

Evolutionary plant breeding as a response to the complexity of climate change

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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 cycle, 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 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, while Deutsch et al. (2018) estimated a 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 vary 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 of several important insects, weeds and pathogens has been documented in the USA (Rosenzweig et al., 2000).

In addition to affecting diseases, insects and weeds in a largely unpredictable and continuously evolving way, a further aspects 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 event, 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; Bøhn 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 defence 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 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 word 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 due to the occurrence of heat waves, floods and fires and indirectly due to its effects on agriculture, food supply and diets (Springmann et al., 2016; Ceccarelli, 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. (2010) 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 declined in Bulgarian winter wheat while 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. Out of 7000 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. Firstly, it makes our crops more vulnerable because their genetic uniformity makes them unable to respond to both short and long terms climate changes (Keneni et al., 2012), and provide 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). Secondly, 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 (Khamisi, 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 (Willet 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 emphasises specific adaptation and therefore leads to selecting different varieties, each adapted to a specific TE. In terms of selection theory, this allows to eliminate genotype x location (GL) interactions keeping only genotype x 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, while 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, while 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 populations: 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 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. Some farmers, however, prefer to grow mixtures from the seed harvested at the end the previous cropping season, thus converting them to dynamic mixtures. Because of natural inter-crossing within the dynamic mixtures, within a few seasons, following segregation, recombination and natural selection, they become populations.

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 F₂ 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).

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 1: 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. However, as the population evolves, 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. 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 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 by the use of 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 normal 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, 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 relying on recombination and selection works on a self-pollinated crop, it should work even better on cross-pollinated crops. In fact, in one of the most recent meta-analysis (Reiss and Drinkwater, 2018), 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 F₂ 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 F₂ to F₅ generations. The average heading time of the populations grown in northern locations shifted gradually towards earliness, while in those grown in more southern locations shifted gradually towards 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: while after 12 generations, not a single line selected from the EPs yielded more than Atlas 46, 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 a) natural selection reduced the frequency of low yielding genotypes and increased mean yield; b) this effect was higher in the EPs than in the mixtures; and c) 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 subsection 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 towards higher yields were also reported by Rasmusson et al. (1967), Soliman and Allard (1991) and more recently by Raggi et al. (2017) and by 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 favourable 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 3600 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 while 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 due 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 towards 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 questions 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 1970's in the UK, 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 threefold 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 cocking.

In 2008 and in 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 2000, 700 and 1600 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, while 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 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 1st, 2022.

By 2017, the three ICARDA EPs had spread widely in Italy (Figure 2), particularly the bread wheat EP, 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 which evolved continuously in Sicily and Tuscany was authorized based on the EU Commission Implementing Decision mentioned earlier. The possibility of legally sell and buy the seed boosted the diffusion which reached 16 regions out of 20 by the end of 2018.

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 project, which started in 2014, by comparing the two populations together with other genetic material in four contrasting locations including the two 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 3 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 four years experiment showed that 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 maintain the seed free of seed-borne diseases and of impurities.

Conclusions

There are a number of points to be made in relation to using heterogeneous material, either populations or 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 favouring 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 even within the same crop, which will be beneficial in increasing diet diversity and ultimately human health.

References

- Allard RW. The Genetics of Host-Pathogen Coevolution: Implications for Genetic Resource Conservation. *Journal of Heredity* 1960; 81 (1): 1–6
- Allard RW. Relationship Between Genetic Diversity and Consistency of Performance in Different Environments. *Crop Science* 1961; 1, 2: 127–133
- Allard RW, Hansche PE. Some parameters of population variability and their implications in plant breeding. *Adv. Agron.* 1964; 16: 281–325
- Akdemir D, Beavis W, Fritsche-Neto R, Singh AK, Isidro-Sánchez J. Multi-objective optimized genomic breeding strategies for sustainable food improvement. *Heredity* 2019; 122: 672–683

499 Bocci R, Bussi B, Petitti M, Franciolini R, Altavilla V, Galluzzi G, Di Luzio P, Migliorini P,
 500 Spagnolo S, Floriddia R, et al. Yield, yield stability and farmers' preferences of evolutionary
 501 populations of bread wheat: a dynamic solution to climate change. *European Journal of*
 502 *Agronomy* 2020; 121
 503
 504 Bonneuil C, Goffaux R, Bonnin I, Montalent P, Hamon C, Balfourier F, Goldringer I. A new
 505 integrative indicator to assess crop genetic diversity. *Ecological Indicators* 2012; 23: 280 –
 506 289
 507
 508 Bonnin I, Bonneuil C, Goffaux R, Montalent P, Goldringer I. Explaining the decrease in the
 509 genetic diversity of wheat in France over the 20th century. *Agriculture, Ecosystems &*
 510 *Environment* 2014; 195:183-192
 511
 512 Bøhn T, Millstone E. The Introduction of Thousands of Tonnes of Glyphosate in the food
 513 Chain—An Evaluation of Glyphosate Tolerant Soybeans. *Foods* 2019; 8: 669
 514
 515 Brumlop S, Pfeiffer T, Finckh MR. Evolutionary Effects on Morphology and Agronomic
 516 Performance of Three Winter Wheat Composite Cross. Populations Maintained for Six Years
 under Organic and Conventional Conditions. *Organic Farming* 2017; 3 (1): 34–50
 517
 518 Brumlop S, Weedon O, Link W, Finckh MR. Effective population size (Ne) of organically and
 519 conventionally grown composite cross winter wheat populations depending on generation.
European Journal of Agronomy 2019; 125:922
 520
 521 Campbell L, Madden LV. Introduction to Plant Disease Epidemiology. John Wiley & Sons,
 New York 1990; pp 560.
 522
 523 Ceccarelli S. Efficiency of plant breeding. *Crop Science* 2015; 55: 87–97
 524
 525 Ceccarelli S. Nurturing diversity in our guts and on our farms to reduce health risks and
 526 increase food system resilience. In Bioversity International, Agrobiodiversity Index Report
 2019: Risk and Resilience. Rome (Italy): Bioversity International, Rome, Italy. 2019; pp 107–
 113.
 527
 528 Colautti RI, Barrett SCH. Rapid Adaptation to Climate Facilitates Range Expansion of an
 Invasive Plant. *Science* 2013; 342: 364–366
 529
 530 Dawson JC, Murphy KM, Jones SS. Decentralized selection and participatory approaches in
 plant breeding for low-input systems. *Euphytica* 2008; 160:143–154
 531
 532 Denison RF, Kiers ET, West SA. Darwinian Agriculture: When Can Humans Find Solutions
 Beyond The Reach of Natural Selection? *The Quarterly Review of Biology* 2003; 78 (2): 148–
 533 168
 534 Deutsch CA, Tewksbury JJ, Tigchelaar M, Battisti DS, Merrill SC, Huey RB, Naylor RL.
 Increase in crop losses to insect pests in a warming climate. *Science* 2018; 361: 916–919
 535
 536 Döring TD, Knapp S, Kovacs G, Murphy K, Wolfe MS. Evolutionary Plant Breeding in
 Cereals—Into a New Era. *Sustainability* 2011; 3: 1944-1971
 537
 538 Döring TF, Annicchiarico P, Clarke S, Haigh Z, Jones HE, Pearce H, Snape J, Zhang J, Wolfe
 539 MS. Comparative analysis of performance and stability among composite cross populations,
 variety mixtures and pure lines of winter wheat in organic and conventional cropping
 540 systems. *Field Crops Research* 2015; 183: 235–245

541 Falconer DS. Introduction to Quantitative Genetics. Oliver and Boyd Ltd., Edinburgh, 1960;
542 1–140

543 FAO. Il patrimonio genetico mondiale decisivo per la sopravvivenza dell'umanità. 2013;
544 Available at: <http://www.fao.org/news/story/it/item/174345/icode/>

545 FAO. The State of the World's Biodiversity for Food and Agriculture, J. Bélanger and D. Pilling
546 (eds.). FAO Commission on Genetic Resources for Food and Agriculture Assessments. Rome
547 2019; 572 pp.

548 FAO, IFAD, UNICEF, WFP and WHO. The State of Food Security and Nutrition in the World
549 2019. Safeguarding against economic slowdowns and downturns. Rome, FAO. 2019;
550 License: CC BY-NC-SA 3.0 IGO

551 Finckh MR, Mundt CC. Stripe Rust, Yield, and Plant Competition in Wheat Cultivar Mixtures.
552 *Phytopathology* 1992; 82: 905-913

553 Finckh M, Gacek E, Goyeau H, Lannou C, Merz U, Mundte CC, Munk L, Nadziak L, Newton
554 AC, de Vallavieille-Popoc C, Wolfe MS. Cereal variety and species mixtures in practice, with
555 emphasis on disease resistance. *Agronomie, EDP Sciences* 2000; 20 (7): 813-837

556 Finckh M, Wolfe M. Diversification strategies. In: Cooke B, Jones D, Kaye B. (eds) The
557 Epidemiology of Plant Diseases. 2006; Springer, Dordrecht Fisher MC, Hawkins NJ, Sanglard
558 D, Gurr SJ. Worldwide emergence of resistance to antifungal drugs challenges human health
559 and food security. *Science* 2018; 360 (6390): 739–742

560 Frankel OH. The development and maintenance of superior genetic stocks. *Heredity* 1950; 4:
561 89–102

562 Goldringer I, Enjalbert J, Raquin A-L, Brabant P. Strong selection in wheat populations during
563 ten generations of dynamic management. *Genetic Selection Evolution* 2001; 33 (Suppl. 1):
564 S441–S463

565 Goldringer I, Prouin C, Rousset M, Galic N, Bonnin I. Rapid differentiation of experimental
566 populations of wheat for heading time in response to local climatic conditions. *Ann. Bot.*
567 2006; 98: 805–817

568 Harlan HV, Martini ML. A composite hybrid mixture. *J. Amer. Soc. Agron.* 1929; 21: 487–490

569 Harlan HV, Martini ML. The Effect of Natural Selection in a Mixture of Barley Varieties.
570 *Journal of Agricultural Research* 1938; 57 (3): 189–199

571 Heeb L, Jenner E, Cock MJW. Climate-smart pest management: building resilience of farms
572 and landscapes to changing pest threats. *J Pest Science* 2019; 92: 951–969

573 Heiman ML, Greenway FL. A healthy gastrointestinal microbiome is dependent on dietary
574 diversity. *Molecular Metabolism* 2016; 5(5): 317–320

575 Hoban AE, Stilling RM, Ryan FJ, Shanahan F, Dinan TG, Claesson MJ, Clarke G, Cryan JF.
576 Regulation of prefrontal cortex myelination by the microbiota. *Translational Psychiatry*
577 2016; 6: e774

578 Hufford MB, Berny Mier y Teran JC, Gepts P. Crop Biodiversity: An Unfinished Magnum Opus
579 of Nature. *Annual Review of Plant Biology* 2019; 70: 727–751

580 Ibrahim KM, Barret JA. Evolution of mildew resistance in a hybrid bulk population of barley.
581 *Heredity* 1991; 67: 247–256
582

583 IPCC. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to
584 the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core
585 Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC 2014 Geneva, Switzerland, 151 pp.
586

587 IPCC. Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of
588 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in
589 the context of strengthening the global response to the threat of climate change,
590 sustainable development, and efforts to eradicate poverty [Masson-Delmotte V, Zhai P,
591 Pörtner H.-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R et
592 al.] 2018. In Press.
593

594 Jackson LF, Webster RK, Allard RW, Kahler AL. Genetic Analysis of Changes in Scald
595 Resistance in Barley Composite Cross V. *Phytopathology* 1982; 72: 1069–1072
596

597 Jacobsen S-E, Sørensen M, Pedersen SM, Weiner J. Using our agrobiodiversity: plant-based
598 solutions to feed the world. *Agronomy for Sustainable Development* 2015; 35: 1217–1235
599

600 Jaramillo F, Destouni G. Comment on “Planetary boundaries: Guiding human development
601 on a changing planet”. *Science* 2015; 348: 1217–1218

602 Kahiluoto H, Kaseva J, Balek J, Olesen J E, Ruiz-Ramos M, Gobin A, Kersebaum KC, Takáč J,
603 Ruget F, Ferrise R. Decline in climate resilience of European wheat. *Proceedings of the*
604 *National Academy of Sciences* 2019; 116: 123–128

605 Khamsi R. A gut feeling about immunity. *Nat. Med.* 2015; 21: 674–676

606 Keneni G, Bekele E, Imtiaz M, Dagne K. Genetic Vulnerability of Modern Crop Cultivars:
607 Causes, Mechanism and Remedies. *International Journal of Plant Research* 2012; 2(3): 69–79

608 Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, Rasmont P, Schweiger O, Colla
609 SR, Richardson LL. Climate change impacts on bumblebees converge across continents.
610 *Science* 2015; 349 (6244): 177–180

611 Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P,
612 Beerli P. The Strength of Phenotypic Selection in Natural Populations. *The American*
613 *Naturalist* 2001; 157: 245–261

614 Knapp S, Döring TF, Jones HE, Snape J, Wingen LU, Wolfe MS, Leverington-Waite M, Griffiths
615 S. Natural Selection Towards Wild-Type in Composite Cross Populations of Winter Wheat.
616 *Frontiers in Plant Science* 2020; 10: 1757

617 Kole C. (ed). Genomic Designing of Climate-Smart Cereal Crops. Springer Nature, 2020;
618 Switzerland
619

620 Kole C, Muthamilarasan M, Henry R, Edwards D, Sharma R, Abberton M, Batley J, Bentley, A,
621 Blakeney M, Bryant J. et al. Application of genomics-assisted breeding for generation of
622 climate resilient crops: progress and prospects. *Front Plant Sci.* 2015; 6: 563

623
624 Landjeva S, Korzun V, Ganeva G. Evaluation of Genetic Diversity Among Bulgarian Winter
625 Wheat (*Triticum aestivum* L.) Varieties During the Period 1925–2003 Using Microsatellites.
626 *Genet Resour Crop Evol* 2006; 53: 1605–1614
627
628 Lehmann P, Ammunét T, Barton M, Battisti A, Eigenbrode SD, Jepsen JU, Kalinkat G,
629 Neuvonen S, Niemelä P, Terblanche JS, Økland B, Björkman C. Complex responses of global
630 insect pests to climate warming. *Frontiers in Ecology and the Environment* 2020; 18 (3): 141-
631 150
632
633 Lipper L, McCarthy N, Zilberman D, Asfaw S, Branca G. (Eds.). Climate Smart Agriculture:
634 Building Resilience to Climate Change. Springer International Publishing 2018; pp 630
635
636 Lucas T, Horton R. The 21st-century great food transformation. *The Lancet* 2019; 393
637 (10170): 386-387
638
639 Matzrafi M, Seiwert B, Reemtsma T, Rubin B, Peleg Z. Climate change increases the risk of
640 herbicide-resistant weeds due to enhanced detoxification. *Planta* 2016; 244: 1217–1227
641
642 McDonald BA, Allard RW, Webster RK. Responses of Two, Three, and Four Component
643 Barley Mixtures to a Variable Pathogen Population. *Crop Science* 1988; 28: 447-452
644
645 McDonald BA, Stukenbrock EH. Rapid emergence of pathogens in agro-ecosystems: global
646 threats to agricultural sustainability and food security. *Trans. R. Soc. B* 2016; 71: 20160026
647
648 Menkir A, Crossa J, Meseka S, Bossey B, Muhyideen O, Riberio PF, Coulibaly M, Yacoubou A-
649 M, Olaoye G, Haruna A. Stacking Tolerance to Drought and Resistance to a Parasitic Weed in
650 Tropical Hybrid Maize for Enhancing Resilience to Stress Combinations. *Front. Plant Sci.*
651 2020; 11: 66
652
653 Mulumba JW, Nankya R, Adokorach J, Kiwuka D, Fadda C, De Santis P, Jarvis DI. A risk-
654 minimizing argument for traditional crop varietal diversity use to reduce pest and disease
655 damage in agricultural ecosystem of Uganda. *Agriculture, Ecosystem and the Environment*
656 2012; 157: 70–86
657
658 Mundt, CC. Use of multiline cultivars and cultivar mixtures for disease management. *Annual*
659 *Review Phytopathology* 2002; 40: 381–410
660
661 Murphy K, Lammer D, Lyon S, Carter B, Jones SS. Breeding for organic and low-input farming
662 systems: An evolutionary–participatory breeding method for inbred cereal grains.
663 *Renewable Agriculture and Food Systems* 2005; 20: 48–55
664
665 Newton AC, Johnson SN, Gregory PJ. Implications of climate change for diseases, crop yields
666 and food security. *Euphytica* 2011; 179: 3–18
667
668 Paillard S, Goldringer I, Enjalbert J, Trottet M, David J, de Vallavieille-Pope C, Brabant P. Evolution of
669 resistance against powdery mildew in winter wheat populations conducted under dynamic
670 management. II. Adult plant resistance. *Theor. Appl. Genet* 2000; 101: 457–462
671
672 Palumbi SR. Humans as the world's greatest evolutionary force. *Science* 2001; 293 (5536): 1786–1790

664 Patel JD, Reinbergs E, Mather DE, Choo TM, Sterling JD. Natural Selection in a Double-
665 Haploid Mixture and a Composite Cross of Barley. *Crop Science* 1987; 27: 474–479

666 Pautasso M, Döring TF, Garbelotto M, Pellis L, Jeger MJ. Impacts of climate change on plant
667 diseases—opinions and trends. *European Journal of Plant Pathology* 2012; 133 (1): 295–313

668 Petitti M, Bocci R, Bussi B, Ceccarelli S, Spillane C, McKeown P. Evolutionary-participatory
669 breeding generates populations adapted for organic agriculture in Italy. 2018; pp 39-41 In:
670 Baćanović-Šišić, J., Dennenmoser, D., Finckh, M.R. (eds), Symposium on Breeding for
671 Diversification, February 2018, University of Kassel, Witzenhausen, Germany. Kassel
672 University Press

673 Phillips SL, Wolfe MS. Evolutionary plant breeding for low input systems. *Journal of*
674 *Agricultural Science* 2005; 143: 245–254

675 Piepho H-P. Recent claim of declining climate resilience in European wheat is not supported
676 by the statistics used. *Proceedings of the National Academy of Sciences* 2019; 116 (22):
677 10625-10626

678 Raggi L, Ceccarelli S, Negri V. Evolution of a barley composite cross-derived population: an
679 insight gained by molecular markers. *The Journal of Agricultural Science* 2016; 154: 23–39

680 Raggi L, Ciancaleoni S, Torricelli R, Terzi V, Ceccarelli S, Negri V. Evolutionary breeding for
681 sustainable agriculture: selection and multi-environment evaluation of barley populations
682 and lines. *Field Crops Research* 2017; 204: 76–88

683 Rahmanian M, Salimi M, Razavi K, Haghparast R, Ceccarelli S. Living Gene Banks in Farmers
684 Fields. *Farming Matters* March 2014; 12–15

685 Ray DK, Gerber JS, MacDonald GK, West PC. Climate variation explains a third of global crop
686 yield variability. *Nature Communications* 2015; 6: 5989

687 Rasmusson DC, Beard BH, Johnson FK. Effect of Natural Selection on Performance of a
688 Barley Population. *Crop Science* 1967; 7: 543–543
689

690 Reiss ER, Drinkwater LE. Cultivar mixtures: a meta-analysis of the effect of intraspecific
691 diversity on crop yield. *Ecological Applications* 2018; 28: 62–77
692

693 Rhoné B, Vitalis R, Goldringer I, Bonnin I. Evolution of flowering time in experimental wheat
694 populations: a comprehensive approach to detect genetic signatures of natural selection.
695 *Evolution* 2010; 64 (7):2110-2125

696 Robinson RA. Breeding for quantitative variables. Part 2: Breeding for durable resistance to
697 crop pests and diseases. In Ceccarelli S, Guimaraes EP, Weltzien E. (Eds) Plant breeding and
698 farmer participation. 2009; pp 367–390. FAO, Rome

699 Rockström J, Steffen W, Noone K, Persson Å, Chapin III FS, Lambin EF, Lenton TM, Scheffer
700 M, Folke C, Schellnhuber HJ, et al. A safe operating space for humanity. *Nature* 2009; 461:
701 472–475

702 Rosenzweig C, Iglesias A, Yang AB, Epstein PR, Chivian E. Climate Change and U.S.
703 Agriculture: The Impacts of Warming and Extreme Weather Events on Productivity,

704 Plant Diseases, and Pests. Center for Health and the Global Environment, Harvard Medical
705 School, 260 Longwood Avenue, Room 262A, Boston, MA 02115 2000; pp 1–47
706

707 Rosenzweig C, Iglesias A, Yang AB, Epstein PR, Chivian E. Climate change and extreme
708 weather events - Implications for food production, plant diseases, and pests. *Global Change*
709 *and Human Health* 2001; 2: 90–104
710

711 Simmonds NW. Variability in Crop Plants, Its Use and Conservation. *Biological Reviews* 1962;
712 37: 422–465

713 Singh M, Grando S, Ceccarelli S. Measures of Repeatability of Genotype by Location
714 Interactions Using Data from Barley Trials in Northern Syria. *Experimental Agriculture* 2006;
715 42: 189-198

716 Singh RK, Chang HW, Yan D, Lee KM, Ucmak D, Wong K. Influence of diet on the gut
717 microbiome and implications for human health. *J. Transl. Med.* 2017; 15: 73

718 Smithson JB, Lenné JM. Varietal mixtures: a viable strategy for sustainable productivity in
719 subsistence agriculture. *Annals of Applied Biology* 1996; 128(1): 127–158
720

721 Soliman KM, Allard RW. Grain Yield of Composite Cross Populations of Barley: Effects of
722 Natural Selection. *Crop Science* 1991; 31: 705–708

723 Springmann M, Mason-D'Croz D, Robinson S, Garnett T, Godfray HCJ. Global and regional
724 health effects of future food production under climate change: a modelling study. *The*
725 *Lancet* 2016; 387 (10031): 1937–1946

726 Steffen W, Richardson K, Rockstrom J, Cornell SE, Fetzer I, Bennett EM, Biggs R, Carpenter
727 SR, de Vries W, de Wit CA, ., et al. Planetary boundaries: Guiding human development on a
728 changing planet. *Science* 2015; 347: 1259855

729 Suneson CA. An Evolutionary Plant Breeding Method. *Agronomy Journal* 1956; 48: 188–191

730 Thrupp L. Linking agricultural biodiversity and food security: the valuable role of
731 agrobiodiversity for sustainable agriculture. *International Affairs* 2000; 76: 265–281

732 Tilman D, Clark M. Global diets link environmental sustainability and human health. *Nature*
733 2014; 515: 518–522

734 van der Wouw M, Kik C, van Hintum T, van Treuren R, Visser B. Genetic erosion in crops:
735 concept, research results and challenges. *Plant Genetic resources: Characterization and*
736 *Utilization* 2010; 8 (1): 1–15

737 Wade MJ, Kalisz S. The causes of natural selection. *Evolution* 1991; 44: 1947 1955

738 Watts N, Amann M, Arnell N, Ayeb-Karlsson S, Belesova K, Berry H, Bouley T, Boykoff M,
739 Byass P, Cai W. The 2018 report of the Lancet Countdown on health and climate change:
740 shaping the health of nations for centuries to come. *The Lancet* 2018; 392 (10163): 2479–
741 2514

742 Weedon OD, Finckh MR. Heterogeneous Winter Wheat Populations Differ in Yield Stability Depending
743 on their Genetic Background and Management System. *Sustainability* 2019; 11(21): 6172

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

747 Wolfe MS, Brändle U, Koller B Limpert E, McDermott JM, Müller K, Schaffner D. Barley
748 mildew in Europe: population biology and host resistance. *Euphytica* 1992; 63: 125–139

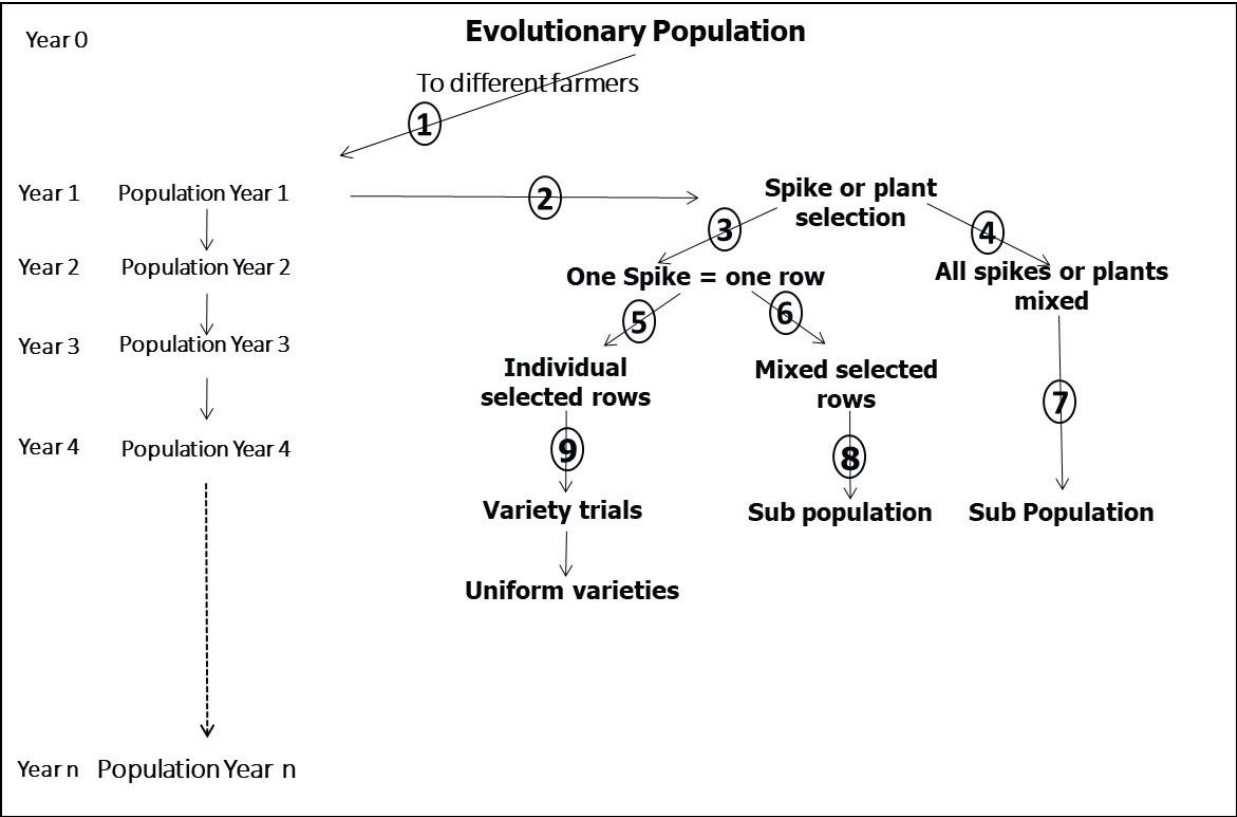
749 Wolfe MS, Ceccarelli S. The need to use more diversity in cereal cropping requires more
750 descriptive precision. *Journal of the Science of Food and Agriculture* 2020; 100: 4119–4123

751 Zampieri M, Weissteiner CJ, Grizzetti B, Toreti A, van den Berg M, Dentener F. Estimating
752 resilience of crop production systems: From theory to practice. *Science of the Total*
753 *Environment* 2020; 735: 139378

754 Zavala JA, Casteel CL, DeLucia EH, Berenbaum MR. Anthropogenic increase in carbon dioxide
755 compromises plant defense against invasive insects. *Proceedings of the National Academy of*
756 *Sciences* 2008; 105 (13): 5129–5133

757 Ziska LH, Dukes JS. *Weed Biology and Climate Change*. Blackwell Publishing Ltd. Ames, Iowa
758 50014-8300, 2010; USA

1



2

3 Figure 1. An evolutionary population is distributed to different farmers and is left evolving
4 independently in each farmer's field (path 1). It can also be subjected to selection (path 2)
5 leading to either improved sub-populations (paths 4-7 or 3-6-8) or uniform varieties (path 3-
6 5-9).

7

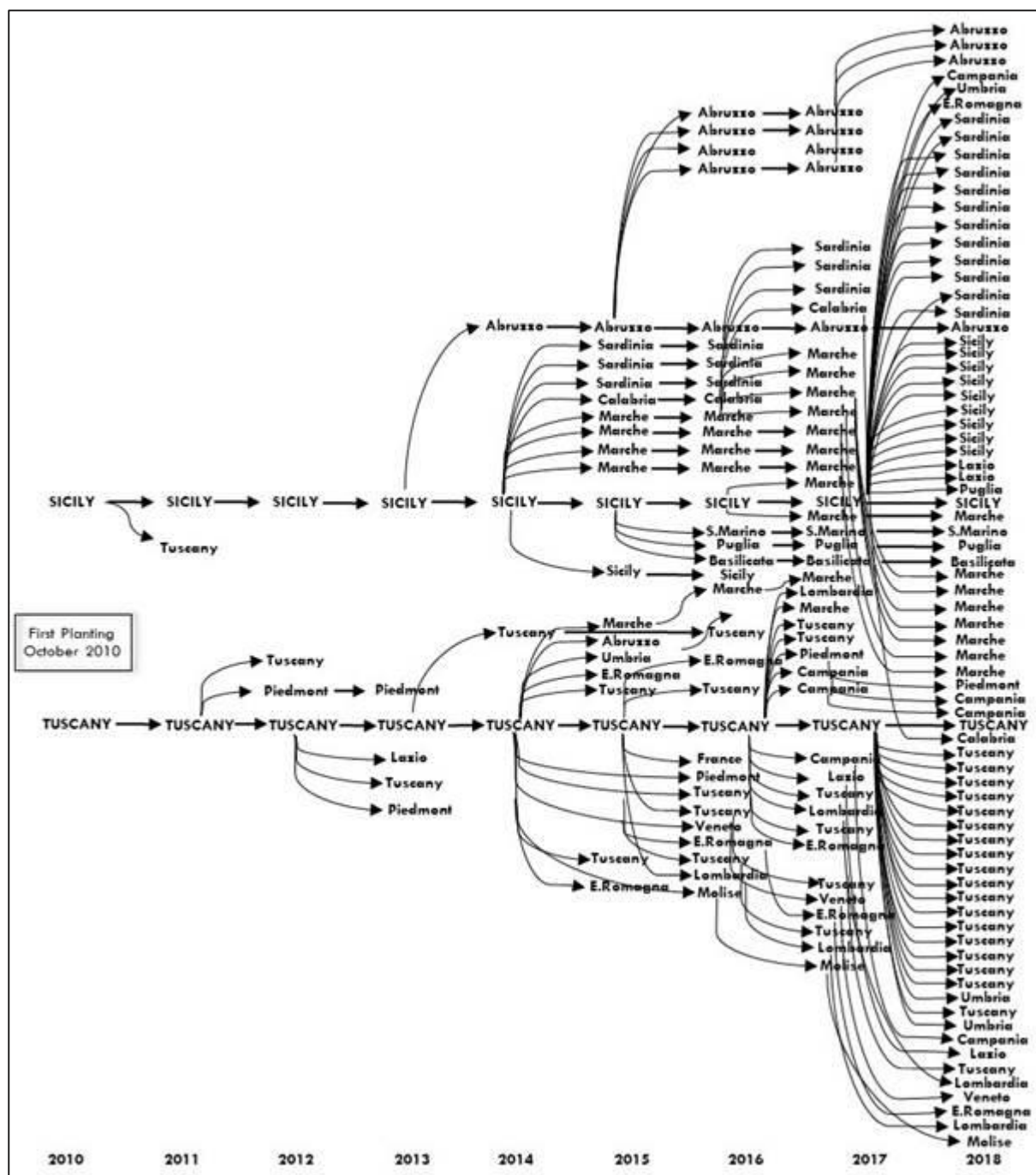


Figure 2. Diffusion throughout Italy of the ICARDA bread wheat EP made in Syria and planted in Sicily and Tuscany, for the first time in 2010.



12

13 Figure 3. The ICARDA evolutionary bread wheat population after 10 years evolution in Sicily
14 (left) and the same population after 10 years evolution in Tuscany (right) grown in Marche,
15 in 2020 (courtesy of Pierluigi Valenti).