Chapter 9
Evolutionary Breeding and Climate Change

Kevin M. Murphy, Arron H. Carter, and Stephen S. Jones

Abstract The genetic uniformity within, and typified by, most monocultural cereal-based systems has been shown to limit the crops' capacity to evolve in response to adverse environmental conditions, thereby leading to a possible decrease in the yield stability of the cropping system. Deployment of significantly increased crop diversity across the global landscape has the potential to reduce the progress of crop epidemics, optimize yield stability, and positively enhance crop resilience in the ever-changing visage of climate-induced stress. One method of increasing genetic diversity within cereal crop populations is through evolutionary breeding (EB). In EB populations of self-pollinating cereals, natural selection acts upon the heterogeneous mixture of genotypes over generations and across environments and traits positively correlated to reproductive capacity increase over time. Crop populations with enhanced genetic diversity mimic natural ecological communities, which are better equipped to adapt to future unpredictable temporal climate shifts than are monocultures. Evolutionary participatory breeding merges the EB method with farmer selection to develop high-yielding, disease-resistant cultivars while maintaining a high degree of genetic variation to allow for adaptability to fluctuations in environmental conditions. The EB method can contribute to the development of cropping systems with greater resilience and yield stability in the climate change era.

K.M. Murphy (✉) • A.H. Carter
Department of Crop and Soil Sciences, Washington State University, Pullman,
WA 99164-6420, USA
e-mail: kmurphy2@wsu.edu

S.S. Jones
Northwestern Washington Research and Extension Center, Washington State University,
Mount Vernon, WA 98273-4768, USA

9.1 Introduction

9.1.1 Climate Change and Crop Resilience

There is much reported unpredictability in future global agriculture due to the considerable variability within and between countries, with some areas potentially benefiting, and others suffering from, climate change (Jones and Thornton 2003; Gregory et al. 2009). Crops that are grown in regions that reach their maximum temperature tolerance, particularly in low-latitude dryland farming systems, are expected to experience yield decreases with even minimal changes in climate (Parry et al. 2005). The distribution of the effects of climate change will almost certainly be uneven, with the livelihoods of subsistence farmers likely being the most negatively affected and the risk of hunger increasing predominantly in the most marginalized economies (Rosenzweig and Parry 1994; Parry et al. 2005). In China, it is clear that the climate has warmed significantly since 1960, with increased frequency of heat waves. However, both geographic and annual variability in water resources prevents an accurate understanding of the impact of climate on China's agriculture (Piao et al. 2010). Regional (within countries rather than across countries) climate simulations and management strategies should be developed to better understand potential crop response to climate change (Piao et al. 2010).

Many complex crop × climate interactions are influenced by crop pathogens and insect pests. Each year, plant diseases account for global harvest losses of approximately 10–16 % (Oerke 2006), and disease resistance in cultivars of wheat, oats, rice, tobacco, and sunflower have been shown to be differentially affected by temperature (Gregory et al. 2009). For example, differential resistance expression has been shown at 10 °C and 25 °C against isolates of *Puccinia recondita* among cultivars of wheat, and similar temperature sensitivities have also been reported to *P. striiformis* in wheat, *P. tritici* in oats, and to *Xanthomonas oryzae* pv. *oryzae* in rice (Martens et al. 1967; Dyck and Johnson 1983; Gerecheter-Amitai et al. 1984; Jones 2003; Garrett et al. 2006). The effectiveness of currently deployed resistance genes has been shown to be compromised, over- or underexpressed when faced with more extreme and variable climatic conditions (Gregory et al. 2009). Resistance genes in barley have been shown to lose gene expression due to drought stress and salt stress as well as to drought stress relief and cold stress relief (Newton and Young 1996; Barker 1998; Stewart 2002; Goodman and Newton 2005). Aphids, one of the most important pests in agriculture throughout the globe, may be able to exploit the changing conditions particularly well due to their short generation time, low developmental threshold temperature, and significant dispersal abilities (Sutherst et al. 2007).

It is impossible to predict annual fluctuations in rainfall and temperature in any given location, much less across locations, thereby making proper varietal selection somewhat of a guessing game. This could become progressively more problematic in the face of increasingly unpredictable environmental fluctuations of a potentially

larger magnitude due to climate change. One way to combat this issue is to deploy inter- and intraspecific crop diversity across the landscape, thereby reducing the progress of crop epidemics and optimizing yield stability (Gregory et al. 2009). Increased crop diversity should positively enhance crop resilience in the ever-changing face of climate-induced stress, resulting in improved crop performance (Newton et al. 2009) and enhanced food security.

9.1.2   *Intraspecific Genetic Diversity*

Because of the predominance of monocultures in cereal crops throughout much of the world, crop diversity occurs at scales where individual genotype unit areas (GUAs) (Mundt and Browning 1985) are often many square kilometers (Newton et al. 2009). The genetic uniformity inherent in monocultures can restrict the crops' ability to tolerate diverse abiotic environmental stresses and pests and diseases, thereby leading to a potential decrease in the stability of the cropping system (Hooper et al. 2005; Hughes et al. 2008).

Niche segregation in the form of light gradient and exposure, soil moisture availability, and rooting depths for mineral uptake often increase complementarity while simultaneously reducing competition (Silverton 2004). Cultivar mixtures, multilines and isogenic lines have the capacity, to varying degrees, to increase the intraspecific genetic diversity in the field, and make small to potentially extreme reductions in GUAs. The use of multilines has been shown repeatedly to effectively reduce yield losses due to disease (Wolfe 1985; Garret and Mundt 1999; Zhu et al. 2000). For example, the multiarchitectural canopy types present in intentional grain mixtures have the capacity to reduce or prevent infection by splash-dispersed pathogens, including Septoria tritici blotch (*Mycosphaerella graminicola*) and glume blotch (*Phaeosphaeria nodorum*) on wheat (Jeger et al. 1981a; Cowger and Mundt 2002) and *R. secalis* infection on barley (Jeger et al. 1981b). Likewise, the severity of barley yellow dwarf virus in oats decreased in mixtures compared to pure lines (Peltonensaino and Karjalainen 1991; Karjalainen and Peltonensaino 1993). In wheat, it has also been shown that only 10–20 % of the variation in yield was attributable to disease in mixtures compared to 52–58 % in monocultures (Finckh and Mundt 1992). This complementation effect among varieties in a mixture aids in a more extensive exploitation of the major limiting resources, and decreases between-plant competition (Doring et al. 2011).

In addition to complementarity, facilitation—a positive interaction in which plants enhance the environment of their neighbors—has also been shown to be augmented through increased genetic diversity in a system (Vandermeer 1989; Long et al. 2007). Facilitation has been reported to be of greatest significance under abiotic stress (Cheng et al. 2006). However, positive effects have been found in high-input systems as well (Hauggaard-Nielsen and Jensen 2005). In barley, direct facilitation among genotypes in mixtures has been shown to impact levels of *Rhynchosporium secalis* infection through microclimatic differences

resulting from the modification of the canopy (Hoad and Wilson 2006). Indirect facilitation occurs as well; for example, mixtures of wheat were shown to significantly enhance control of *Polymyxa graminis*, the vector for wheat soil-borne mosaic virus, thus reducing the incidence of this disease (Hariri et al. 2001). Variety mixtures can also aid in disease control by increasing the physical distance between susceptible genotypes with the resistant plants acting as barriers to these foliar pathogens (Garret and Mundt 1999).

9.1.3   Towards Global Crop Resilience and Yield Stability

Yield stability across contrasting environmental conditions will be of paramount concern throughout the climate change era, particularly in the low latitude regions of the world and those areas with marginalized economies and/or dependent on rainfed cropping systems. Historical trends clearly point to evidence of seasonally and regionally altered precipitation distributions, which will have implications on changes in cropping systems and pathogen and pest incidence and severity (Barnett et al. 2006; Chakraborty and Newton 2011). Varietal mixtures typically stabilize grain yield and minimize disease-induced yield losses as well as yield losses due to abiotic stresses (Finckh et al. 2000). In comparison with monocultures, spring barley mixtures were found to be more stable for both actual yield and for yield ranking across 17 different environments in Denmark (Ostegaard et al. 2005). Using biplot analysis methods and variance models to assess yield stability, Cowger and Weisz (2008) found that mixtures of winter wheat were more stable than their individual components. Smithson and Lenne (1996) showed that yield stability of mixtures increased with the number of genotypes. Yield stability in mixtures is often due to the compensatory effect found when the loss of performance of one or more genotype in a mixture is compensated by the improvement in performance of other genotypes (Yachi and Loreau 1999; Swanston and Newton 2004; Newton et al. 2009; Doring et al. 2011).

   Chakraborty and Newton (2011) suggest that strategies for establishing greater resilience and yield stability in crops should focus on the introduction of increased genetic variability, both within and between cultivars, into agricultural systems. Crop populations with this added genetic diversity can then mimic natural ecological communities, which are better equipped to adapt to future unpredictable temporal climate shifts than are monocultures. Genetically uniform cultivars have been shown to lack the ability to adjust and adapt to highly unpredictable, in direction and range, environmental fluctuations and novel stress factors (Verboom et al. 2010). As compared to monocultures, in which the use of major genes for resistance to pathogens often leads to strong selection on pathogen populations to overcome these genes (Pangga et al. 2011), genetically diverse, heterogeneous cropping systems can potentially adapt to evolving pathogen threats resulting in durable disease resistance and stable, resilient farming systems (Huang et al. 1994; Allard 1999; Chakraborty and Newton 2011).

9.2 Evolutionary Breeding

Many decades before warnings of climate change emerged in the scientific literature, Harry Harlan, a plant explorer and cereal geneticist of the United States Department of Agriculture (USDA) constructed his first barley composite cross populations (Harlan et al. 1940). For example, Barley Composite Cross II (CC II), one of the most widely studied of Harlan's composite cross populations, was created in 1929 through the hybridization of 30 diverse barley cultivars from around the world in all possible cross combinations (Harlan and Martini 1929). CC II and other composite cross populations were grown annually, first at the University of California at Davis and later in other environments, under the typical agronomic conditions of the time period, and harvested at maturity without any targeted selection by the researchers (Suneson 1956; Ramage 1987; Murphy et al. 2005). These populations were subjected to natural selection through temporal and spatial fluctuations in rainfall and temperature, similar to, though perhaps of less magnitude than, the climatic fluctuations of the present day.

9.2.1 Natural Selection and Fitness in Heterogeneous Populations

Natural selection acts upon a heterogeneous mixture of competing genotypes that undergo continual recombination and subsequent segregation and selection over many generations. Jain (1961) describes three quantifiable components of fitness in self-pollinating, annual cereals (1) the ability of a plant to germinate and emerge, (2) the survival of the plant to the reproductive growth stage, and (3) the number of seeds produced per plant. Natural selection in the barley composite cross population was shown to favor high-yielding genotypes as a result of the relationship between the yield capacity of an individual plant and its fitness components (Allard 1999). Traits positively correlated to the reproductive capacity of a self-pollinating cereal, including spike weight, number of seeds per plant and seed yield, have all been shown to increase over time through the effects of natural selection found in evolutionary breeding of barley populations (Allard 1990). For example, reproductive capacity over 50 generations of evolutionary breeding of CC II consistently kept yield performance within 95 % of the most current highest yielding varieties (Allard 1990).

Coefficients of variability are an indicator of yield stability across years and locations. In comparison with the high-yielding cultivar Atlas, Suneson (1956) reported a coefficient of variability across environments almost twice as low in CCII over an 18-year time period (1937–1955). CCII progressed from F_{11} to F_{29} during this time period. Newer composite crosses in the same study, including CCV (F_{15}), CCXII (F_{14}), and CCXIV (F_{12}) had yields similar to Atlas in 1955. Similarly, in a study comparing seed yields of lima bean composite cross populations, pure

lines and seed mixture over 4 years in California, the CC populations outproduced both the mixtures and the pure lines (Allard 1961). To minimize the effects of genotypic variation, both the mixtures and populations were developed using the pure lima bean lines in this study as parents. Suneson (1956) estimated that 15 generations of natural selection in barley was sufficient time for the composite crosses to have improved fitness traits compared to the parent genotypes.

Natural selection must favor genotypes with superior agronomic performance, otherwise the composite populations will not reach optimal fitness levels (Phillips and Wolfe 2005). Jain and Qualset (1975) suggested that stabilizing natural selection was the driving force for many traits, including seed size, spike length, days to heading and spike density, whereas directional selection was the primary selective force influencing seed number per plant. Evolutionary breeding is clearly most effective in increasing grain yield when selection pressures are constant and directional (Degago and Caviness 1987), although disruptional selection can also be effective in increasing yield. For example, even under conditions that fluctuated significantly in rainfall, temperature and day length, segregating bean populations showed a mean yield gain of 2.5 % over a 17-year time period when compared to the mean of the parents (Corte et al. 2002). In fact, the utilization of different sites with contrasting, disruptional selection pressures has been recommended as an effective method to maintain genetic diversity of disease-resistant genes within a population, thereby increasing the overall fitness of the population (Paillard et al. 2000; Phillips and Wolfe 2005).

9.2.2 Yield of Composite Cross Populations in Marginal Environments

Reduced temporal predictability of biotic and abiotic stresses in marginal environments coupled with low-input systems can make it difficult to accurately select pure line cultivars that will perform best from year to year in these challenged agronomic systems (Phillips and Wolfe 2005). These marginal environments are perhaps where the deployment of CC populations would be most effective. Many marginal environments lack a buffering or adaptive capacity, and it is the countries, regions, and societal groups with limited adaptive capacity that face the most significant threat to food security (von Braun 2007).

CCII (F_{15} to F_{37}) was shown to be equal to the yield of the best control cultivars in marginally productive environments in Montana, USA, but when grown in highly productive environments in Montana and California, was susceptible to disease and lodging (Hockett et al. 1983). Additionally, bulk F_2 populations of wheat were found to yield more than the parent cultivars by up to 26 %, but only when grown in marginal conditions (Qualset 1968). Several generations of CCV in barley were shown to have superior yields during periods of drought when compared to commercial cultivars when grown over an 18-year period in Cambridge,

UK. However, the reverse was true under the favorable agronomic conditions, which predominated during that time span (Danquah and Barret 2002). Soliman and Allard (1991) found that barley composite crosses showed significantly more yield stability across a range of marginal environments when compared to commercial cultivars. When grown in favorable agronomic environments, however, these same commercial cultivars yielded significantly higher than the composite crosses.

Because of the various resources that trigger plant-to-plant competition in cereals, including light, moisture, and nutrients, Frey and Maldonado (1967) suggested that the benefits of heterogeneous cereal populations are more clearly seen in resource-limiting environments. Likewise, Danquah and Barret (2002) established that advanced generations of barley composite cross populations were responsive and well suited to marginal, fluctuating, and stressed environments. Yield increases of 57 % over 6 years, or an average of 9.5 % per year, were found in a barley population derived from the mixing of 6,000 entries from the world barley collection and grown under late planting induced stress (Rasmusson et al. 1967).

9.3 Evolutionary Participatory Breeding

On the basis of the limitations inherent in reliance solely upon natural selection within heterogeneous populations, researchers have suggested the utilization of artificial selection within composite cross populations to drive each population in the desired direction for nonfitness-related traits of interest (Mak and Harvey 1982; Patel et al. 1987). This artificial selection may be carried out by breeders on research stations and farmers' fields, as well as by farmers in their own fields.

In regard to the latter option, farmer participatory breeding has been shown to be effective in selecting varieties of major cereal crops, including barley, maize, wheat, and rice (Sthapit et al. 1996; Bänziger and Cooper 2001; Ceccarelli et al. 2001; Witcombe et al. 2003; Thapa et al. 2009; Bachmann 2010; Medina 2012). In fact, farmers have been shown to be as capable as plant breeders in selecting high-yielding varieties on research stations, and when selection occurred on farmers' individual fields, more proficient than plant breeders in selecting high-yielding varieties (Ceccarelli et al. 2000). Evolutionary participatory breeding (EPB) merges the evolutionary breeding method described above with farmer participatory breeding to develop high-yielding, disease-resistant cultivars of desired quality while maintaining a high degree of genetic variation to allow for adaptability to fluctuations in environmental conditions (Murphy et al. 2005). For a complete review of the EPB process, please refer to Murphy et al. (2005). Below is a case study that will illustrate EPB in wheat.

9.3.1 Case Study of EPB in Wheat

In 2002, Lexi Roach, an 8th grader at Kahlotus, WA middle school, drove two hours from her family farm in Kahlotus, WA to Pullman, WA, with her grandfather Jim Moore. Jim and his family grow winter wheat on approximately 10,000 acres of farmland in a low-rainfall, rain-fed environment (~200–250 mm precipitation per year) in South-Central Washington State. In this environment, it typically takes 2 years of moisture to raise one crop of winter wheat. The only nonirrigated rotation in the area is winter wheat in Year 1 followed by fallow (tillage or chemical) in Year 2.

Lexi and Jim were traveling to Pullman to make crosses between varieties of wheat that did well on their farm, and took the initial step in the EPB process. Working with Kerry Balow in the winter wheat program, three crosses were successfully completed. F_1 seed was obtained and advanced to the F_2 in the greenhouses at Washington State University (WSU) in Pullman. This seed was then planted on their farm using small, plot-scale breeding equipment. In the F_3 to F_8, seed from each population was planted each year in the late summer, subjected to natural selection and to farmer selection by Lexi and Jim, and then harvested in bulk, subsampled, and replanted.

The seed was typically planted 5–7″ deep in order to reach available moisture, thereby selecting for genotypes with strong emergence qualities, including longer coleoptiles and perhaps faster germination and shoot initiation. Each summer, individual plants that were susceptible to yellow rust were pulled out of the population by Lexi and Jim and the farm crew.

By 2009, one of the populations, now called Lexi II, proved to be the highest yielding and was included as "WA 8094" in the WSU Statewide Variety Testing program and grown in yield trials along with 59 of the most promising varieties from 11 regional breeding programs at over 16 locations in high, medium, and low rainfall regions across the state. In the low rainfall zone, six locations including Connell, Harrington, Horse Heaven, Lind, Ritzville, and St. Andrews, were represented. When compared to the top five varieties (by acreage) grown in Washington State in 2009–2010, WA8094 yielded significantly lower than "Xerpha," the highest yielding of the dominant varieties (Table 9.1). However, WA8094 yielded the same as the most widely grown variety statewide in dry areas, "Eltan," and yielded significantly higher than "ORCF-102," "WB-528," and "Madsen" (ranked 2, 4, and 5 respectively in Washington acreage) when averaged across the six low rainfall locations (Table 9.1). In this same year, at the St. Andrews location, WA8094 was the top yielder surpassing all of the 59 other varieties.

In 2010–2011, WA8094 yielded lower than Xerpha and ORCF-102, and was statistically equal to Eltan, WB-528, and AP 700 CL (which had replaced Madsen as the 5th most widely grown soft white winter wheat variety in Washington State, when averaged across all six locations (Table 9.2).

Although WA8094 has a very high yield potential under this selection criteria, there are other disease factors that need to be taken into account. New shifts in

Table 9.1   2010 Soft white winter wheat variety yield (bu/a) trial

Variety	WA Acreage Rank (2010)	Connell	Harrington	Horse Heaven	Lind	Ritzville	St. Andrews	Average yield
Xerpha	3	67	59	46	51	64	66	59
Eltan	1	65	50	38	45	68	57	54
WA 8094	na	59	50	38	45	55	75	54
ORCF-102	2	54	53	37	44	59	48	49
Madsen	5	47	49	34	45	63	43	47
WB-528	4	46	46	42	39	51	50	46
lsd ($P = 0.10$)		7	9	4	5	9	14	4

Table 9.2   2011 Soft white winter wheat variety yield (bu/a) trial

Variety	WA Acreage Rank (2011)	Connell	Harrington	Horse Heaven	Lind	Ritzville	St. Andrews	Average yield
Xerpha	3	56	64	69	53	88	68	66
ORCF-102	1	71	64	67	43	77	63	66
Eltan	2	56	61	62	48	77	82	64
WB-528	4	67	63	64	39	75	50	60
WA 8094	na	53	56	65	43	74	63	59
AP 700 CL	5	69	58	55	38	75	57	59
lsd ($P = 0.10$)		10	9	10	11	11	20	5

pathogen races warrant the need for selection each year. During the F_3 to F_8 stages when WA8094 was selected on farm, it was resistant to local races of yellow rust. Two years after commercial production on the farm, a new race entered the area which is virulent on WA8094. Currently, fungicide applications are needed to protect the yield potential of this line. Similarly, a long, cool growing season in 2011 caused aphid populations to increase, and resulted in a severe case of the aphid transmitted barley yellow dwarf virus (BYDV). Since this growing region seldom sees aphid problems, WA8094 was highly susceptible to BYDV, a problem attributed mainly to changing climate variables. As climate change will not only change the agronomic growing conditions but also pest populations, concurrent production and selection fields are needed to maintain identification of high-yielding adapted lines with excellent resistance to changing pest populations.

The fact that a bulk population with recurrent, farmer imposed, natural and intentional selection could rank high in an elite yield nursery demonstrates with some clarity the potential for this method. Continued annual selection under changing environmental and disease pressures will maintain populations of adapted and resistant material. As our climate becomes less predictable we will be well served to not only increase the diversity in our fields but also in the approaches that we take towards crop improvement.

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