

SPECIAL ISSUE ARTICLE

Enhancing crop diversity for food security in the face of climate uncertainty

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SUMMARY

Global agriculture is dominated by a handful of species that currently supply a huge proportion of our food and feed. It additionally faces the massive challenge of providing food for 10 billion people by 2050, despite increasing environmental deterioration. One way to better plan production in the face of current and continuing climate change is to better understand how our domestication of these crops included their adaptation to environments that were highly distinct from those of their centre of origin. There are many prominent examples of this, including the development of temperate *Zea mays* (maize) and the alteration of day-length requirements in *Solanum tuberosum* (potato). Despite the pre-eminence of some 15 crops, more than 50 000 species are edible, with 7000 of these considered semi-cultivated. Opportunities afforded by next-generation sequencing technologies alongside other methods, including metabolomics and high-throughput phenotyping, are starting to contribute to a better characterization of a handful of these species. Moreover, the first examples of *de novo* domestication have appeared, whereby key target genes are modified in a wild species in order to confer predictable traits of agronomic value. Here, we review the scale of the challenge, drawing extensively on the characterization of past agriculture to suggest informed strategies upon which the breeding of future climate-resilient crops can be based.

Keywords: adaptation, (*de novo*) domestication, food security, temperature stress, water deficit stress.

CURRENT CHALLENGES TO GLOBAL AGRICULTURE

Crops that currently support humankind were domesticated from their wild progenitors over the past 12 000 years. The extent of crop domestication remains variable: out of more than 50 000 plant species considered edible, around 7000 are considered semi-cultivated and only 250 are fully domesticated (Gruber, 2017). A core group of 150 species are cultivated at large scale today and 70% of the calories consumed by humans come from only 15 crop species, from which a handful of cereals contribute more than 50% (FAOSTAT, 2019). Cereal crops are a great source of carbohydrates in the form of starch, but they are low in proteins, minerals and vitamins (Yu and Tian, 2018). This leads to the problem of 'hidden hunger' whereby daily calorific needs are met but nutritional content, particularly iron, zinc and vitamins, but also phytonutrients with

antioxidant potential, is insufficient to sustain good health and development (Martin, 2018; Tiozon et al., 2021; Van Der Straeten et al., 2020). In fact, the calorie supply worldwide is 23% higher than that required, even though its uneven distribution causes almost 800 million people to be hungry (Gould, 2017). This excessive production of nutritionally devoid calories is reflected in the fact that 1.9 billion people are obese or overweight (Blüher, 2019), whereas 2 billion people have sufficient caloric intake but suffer some form of nutrient deficiency (Gödecke et al., 2018).

Agricultural intensification resulting from the development of new technologies, such as the discovery of hybrid vigour in *Zea mays* (maize) in the 1930s (Xiao et al., 2021) and the high yield of semi-dwarf *Triticum aestivum* (wheat) and *Oryza sativa* (rice) varieties during the 'Green Revolution' in the 1950s (Khush, 2001), allowed the tripling of

cereal yield despite the global area of cereal cultivation remaining largely unchanged over this period (Evenson and Gollin, 2003). However, the high demand of inputs (water, fertilizer, pesticides, mechanization) resulted in falling groundwater tables, water pollution and eutrophication, soil degradation and biodiversity loss (Tilman et al., 2002). Moreover, rural population displacement led to rapid and disorganized urbanization, particularly in developing countries (Perkins, 1997). The negative environmental and demographic consequences of the Green Revolution indicate that future agriculture should find new avenues to achieve the goal of long-term sustainability (Flavell, 2016; Pingali, 2012). The United Nations (UN) estimates that the current population of 7.7 billion will reach 9.7 billion in 2050, an increase of 2 billion over the next 30 years (United Nations, 2019). Future agriculture thus faces multiple challenges: a growing population, a changing climate and declining environmental conditions, particularly soil quality (Gao, 2021; Tian et al., 2021). To meet all of these in a sustainable manner is ultimately the grand challenge of 21st-century agriculture (Fernie and Sonnewald, 2021).

To meet this challenge, crop yields need to be increased by exploiting less prime agricultural ground, and with recourse to lower quantities of pesticides and fertilizers (Reynolds et al., 2021). Furthermore, high-quality, and not just high-quantity, crop production needs to be established in order to ensure proper nutrition (Van Der Straeten et al., 2020). New strategies will clearly be needed to achieve this. Central to their development will be the better matching of crops with their (future) environment, to ensure yield and nutritional stability (Mickelbart et al., 2015). We will outline possible strategies by which this could potentially be achieved. To uncover

routes for meeting this challenge, we postulate looking back at how nature, under anthropic and non-anthropocentric guidance, has previously tackled this problem. Before doing so, however, a further complication – climate change – needs to be addressed, as the difficulties in accurately predicting this means that the rational design of future crops is effectively aiming at a moving target. As such, considerable flexibility will need to be built into such designs.

AGRICULTURE HAS ALWAYS BEEN CONDITIONED BY CLIMATIC EVENTS

There is increasing evidence that the origin of agriculture is closely tied to climate events. The protracted transition from gathering crops in the wild to the beginning of agriculture may have been caused by climate constraints (Darlington, 1969). Indeed, these ‘silent millennia’ during the Pleistocene (from 2.5 million years to 12 000 years before present) were characterized by cold and dry weather punctuated by abrupt climate changes (Alley, 2000). The simultaneous origin of sedentary, agriculture-based societies in at least 10 geographically independent areas of the world coincides with the start of the current interglacial period (the Holocene), around 12 000 years ago (Figure 1) (Richerson et al., 2001). Clearly other factors may have been important, but the relatively warm conditions and increased local rainfall patterns are likely to have played a role in the establishment of the first agricultural societies (Ferrio et al., 2011). Since this date, unusually stable climate has become the norm, and a new glacial cycle is not expected within the next 50 000 years (Ganopolski et al., 2016). In keeping with this, climatic anomalies such as the Iron Age Cold Epoch (900–300 years before the current era,

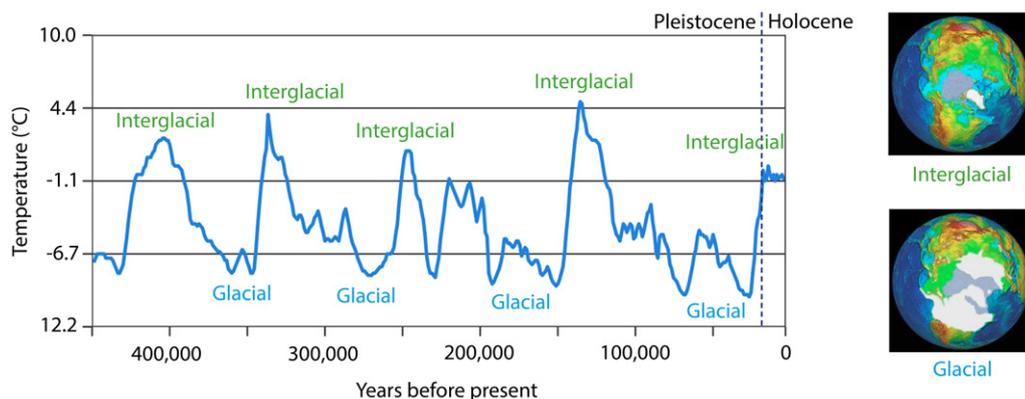


Figure 1. Climate change conditioned the appearance of agriculture. The appearance of agriculture coincided with changes in global climate at the transition from the Pleistocene to the Holocene (11 500 years BP): (a) Glacial–interglacial cycles over the past 450 000 years; the y-axis shows the mean surface temperature difference compared with the current mean surface temperature. (b) Summer ice coverage of the Northern hemisphere during the last glacial period (18 000 years BP) and today. Key: white, continental ice; light blue, sea ice; green, land above sea level. Glacial periods are marked by a drop in temperature and glacial advancement, leading to significant ice coverage. Glacial periods usually last between seven and nine times longer than interglacial periods. The current interglacial period is characterized by an unusually long stretch of stable global temperatures. Source: the US National Oceanic and Atmospheric Administration (NOAA, <https://www.noaa.gov>; used with permission).

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BCE), the Roman Warm Period (250 BCE–400 CE) and the Little Ice Age (1400–1850 CE) were associated with disruptions in food supply and human population (Bevan et al., 2017). However, these events were localized phenomena, in contrast with the accelerated global increase in temperature starting in the second half of the last century (Neukom et al., 2019). The resulting climate uncertainty is a challenge to the sustainable intensification of agriculture, required to support a growing world population in the coming decades.

The impact of changing climate has a parallel with domesticated crops being exposed to new conditions when geographically expanding out of their centres of origin. This being particularly pertinent in the exchange between Eurasia and the Americas. The expanded latitudinal range of many crops required changes in developmental progression, duration of growth cycle and time to reproduction. A general pattern is that grain crops are of temperate origin, whereas most leaf and fruit crops are tropical (Milla and Osborne, 2021). Varying latitudes differ primarily in day length between summer and winter, but also in temperature, precipitation regime and soil properties (e.g. precipitation and soil weathering tend to be more intense in tropical areas). Plants are highly adapted to their local conditions, and their growth and reproduction is temporally adjusted to respond to, and even anticipate, environmental cues. Human migration and trade transferred crops from their centres of origin to new latitudes. Although this may be advantageous because of the absence of pathogens that evolved in the centre of origin, there is the need for changes in physiological responses that would be 'maladaptive' in their new environments. For instance, photoperiodism (the control of development through the recognition of day length) and vernalization (the requirement of a cold period to induce flowering) responses were altered in crops during domestication and breeding.

Glycine max (soybean) is perhaps one of the most extreme cases, as it originated from a temperate region in north-eastern China (30°N–35°N) (Hymowitz, 1970) but is now cultivated over an enormous range of latitudes ranging between 50°N and 40°S (Chen et al., 2020), including soybean fields over the equator line in the state of Roraima (Brazil). Crops of the Compositae family, such as *Lactuca sativa* (lettuce), were also selected to avoid precocious flowering in tropical environments (Han et al., 2021). On the other hand, the transfer of tropical crops to temperate regions required an alteration of physiological responses controlled by short days, as this would coincide with a rigorous winter in the new environment. This was the case for *Solanum tuberosum* (potato), which was selected to produce tubers in long-day conditions, as opposed to its original short-day tuberization response near the equator (Ames and Spooner, 2008; Kloosterman et al., 2013).

Similarly, to adapt to longer summer days, tomato (*Solanum lycopersicum*) suffered a profound alteration in its circadian clock machinery when it was transferred to Europe (Müller et al., 2015). Moreover, the quantitative short-day flowering response of tomato was neutralized through the combination of mutations in two genes of the *CETS* family: *SP5G*, which represses flowering under long days (Soyk et al., 2017), and *SP11B*, which induces flowering under short days (Song et al., 2020). Similar mutations in genes of the *CETS* family have allowed the latitudinal spread of soybean (Chen et al., 2020), *Manihoc esculenta* (cassava; Adeyemo et al., 2019) and *Helianthus annuus* (sunflower; Blackman et al., 2010). This suggests that fine-tuning the molecular networks controlling endogenous rhythms and photoperiodic regulation of flowering could be key targets to breed crops adapted to novel climates (Steed et al., 2021). Circadian oscillator genes are similar between crops, so genes like *EARLY FLOWERING 3 (ELF3)*, *LUX ARRHYTHMO (LUX)*, *GIGANTEA (GI)* and the *PSEUDO RESPONSE REGULATOR (PRR)* family could be tailored to suit specific growth conditions (reviewed in Steed et al., 2021).

An example of successful adaptation to varying climate, although over a spatial instead of a temporal range, is the highly diversified food basis of the Inca Empire in South America (National Research Council, 1989). Whereas the Eurasian landmass is elongated longitudinally along a temperate latitude, allowing a relatively smooth flow of people and crops along the east–west axis, South America extends primarily along a north–south axis marked by the altitudinal gradient created by the Andes Mountains (Diamond, 2002). The Andean region was different to other centres of crop domestication in that it lacked flat, fertile land with good access to water (Warnock, 1991). The Incas negotiated this adverse topography by creating a network of terraces supported by a highly sophisticated irrigation system, where they cultivated 70 different crops specifically adapted to local conditions from 1000 to more than 4500 m a.s.l. They developed more than 50 varieties of maize and 4000 varieties of potatoes, which supply valuable diversity for breeding programmes today (de Haan and Rodriguez, 2016; Zambrano et al., 2021). The diversified food production matrix was complemented by a system of storage that included freeze-drying potatoes into 'chuño', which could then be preserved for more than a year without spoiling (De Jong, 2016). This provided food and nutrition security for a large population and buffered them against bad harvests, caused by the frequent droughts and floods that are typical of the Andean region.

Although the potato eventually became a staple source of carbohydrates worldwide, other important 'lost crops' of the Incas that were overlooked by the European conquerors are now gaining potential again as sources of diversity in a changing climate. These include the highly

resilient and protein-rich pseudo-cereals *Chenopodium quinoa* (quinoa; (López-Marqués et al., 2020) and *Amaranthus* spp. (amaranth; Joshi et al., 2018). Other species of interest are *Lupinus mutabilis* (tarwi), a legume with protein and oil contents comparable with those of soybean (Atchison et al., 2016), and *Annona cherimola* (cherimoya), a fruit crop with excellent organoleptic and nutritional properties (Larranaga et al., 2017). The enormous varietal diversity in these crops and their wild relatives represents a rich source to tap for future food and nutrition security in the face of climate change (Castañeda-Álvarez et al., 2016).

PREDICTED CLIMATE-CHANGE SCENARIOS AND THEIR IMPACT ON AGRICULTURE

This year marks the 50th anniversary of the Study of Man's Impact on the Climate (SMIC): Inadvertent Climate Modification (SMIC Report, 1971). The report, written by a panel of distinguished scientists, warned for the first time of an international problem of unprecedented scope. It described how carbon dioxide (CO₂), methane (CH₄), nitrous oxide (N₂O) and fluorinated gases produced by human activities absorb infrared radiation emitted from the Earth's surface, trapping it in the atmosphere and leading to warming, which became popularized in the media as the 'greenhouse effect'. The evidence of human impact on climate was so convincing that it served as a trigger to convene the first UN Conference on the Human Environment (Stockholm, 1972 – now known as 'Earth Summits') and to create the UN Environmental Program, with headquarters in Nairobi, Kenya. The goal of these institutions was to implement measures to reduce the emission of greenhouse gases, particularly CO₂ derived from the use of fossil fuels. However, an international mechanism with enforcement authority was not established until 1997, when the Kyoto Protocol was adopted (but because of a complex ratification mechanism this only came into force in 2005) (Bazerman, 2006). The effectiveness of the Kyoto Protocol in mitigating climate change is still a subject of debate, with evidence for (Maamoun, 2019) and against (Almer and Winkler, 2017) a discernible positive impact. The most recent report of the Intergovernmental Panel on Climate Change (IPCC) states that global mean temperature has increased faster since 1970 than in any other 50-year period over the last 2000 years, very likely because of greenhouse gases: atmospheric CO₂ concentrations were higher in 2019 than at any time during the last 2 million years and concentrations of CH₄ and N₂O were higher than at any time in at least 800 000 years (IPCC, 2021).

Even though future climate is hard to predict, the current consensus is that the planetary mean surface temperature will continue to increase steadily over the current century. A wide range of scenarios is possible, the outcomes of which depend on greenhouse gas emission volumes (McCarl et al., 2016). Under all scenarios of near-term

anthropogenic emissions of greenhouse gases, a virtually irreversible global mean temperature increase of 1.5°C is expected by 2040 (IPCC, 2021). It is anticipated that, if not restricted to 1–2°C by the end of the century, global warming will compromise at least one-third of crop and livestock production by moving them outside of a 'safe climatic space' (Kummu et al., 2021). The demand for food is expected to peak in 2050, so the coming two decades are going to be critical in conditioning future scenarios (Lobell and Tebaldi, 2014). Climate change has, in fact, already slowed growth in agricultural productivity, particularly in warmer, tropical regions (Ortiz-Bobea et al., 2021). However, in some of the highest latitudes of the northern hemisphere, where agriculture is currently limited by cold temperatures, a warmer climate may, conversely, improve yield and productivity (Butler et al., 2018).

Increased temperature and more frequent heatwaves will have a strong impact on agriculture in tropical regions but also in some temperate countries (Figure 2). Globally, 31% of agricultural areas are considered at 'high risk' of heat stress in the 21st century (Kummu et al., 2021). The yield of the world's four major crops is threatened by increased temperatures (Zhao et al., 2017). Climate risks could thus lead to food shortages, population displacement and other forms of social disruption (Woodward, 2019). Moderately elevated temperatures will affect all stages and processes of plant development (Lippmann et al., 2019). The expected adverse effects of high temperature on crop growth include decreased seed development and germination (Suriyasak et al., 2020), increased incidence of plant disease and herbivory (Ristaino et al., 2021), altered rates of respiration (Scafaro et al., 2021), photosynthesis (Moore et al., 2021) and photorespiration (Dusenge et al., 2019), and alterations in flowering time (Cao et al., 2021). Moreover, the effects of increased night-time temperature are expected to be particularly detrimental for crop yield (Sadok and Jagadish, 2020). The increased frequency of heatwaves, and indeed other episodes of extreme temperature, may be particularly detrimental to crop yield, as they could lead to simultaneous yield reductions worldwide (Gaupp et al., 2020; Tigchelaar et al., 2018). The physiological impact of heatwaves is an area of intense continuing research (Breshears et al., 2021). Heat stress is especially challenging to study, as the final effects depend on highly dynamic and complex interactions with ambient CO₂ concentration and water and nutrient availability (Moore et al., 2021). Recent insight from the model plant *Arabidopsis* has shown that there is a considerably epigenetic aspect of plant temperature responses (Pandey et al., 2021), whereas a recent paper indicates that prion-like domains in the circadian clock evening complex constituent EARLY FLOWERING 3 (ELF3) play an important role in guiding the response of plants to temperature (Jung et al., 2020).

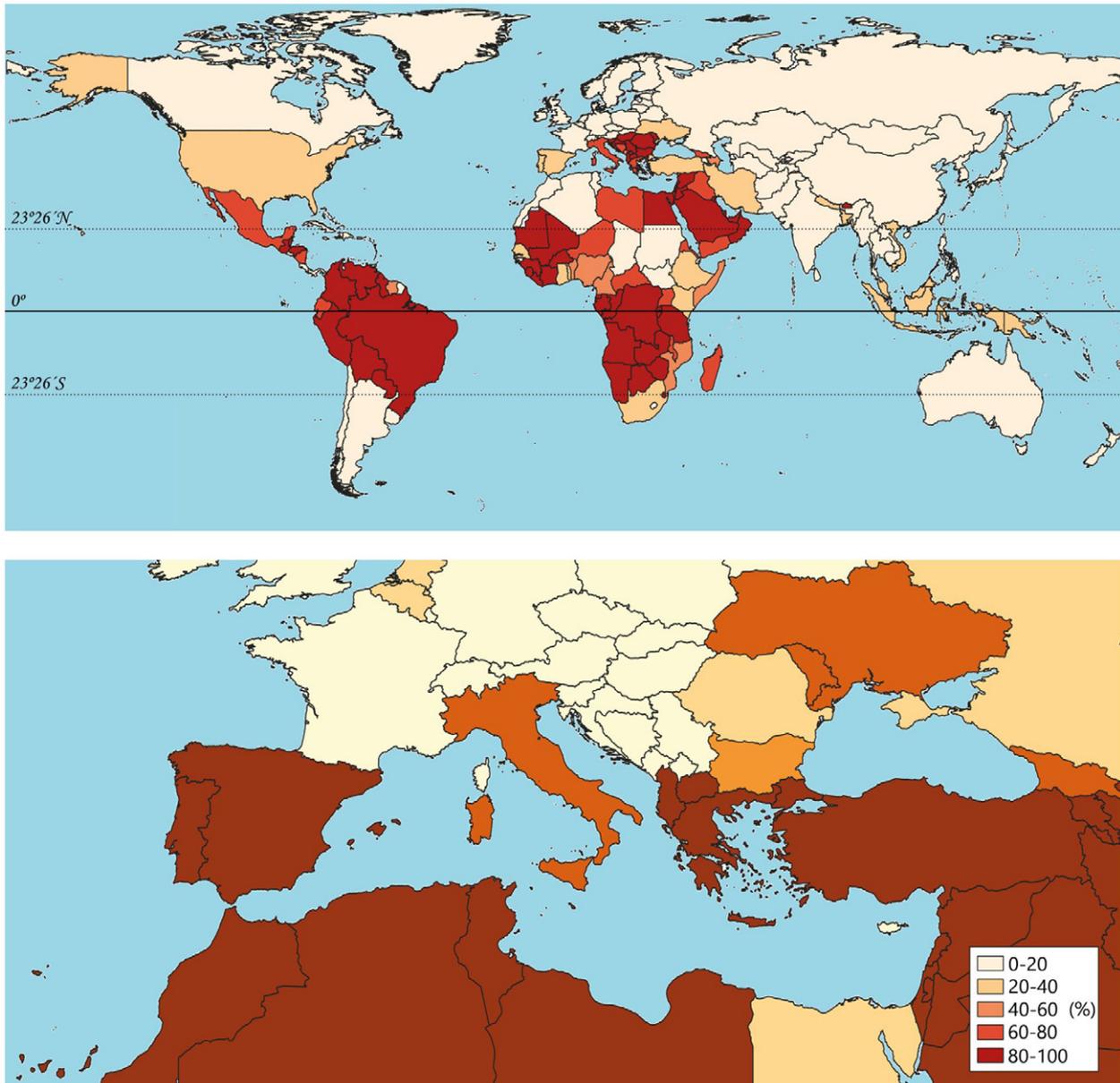


Figure 2. Climate change is expected to have a strong impact on agriculture. Top graph: proportion of agricultural area (by country) projected to be exposed to heat stress worldwide by 2040. Bottom graph: proportion of agricultural area (by country) projected to be exposed to water stress in the Mediterranean and Black Sea basin areas by 2040 (source: Four Twenty Seven, part of Moody's ESG Solutions, <https://esg.moody's.io/climate-solutions>). Note that the maps present exposure to these hazards and do not consider adaptation measures. Water stress only captures changes in blue water from rainfall and run-off and consumption demand, and many countries have strong desalination programmes, which may or may not benefit inland agriculture.

One further complicating factor will be the occurrence of simultaneous stresses. Increased atmospheric and oceanic temperature is leading to an altered distribution of rainfall, exacerbating flooding in some areas and drought in others. Thus, the detrimental effects of high temperature and drought could be compounded (Mazdiyasi and Agha-Kouchak, 2015). Given that crop yield is strongly correlated with water and nitrogen use (Sinclair and Rufty, 2012), farmers have increased output by ensuring an appropriate

supply of both resources (Sadras and Richards, 2014). It has been argued that breeding under 'ideal' resource supply may have left crops more susceptible to abiotic stresses, such as water and nitrogen deficiency (Snowdon et al., 2021). However, the finding that nitrogen overfertilization has compromised nitrogen-use efficiency in rice and that this can be set right by reintroducing landrace alleles of a single transcription factor (Liu et al., 2021) strongly supports this being the case. Moreover, in maize

grown in the USA, for instance, breeding for higher yield has increased its susceptibility to drought – mostly as an indirect consequence of higher growth density (Lobell et al., 2014). As in the case of temperature, drought will impact crop yield at different scales ranging from episodes of severe water scarcity to a general long-term reduction in rainfall (increased aridity) (Passioura, 2006). Clearly, different strategies will be required to cope with either scenario. Climate models project that rising temperatures will lead to changes in rainfall patterns that exacerbate current trends: dry regions will get drier and wet regions will become wetter. The Mediterranean basin, for instance, is particularly susceptible to drought (Cook et al., 2016), so a large share of the agricultural output in countries of Southern Europe and North Africa is expected to be compromised (Figure 2). Entire agriculture-based industries, like wine production in Southern Europe, could be disrupted (Santos et al., 2020).

When taken together, all these factors suggest that diversifying the agricultural base of crops beyond the handful of species upon which humans currently rely would be most prudent. From a plant biologist's perspective, climate change is particularly challenging as understanding one stress at a time will now not be sufficient, as it is necessary to understand the effects of the simultaneous application of multiple stresses (Zandalinas et al., 2021). Crops have been domesticated and bred for high productivity under mild, stable environmental conditions. However, many of their wild relatives have valuable adaptations that allow them to thrive in climate extremes. A deeper understanding of the dynamics of the domestication process and the underlying genetic and physiological changes produced by selection would be valuable to create new crops for the future.

CROP DOMESTICATION IS A HIGHLY DYNAMIC PROCESS

Domestication is an evolutionary process whereby the traits of plants and animals are altered to make them better adapted to an agricultural environment (Darwin, 1868). As mentioned above, starting 12 000 years ago, a set of 'core' crops (mostly cereals and legumes) were domesticated in at least 10 different areas of the world as sources of carbohydrates and proteins. These crops supplemented existing animal sources of food and subsequently paved the way for the domestication of leafy vegetable crops, spices, oil crops and most fruits (Milla and Osborne, 2021). One of the key outstanding questions surrounding this process is why these particular species were successfully domesticated and not others. The advent of tools for high-throughput long-read genome sequencing has allowed the analysis of hundreds of accessions of crops and their wild relatives, to construct 'pan-genomes' of the species (Tranchant-Dubreuil et al., 2019). Such studies are revealing that, whereas single domestication events occurred for

crops such as rice (Choi et al., 2017), maize (Matsuoka et al., 2002) or potato (Spooner et al., 2007), other species were domesticated multiple times, for instance *Phaseolus vulgaris* (the common bean; Bitocchi et al., 2013), *Pisum sativum* (pea; Trněný et al., 2018), *Cucumis melo* (melon; Zhao et al., 2019), *Prunus armeniaca* (apricot; Liu et al., 2019), *Mangifera indica* (mango; Warschefsky and Wetberg, 2019) and tomato (Razifard et al., 2020). This suggests that some species harbour traits that predispose them to be easily domesticated. A deeper understanding of these traits will prove highly valuable for future plant breeding.

It is becoming increasingly clear that domestication is a highly dynamic, reversible and open-ended process. First, human selection targets change over time, according to their needs, the prevailing environmental conditions and the agronomic management systems employed. This can be illustrated by changes in crop height. Annual seed crops such as *Hordeum vulgare* (barley), *Secale cereale* (rye), *Sorghum bicolor* (sorghum), maize, rice and wheat, as well as soybean, are grown in dense stands, leading to high competition for light. Under early cultural conditions small increases in height arising from natural selection probably added up, independently of human selection, to produce very tall plants: heights of more than 3 m for maize in the USA, 4 m for sunflower in Russia and 4 m for sorghum in Nigeria have been recorded in the last century (Donald and Hamblin, 1983). However, the 'ideal' height is determined by a trade-off between the positive effects of increases, such as suppressing weed competition or increased vegetative mass that can be used for fibre or fuel, and the numerous negative effects, such as a higher tendency to lodge, disorganized light profile, reduced seed production, harvest problems, heavy water use, low harvest index, prolonged growth cycle and late maturity. Over time, breeders resorted to deliberately reducing plant height to reduce the duration of the growth cycle and increase the harvest index, a trend that accelerated particularly during the Green Revolution, when dwarfing genes were bred into wheat and rice (Peng et al., 1999; Sasaki et al., 2002).

Domestication is a reversible process in that the genetic modifications acquired through human agency can be quickly undone if selection is relaxed (Scossa and Fernie, 2021; Wu et al., 2021). Indeed, de-domestication or feralization has recently received considerable research interest, with most effort focused on de-domesticated or weedy cereals – mainly rice, but also barley and wheat (Guo et al., 2020; Li et al., 2015; Zeng et al., 2018). Although de-domesticates evolve from domesticated species and are characterized by de-domestication syndromes, the process is not a mere reversal of domestication, with different genomic loci being involved (Wu et al., 2021). That said, although 14 independent de-domestication events have been suggested in crops, few of them have been

supported with genomic data (Wu et al., 2021). Domesticates can be further defined as endo-, exoendo- or exoferal. The first of these include some weedy rice species, Tibetan semi-wild wheat, and feral rye, feral apple and feral olive, and are the result of spontaneous mutations in genes underlying key traits (Burger et al., 2006; Cronin et al., 2020; Guo et al., 2020; Londo and Schaal, 2007; Mekuria et al., 2002). The second includes some other weedy rice species, Tibetan weedy barley and feral Callery pear, all of which result from hybridization within landraces or different genotypes (Ishikawa et al., 2005; Pourkheirandish et al., 2018; Wu et al., 2021; Zeng et al., 2018). Exoferal genotypes arise from the genomic introgression from wild relatives or by crop-wild hybridization, such as that which brought about feral *Solanum melongena* (eggplant), *Raphanus raphanistrum* (California wild radish), *Sorghum halepense* (johnsongrass), weedy sunflower, *Beta vulgaris* (weed beet) and *Cynara cardunculus* (wild artichoke thistle) (Huang et al., 2017; Page et al., 2019; Presotto et al., 2011; Song et al., 2014). The study of these processes has been postulated to provide a richer understanding of domestication and, indeed, introgression breeding underlies much of the reintroduction of biotic stress resistance in the major crops (Hajjar and Hodgkin, 2007).

Lastly, domestication should be considered an open-ended and ongoing process. It has been proposed that breeding should be guided by modelling 'ideal' plants for specific environments (Donald, 1968). Using physiological knowledge and targeting the genes controlling relevant agronomic traits, crops could be created by design as well as empirically, as has been done conventionally. Plants are highly plastic, adaptable and have been endowed by evolution with a high capacity for 'problem solving', which could be considered a form of intelligence (Trewavas, 2016). For instance, plants grown in dense stands will compete with one another for soil volume and access to water, nutrients and sunlight; mechanisms of kin recognition could be operating here (Anten and Chen, 2021). The evolutionary solutions that plants produce for this sort of challenge are seldom aligned with human interests: traits that increase fitness in nature may reduce yield under cultivation, and vice versa. A classic example is 'drought tolerance' in situations of extreme water scarcity, where plants are endowed with mechanisms for survival and reproduction but not for maintaining yield (Passioura, 1996). In opposition of the view of domestication as an open-ended and continuing process is the separation between domestication and improvement as two recognizably distinct and sequential events (Olsen and Wendel, 2013). This distinction is increasingly coming into question (Parker et al., 2021), given the different combinations of morphological, physiological and biochemical traits found in each crop in each stage of domestication (Pickersgill, 2018).

CROP DIVERSIFICATION THROUGH *DE NOVO* DOMESTICATION OF WILD SPECIES

The idea of creating new crops is not new: inducing mutations to retrieve desirable agronomic traits in wild species (IAEA, 1989), or using homologous variation between crops to guide trait stacking (Smartt, 1990), had been proposed as an avenue to increase crop diversity, particularly for marginal environments. However, the technical challenges of such empirical approaches have been insurmountable most of the time (DeHaan et al., 2016). Increased knowledge about the genetic basis of domestication, coupled with the advent of gene-editing technology, allowed a resurgence of the *de novo* domestication approach through the rational design of ideotypes (Sedbrook et al., 2014; Zsögön et al., 2017). The basic concept is to select a wild relative of a crop that has some polygenic trait of interest (which would be very difficult to introduce into crops using conventional breeding), such as drought or heat resistance, and then improve its yield by creating mutations that mimic the domestication and breeding events in existing crops (Gasparini et al., 2021). Clearly, an iterative process that encompasses conventional breeding needs to follow, to allow the widespread cultivation of the new crops (Van Tassel et al., 2020). Proof-of-concept demonstrations for the first steps of *de novo* domestication of a wild relative of tomato (*Solanum pimpinellifolium*) (Li et al., 2018a; Zsögön et al., 2018) and in the orphan Solanaceae crop *Physalis pruinose* (groundcherry) (Lemmon et al., 2018) provided a boost for the concept to gain acceptance and momentum (Fernie and Yan, 2019, 2020; Gasparini et al., 2021; Schindele et al., 2020; Wolter et al., 2019). Targeted modifications resulting in predictable phenotypic outcomes were performed in the aforementioned Solanaceae species to improve their agronomic potential, following the concept of ideotype breeding originally proposed by Donald (1968).

Following on from the examples in wild species of tomato and groundcherry, a multinational research effort recently culminated in the establishment of a route to a newly domesticated wild allotetraploid rice cultivar (Yu et al., 2021). The polyploidization of rice has long been sought as polyploid plants often harbour significant advantages with regard to biomass yield, vigour and the ability to robustly adapt to environmental changes (Comai, 2005; Fang and Morrell, 2016; Van de Peer et al., 2017). This is of particular importance for rice, which is now the main source of calories for half of the world's population (Huang et al., 2012). As mentioned above, the domestication of rice selected a range of important agronomic traits, including seed shattering, erect stand, panicle shape, awn length, grain size and quality, and hull colour (Chen et al., 2019). Although this knowledge has been used to breed new elite varieties via rational design (Zeng et al., 2017), new

strategies for rice improvement are urgently needed. The work presented by Yu et al. (2021) represents the first major outcome of the Future Crops Design project (Tian et al., 2021), which aims to develop a road map for the rapid design of customized future crops using cutting-edge technologies.

In their study, Yu et al. proposed an approach to create a polyploid rice alternative through the polyploidization of cultivated diploid rice species, which has proven difficult because of the restricted genetic background (Xu et al., 2014). By contrast, they used the *de novo* domestication route by developing an efficient transformation system, thus facilitating the gene editing of the allotetraploid *Oryza alta*. This was coupled with a high-quality genome assembly of this wild rice species, which was additionally demonstrated to have good callus induction and regeneration capacities. Following this foundational work, six agronomically important traits, namely shattering, awn length, hull colour, pericarp colour, panicle shape and grain width, were rapidly improved in *O. alta*, thereby demonstrating the feasibility of its *de novo* domestication. This study illustrates the importance of developing transformation systems and genome sequences as enabling steps for this process. The development of a high-quality genome sequence of a polyploid plant is by no means trivial; however, it has been achieved for wheat (*T. aestivum*) (Brenchley et al., 2012), *Brassica napus* (Chalhoub et al., 2014), *Gossypium* spp. (cotton) (Li et al., 2015), *Saccharum officinarum* (sugarcane) (Zhang et al., 2018), *Ipomoea batatas* (sweet potato) (Yang et al., 2017), the Ethiopian cereal crop *Eragrostis tef* (tef) (VanBuren et al., 2020) and now the wild rice *O. alta* (Yu et al., 2021). A further advantage of using wild rice, which is pertinent in the context of this special issue, is that it has many advantages over domesticated rice, such as superior biotic and abiotic stress resistance (Zhang et al., 2018), which are key factors with regards to imminent climate change (Prusty et al., 2018).

As mentioned above another domesticated cereal with enormous potential to thrive under the new climate is tef, a crop originating in the Ethiopian highlands. Like maize, tef is a plant with C4 photosynthesis, which concentrates CO₂ around the Rubisco enzyme, avoiding photorespiration and allowing lower stomatal conductance. As photorespiration is higher in high temperatures and stomatal conductance also means water loss, C4 plants tend to be more efficient in hot and dry conditions, making them hardy and drought tolerant (Kebede et al., 1989). However, the tef seeds are small and the plants tiller profusely, and are tall, leaving them prone to lodging (Habtegebrial et al., 2007). These features render the crop less productive, compared with other cereals, and less responsive to nitrogen fertilizers, which tend to disproportionately increase vegetative growth, leading to lodging (D'Andrea, 2008). Breeding programmes using ethyl methanesulfonate (EMS)-

induced mutagenesis have attempted to retrieve mutations that cause plant dwarfing and prevent lodging (Zhu et al., 2012). Using knowledge gained in other cereals about the genetic basis of seed size (Calderini et al., 2021), and of dwarfism (Würschum et al., 2017), could allow the implementation of gene-editing techniques to accelerate the improvement of tef and other orphan crops (Numan et al., 2021; Tadele, 2019). Another such example is *Tylosema esculentum*, commonly known as the morama bean, which is an excellent source of good-quality protein (29–39%); its oil (24–48%) is rich in mono- and di-unsaturated fatty acids and contains no cholesterol. Morama is a good source of micronutrients such as calcium, iron, zinc, phosphate, magnesium and B vitamins, including folate, as well as phytonutrients, including phenolics (Jackson et al., 2010). With the limitations of space here, we cannot detail the many further examples that have been reviewed and therefore refer the interested reader to recent reviews that provide more detail (Fernie and Yan, 2019; Jamnadass et al., 2020; Nasti and Voytas, 2021; Riggins and Mumm, 2021; Ye and Fan, 2020).

One advantage of gene editing over conventional mutagenesis is the predictability of the genetic pathway that will be changed. This allows the use of the body of physiological knowledge accumulated over decades. For example, although different hormonal pathways can lead to dwarfism, it is now possible to test the best option, based on the pathways that were naturally selected in the past. In rice and wheat, two C3 crops, the dwarfism used in the Green Revolution is based on the gibberellin (GA) pathway (Peng et al., 1999; Sasaki et al., 2002). In the case of rice, which is a diploid plant, a recessive loss-of-function mutation in the GA biosynthesis gene *GA20ox* was selected (Sasaki et al., 2002). On the other hand, in wheat, which is hexaploid, a dominant gain-of-function mutation in the DELLA protein, a repressor of the GA signalling pathway, was selected (Peng et al., 1999). Although dwarfism has not been exploited in C4 crops to the same extent as in C3 crops, it was introduced in sorghum, along with photoperiod insensitivity, as adaptations to more temperate climates (Thurber et al., 2013). However, unlike rice and wheat, in the case of sorghum the mutation responsible for dwarfism impairs polar auxin transport, leading to reduced internode elongation (Multani et al., 2003). Mutations in GA biosynthesis, on the other hand, pleiotropically induce culm bending in sorghum, which is an undesirable agronomic trait (Ordonio et al., 2014).

INTRODUCING DIVERSITY AND RESILIENCE INTO FUTURE CROPS

In 2010, the Food and Agriculture Organization of the United Nations (FAO) introduced the concept of 'climate-smart agriculture' to cope with future threats to food security and climate change. One of the key drivers of the

'climate-responsible' intensification of agriculture is diversification. However, the conservation of agro-biodiversity, which is a source of genetic resources, must be strongly linked to their use, either actual or potential (Maxted et al., 2012). Genomic analyses are widening to capture the large-scale range of ecological variation in crops (Tranchant-Dubreuil et al., 2019). They now include wild species, landraces and cultivars, and aim at identifying relevant genetic signatures for valuable agronomic traits (Zhang and Batley, 2020). This is a fundamental first step, which in an ideal pipeline should be followed by physiological characterization, the identification of the genetic basis of valuable physiological traits and manipulation using state-of-the-art breeding tools. One such example is work on potato, a key tuber crop with broad genetic variation in the form of wild species and landraces, but with challenging breeding because of its polyploid nature and vegetative reproduction (Bradshaw et al., 2006). A road map has been laid out to convert potato into a diploid crop (Jansky et al., 2016), which was followed by a thorough characterization of potato natural variation at the genomic level (Li et al., 2018b; Zhou et al., 2020). The physiological characterization of wild germplasm for heat tolerance (Guedes et al., 2019) and drought tolerance (Ibañez et al., 2021), and biotechnological manipulation (Lehretz et al., 2019, 2020), creates a complete synergistic portfolio with great potential for success.

Changing highly engrained dietary habits is probably more challenging than breeding new crops and creating resilient agricultural systems (Fanzo et al., 2013). However, past experiences show that it is possible through a combination of policy and individual endeavour. As recently as 300 years ago, European peasants were reluctant to grow potatoes for a variety of reasons, including superstition, their resemblance with poisonous nightshade or simply taste preferences (De Jong, 2016). Today, Europe is responsible for 30% of the total production of potato worldwide, and Germany, France, the Netherlands and Poland are among the top-10 world producers (FAOSTAT, 2019). Another example of the rapid adoption of a new crop is *Actinidia deliciosa* (kiwifruit). The first commercial orchard of kiwifruit was established in New Zealand in the 1930s (Ferguson, 2004). In less than a century, the total world production has reached well over 4 million tonnes per year and could expand and diversify through the exploitation of closely related species: *Actinidia arguta* (already grown at low scale in Europe and the USA), *Actinidia kolomikta* (high in vitamin C and adapted to colder areas) or *Actinidia eriantha* (high in vitamin C) (Ferguson, 2013). One of the key reasons behind the commercial success of the kiwifruit is the post-harvest qualities of the fruit, which can be stored for a long period of time at 0°C, making it very suitable for long-distance commercialization. Thus, the appropriate selection of wild, semi-domesticated or

incompletely domesticated plant species, based on their physiological and yield traits, will be key to increase crop diversity.

When the genetic basis of the relevant traits is unknown or is difficult to replicate, controlled introgression through wide crosses followed by selection represents a viable alternative (Fernie and Yan, 2019), especially given recent advances in crop genomics and molecular-assisted breeding (Purugganan and Jackson, 2021; Thudi et al., 2021). The burgeoning interest in this approach is leading to the gradual emergence of a consensus road map. As an initial step in this process, diversifying our knowledge of crop biology is essential given that our current understanding of the physiology, stress tolerance and optimal growth conditions of all but our major grass crops is relatively poor. For example, as mentioned above, cassava, the fourth highest yielding crop on the planet, has only recently started to be subjected to comprehensive investigation (Sonnewald et al., 2020). A better understanding of such crops, as well as the so-called orphan crops and semi-domesticates (and their wild relatives), will allow us to make informed decisions as to the best starting material for a given agronomic niche. This will require testing at multiple levels, including plant performance under optimal and suboptimal growth conditions, yield studies and ultimately also chemical compositional quality analysis. As a second step, the ability to introduce traits of interest becomes crucial; however, gene editing and transgenesis are not the only tools available here, with the introgression of known domestication genes also being possible. Naturally, these new variants must be tested in comparison both with their progenitors and with the crops that they are envisaged to replace, or alternatively must be subjected to further improvement cycles. Thus, this is no trivial undertaking. However, it is our belief that crop breeding for climate change must exploit every available tool to ensure food security and nutrition, from empirical crosses and selection to domestication of wild relatives.

CONCLUSION

We have attempted to provide a few tangible routes towards securing nutritious and high-yielding foodstuffs in the face of a changing climate. As we document above, since its inception agriculture has faced climatic uncertainties and most crops are arguably now not grown in their optimal environments, or at least not in the optimal environments of their progenitors. Climate change has numerous consequences for agriculture, some of them more certain than others. We have therefore focused this review on elevated temperature and reduced precipitation. Although several excellent reviews exist on both of these challenges, independently, it is likely that the understanding of simultaneous multiple stresses will ultimately be more relevant (Obata et al., 2015; Zandalinas et al., 2021).

We are fortunate to be able to count on a wide range of genetic and analytical resources, ranging from those that can be used to understand domestication to those recently developed for genome editing, that have been demonstrated to work highly effectively in multi-site interventions. The *de novo* domestication strategy of carefully selecting a wild species that is already by nature drought and heat resistant, and then improving its yield by introducing mutations that mimic the domestication events of the major crops of today, followed by iterations of conventional breeding, is one avenue to increase future crop resilience.

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