

CLIMATE CHANGE AND AGRICULTURE PAPER

Plant breeding and climate changes

S. CECCARELLI^{1*}, S. GRANDO¹, M. MAATOUGUI¹, M. MICHAEL¹, M. SLASH¹,
R. HAGHPARAST², M. RAHMANIAN³, A. TAHERI³, A. AL-YASSIN^{4†},
A. BENBELKACEM⁵, M. LABDI⁶, H. MIMOUN⁶ AND M. NACHIT¹

¹ ICARDA – BIGM, Aleppo, Syrian Arab Republic

² Dryland Agricultural Research Institute – Cereal, Kermanshah, Islamic Republic of Iran

³ CENESTA, Tehran, Islamic Republic of Iran

⁴ NCARE, Amman, Jordan

⁵ INRAA, El Khroub, Algeria

⁶ INRAA, Sidi Bel Abbes, Algeria

(Revised MS received 19 May 2010; Accepted 10 June 2010; First published online 16 August 2010)

SUMMARY

Climate change is now unequivocal, particularly in terms of increasing temperature, increasing CO₂ concentration, widespread melting of snow and ice and rising global average sea level, while the increase in the frequency of drought is very probable but not as certain.

However, climate changes are not new and some of them have had dramatic impacts, such as the appearance of leaves about 400 million years ago as a response to a drastic decrease in CO₂ concentration, the birth of agriculture due to the end of the last ice age about 11 000 years ago and the collapse of civilizations due to the late Holocene droughts between 5000 and 1000 years ago.

The climate changes that are occurring at present will have – and are already having – an adverse effect on food production and food quality with the poorest farmers and the poorest countries most at risk. The adverse effect is a consequence of the expected or probable increased frequency of some abiotic stresses such as heat and drought, and of the increased frequency of biotic stresses (pests and diseases). In addition, climate change is also expected to cause losses of biodiversity, mainly in more marginal environments.

Plant breeding has addressed both abiotic and biotic stresses. Strategies of adaptation to climate changes may include a more accurate matching of phenology to moisture availability using photoperiod-temperature response, increased access to a suite of varieties with different duration to escape or avoid predictable occurrences of stress at critical periods in crop life cycles, improved water use efficiency and a re-emphasis on population breeding in the form of evolutionary participatory plant breeding to provide a buffer against increasing unpredictability. ICARDA, in collaboration with scientists in Iran, Algeria, Jordan, Eritrea and Morocco, has recently started evolutionary participatory programmes for barley and durum wheat. These measures will go hand in hand with breeding for resistance to biotic stresses and with an efficient system of variety delivery to farmers.

CLIMATE CHANGES TODAY

Today, nobody questions whether climate changes are occurring or not and the discussion has shifted

from whether they are happening to what to do about them.

The most recent evidence from the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2007) indicates that the warming of the climate system is unequivocal, as it is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice and rising global average sea level.

* To whom all correspondence should be addressed.
Email: s.ceccarelli@cgiar.org

† Present address ICARDA – BIGM, Aleppo, Syrian Arab Republic.

The report states:

- Eleven of the last 12 years (1995–2006) rank among the 12 warmest years in the instrumental record of global surface temperature (since 1850).
- The temperature increase is widespread over the globe, and is greater at higher northern latitudes. Land regions have warmed faster than the oceans.
- The rising sea level is consistent with warming. The global average sea level has risen since 1961 at an average rate of 1.8 mm/year and since 1993 at 3.1 mm/year, with contributions from thermal expansion, melting glaciers and ice caps and the polar ice sheets.
- Observed decreases in snow and ice extent are also consistent with warming. Satellite data since 1978 show that the annual average Arctic sea ice extent has shrunk by 2.7% per decade, with larger decreases in summer of 7.4% per decade. Mountain glaciers and snow cover on an average have declined in both hemispheres (IPCC 2007).

It is very probable that over the past 50 years, cold days, cold nights and frosts have become less frequent over most land areas, and hot days and hot nights have become more frequent. Heat waves have become more frequent over most land areas, the frequency of heavy precipitation events has increased over most areas, and since 1975 the incidence of extreme high sea levels has increased worldwide. There is also observational evidence of an increase in intense tropical cyclone activity in the North Atlantic since around 1970, with limited evidence of increases elsewhere. There is no clear trend in the annual numbers of tropical cyclones, but there is evidence of increased intensity (IPCC 2007).

Changes in snow, ice and frozen ground have resulted in more, and larger, glacial lakes, increased ground instability in mountain and other permafrost regions, and led to changes in some Arctic and Antarctic ecosystems (Walker 2007).

Projections to the year 2100 indicate that CO₂ emissions are expected to increase by 400% and CO₂ atmospheric concentration is expected to increase by 100% (Fig. 1, modified from Cline 2007).

Some studies have predicted increasingly severe future impacts with potentially high extinction rates in natural ecosystems around the world (Williams *et al.* 2003; Thomas *et al.* 2004).

CLIMATE CHANGES IN HISTORY

Even though climate change is one of the major current global concerns, it is not new. Several climate changes have occurred before, with dramatic consequences. Among them is the decrease in CO₂ content, which took place 350 million years ago and which is considered to be responsible for the appearance of leaves – the first plants were leafless and it took

c. 40–50 million years for leaves to appear (Beerling *et al.* 2001).

The second climate change was that induced by perhaps the most massive volcanic eruption in Earth history, which took place during the end-Permian (about 250 million years ago) in Siberia when up to 4 million km³ of lava erupted onto the Earth's surface (Beerling 2007). The remnants of that eruption today cover an area of 5 million km². This massive eruption caused, directly or indirectly through the formation of organohalogens, a worldwide depletion of the ozone layer. The consequent burst of ultraviolet radiation explains why the peak eruption phase coincides with the timing of the mass extinction that wiped out 0.95 of all species (Beerling 2007).

The third major climate change was the end of the last ice age (between 15000 and 13500 years ago), with the main consequence that much of the earth became subject to long dry seasons. This created favourable conditions for annual plants which can survive dry seasons either as dormant seeds or as tubers. This eventually led to agriculture as we know it today, in the Fertile Crescent, around 11000 years ago, and soon after in other areas.

The fourth climate change is the so-called Holocene flooding, which took place about 9000 years ago and is now believed to be associated with the final collapse of the ice sheet, resulting in a global sea level rise of up to 1.4 m (Turney & Brown 2007). Land lost from rising sea levels drove mass migration to the North West and this could explain how domesticated plants and animals, which by then had already reached modern Greece, started moving towards the Balkans and eventually into Europe.

During the last 5000 years, drought, or more generally limited water availability, has historically been the main factor limiting crop production. Water availability has been associated with the rise of multiple civilizations, while drought has caused the collapse of empires and societies such as the Akkadian Empire (Mesopotamia, *c.* 6200 years ago), the Classic Maya (Yucatan Peninsula, *c.* 1400 years ago), the Moche IV–V Transformation (coastal Peru, *c.* 1700 years ago) (de Menocal 2001) and the early bronze society in the southern part of the Fertile Crescent (Rosen 1990).

CLIMATE CHANGES, FOOD AND AGRICULTURE

Using the results from formal economic models, it is estimated (Stern 2005) that, in the absence of effective counteraction, the overall costs and risks of climate change will be equivalent to a 5% decrease in global gross domestic product (GDP) each year. If a wider range of risks and impacts is taken into account, the estimates of damage could rise to a 20% decrease in GDP or more, with a disproportionate burden on and

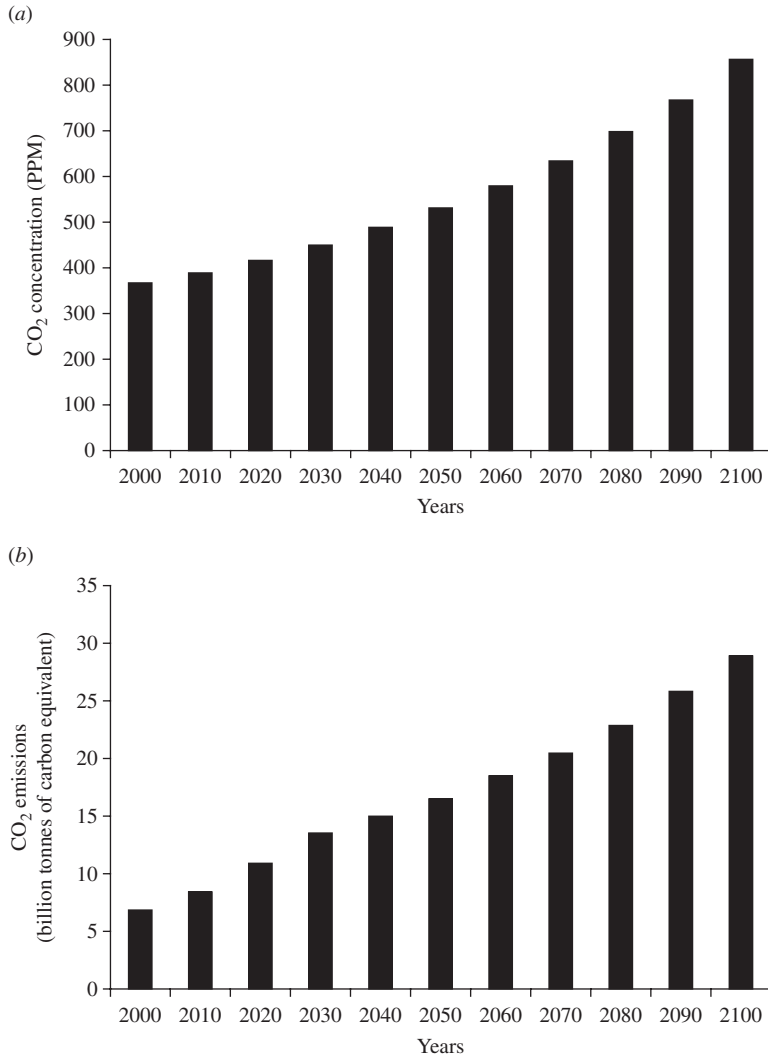


Fig. 1. Projected atmospheric CO₂ concentration in parts per million of CO₂ (a) and projected emission in billion tonnes of carbon equivalent (b) (modified from Cline 2007).

an increased risk of famine in the poorest countries (Altieri & Koohafkan 2003).

The majority of the world's rural poor (about 370 million of the poorest people on the planet) live in areas that are resource-poor, highly heterogeneous and risk-prone. The worst poverty is often located in arid or semi-arid zones, and in mountains and hills that are ecologically vulnerable (Conway 1997). In many countries, more people, particularly those at lower-income levels, are now forced to live in marginal areas (i.e. floodplains, exposed hillsides, arid or semi-arid lands), putting them at risk from the negative impacts of climate variability and change.

Climate changes are predicted to have adverse impacts on food production, food quality (Atkinson *et al.* 2008) and food security. One of the most recent predictions (Tubiello & Fischer 2007) is that the number of undernourished people would have increased by 150% in the Middle East and North Africa and by 300% in sub-Saharan Africa by the year 2080, compared to 1990 (Table 1).

Agriculture is extremely vulnerable to climate change. Higher temperatures eventually reduce crop yields without discouraging weed, disease and pest challenges. Changes in precipitation patterns increase the likelihood of short-term crop failures and

Table 1. *Expected number of undernourished in millions, incorporating the effect of climate (using data taken from Tubiello & Fischer 2007)*

	1990	2020	2050	2080	2080/ 1990
Developing countries	885	772	579	554	0.6
Asia, developing	659	390	123	73	0.1
Sub-Saharan Africa	138	273	359	410	3.0
Latin America	54	53	40	23	0.4
Middle East and North Africa	33	55	56	48	1.5

long-term declines in production. Although there will be gains in some crops in some regions of the world, the overall impact of climate change on agriculture is expected to be negative, threatening global food security (Nelson *et al.* 2009).

Food insecurity would probably increase under climate change, unless early warning systems and development programmes are used more effectively (Brown & Funk 2008). Currently, millions of hungry people subsist on what they produce. If climate change reduces production while populations increase, there is likely to be more hunger. Lobell *et al.* (2008) showed that increasing temperatures and declining precipitation over semi-arid regions are likely to reduce yields of maize, wheat, rice and other primary crops in the next two decades. These changes could have a substantial negative impact on global food security.

In addition, the impacts of climate change include reductions in calorie consumption and increases child malnutrition. Thus, aggressive agricultural productivity investments are needed to raise calorie consumption enough to offset the negative impacts of climate change on the health and well being of children (Nelson *et al.* 2009).

HOW DO PEOPLE RESPOND TO CLIMATE CHANGES?

Although the debate about climate changes is relatively recent, people have been adapting to climate changes for thousands of years, for example, in Africa. In general, people seem to have adapted best when working as a community rather than as individuals. The four main strategies of adaptation have been: (i) changes in agricultural practices, (ii) formation of social networks, (iii) embarking on commercial projects, such as investing in livestock and (iv) seeking work in distant areas. The first three of these strategies rely on people working together to improve their community (Giles 2007).

In coping continuously with extreme weather events and climate variability, farmers living in harsh environments in Africa, Asia and Latin America have developed and/or inherited complex farming systems that have the potential to bring solutions to many of the uncertainties facing humanity in an era of climate change (Altieri & Koohafkan 2003). These systems have been managed in ingenious ways, allowing small farming families to meet their subsistence needs in the midst of environmental variability without depending much on modern agricultural technologies (Denevan 1995). These systems can still be found throughout the world, covering some 5 million ha. Such systems are of global importance to agriculture and food production, and are based on the cultivation of a diversity of crops and varieties in time and space that have allowed traditional farmers to avert risks and maximize harvest security in uncertain and marginal environments, under low levels of technology and with limited environmental impact (Altieri & Koohafkan 2003). One of the salient features of traditional farming systems is their high degree of biodiversity, in particular, the plant diversity in the form of poly-cultures and/or agro-forestry patterns. This strategy of minimizing risk by planting several species and varieties of crops makes the system more resilient to weather events, climate variability and change, and is more resistant to the adverse effects of pests and diseases, while at the same time stabilizing yields over the long term, promoting diet diversity and maximizing returns even with low levels of technology and limited resources (Altieri & Koohafkan 2003).

The term 'autonomous adaptation' is used to define responses that will be implemented by individual farmers, rural communities and/or farmers' organizations, depending on perceived or real climate change in the coming decades, and without intervention and/or co-ordination by regional and national governments and international agreements. To this end, pressure to cultivate marginal land, or to adopt unsustainable cultivation practices as yields drop, may increase land degradation and endanger the biodiversity of both wild and domestic species, possibly jeopardizing future ability to respond to increasing climate risk later in the century.

One of the options for autonomous adaptation includes the adoption of varieties/species with, for example, increased resistance to heat shock and drought (Bates *et al.* 2008).

HOW DO CROPS RESPOND TO CLIMATE CHANGES?

Adapting crops to climate changes has become an urgent challenge which requires some knowledge on how crops respond to those changes. In fact, plants have responded to increasing CO₂ concentration from pre-industrial to modern times by decreasing stomatal

density – reversing the change described earlier which led to the appearance of leaves – as shown by the analysis of specimens collected from herbaria over the past 200 years (Woodward 1987). In *Arabidopsis thaliana*, the ability to respond to increasing CO₂ concentration with a decrease in the number of stomata is under genetic control (Gray *et al.* 2000); with the dominant allele (*HIC*=high carbon dioxide) preventing changes in the number of stomata. In the presence of the recessive *hic* allele, there is an increase of up to 42% in stomatal density in response to a doubling of CO₂. Stomatal density varies widely within species: for example, in barley, stomatal density varies from 39 to 98 stomata/mm² (Miskin & Rasmusson 1970) suggesting that the crop has the capacity to adapt.

Currently, it is fairly well known how plants respond to an increase in CO₂ concentration, which has both direct and indirect effects on crops. Direct effects (also known as CO₂-fertilization effects) are those affecting crops by the presence of CO₂ in ambient air, which is currently sub-optimal for C3-type plants like wheat and barley. In fact, in C3 plants, mesophyll cells containing ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) are in direct contact with the intercellular air space that is connected to the atmosphere via stomatal pores in the epidermis. Hence, in C3 crops, rising CO₂ increases net photosynthetic CO₂ uptake, because RuBisCO is not CO₂-saturated in today's atmosphere and because CO₂ inhibits the competing oxygenation reaction, leading to photorespiration. CO₂-fertilization effects can include an increase in photosynthetic rate, reduction of transpiration rate through decreased stomatal conductance, higher water use efficiency (WUE) and a lower probability of water stress occurrence. As a consequence, crop growth and biomass production may increase by up to 30% for C3 plants at doubled ambient CO₂; however, other experiments show biomass increases of only 10–20% under doubled CO₂ conditions. In theory, at 25 °C, an increase in CO₂ from the current 380–550 ppm (air dry mole fraction), projected for the year 2050, would increase photosynthesis by 38% in C3 plants. In contrast, in C4 plants (e.g. maize and sorghum) RuBisCO is localized in the bundle sheath cells in which CO₂ concentration is 3 to 6 times higher than atmospheric CO₂. This concentration is sufficient to saturate RuBisCO and in theory would prevent any increase in CO₂ uptake with rising CO₂. However, even in C4 plants, an increase in WUE via a reduction in stomatal conductance caused by an increase in CO₂ may still increase yield (Long *et al.* 2006).

However, the estimates of the CO₂-fertilization effects have been derived from enclosure studies conducted in the 1980s (Kimball 1983; Cure & Acock 1986; Allen *et al.* 1987), and currently they appear to be overestimated (Long *et al.* 2006).

Table 2. Percentage increases in yield, biomass and photosynthesis of crops grown at elevated CO₂ (550) in enclosure studies v. FACE experiments (adapted from Long *et al.* 2006)

Source	Rice	Soybean	Wheat	C ₄ crops
Yield				
Allen <i>et al.</i> (1987)	–	26	–	–
Cure & Acock (1986)	11	22	19	27
Kimball (1983)	19	21	28	–
Enclosure studies	–	32	31	18
FACE studies	12	14	13	0*
Biomass				
Allen <i>et al.</i> (1987)	–	35	–	–
Cure & Acock (1986)	21	30	24	8
FACE studies	13	25	10	0*
Photosynthesis				
Cure & Acock (1986)	35	32	21	4
FACE studies	9	19	13	6

* Data from only 1 year (Leakey *et al.* 2006).

In fact, free-air concentration enrichment (FACE) experiments, representing the best simulation of elevated CO₂ concentrations in the future, give much lower (c. half) estimates of increased yields due to CO₂ fertilization (Table 2).

Indirect effects (also known as weather effects) are the effects of solar radiation, precipitation and air temperature. Keeping management the same, cereals yields typically decrease with increasing temperatures and increase with increased solar radiation. If water is limited, yields eventually decrease because of higher evapotranspiration. Precipitation will obviously have a positive effect when it reduces water stress but can also have a negative effect such as, for example, through water logging.

In addition to CO₂, nitrogen (N) deposition is also expected to increase further (IPCC 2007) and it is known that increasing N supply frequently results in declining species diversity (Clark & Tilman 2008). In a long-term open-air experiment, grassland assemblages planted with 16 species were grown under all combinations of ambient and elevated CO₂ and ambient and elevated N. Over 10 years, elevated N reduced species diversity by 16% at ambient CO₂ but by just 8% at elevated CO₂. Although the projected increase in atmospheric CO₂ and global warming may enhance food production to some extent in the temperate developed countries, it is likely to reduce both arable area and yield per crop in many less-developed ones (Evans 2005).

The most likely scenario within which plant breeding targets need establishing is the following:

- Higher temperatures, which will reduce crop productivity, are certain.
- Increase in CO₂ concentration is certain with both direct and indirect effects.
- Increasing frequency of drought is highly probable.
- Increase in the areas affected by salinity is highly probable.
- Increasing frequency of biotic stress is also highly probable.

Given this scenario, and given that plant breeding has been a success story in increasing yield (Dixon *et al.* 2006), plant breeding may help in developing new cultivars with enhanced traits better suited to adapt to climate change conditions using both conventional and genomic technologies (Habash *et al.* 2009). These traits include drought and temperature stress resistance; resistance to pests and disease – which continue to cause crop losses (Oerke 2006), salinity and water logging (Humphreys 2005). Breeding for drought resistance has historically been one of the most important and common objectives of several breeding programmes for all the major food crops in most countries (Ceccarelli *et al.* 2004, 2007). Opportunities for new cultivars with increased drought tolerance include changes in phenology or enhanced responses to elevated CO₂. With respect to water, a number of studies have documented genetic modifications to major crop species (e.g. maize and soybeans) that have increased their water-deficit tolerance (Drennen *et al.* 1993; Kishor *et al.* 1995; Pilon-Smits *et al.* 1995; Cheikh *et al.* 2000), although this may not extend to a wide range of crops. In general, too little is known currently about how the desired traits achieved by genetic modification perform in real farming and forestry applications (Sinclair & Purcell 2005).

Thermal tolerances of many organisms have been shown to be proportional to the magnitude of temperature variation they experience: lower thermal limits differ more among species than upper thermal limits (Addo-Bediako *et al.* 2000). Therefore, a crop, such as barley, which has colonized a wide diversity of thermal climates, may harbour enough genetic diversity to breed successfully for enhanced thermal tolerance.

Soil moisture reduction due to precipitation changes could affect natural systems in several ways. There are projections of significant extinctions in both plant and animal species. Over 5000 plant species could be impacted by climate change, mainly due to the loss of suitable habitats. By 2050, the extent of the Fynbos Biome (Ericaceae-dominated ecosystem of South Africa, which is an International Union for the Conservation of Nature and Natural Resources

(IUCN) ‘hotspot’) is projected to decrease by 51–61% due to decreased winter precipitation. The succulent Karoo Biome, which includes 2800 plant species at increased risk of extinction, is projected to expand south-eastwards, and about 2% of the family Proteaceae is projected to become extinct. These plants are closely associated with birds that have specialized in feeding on them. Some mammal species, such as the zebra and nyala, which have been shown to be vulnerable to drought-induced changes in food availability, are widely projected to suffer losses. In some wildlife management areas, such as the Kruger and Hwange National Parks, wildlife populations are already dependent on water supplies supplemented by borehole water (Bates *et al.* 2008).

With the gradual reduction in rainfall during the growing season, aridity in central and west Asia has increased in recent years, reducing the growth of grasslands and ground cover (Bou-Zeid & El-Fadel 2002). The reduction of ground cover has led to increased reflection of solar radiation, such that more soil moisture evaporates and the ground becomes increasingly drier in a feedback process, thus adding to the acceleration of grassland degradation (Zhang *et al.* 2003). Recently, it has been reported that the Yangtze river basin has become hotter and it is expected that the temperature will increase by up to 2 °C by 2050 relative to 1950 (Ming 2009). This temperature increase will reduce rice production by up to 41% by the end of the 21st century and maize production by up to 50% by 2080.

The negative impact of climate changes on agriculture and therefore on food production is aggravated by the greater uniformity that exists now, particularly in the agricultural crops of developed countries compared to 150–200 years ago. The decline in agricultural biodiversity can be quantified. While it is estimated that there are c. 250 000 plant species, of which about 50 000 are edible, in fact not more than 250 are used – out of which 15 crops provide 0.9 of the calories in the human diet and three of them, namely wheat, rice and maize, provide 0.6%. In these three crops, modern plant breeding has been particularly successful and movement towards genetic uniformity has been rapid – the most widely grown varieties of these three crops are closely related and genetically uniform (pure lines in wheat and rice and hybrids in maize). The major consequence of the dependence of modern agriculture on a small number of varieties for the major crops (Altieri 1995) is that the main sources of food are more genetically vulnerable than ever before, i.e. food security is potentially in danger. A number of plant breeders have warned that conventional plant breeding by continuously crossing between elite germplasm lines would lead to the extinction of diverse cultivars and non-domesticated plants (Vavilov 1992; Flora 2001; Gepts 2006; Mendum & Glenna 2010) and climate change may exacerbate the

crisis. Gepts (2006) claims that the current industrial agriculture system is 'the single most important threat to biodiversity'. The threat has become real with the rapid spreading of diseases such as UG99 (a new race of stem rust of wheat caused by *Puccinia graminis triticii*, detected for the first time in Uganda in 1999, which is virulent to most wheat varieties and causes losses up to complete loss of the crop; Pretorius *et al.* 2000; Singh *et al.* 2006), but applies equally well to climate changes as the current predominant uniformity does not allow the crops to evolve and adapt to the new environmental conditions. The expected increase of biofuel monoculture production may lead to increased rates of biodiversity loss and genetic erosion. Another serious consequence of the loss of biodiversity has been the displacement of locally adapted varieties which may hold the secret of adaptation to the future climate (Ceccarelli & Grando 2000; Sarker & Erskine 2006; Rodriguez *et al.* 2008; Abay & Bjørnstad 2009).

COMBINING PARTICIPATION AND EVOLUTION: PARTICIPATORY-EVOLUTIONARY PLANT BREEDING

One of the fundamental breeding strategies to cope with the challenge posed by climate changes is to improve adaptation to what will probably be a shorter crop season by matching phenology to moisture availability. This should not pose major problems, because the photoperiod-temperature response is highly heritable. Other strategies include increased access to a suite of varieties with different growth durations to escape or avoid predictable occurrences of stress at critical periods in crop life cycles, shifting temperature optima for crop growth and re-emphasizing population breeding.

In all cases, the emphasis will be on identifying and using sources of genetic variation for tolerance/resistance to a higher level of abiotic stresses. The two most obvious sources of novel genetic variation are the gene banks (ICARDA has one of the largest gene banks with more than 120 000 accessions of several species including important food and feed crops such as barley, wheat, lentil, chickpea, vetch, etc.) and/or the farmers' fields. Currently, there are several international projects aiming at the identification of genes associated with superior adaptation to higher temperatures and drought. At ICARDA, as elsewhere, it has been found that landraces and, when available, wild relatives harbour a large amount of genetic variation some of which is of immediate use in breeding for drought and high-temperature resistance (Ceccarelli *et al.* 1991; Grando *et al.* 2001).

The major difference between the two sources of genetic variation is that the first is static, in the sense that it represents the genetic variation available in the

collection sites at the time the collection was made, while the second is dynamic, because landraces and wild relatives are heterogeneous populations and, as such, they evolve and can generate continuously novel genetic variation.

Adaptive capacity in its broadest sense includes both evolutionary changes and plastic ecological responses. In the climate change literature, it also refers to the capacity of humans to manage, adapt and minimize impacts (Williams *et al.* 2008). All organisms are expected to have some intrinsic capacity to adapt to changing conditions; this may be via ecological (i.e. physiological and/or behavioural plasticity) or evolutionary adaptation (i.e. through natural selection acting on quantitative traits). There is now evidence in the scientific literature that evolutionary adaptation has occurred in a number of species in response to climate change both in the long term as seen earlier in the case of stomata (Woodward 1987) or over a relatively short term, e.g. 5–30 years (Bradshaw & Holzapfel 2006). However, this is unlikely to be the case for the majority of species and, additionally, the capacity for evolutionary adaptation is probably the most difficult trait to quantify across many species (Williams *et al.* 2008).

Recently, Morran *et al.* (2009) used experimental evolution to test the hypothesis that outcrossing populations are able to adapt more rapidly to environmental changes than self-fertilizing organisms as suggested by Stebbins (1957), Maynard Smith (1978) and Crow (1992), explaining why the majority of plants and animals reproduce by outcrossing as opposed to selfing. The advantage of outcrossing is to provide a more effective means of recombination and thereby generating the genetic variation necessary to adapt to a novel environment (Crow 1992). The experiment of Morran *et al.* (2009) suggests that even outcrossing rates lower than 0.05, therefore comparable with those observed in self-pollinated crops such as barley, wheat and rice (outcrossing rates as high as 0.07 have been reported in barley (Marshall & Allard 1970; Allard *et al.* 1972) and 0.035 in wheat (Lawrie *et al.* 2006) allowed adaptation to stress environments as indicated by a greater fitness, accompanied by an increase in the outcrossing rates. The experiment by Morran *et al.* (2009), even though conducted on a nematode, is relevant for both self- and cross-pollinated crops and provides some justifications for evolutionary plant breeding, a breeding method introduced by Suneson more than 50 years ago. Working with barley (Suneson 1956), followed the assumption of Harlan & Martini (1929) and of Allard (1960) that with bulk breeding natural selection will, over time, evolve superior genotypes of self-pollinated plants. The core features (of the evolutionary breeding method) are a broadly diversified germplasm and a prolonged subjection of the mass of the progeny to

competitive natural selection in the area of contemplated use. Results showed that traits relating to reproductive capacity, such as higher seed yields, larger numbers of seeds/plant and greater spike weight, increase in populations due to natural selection over time.

The advantages of evolutionary participatory plant breeding (PPB) have been reviewed recently by Phillips & Wolfe (2005) and Murphy *et al.* (2005) using studies on yield, disease resistance and quality.

During periods of drought, the yield of bulk populations increases over commercial cultivars selected under high input, but these yield advantages do not hold when conditions are agronomically favourable (Danquah & Barrett 2002); in dry bean, Corte *et al.* (2002) found a mean yield increase of 2.5% per generation over the mean of the parents. This indicates that natural selection will favour high-yielding genotypes in environments with fluctuating biotic and abiotic selection pressures, a condition typical of most agro-ecosystems. The positive effect on the control of persistent and flexible diseases of increasing genetic diversity has been shown with the use of multilines (Wolfe 1985; Garrett & Mundt 1999; Zhu *et al.* 2000). A genetically diverse bulk population allows for adaptation to disease through the establishment of a self-regulating plant–pathogen evolutionary system (Allard 1990). An example of this has been documented in barley for resistance to scald (caused by *Rynchosporium secalis*), where a reversal from an excess of susceptible families in the earlier generations to a greater proportion of resistant families after 45 generations was observed (Muona *et al.* 1982). In soybean, where F₅ bulk populations were grown on soybean cyst nematode-infested soil, the proportion of resistant plants increased from 0.05 to 0.40, while the proportion remained at 0.05 when grown on uninfected soil (Hartwig *et al.* 1982).

Unlike yield and disease, quality is not directly influenced by natural selection and therefore, if quality is an important breeding objective, it is important to include high-quality parents in the crossing design.

At ICARDA, evolutionary plant breeding is being combined with PPB, which is seen by several scientists as a way to overcome the limitations of conventional breeding by offering farmers the possibility to choose, in their own environment, which varieties better suit their needs and conditions. PPB exploits the potential gains of breeding for specific adaptation through decentralized selection, defined as selection in the target environment (Ceccarelli & Grando 2007).

Evolutionary breeding at ICARDA is combined with participatory programmes in barley and wheat implemented in Syria, Jordan, Iran, Eritrea and Algeria. The aim is to increase the probability of recombination within a population which is

constituted deliberately to harbour a very large amount of genetic variation. In the case of barley, such a population consists of a mixture of nearly 1600 F₂ (Ceccarelli 2009), while, in the case of durum wheat, the population consists of a mixture of slightly more than 700 crosses. The barley population has been planted at 19 locations in five countries, while the durum wheat population has been planted at five locations. Both populations will be left evolving under the pressure of changing climate conditions with the expectation that the frequency of genotypes with adaptation to the conditions (climate, soil, agronomic practices and biotic stresses) of the location where each year the population is grown. The simplest and cheapest way of implementing evolutionary breeding is for the farmers to plant and harvest in the same location. However, it is also possible to plant samples in other locations affected by different stresses or different combinations of stresses by sharing the population with other farmers.

The breeder and the farmers can superimpose artificial selection with criteria that may change from location to location and with time. While the population is evolving, lines can be derived and tested as pure lines in the participatory breeding programmes, or can be used as multilines, or a subsample of the population can be directly used for cultivation exploiting the advantages of genetic diversity described earlier. The key aspect of the method is that, while the lines are continuously extracted, the population is left evolving for an indefinite amount of time, thus becoming a unique source of continuously better-adapted genetic material directly in the hands of the farmers. In all the countries where the barley evolutionary population was grown in 2008/09, the farmers shared the excess seed with others so that the population is rapidly spreading. This guarantees that the improved material will be readily available to farmers without the bureaucratic and inefficient systems of variety release and formal seed production.

In conclusion, the major danger is that discussions on the adaptation of crops to climate changes are often undertaken by those who are isolated both from the outside climate and from the people who will be most affected by its changes.

The analysis of the problems and the search for solutions can be returned to the thousands of small holder/traditional family farming communities and indigenous peoples in the developing world, which will be most affected by climatic changes. In addition, the indigenous knowledge of agricultural systems can be combined with scientific knowledge. By making use of lessons learnt from the past, it may be possible to provide better-adapted varieties that together with appropriate agronomic techniques can help millions of rural people to reduce their vulnerability to the impact of climate change.

REFERENCES

- ABAY, F. & BJØRNSTAD, A. (2009). Specific adaptation of barley varieties in different locations in Ethiopia. *Euphytica* **167**, 181–195.
- ADDO-BEDIAKO, A., CHOWN, S. L. & GASTON, K. J. (2000). Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society of London B* **267**, 739–745.
- ALLARD, R. W. (1960). *Principles of Plant Breeding*. New York: John Wiley and Sons.
- ALLARD, R. W. (1990). The genetics of host–pathogen coevolution: implications for genetic resource conservation. *Journal of Heredity* **81**, 1–6.
- ALLARD, R. W., BABEL, G. R., CLEGG, M. T. & KAHLER, A. L. (1972). Evidence for coadaptation in *Avena barbata*. *Proceedings of the National Academy of Sciences, USA* **69**, 3043–3048.
- ALLEN, L. H. JR, BOOTE, K. J., JONES, J. W., JONES, P. H., VALLE, R. R., ACOCK, B., ROGERS, H. H. & DAHLMAN, R. C. (1987). Response of vegetation to rising carbon dioxide: Photosynthesis, biomass, and seed yield of soybean. *Global Biogeochemical Cycles* **1**, 1–14.
- ALTIERI, M. A. (1995). *Agroecology: The Science of Sustainable Agriculture*. Boulder, CO: Westview Press.
- ALTIERI, M. A. & KOOHAFKAN, P. (2003). *Enduring Farms: Climate Change, Smallholders and Traditional Farming Communities*. Third World Network Environmental & Development Series 6. Penang, Malaysia: TWN.
- ATKINSON, M. D., KETTLEWELL, P. S., POULTON, P. R. & HOLLINS, P. D. (2008). Grain quality in the Broadbalk wheat experiment and the winter North Atlantic oscillation. *Journal of Agricultural Science, Cambridge* **146**, 541–549.
- BATES, B. C., KUNDZEWICZ, Z. W., WU, S. & PALUTIKOF, J. P. (2008). *Climate Change and Water*. Technical Paper of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC Secretariat.
- BEERLING, D. J. (2007). *The Emerald Planet: How Plants Changed Earth's History*. Oxford, UK: Oxford University Press.
- BEERLING, D. J., OSBORNE, C. P. & CHALONER, W. G. (2001). Evolution of leaf-form in land plants linked to atmospheric CO₂ decline in the Late Palaeozoic era. *Nature* **410**, 352–354.
- BOU-ZEID, E. & EL-FADEL, M. (2002). Climate change and water resources in Lebanon and the Middle East. *Journal of Water Resources Planning and Management* **128**, 343–355.
- BRADSHAW, W. E. & HOLZAPFEL, C. M. (2006). Evolutionary response to rapid climate change. *Science* **312**, 1477–1478.
- BROWN, M. E. & FUNK, C. C. (2008). Food security under climate change. *Science* **319**, 580–581.
- CECCARELLI, S. (2009). Evolution, plant breeding and biodiversity. *Journal of Agriculture and Environment for International Development* **103**, 131–145.
- CECCARELLI, S. & GRANDO, S. (2000). Barley landraces from the Fertile Crescent: a lesson for plant breeders. In *Diversity in the Field: On-farm Conservation of Crop Diversity* (Ed. S. B. Brush), pp. 51–76. Boca Raton, FL: IDRC.
- CECCARELLI, S. & GRANDO, S. (2007). Decentralized-participatory plant breeding: an example of demand driven research. *Euphytica* **155**, 349–360.
- CECCARELLI, S., VALKOUN, J., ERSKINE, W., WEIGAND, S., MILLER, R. & VAN LEUR, J. A. G. (1991). Plant genetic resources and plant improvement as tools to develop sustainable agriculture. *Experimental Agriculture* **28**, 89–98.
- CECCARELLI, S., GRANDO, S., BAUM, M. & UDUPA, S. M. (2004). Breeding for drought resistance in a changing climate. In *Challenges and Strategies for Dryland Agriculture* (Eds S. C. Rao & J. Ryan), pp. 167–190. CSSA Special Publication No. 32. Madison, WI: ASA and CSSA.
- CECCARELLI, S., GRANDO, S. & BAUM, M. (2007). Participatory plant breeding in water-limited environments. *Experimental Agriculture* **43**, 411–435.
- CHEIKH, N., MILLER, P. W. & KISHORE, G. (2000). Role of biotechnology in crop productivity in a changing environment. In *Climate Change and Global Crop Productivity* (Eds K. R. Reddy & H. F. Hodges), pp. 425–436. New York, NY: CAB International.
- CLARK, C. M. & TILMAN, D. (2008). Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature* **451**, 712–715.
- CLINE, W. R. (2007). *Global Warming and Agriculture: Impact Estimates by Country*, Washington, DC: Peterson Institute for International Economics.
- CONWAY, G. R. (1997). *The Doubly Green Revolution: Food for All in the Twenty-First Century*. Ithaca, NY: Cornell University Press.
- CORTE, H. R., RAMALHOL, M. A. P., GONCALVES, F. M. A. & ABREU, A. D. F. B. (2002). Natural selection for grain yield in dry bean populations bred by the bulk method. *Euphytica* **123**, 387–393.
- CROW, J. F. (1992). An advantage of sexual reproduction in a rapidly changing environment. *Journal of Heredity* **83**, 169–173.
- CURE, J. D. & ACOCK, B. (1986). Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forestry Meteorology* **38**, 127–145.
- DANQUAH, E. Y. & BARRETT, J. A. (2002). Grain yield in composite cross five of barley: Effects of natural selection. *Journal of Agricultural Science, Cambridge* **138**, 171–176.
- DEMENOCAL, P. B. (2001). Cultural responses to climate change during the late Holocene. *Science* **292**, 667–673.
- DENEVAN, W. M. (1995). Prehistoric agricultural methods as models for sustainability. *Advances in Plant Pathology* **11**, 21–43.
- DIXON, J., NALLEY, L., KOSINA, P., LA ROVERE, R., HELLIN, J. & AQUINO, P. (2006). Adoption and economic impact of improved wheat varieties in the developing world. *Journal of Agricultural Science, Cambridge* **144**, 489–502.
- DRENNEN, P. M., SMITH, M., GOLDSWORTHY, D. & VAN STATEN, J. (1993). The occurrence of trahaolose in the leaves of the desiccation tolerant angiosperm *Myronthamnus flabellifolius* Welw. *Journal of Plant Physiology* **142**, 493–496.
- EVANS, L. T. (2005). The changing context for agricultural science. *Journal of Agricultural Science, Cambridge* **143**, 7–10.
- FLORA, C. (2001). *Interactions between Agroecosystems and Rural Communities*. Boca Raton, FL: CRC Press.
- GARRETT, K. A. & MUNDT, C. C. (1999). Epidemiology in mixed host populations. *Phytopathology* **89**, 984–990.

- GEPTS, P. (2006). Plant genetic resources conservation and utilization: the accomplishment and future of a societal insurance policy. *Crop Science* **46**, 2278–2292.
- GILES, J. (2007). How to survive a warming world. *Nature* **446**, 716–717.
- GRANDO, S., VON BOTHMER, R. & CECCARELLI, S. (2001). Genetic diversity of barley: use of locally adapted germplasm to enhance yield and yield stability of barley in dry areas. In *Broadening the Genetic Base of Crop Production* (Eds H.D. Cooper, C. Spillane & T. Hodgink), pp. 351–372. New York/Rome: CABI/FAO/IPRI.
- GRAY, J.E., HOLROYD, G.H., VAN DER LEE, F.M., BAHRAMI, A.R., SIMONS, P.C., WOODWARD, F.I., SCHUCH, W. & HETHERINGTON, A.M. (2000). The HIC signaling pathway links CO₂ perception to stomatal development. *Nature* **408**, 713–716.
- HABASH, D.Z., KEHEL, Z. & NACHIT, M. (2009). Genomic approaches for designing durum wheat ready for climate change with a focus on drought. *Journal of Experimental Botany* **60**, 2805–2815.
- HARLAN, H.V. & MARTINI, M.L. (1929). A composite hybrid mixture. *Journal of the American Society of Agronomy* **21**, 487–490.
- HARTWIG, E.E., KILEN, T.C., YOUNG, L.D. & EDWARDS, C.J. Jr. (1982). Effects of natural selection in segregating soybean populations exposed to phytophthora rot or soybean cyst nematodes. *Crop Science* **22**, 588–590.
- HUMPHREYS, M.O. (2005). Genetic improvement of forage crops – past, present and future. *Journal of Agricultural Science, Cambridge* **143**, 441–448.
- IPCC (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE). (2007). *Climate Change 2007. The Physical Science Basis: Summary for Policymakers*. Geneva, Switzerland: IPCC Secretariat.
- KIMBALL, B.A. (1983). Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal* **75**, 779–788.
- KISHOR, P.B.K., HONG, Z., MIAO, G., HU, C. & VERMA, D. (1995). Overexpression of $\Delta 1$ -pyrroline-5-carboxylase synthase increases proline production and confers osmotic tolerance in transgenic plants. *Journal of Plant Physiology* **108**, 1387–1394.
- LAWRIE, R.G., MATUS-CÁDIZ, M.A. & HUCL, P. (2006). Estimating out-crossing rates in spring wheat cultivars using the contact method. *Crop Science* **46**, 247–249.
- LEAKEY, A.B.D., URIBELARREA, M., AINSWORTH, E.A., NAIDU, S.L., ROGERS, A., ORT, D.R. & LONG, S.P. (2006). Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO₂ concentration in the absence of drought. *Plant Physiology* **140**, 779–790.
- LOBELL, D.B., BURKE, M.B., TEBALDI, C., MASTRANDREA, M.D., FALCON, W.P. & NAYLOR, R.L. (2008). Prioritizing climate change adaptation needs for food security in 2030. *Science* **319**, 607–610.
- LONG, S.P., AINSWORTH, E.A., LEAKEY, A.B.D., NÖSBERGER, J. & ORT, D.R. (2006). Food for thought: lower-than-expected crop yield stimulation with rising CO₂ concentrations. *Science* **312**, 1918–1921.
- MARSHALL, D.R. & ALLARD, R.W. (1970). Maintenance of isozyme polymorphisms in natural populations of *Avena barbata*. *Genetics* **66**, 393–399.
- MAYNARD SMITH, J. (1978). *The Evolution of Sex*. Cambridge, UK: Cambridge University Press.
- MENDUM, R. & GLENN, L.L. (2010). Socioeconomic obstacles to establishing a participatory plant breeding program for organic growers in the United States. *Sustainability* **2**, 73–91.
- MING, X. (2009). *Yangtze River Basin Climate Change Vulnerability and Adaptation Report*. Beijing, China: WWF.
- MISKIN, K.E. & RASMUSSEN, D.C. (1970). Frequency and distribution of stomata in barley. *Crop Science* **10**, 575–578.
- MORRAN, L.T., PARMENTER, M.D. & PHILLIPS, P.C. (2009). Mutation load and rapid adaptation favour outcrossing over self-fertilization. *Nature* **462**, 350–352.
- MUONA, O., ALLARD, R.W. & WEBSTER, R.K. (1982). Evolution of resistance to *Rhynchosporium secalis* (Oud.) Davis in barley composite cross II. *Theoretical and Applied Genetics* **61**, 209–214.
- MURPHY, K., LAMMER, D., LYON, S., CARTER, B. & JONES, S.S. (2005). Breeding for organic and low-input farming systems: an evolutionary-participatory breeding method for inbred cereal grains. *Renewable Agriculture and Food Systems* **20**, 48–55.
- NELSON, G.C., ROSEGRANT, M.W., KOO, J., ROBERTSON, R., SULSER, T., ZHU, T., RINGLER, C., MSANGI, S., PALAZZO, A., BATKA, M., MAGALHAES, M., VALMONTE-SANTOS, R., EWING, M. & LEE, D. (2009). *Climate Change: Impact on Agriculture and Costs of Adaptation*. Food Policy Report. Washington, DC: International Food Policy Research Institute.
- OERKE, E.-C. (2006). Crop losses to pests. *Journal of Agricultural Science, Cambridge* **144**, 31–43.
- PHILLIPS, S.L. & WOLFE, M.S. (2005). Evolutionary plant breeding for low input systems. *Journal of Agricultural Science, Cambridge* **143**, 245–254.
- PILON-SMITS, E.A.H., EBSKAMP, M.J.M., PAUL, M.J., JEUKEN, M.J.W., WEISBEEK, P.J. & SMEEKENS, S.C.M. (1995). Improved performance of transgenic fructan-accumulating tobacco under drought stress. *Plant Physiology* **107**, 125–130.
- PRETORIUS, Z.A., SINGH, R.P., WAGOIRE, W.W. & PAYNE, T.S. (2000). Detection of virulence to wheat stem rust resistance gene Sr31 in *Puccinia graminis* f. sp. *tritici* in Uganda. *Plant Disease* **84**, 203.
- RODRIGUEZ, M., RAU, D., PAPA, R. & ATTENE, G. (2008). Genotype by environment interactions in barley (*Hordeum vulgare* L.): different responses of landraces, recombinant inbred lines and varieties to Mediterranean environment. *Euphytica* **163**, 231–247.
- ROSEN, A.M. (1990). Environmental change at the end of early Bronze Age Palestine. In *L'urbanisation de la Palestine à l'âge du Bronze ancien* (Ed. P. De Miroschedji), pp. 247–255. Oxford, UK: BAR International.
- SARKER, A. & ERSKINE, W. (2006). Recent progress in the ancient lentil. *Journal of Agricultural Science, Cambridge* **144**, 19–29.
- SINCLAIR, T.R. & PURCELL, L.C. (2005). Is a physiological perspective relevant in a 'genocentric' age? *Journal of Experimental Botany* **56**, 2777–2782.
- SINGH, R.P., HODSON, D.P., JIN, Y., HUERTA-ESPINO, J., KINYUA, M.G., WANYERA, R., NJAU, P. & WARD, R.W. (2006). Current status, likely migration and strategies to

- mitigate the threat to wheat production from race Ug99 (TTKS) of stem rust pathogen. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* **4**, 1–13.
- STEBBINS, G. L. (1957). Self-fertilization and population variation in higher plants. *American Naturalist* **91**, 337–354.
- STERN, N. (2005). *Stern Review on the Economics of Climate Change*. Cambridge, UK: Cambridge University Press. Available online at http://webarchive.nationalarchives.gov.uk/20100407010852/http://www.hm-treasury.gov.uk/stern_review_report.htm (verified 15 July 2010).
- SUNESON, C. A. (1956). An evolutionary plant breeding method. *Agronomy Journal* **48**, 188–191.
- THOMAS, C. D., CAMERON, A., GREEN, R. E., BAKKENES, M., BEAUMONT, L. J., COLLINGHAM, Y. C., ERASMUS, B. F. N., DE SIQUEIRA, M. F., GRAINGER, A., HANNAH, L., HUGHES, L., HUNTLEY, B., VAN JAARSVELD, A. S., MIDGLEY, G. F., MILES, L., ORTEGA-HUERTA, M. A., PERSON, A. T., PHILLIPS, O. L. & WILLIAMS, S. E. (2004). Extinction risk from climate change. *Nature* **427**, 145–148.
- TUBIELLO, F. N. & FISCHER, G. (2007). Reducing climate change impacts on agriculture: global and regional effects of mitigation, 2000–2080. *Technological Forecasting and Social Change* **74**, 1030–1056.
- TURNERY, C. S. M. & BROWN, H. (2007). Catastrophic early Holocene sea level rise, human migration and the Neolithic transition in Europe. *Quaternary Science Reviews* **26**, 2036–2041.
- VAVILOV, N. I. (1992). *Origin and Geography of Cultivated Plants*. Cambridge, UK: Cambridge University Press.
- WALKER, G. (2007). A world melting from the top down. *Nature* **446**, 718–721.
- WILLIAMS, S. E., BOLITHO, E. E. & FOX, S. (2003). Climate change in Australian tropical rainforests: An impending environmental catastrophe. *Proceedings of the Royal Society of London B* **270**, 1887–1892.
- WILLIAMS, S. E., SHOO, L. P., ISAAC, J. L., HOFFMANN, A. A. & LANGHAM, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* **6**, e325. doi:10.1371/journal.pbio.0060325.
- WOLFE, M. S. (1985). The current status and prospects of multiline cultivars and variety mixtures for disease resistance. *Annual Review of Phytopathology* **23**, 251–273.
- WOODWARD, F. I. (1987). Stomatal numbers are sensitive to increases in CO₂ from preindustrial levels. *Nature* **327**, 617–618.
- ZHANG, Y., CHEN, W. & CIHLAR, J. (2003). A process-based model for quantifying the impact of climate change on permafrost thermal regimes. *Journal Geophysical Research* **108**, 4695. doi:10.1029/2002JD003354.
- ZHU, Y., CHEN, H., FAN, J., WANG, Y., LI, Y., CHEN, J., FAN, J. X., YANG, S., HU, L., LEUNG, H., MEW, T. W., TENG, P. S., WANG, Z. & MUNDT, C. C. (2000). Genetic diversity and disease control in rice. *Nature* **406**, 718–722.