradually toward earliness, whereas in those grown in more southern locations shifted gradually toward lateness (Allard and Hansche, 1964).

Similar results were obtained with an EP of bread wheat developed by crossing 16 parents. The population was grown for 10 generations in seven locations all over France. After 10 generations, the population that evolved in northern France was significantly later heading than the population that evolved in southern France with a much warmer climate (Goldringer et al., 2006). The response to selection was found associated with genes with a strong effect on flowering time (Rhoné et al., 2010).

Evolutionary Populations and Yield

Suneson (1956) was one of the first to show the ability of EPs (four different barley CCs grown in California) to evolve to produce higher yields than the widely grown variety Atlas 46 (a parent of all the CCs). Another interesting feature of this experiment was the demonstration of the potential of using artificial line-selection within an evolving EP: after 12 generations, not a single line selected from the EPs yielded more than Atlas 46, whereas after 20 generations a line out-yielded Atlas 46 by 37% and, after 24 generations, three top selections out-yielded Atlas 46 by 56%.

One of the classical experiments throwing lights not only on the effects of natural selection on grain yield but also on how they can vary with environment and type of heterogeneous populations is the one of Patel

et al. (1987). This experiment showed that (1) natural selection reduced the frequency of low-yielding genotypes and increased mean yield; (2) this effect was higher in the EPs than in the mixtures; and (3) natural selection improved yield when the method was used within the intended region of adaptation. This fits with the original description of the core features of evolutionary breeding by Suneson (1956) as “a broadly diversified germplasm and a prolonged subjection of the mass of the progeny to competitive natural selection in the area of contemplated use.”

Experiments showing the evolution of both EPs and mixtures toward higher yields were also reported by Rasmusson et al. (1967) and Soliman and Allard (1991), and more recently by Raggi et al. (2017) and Bocci et al. (2020). Murphy et al. (2005) reviewed the yield advantages of EPs and mixtures underlining that the advantage is evident under drought but tend to disappear under more favorable conditions. The dynamics of yield evolution in evolutionary populations has been described in detail by Döring et al. (2011). Brumlop et al., 2017 showed that EPs are comparable with modern cultivars in yielding ability under organic conditions.

Evolutionary Populations and Yield Stability

The buffering ability of heterogeneous populations is expected to be higher than that of uniform material. One of the most convincing proof that this is indeed the case comes from an experiment conducted in 1961 (Allard, 1961), which showed how the stability of EPs is greater than the stability of mixtures, which in turn is higher than that of pure lines.

A meta-analysis of 91 studies and more than 3,600 observations concluded that cultivar mixtures are a viable strategy to increase diversity in agroecosystems, increasing yield and yield stability as well as disease resistance (Reiss and Drinkwater, 2018).

The genetic background affects yield stability of EPs: those with a wide genetic basis have a better dynamic stability, whereas those with a narrow genetic basis tend to have a better static stability (Weedon and Finckh, 2019). Döring et al. (2015) found an advantage of EPs and mixtures over the mean of their components in terms of cultivar superiority. Raggi et al. (2017) identified barley EPs combining high yield and stability across years and locations.

Evolutionary Populations and Pest Resistance

Evolution of resistance to pests and in particular to diseases has been the most widely documented advantage of EPs and mixtures. Simmonds (1962) reported several cases of reduced severity and incidence of diseases in mixtures of crops. In a review of mixture cultivation in both developing and developed countries, Smithson and Lenné (1996) suggested more durable resistance to insect and diseases as one of the perceived advantages of mixtures over their components and possibly one of the reasons for larger and more stable yields. The most important mechanism to explain the reduction in severity of diseases in mixtures is the dilution of inoculum that occurs owing to the distance between plants of the same genotype (Mundt, 2002). There is also a large variation in the efficacy of mixtures in reducing disease incidence.

A larger than expected number of families resistant to more than one race and a high proportion of segregating families even after several generations of selfing suggested a higher than expected outcrossing rate or a larger advantage of heterozygotes (Jackson et al., 1982). The frequency of resistance alleles that protected against the most damaging pathotypes increases sharply in the host populations, indicating that the evolutionary processes that take place in genetically variable populations propagated under conditions of cultivation can be highly effective in increasing the frequency of desirable alleles and useful multilocus genotypes (Allard, 1990).

The evolution of resistance to powdery mildew in three subpopulations of the same Composite Cross showed that (1) there have been large directional shifts toward increased resistance, (2) there are differences between the three populations in the rate of increase of the frequency of resistant plants, and (c) there was a strong increase in the frequency of resistant plants at almost the same time in the three populations (Ibrahim and Barret, 1991).

Evolution of resistance to powdery mildew was found in populations of bread wheat with the highest level of adult resistance developed when the populations evolved in sites where powdery mildew pressure is known to be high (Paillard et al., 2000).

More recently, agricultural diversity measured by the richness in variety diversity has been shown to be associated with a decrease in the average damage level in banana, plantain, and bean in Uganda (Mulumba et al., 2012).

The advantage of mixture in reducing the incidence and severity of fungal diseases has been demonstrated in several studies (McDonald et al., 1988; Finckh and Mundt, 1992; Finckh et al., 2000; Finckh and Wolfe, 2006).

The Speed of Evolution

One of the advantages of EPs is its ability to evolve and adapt to new environments. One question frequently asked by farmers interested in starting the cultivation of EPs is how quickly they adapt to a new environment. In selection theory terms the answer to this question depends on the magnitude of genetic diversity available in the population for traits associated with adaptation, the heritability of those traits, and the magnitude and consistency of directional selection (Kingsolver et al., 2001). In bread wheat we found evidence of divergent selection after 5 years of evolution in contrasting locations (Bocci et al., 2020). Goldringer et al. (2006) found that, after 10 years, populations diverged significantly for days to maturity along a north-south gradient in France.

THE USE OF EVOLUTIONARY POPULATIONS AND MIXTURES

Despite this very rich body of research, and until recently, there has been only one example of large-scale use of the advantages of heterogeneous populations, and this refers only to mixtures and not to populations. During the 1970s in the United Kingdom, static mixtures proved highly successful in slowing development of diseases, particularly powdery mildew. This approach was taken to the former German Democratic Republic where it was built up to cover an area of some 350,000 hectares, effectively the whole of the spring barley area, leading to a massive reduction of the percentage of fields affected by severe mildew epidemics from 50% to 10% and a 3-fold reduction of the percentage of fields sprayed with fungicides (Wolfe et al., 1992).

One possible explanation for the very limited practical exploitation of the evidence of the multiple benefits of cultivating heterogeneous material is that such material does not fit with the requirement for variety registration. Other reasons that make uniformity desirable is the uniform response of a crop to agronomic treatments and uniform response to processing and cooking.

In 2008 and 2009, while working at the International Center for Agricultural Research in the Dry Areas (ICARDA), then in Aleppo, Syria, we made three EPs by mixing 2,000, 700, and 1,600 segregating populations of bread wheat, durum wheat, and barley, respectively, derived from crosses between widely diverse parents from all over the world, including old local varieties and, in the case of barley, the wild progenitor of the crop. The barley EP was sent to Syria, Algeria, Eritrea, Jordan, and Iran, whereas the two wheat EPs were sent to Syria, Morocco, Algeria, and Jordan. We will refer to these three EPs as “ICARDA EPs.”

In Iran, the ICARDA barley EPs were used as an inspiration to constitute a bread wheat EP made with local breeding material. This EP eventually spread in several provinces as farmers and bakers were pleased with the bread made from the EP, which was marketed in local artisanal bakeries (Rahmanian et al., 2014).

By the time it was found that the bread obtained from the bread wheat EP was a commercial success in Iran, the three ICARDA EPs were already spreading in Italy. In fact, beginning in 2010, there has been in Europe a growing interest in supporting projects with a focus on diversity, and it was within the framework of one of these European projects that the three populations were introduced in Italy in 2010.

In 2014, perhaps acknowledging that some outputs of the projects the European Union (EU) was financing could be heterogeneous material, which did not have a legal status, the EU Commission issued on March 18, 2014, a “Commission Implementing Decision.” With such a decision, the EU Commission organized a “temporary experiment at Union level for the purpose of assessing whether the production, with a view to marketing, and marketing, under certain conditions, of seed from populations belonging to the species Oats, Wheat, Barley and Corn, may constitute an improved alternative to the exclusion of the marketing of seed not complying with the requirements ...,” which made it possible, in Europe, to market

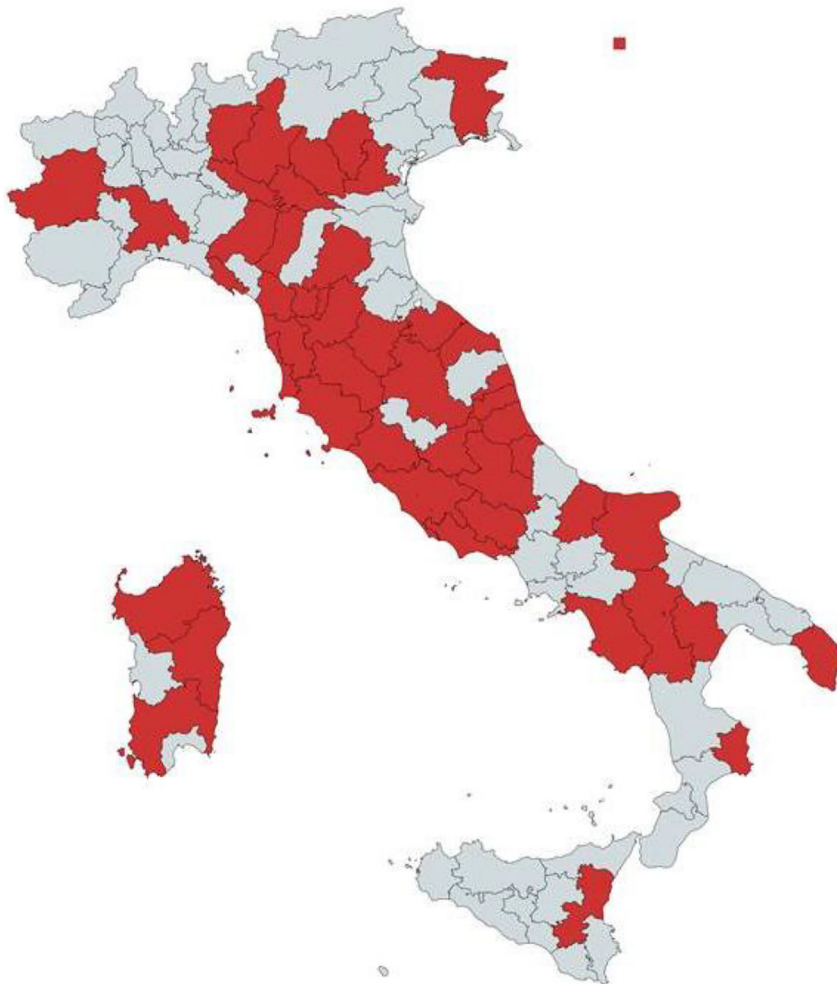


Figure 3. Current Diffusion, Throughout Italy, of the ICARDA Bread Wheat EP Made in Syria and Planted in Sicily and Tuscany, for the First Time in 2010

experimentally heterogeneous materials of oats, barley, maize, and wheat up to 29 February, 2021, after their approval by the designated authors (Petitti et al., 2018).

This had made possible the official certification and authorization to sell and buy seed of the populations, but most importantly for farmers, to become the producers of their own seed throughout the years. The possibility of using heterogeneous material, hence populations and mixtures, has been extended to all crops with the new EU regulations on organic agriculture effective on January 1, 2022.

By 2018, the three ICARDA EPs had spread widely in Italy, particularly the bread wheat EP, which within less than 10 years reached several regions (Figure 3), as several artisanal bakeries confirmed the quality and the consumer acceptance of the bread, which had been found earlier in Iran. The two regions where the EP was first planted (Sicily and Tuscany) are those where the two EPs were cultivated continuously on the same farms, using part of the seed harvested the previous year.

After a slow rate of diffusion during the first four years, the diffusion accelerated and the major increase took place after 2017. In that year the sale of the seed of the two populations that evolved continuously in Sicily and Tuscany was authorized based on the EU Commission Implementing Decision mentioned earlier. The possibility of legally selling and buying the seed boosted the diffusion that reached 16 regions out of 20 by the end of 2018.



Figure 4. Divergent Evolution of a Bread Wheat Evolutionary Population after Ten Years of Cultivation in Two Contrasting Locations

The ICARDA evolutionary bread wheat population after 10 years evolution in Sicily (left) and the same population after 10 years evolution in Tuscany (right) grown side by side in March 2020 (courtesy of Pierluigi Valenti).

The two farms where the populations evolved continuously since 2010 differed in rainfall and temperature, with Sicily being systematically drier and warmer than the farm in Tuscany (Petitti et al., 2018). The two populations, which evolved continuously in the two farms offered therefore the possibility of studying whether there was evidence of any divergent selection. This was done within the framework of one of the EU projects, which started in 2014, by comparing the two populations together with other genetic materials in four contrasting locations, including the two original farms, during four cropping seasons (from 2014/2015 till 2017/2018). The experiment showed that the EP became specifically adapted to the region where they were cultivated in which they also exhibited a high temporal stability (Bocci et al., 2020). One example of divergent evolution is shown in Figure 4 where on the left are two hectares of the same original population after 10 years of evolution in Sicily (south Italy) and on the right the same population after 10 years of evolution in Tuscany (Central Italy). A 4-year experiment showed that the same original EP grown continuously in different locations evolved into locally adapted populations with significant differences in important quantitative traits such as grain yield and plant height (Bocci et al., 2020).

The experiment continues by addressing the issue of seed circulation and seed sharing among farmers to define the area of adaptation of each population. The strategy we follow consists in recommending the exchange of a sufficient *number* (rather than quantity) of seed to allow the population to adapt to a new environment. Farmers and institutions should monitor these exchanges.

This is a particularly important issue because free seed circulation can easily cause uncontrolled spreading of seed-borne diseases. This can be avoided not only with training of farmers but also with the involvement of small seed companies, which assist farmers in producing and maintaining the seed free of seed-borne diseases and impurities.

CONCLUSIONS

There are a number of points to be made in relation to using heterogeneous material, either populations or dynamic mixtures, as farmers' main crops. The first is that they represent a dynamic response to the complexity of climate change not only in its physical characteristics (temperature and rainfall) but also in

its biotic aspects and in its location specificity. EPs and mixtures, with their capacity to evolve in response to both biotic and abiotic stresses, as long as they maintain sufficient genetic diversity, appears to be the quickest, cost-effective, and evolving solution to such a complex and evolving problem with the additional advantage of increasing yield gains resulting from a combination of natural and artificial selection and genetic recombination.

The second is their ability to control pests, which makes them particularly suited to organic systems, representing an ecological solution to pest control—because they do not create a selection pressure favoring the evolution of resistance. This will fill an important gap represented by the scarce availability of varieties specifically adapted to organic conditions.

The third, which is a consequence of the first two, is that they represent at the same time a mitigation and an adaptation strategy. A mitigation strategy because they reduce considerably the use of chemical inputs, and an adaptation strategy associated with their ability to continuously evolve to adapt to new combinations of biotic and abiotic stresses.

Finally, as they evolve, they generate a continuous flow of novel cultivated agro biodiversity both in space (because of divergent evolution in different location) and in time (because of evolution within the same location) even within the same crop, which will be beneficial in increasing diet diversity and ultimately human health.

LIMITATIONS OF THE STUDY

One limitation of the study is the difficulty in accurately tracing the spreading of the evolutionary populations to be able to assess their full impact.

RESOURCE AVAILABILITY

Lead Contact

Salvatore Ceccarelli (ceccarelli.salvatore83@gmail.com).

Materials Availability

This study did not use or generate any reagents.

Data and Code Availability

There were no datasets used to support the views presented in this paper beyond those cited in the literature.

ACKNOWLEDGMENTS

We are grateful to the International Center for Agricultural Research in Dry Areas (ICARDA) for the facilities and the germplasm, which make possible the constitution of the evolutionary populations, and to three anonymous reviewers for their constructive remarks.

AUTHOR CONTRIBUTIONS

The authors contributed equally to the paper.

REFERENCES

- Akdemir, D., Beavis, W., Fritsche-Neto, R., Singh, A.K., and Isidro-Sánchez, J. (2019). Multi-objective optimized genomic breeding strategies for sustainable food improvement. *Heredity* 122, 672–683.
- Allard, R.W. (1961). Relationship between genetic diversity and consistency of performance in different environments. *Crop Sci.* 1, 127–133.
- Allard, R.W. (1990). The genetics of host-pathogen coevolution: implications for genetic resource conservation. *J. Hered.* 81, 1–6.
- Allard, R.W., and Hansche, P.E. (1964). Some parameters of population variability and their implications in plant breeding. *Adv. Agron.* 16, 281–325.
- Bocci, R., Bussi, B., Petitti, M., Franciolini, R., Altavilla, V., Galluzzi, G., Di Luzio, P., Migliorini, P., Spagnolo, S., Floriddia, R., et al. (2020). Yield, yield stability and farmers' preferences of evolutionary populations of bread wheat: a dynamic solution to climate change. *Eur. J. Agron.* 121, 126156.
- Bøhn, T., and Millstone, E. (2019). The introduction of thousands of tonnes of glyphosate in the food chain—an evaluation of glyphosate tolerant soybeans. *Foods* 8, 669.
- Bonneuil, C., Goffaux, R., Bonnin, I., Montalent, P., Hamon, C., Balfourier, F., and Goldringer, I. (2012). A new integrative indicator to assess crop genetic diversity. *Ecol. Indic.* 23, 280–289.
- Bonnin, I., Bonneuil, C., Goffaux, R., Montalent, P., and Goldringer, I. (2014). Explaining the decrease in the genetic diversity of wheat in

- France over the 20th century. *Agric. Ecosyst. Environ.* 195, 183–192.
- Brumlop, S., Pfeiffer, T., and Finckh, M.R. (2017). Evolutionary effects on morphology and agronomic performance of three winter wheat composite cross populations maintained for six years under organic and conventional conditions. *Org. Farming* 3, 34–50.
- Brumlop, S., Weedon, O., Link, W., and Finckh, M.R. (2019). Effective population size (N_e) of organically and conventionally grown composite cross winter wheat populations depending on generation. *Eur. J. Agron.* 109, 125922.
- Campbell, L., and Madden, L.V. (1990). *Introduction to Plant Disease Epidemiology* (John Wiley & Sons), p. 532.
- Ceccarelli, S. (2015). Efficiency of plant breeding. *Crop Sci.* 55, 87–97.
- Ceccarelli, S. (2019). Nurturing diversity in our guts and on our farms to reduce health risks and increase food system resilience. In *Agrobiodiversity Index Report 2019: Risk and Resilience*, Bioversity International., ed. (Bioversity International), pp. 107–113.
- Colautti, R.I., and Barrett, S.C.H. (2013). Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science* 342, 364–366.
- Dawson, J.C., Murphy, K.M., and Jones, S.S. (2008). Decentralized selection and participatory approaches in plant breeding for low-input systems. *Euphytica* 160, 143–154.
- Denison, R.F., Kiers, E.T., and West, S.A. (2003). Darwinian agriculture: when can humans find solutions beyond the reach of natural selection? *Q. Rev. Biol.* 78, 148–168.
- Deutsch, C.A., Tewksbury, J.J., Tigchelaar, M., Battisti, D.S., Merrill, S.C., Huey, R.B., and Naylor, R.L. (2018). Increase in crop losses to insect pests in a warming climate. *Science* 361, 916–919.
- Döring, T.D., Knapp, S., Kovacs, G., Murphy, K., and Wolfe, M.S. (2011). Evolutionary plant breeding in cereals—into a new era. *Sustainability* 3, 1944–1971.
- Döring, T.F., Annicchiarico, P., Clarke, S., Haigh, Z., Jones, H.E., Pearce, H., Snape, J., Zhang, J., and Wolfe, M.S. (2015). Comparative analysis of performance and stability among composite cross populations, variety mixtures and pure lines of winter wheat in organic and conventional cropping systems. *Field Crops Res.* 183, 235–245.
- D’Amato, A.W., Bradford, J.B., Fraver, S., and Palik, B.J. (2011). Forest management for mitigation and adaptation to climate change: insights from long-term silviculture experiments. *For. Ecol. Manag.* 262, 803–816.
- Falconer, D.S. (1960). *Introduction to Quantitative Genetics* (Oliver and Boyd Ltd), pp. 1–140.
- FAO (2013). Il patrimonio genetico mondiale decisivo per la sopravvivenza dell’umanità. <http://www.fao.org/news/story/it/item/174345/icode/>.
- FAO. (2019). The State of the World’s Biodiversity for Food and Agriculture. In *FAO Commission on Genetic Resources for Food and Agriculture* Assessments, J. Bélanger and D. Pilling, eds. (FAO), p. 572.
- FAO, IFAD, UNICEF, WFP and WHO (2019). The State of Food Security and Nutrition in the World 2019. Safeguarding against Economic Slowdowns and Downturns (FAO).
- Finckh, M.R., and Mundt, C.C. (1992). Stripe rust, yield, and plant competition in wheat cultivar mixtures. *Phytopathology* 82, 905–913.
- Finckh, M.R., and Wolfe, M.S. (2006). Diversification strategies. In *The Epidemiology of Plant Diseases*, B. Cooke, D. Jones, and B. Kaye, eds. (Springer), pp. 269–307.
- Finckh, M.R., Gacek, E., Goyeau, H., Lannou, C., Merz, U., Mundt, C.C., Munk, L., Nadziak, L., Newton, A.C., de Vallaville-Pope, C., and Wolfe, M.S. (2000). Cereal variety and species mixtures in practice, with emphasis on disease resistance. *Agronomie. EDP Sci.* 20, 813–837.
- Fisher, M.C., Hawkins, N.J., Sanglard, D., and Gurr, S.J. (2018). Worldwide emergence of resistance to antifungal drugs challenges human health and food security. *Science* 360, 739–742.
- Frankel, O.H. (1950). The development and maintenance of superior genetic stocks. *Heredity* 4, 89–102.
- Goldringer, I., Enjalbert, J., Raquin, A.-L., and Brabant, P. (2001). Strong selection in wheat populations during ten generations of dynamic management. *Genet. Sel. Evol.* 33, S441–S463.
- Goldringer, I., Prouin, C., Rousset, M., Galic, N., and Bonnin, I. (2006). Rapid differentiation of experimental populations of wheat for heading time in response to local climatic conditions. *Ann. Bot.* 98, 805–817.
- Harlan, H.V., and Martini, M.L. (1929). A composite hybrid mixture. *J. Amer. Soc. Agron.* 21, 487–490.
- Harlan, H.V., and Martini, M.L. (1938). The effect of natural selection in a mixture of barley varieties. *J. Agric. Res.* 57, 189–199.
- Heeb, L., Jenner, E., and Cock, M.J.W. (2019). Climate-smart pest management: building resilience of farms and landscapes to changing pest threats. *J. Pest Sci.* 92, 951–969.
- Heiman, M.L., and Greenway, F.L. (2016). A healthy gastrointestinal microbiome is dependent on dietary diversity. *Mol. Metab.* 5, 317–320.
- Hoban, A.E., Stilling, R.M., Ryan, F.J., Shanahan, F., Dinan, T.G., Claesson, M.J., Clarke, G., and Cryan, J.F. (2016). Regulation of prefrontal cortex myelination by the microbiota. *Transl. Psychiatry* 6, e774.
- Hufford, M.B., Berny Mier y Teran, J.C., and Gepts, P. (2019). Crop biodiversity: an unfinished magnum opus of nature. *Annu. Rev. Plant Biol.* 70, 727–751.
- Ibrahim, K.M., and Barret, J.A. (1991). Evolution of mildew resistance in a hybrid bulk population of barley. *Heredity* 67, 247–256.
- IPCC (2014). Climate change 2014: synthesis report. In *Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change*, R.K. Pachauri and L.A. Meyer, eds. (IPCC 2014), p. 151.
- IPCC (2018). Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways. In *The Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty*, V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, and et al., eds..
- Jackson, L.F., Webster, R.K., Allard, R.W., and Kahler, A.L. (1982). Genetic analysis of changes in scald resistance in barley composite cross V. *Phytopathology* 72, 1069–1072.
- Jacobsen, S.-E., Sørensen, M., Pedersen, S.M., and Weiner, J. (2015). Using our agrobiodiversity: plant-based solutions to feed the world. *Sustain. Dev.* 35, 1217–1235.
- Jaramillo, F., and Destouni, G. (2015). Comment on “Planetary boundaries: guiding human development on a changing planet”. *Science* 348, 1217–1218.
- Kahiluoto, H., Kaseva, J., Balek, J., Olesen, J.E., Ruiz-Ramos, M., Gobin, A., Kersebaum, K.C., Takács, J., Ruget, F., and Ferrise, R. (2019). Decline in climate resilience of European wheat. *Proc. Natl. Acad. Sci. U S A* 116, 123–128.
- Kenen, G., Bekele, E., Imtiaz, M., and Dagne, K. (2012). Genetic vulnerability of modern crop cultivars: causes, mechanism and remedies. *Int. J. Plant Res.* 2, 69–79.
- Kerr, J.T., Pindar, A., Galpern, P., Packer, L., Potts, S.G., Roberts, S.M., Rasmont, P., Schweiger, O., Colla, S.R., and Richardson, L.L. (2015). Climate change impacts on bumblebees converge across continents. *Science*, 177–180.
- Khamsi, R. (2015). A gut feeling about immunity. *Nat. Med.* 21, 674–676.
- Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., Hoang, A., Gibert, P., and Beerli, P. (2001). The strength of phenotypic selection in natural populations. *Am. Nat.* 157, 245–261.
- Knapp, S., Döring, T.F., Jones, H.E., Snape, J., Wingen, L.U., Wolfe, M.S., Leverington-Waite, M., and Griffiths, S. (2020). Natural selection towards wild-type in composite cross populations of winter wheat. *Front. Plant Sci.* 10, 1757.
- C. Kole, ed. (2020). *Genomic Designing of Climate-Smart Cereal Crops* (Springer Nature), p. 307.
- Kole, C., Muthamilarasan, M., Henry, R., Edwards, D., Sharma, R., Abberton, M., Batley, J., Bentley, A., Blakeney, M., Bryant, J., et al. (2015). Application of genomics-assisted breeding for generation of climate resilient crops: progress and prospects. *Front. Plant Sci.* 6, 563.
- Landjeva, S., Korzun, V., and Ganeva, G. (2006). Evaluation of genetic diversity among Bulgarian winter wheat (*Triticum aestivum* L.) varieties during the period 1925–2003 using

- microsatellites. *Genet. Resour. Crop Evol.* 53, 1605–1614.
- Lehmann, P., Ammunet, T., Barton, M., Battisti, A., Eigenbrode, S.D., Jepsen, J.U., Kalinkat, G., Neuvonen, S., Niemelä, P., Terblanche, J.S., et al. (2020). Complex responses of global insect pests to climate warming. *Front. Ecol. Environ.* 18, 141–150.
- L. Lipper, N. McCarthy, D. Zilberman, S. Asfaw, and G. Branca, eds. (2018). *Climate Smart Agriculture: Building Resilience to Climate Change* (Springer International Publishing), p. 630.
- Lucas, T., and Horton, R. (2019). The 21st-century great food transformation. *The Lancet* 393, 386–387.
- Matzrafi, M., Seiwert, B., Reemtsma, T., Rubin, B., and Peleg, Z. (2016). Climate change increases the risk of herbicide-resistant weeds due to enhanced detoxification. *Planta* 244, 1217–1227.
- McDonald, B.A., and Stukenbrock, E.H. (2016). Rapid emergence of pathogens in agro-ecosystems: global threats to agricultural sustainability and food security. *Trans. R. Soc. B* 71, 20160026.
- McDonald, B.A., Allard, R.W., and Webster, R.K. (1988). Responses of two, three, and four component barley mixtures to a variable pathogen population. *Crop Sci.* 28, 447–452.
- Menkir, A., Crossa, J., Meseka, S., Bossey, B., Muhyideen, O., Riberio, P.F., Coulibaly, M., Yacoubou, A.-M., Olaoye, G., and Haruna, A. (2020). Stacking tolerance to drought and resistance to a parasitic weed in tropical hybrid maize for enhancing resilience to stress combinations. *Front. Plant Sci.* 11, 66.
- Mulumba, J.W., Nankya, R., Adokorach, J., Kiwuka, D., Fadda, C., De Santis, P., and Jarvis, D.I. (2012). A risk-minimizing argument for traditional crop varietal diversity use to reduce pest and disease damage in agricultural ecosystem of Uganda. *Agric. Ecosyst. Environ.* 157, 70–86.
- Mundt, C.C. (2002). Use of multiline cultivars and cultivar mixtures for disease management. *Annu. Rev. Phytopathol.* 40, 381–410.
- Murphy, K., Lammer, D., Lyon, S., Carter, B., and Jones, S.S. (2005). Breeding for organic and low-input farming systems: an evolutionary-participatory breeding method for inbred cereal grains. *Renew. Agric. Food Syst.* 20, 48–55.
- Newton, A.C., Johnson, S.N., and Gregory, P.J. (2011). Implications of climate change for diseases, crop yields and food security. *Euphytica* 179, 3–18.
- Paillard, S., Goldringer, I., Enjalbert, J., Trottet, M., David, J., de Vallavieille-Pope, C., and Brabant, P. (2000). Evolution of resistance against powdery mildew in winter wheat populations conducted under dynamic management. II. Adult plant resistance. *Theor. Appl. Genet.* 101, 457–462.
- Palumbi, S.R. (2001). Humans as the world's greatest evolutionary force. *Science* 293, 1786–1790.
- Patel, J.D., Reinbergs, E., Mather, D.E., Choo, T.M., and Sterling, J.D. (1987). Natural selection in a double-haploid mixture and a composite cross of barley. *Crop Sci.* 27, 474–479.
- Pautasso, M., Döring, T.F., Garbelotto, M., Pellis, L., and Jeger, M.J. (2012). Impacts of climate change on plant diseases—opinions and trends. *Eur. J. Plant Pathol.* 133, 295–313.
- Petitti, M., Bocci, R., Bussi, B., Ceccarelli, S., Spillane, C., and McKeown, P. (2018). Evolutionary-participatory breeding generates populations adapted for organic agriculture in Italy. In *Symposium on Breeding for Diversification*, February 2018, University of Kassel, Witzenhausen, Germany, J. Bačanović-Šišić, D. Dennenmoser, and M.R. Finckh, eds. (Kassel University Press), pp. 39–41.
- Phillips, S.L., and Wolfe, M.S. (2005). Evolutionary plant breeding for low input systems. *J. Agric. Sci.* 143, 245–254.
- Piepho, H.-P. (2019). Recent claim of declining climate resilience in European wheat is not supported by the statistics used. *Proc. Natl. Acad. Sci. U S A* 116, 10625–10626.
- Raggi, L., Ceccarelli, S., and Negri, V. (2016). Evolution of a barley composite cross-derived population: an insight gained by molecular markers. *J. Agric. Sci.* 154, 23–39.
- Raggi, L., Ciancaleoni, S., Torricelli, R., Terzi, V., Ceccarelli, S., and Negri, V. (2017). Evolutionary breeding for sustainable agriculture: selection and multi-environment evaluation of barley populations and lines. *Field Crops Res.* 204, 76–88.
- Rahmanian, M., Salimi, M., Razavi, K., Haghighparast, R., and Ceccarelli, S. (2014). Living gene banks in farmers fields. *Farming Matters* 2014, 12–15.
- Rasmusson, D.C., Beard, B.H., and Johnson, F.K. (1967). Effect of natural selection on performance of a barley population. *Crop Sci.* 7, 543.
- Ray, D.K., Gerber, J.S., MacDonald, G.K., and West, P.C. (2015). Climate variation explains a third of global crop yield variability. *Nat. Commun.* 6, 5989.
- Reiss, E.R., and Drinkwater, L.E. (2018). Cultivar mixtures: a meta-analysis of the effect of intraspecific diversity on crop yield. *Ecol. Appl.* 28, 62–77.
- Rhoné, B., Vitalis, R., Goldringer, I., and Bonnin, I. (2010). Evolution of flowering time in experimental wheat populations: a comprehensive approach to detect genetic signatures of natural selection. *Evolution* 64, 2110–2125.
- Robinson, R.A. (2009). Breeding for quantitative variables. Part 2: breeding for durable resistance to crop pests and diseases. In *Plant Breeding and Farmer Participation*, S. Ceccarelli, E.P. Guimaraes, and E. Weltzien, eds. (FAO), pp. 367–390.
- Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., III, Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., et al. (2009). A safe operating space for humanity. *Nature* 461, 472–475.
- Rosenzweig, C., Iglesias, A., Yang, A.B., Epstein, P.R., and Chivian, E. (2000). *Climate Change and U.S. Agriculture: The Impacts of Warming and Extreme Weather Events on Productivity, Plant Diseases, and Pests* (Center for Health and the Global Environment, Harvard Medical School), pp. 1–47.
- Rosenzweig, C., Iglesias, A., Yang, A.B., Epstein, P.R., and Chivian, E. (2001). Climate change and extreme weather events - implications for food production, plant diseases, and pests. *Glob. Change Hum. Health* 2, 90–104.
- Schnell, F.W. (1982). A synoptic study of the methods and categories of plant breeding. *Z. Pflanzenzücht.* 89, 1–18.
- Simmonds, N.W. (1962). Variability in crop plants, its use and conservation. *Biol. Rev.* 37, 422–465.
- Singh, M., Grando, S., and Ceccarelli, S. (2006). Measures of repeatability of genotype by location interactions using data from barley trials in northern Syria. *Exp. Agric.* 42, 189–198.
- Singh, R.K., Chang, H.W., Yan, D., Lee, K.M., Ucmak, D., and Wong, K. (2017). Influence of diet on the gut microbiome and implications for human health. *J. Transl. Med.* 15, 73.
- Smithson, J.B., and Lenné, J.M. (1996). Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. *Ann. Appl. Biol.* 128, 127–158.
- Soliman, K.M., and Allard, R.W. (1991). Grain yield of composite cross populations of barley: effects of natural selection. *Crop Sci.* 31, 705–708.
- Springmann, M., Mason-D'Croz, D., Robinson, S., Garnett, T., and Godfray, H.C.J. (2016). Global and regional health effects of future food production under climate change: a modelling study. *Lancet* 387, 1937–1946.
- Steffen, W., Richardson, K., Rockstrom, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., de Vries, W., de Wit, C.A., et al. (2015). Planetary boundaries: guiding human development on a changing planet. *Science* 347, 1259855.
- Suneson, C.A. (1956). An evolutionary plant breeding method. *Agron. J.* 48, 188–191.
- Thrupp, L. (2000). Linking agricultural biodiversity and food security: the valuable role of agrobiodiversity for sustainable agriculture. *Int. Aff.* 76, 265–281.
- Tilman, D., and Clark, M. (2014). Global diets link environmental sustainability and human health. *Nature* 515, 518–522.
- Wade, M.J., and Kalisz, S. (1991). The causes of natural selection. *Evolution* 44, 1947–1955.
- Watts, N., Amann, M., Arnell, N., Ayeb-Karlsson, S., Belesova, K., Berry, H., Bouley, T., Boykoff, M., Byass, P., and Cai, W. (2018). The 2018 report of the Lancet Countdown on health and climate change: shaping the health of nations for centuries to come. *Lancet* 392, 2479–2514.
- Weedon, O.D., and Finckh, M.R. (2019). Heterogeneous winter wheat populations differ in yield stability depending on their genetic

background and management system. *Sustainability* 11, 6172.

Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., Garnett, T., Tilman, D., DeClerck, F., and Wood, A. (2019). Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. *Lancet* 393, 447–492.

Wolfe, M.S., and Ceccarelli, S. (2020). The need to use more diversity in cereal cropping requires more descriptive precision. *J. Sci. Food Agric.* 100, 4119–4123.

Wolfe, M.S., Brändle, U., Koller, B., Limpert, E., McDermott, J.M., Müller, K., and Schaffner, D. (1992). Barley mildew in Europe: population biology and host resistance. *Euphytica* 63, 125–139.

van der Wouw, M., Kik, C., van Hintum, T., van Treuren, R., and Visser, B. (2010). Genetic erosion in crops: concept, research results and challenges. *Plant Genet. Resour.* 8, 1–15.

Zampieri, M., Weissteiner, C.J., Grizzetti, B., Toreti, A., van den Berg, M., and Dentener, F.

(2020). Estimating resilience of crop production systems: from theory to practice. *Sci. Total Environ.* 735, 139378.

Zavala, J.A., Casteel, C.L., DeLucia, E.H., and Berenbaum, M.R. (2008). Anthropogenic increase in carbon dioxide compromises plant defense against invasive insects. *Proc. Natl. Acad. Sci. U S A* 105, 5129–5133.

Ziska, L.H., and Dukes, J.S. (2010). *Weed Biology and Climate Change* (Blackwell Publishing Ltd), p. 248.