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IMPROVING AGRICULTURAL PRODUCTION AND FOOD SECURITY UNDER CLIMATE CHANGE CONDITIONS

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Abstract

Climate change represents a major challenge for food security in the coming years, as it is causing a significant reduction of crop yields worldwide, primarily due to the increase in the intensity and frequency of drought periods and the progressive salinisation of irrigated farmland. The best strategy to improve agricultural production appears to be the development of drought and salt-tolerant crop cultivars. Intensive research and promising results in recent years show that this objective will be reached soon, applying classical breeding (supported by modern molecular tools) and plant genetic transformation. In addition, domestication and commercial cultivation of stress-tolerant wild species will also help increase food production. In the meantime, other strategies will contribute, even if more modestly, to enhance stress tolerance and improve crop yields in the frame of sustainable agriculture. They could include using 'new generation' controlled-release fertilisers to optimise plant nutrition or applying a collection of unrelated substances and beneficial microorganisms with activity as 'biostimulants'. In this paper, some examples of these approaches will be discussed, with reference to recent reviews for further reading.

***Key words**: climate change, abiotic stress, drought and salt tolerance, food security, crop yields.*

INTRODUCTION

The current world population, about 7,900 million people, is expected to grow, reaching almost 10,000 million by 2050. Global food production must increase by more than 50% over present values to feed all those people. This target, *a priori*, would seem relatively easy to reach if we look back a few decades. In 50 years, from 1960 to 2009, the human population on earth more than doubled (from 3 x 10^9 to 6.8 x 10^9 people), and we could still increase the (average) available food ca. 30%, to almost 3,000 Kcal per capita per day. Therefore, one can ask why more than 800 million people are undernourished globally, and about 10 million are expected to die of hunger this year (Stop the hunger, 2022). Evidently, all that food is not evenly distributed, with some western countries enjoying food supplies per person two to three-fold higher than many poor African countries (FAOSTAT, 2022). Notwithstanding political and logistic issues, one could think that a fairer food distribution worldwide would solve the hunger problem. However, unfortunately, if we maintain the current agricultural practices and our present major crop cultivars, the expected improvement in crop yields in the next decades will not be sufficient to cope with population growth, even assuming a better share of the available resources. Even though agricultural production is still increasing, both in absolute and *per capita* terms, the *increase rate* has been declining since the mid-1980s. In fact, the global production of major cultivated species, such as grain crops, did not increase at all during the last ten years (Figure 1).

Figure 1. Total global grain production from 2008/2009 to 2020/2021 (million metric tons).
Source: Statista (2022)

This paper will first describe the present and foreseeable situation of agricultural production in a climate change scenario, which will not allow enhancing crop yields using the strategies that were so successful some decades ago. Then, different approaches that could help reach the objective of increasing food production in the coming decades will be presented, mostly based on the generation of drought and salt-tolerant crop varieties better adapted to the new environmental conditions. This review aims to provide a broad overview of complementary strategies that can be used to improve plant tolerance to these abiotic stresses, with a few examples mentioned in each section. This structure does not allow going into much detail, but references to more specific reviews are included for further reading.

INCREASE IN FOOD PRODUCTION IN THE PAST: THE 'GREEN REVOLUTION'

From the middle of the 20th century, a series of scientific and technical advances in agriculture allowed huge increases in crop yields, first in staple crops such as wheat, maise and rice, later on, extended to other species. The development of new, more productive varieties of these major crops constituted the basis of what was known as the 'Green Revolution' (GR) of the 1960s and 1970s. Higher agricultural productivity also depended on the massive use of agrochemicals: pesticides, herbicides, and chemical fertilisers, on the mechanisation of labour, the increase in the area of irrigated land and the use of greenhouses to extend the cultivation period of many crops (Evenson & Gollin, 2003; Pingali, 2012; Llewellyn, 2018).

The Green Revolution also had adverse effects, not considered relevant at the time but with critical consequences for the future. First, those cultivars providing high yields are heavily dependent on high-input, intensive production practices that are not sustainable. Second, modern industrial agriculture is based on a narrow range of crop species and, within each species, relatively few cultivars, which have substituted a vast number of previously grown genotypes. As a result, thousands of less productive local varieties and landraces have been lost, in many cases forever, although some are stored in seed banks. This represents a huge loss of genetic diversity ('genetic erosion') and reduced opportunities to find new sources of genetic variability for breeding if we need to improve other traits than yield in response to new challenges, such as adaptation to harsher environmental conditions (Fita et al., 2015; Govindaraj et al., 2015; Khoury et al., 2022). This is, in fact, the current situation as climate change is increasing the level of environmental stress affecting crops in the field in many regions of the world.

The second 'Green Revolution'. Further increases in crop yields and, consequently, food and feed production were possible with the large-scale cultivation of biotechnological (transgenic) crops, which started in 1996. Herbicide-tolerant (HT) and insect-resistant (IR) soybean, maise and rapeseed (plus cotton, as a non-food crop) represent, by large, the so-called 'first generation' of transgenic crops providing higher average yields than their conventional counterparts. They have been progressively joined by other 'minor' GM crops (sugar beet, alfalfa, papaya, squash, poplar, tomato, potato, eggplant…) expressing the same or additional traits (James, 2000; Paul et al., 2018; Kumar et al., 2020; Abdallah et al., 2021).

We should also mention the cultivation of 'second generation' GM crops with improved nutritional properties, with the iconic 'golden rice' (Golden Rice Humanitarian Board, 2022) as the best-known example of both, a successful technical achievement and a target for anti-GMO organisations. Therefore, these biotechnological crops may contribute to the needed increase in food production but also help overcome micronutrient deficiencies in staple crops, a severe health problem in developing countries

However, we should not forget that GM crops have been developed from previously improved, GR-derived varieties. Therefore, they do not solve the drawbacks and limitations of our present agricultural systems regarding high-input requirements, low genetic diversity or sustainability issues.

REDUCTION ON FOOD PRODUCTION: CLIMATE CHANGE AND BEYOND

Concerning food production, the situation currently faced by agriculture (and humankind) is utterly different from 50 years ago. Climate change has become a 'climate emergency', and its forecasted effects are already affecting our crops. The increase of average temperatures worldwide and the more frequent, longer and more intense extreme weather phenomena, such as droughts, heatwaves, hail, heavy rains and floods, or out-of-season frosts, all contribute to reducing the crop yields. Another serious problem is the progressive salinisation of irrigated cropland due to the accumulation in the soil of toxic ions dissolved in the irrigation water. This 'secondary' salinisation has a relatively strong effect on global food production, as the areas cultivated under irrigation, especially in arid and semiarid regions, represent the most productive farmland in the world, accounting for less than 20% of total cropland but providing around 40% of all our food (Lobell & Gourdji, 2012; Ray et al., 2019; Akbari et al., 2020; Brás et al., 2021).

On the other hand, there is also a growing limitation of the availability of good-quality water for irrigation, not only because of lower precipitations but also due to its increasing use for human consumption and industry. All these factors are causing the spreading of desertification. Moreover, other socioeconomic changes, such as abandonment of cultivated fields by migration of the rural population to big cities, or the modification in land use in many areas due to urbanisation, industry and tourism, are also contributing to a progressive reduction of the land available for agriculture.

Finally, there is the need to develop more sustainable agriculture. All actions undertaken to improve crop yields should be carried out without depletion of natural resources and further degradation of the environment (Velten et al., 2015).

'CANs' and 'CANNOTs'

Under the present circumstances, some apparently straightforward strategies to increase food production cannot be used. For example, we cannot significantly increase the area of arable land, which is actually decreasing, as mentioned above. Marginal soils represent a relatively large proportion of the land surface but are not cultivable with the present crop varieties because they are arid or naturally saline, or alkaline soils. Other possibilities to enlarge the area available for agriculture would require using lands of high ecological value, such as rainforests. Unfortunately, this is already happening but should not be promoted as a sensible solution for the future. We also cannot increase the area of irrigated land because not enough water will be available; the use of low-quality, saline water for irrigation is a growing necessity, which is already reducing average crop yields in many irrigated areas. In any case, improving the productivity of conventional crops by a large increase in the use of toxic and contaminating agrochemicals, or non-renewable fertilisers like mineral phosphate, should not be considered, as it would be an unsustainable approach.

On the other hand, there is room for improving global crop yields by increasing the (relative) area of the current main biotech crops; that is, HT and IR (or HT and IR stacked traits) soybean, maise and rapeseed. Only minor improvements are possible in the main growing countries since the adoption rate of these transgenic crops is already extremely high, such as in Argentina, where practically 100% of the cultivated soybeans are transgenic. However, these crops could be grown in other countries, which are not cultivating transgenic plants at present, or have lower adoption rates; in Spain, for example, *Bt* maize represents only about 30% of all grown conventional maize varieties. Moreover, many other biotech crops expressing the same and other traits are currently in development in public research institutions and private companies, many at the level of field trials or already grown commercially at a small scale in different countries. All these biotech crops will provide higher mean yields than the corresponding conventional cultivars, thus contributing to increasing the amount (or, in some cases, the nutritional quality) of the produced food (ISAAA, 2019).

The large-scale cultivation of biotech crops also has a negative side, as in some cases is leading to the destruction of forests, grasslands and other ecologically interesting areas, for example, in Brazil and Argentina. Apart from reducing biodiversity (and agrobiodiversity), the problems associated with this kind of 'monocultures' are well known, historically (Kennedy, 1999).

In any case, unfortunately, the expected improvement of crop yields based on increasing the area of biotech crops worldwide is not so substantial as to allow copping with population growth.

STRATEGIES TO INCREASE FOOD PRODUCTION IN A CLIMATE CHANGE SCENARIO

The higher CO_2 atmospheric concentrations, enhancing photosynthetic activity, and the increase in average temperatures will have some positive effects on the agriculture of some northern areas of the world. However, this will not compensate for the by far more important global negative effects of climate change, which is causing a general increase in the level of abiotic stress affecting plants in the field. Abiotic stresses, especially drought and soil salinity, are the major environmental adverse conditions that reduce agricultural yields worldwide. Indeed, for all major crops, average yields are generally only a fraction of recorded record yields, and the difference is primarily due to losses caused by abiotic environmental stress factors during plant growth (Table 1).

Table 1. Yield losses (as percentage of record yields) due to abiotic stress conditions in some major crops (adapted from Buchanan et al., 2000)

Crop	**Record yield** (kg/ha)	**Average yield** (kg/ha)	**Yield losses** (abiotic) (%)
sugar beet	121,000	42,600	51
potato	94,100	28,300	54
soybean	7,400	1,600	69
maize	19,300	4,600	66
barley	11,400	2,000	75
wheat	14,500	1,900	82
sorghum	20,100	2,800	81

Therefore, developing new cultivars with enhanced tolerance to salt stress and water deficit appears to be the most promising strategy to increase crop yields and food production rapidly.

Drought-tolerant plants would allow reducing yield losses under conditions of low precipitation in rainfed farmland or limited artificial irrigation. On the other hand, salt-tolerant crops will maintain yields despite the progressive salinisation of the soil or if low-quality, brackish water is used for irrigation. Both stress-tolerant crop cultivars will allow extending the area available for agriculture; recovering farmland abandoned because of prolonged drought periods or soil salinisation. It would also be possible to cultivate marginal lands not previously used for agriculture because they are naturally saline or alkaline and do not allow the growth of our current crop varieties. In addition, these stress-tolerant cultivars will contribute to sustainable agriculture as they will not compete with conventional crops for limited resources such as fertile land and good-quality irrigation water.

The generation of drought and salt-tolerant cultivars is not an easy task but would be critical for food security in the decades ahead. Therefore, all available approaches should be considered when addressing this problem, as briefly described in the following sections.

STRESS-TOLERANT CROP CULTIVARS OBTAINED BY 'CLASSICAL' BREEDING TECHNIQUES

Modern crop cultivars have been primarily bred for improved yields under optimal - artificial - growth conditions; that is, for industrialised, high-input agriculture, requiring large amounts of pesticides, herbicides, and chemical fertilisers, and adapted to the mechanisation of agricultural practices. Enhancing the resistance to specific viral and bacterial pathogens has also been a common breeding aim, relatively simple to achieve, as this trait is often dependent on a single resistance gene (Anderson et al., 2010). On the other hand, drought or salt tolerance are complex traits depending on many different genes or QTLs (quantitative trait loci). In addition, there are limited sources of genetic variability for abiotic stress tolerance, a problem exacerbated by the 'genetic erosion' derived, as a side effect, from the Green Revolution, which caused a huge reduction in the number of cultivated plant varieties. Many of those neglected landraces, local varieties and minor commercial cultivars provided lower yields but probably were better adapted to local, often more stressful environmental conditions. The number of drought or salt-tolerant wild relatives of our major crops, another possible source of genetic variability, is also limited. Furthermore, even when crop wild relatives adapted to arid or saline habitats are known, their direct use in breeding programmes is not possible because of crossing barriers with the cultivated species or the presence of unfavourable characters in the wild species.

This situation explains why traditional breeding has not been very successful in the past in the development of cultivars tolerant to abiotic environmental stress, compared to the enhancement of other important traits, such as yield or pathogen resistance. Nevertheless, there are some successful examples of new cultivars with improved tolerance to drought (Bolaños & Edmeades, 1993; Ashraf, 2010) or salinity (Subbarao et al., 1990; Ashraf & O'Leary, 1996) generated by conventional breeding techniques.

Nowadays, the breeder has access to new tools that substantially improve the efficiency of breeding programmes, reducing the time necessary to develop new varieties or overcoming crossing barriers. They include a variety of molecular methods, such as the use of molecular markers – for marker-assisted selection, genetic mapping, or genetic fingerprinting - generation of variability by mutagenesis, or high-throughput genomic techniques (association mapping, 'breeding by design', genomic selection, genotyping by sequencing, Targeting Induced Local Lesions in Genomes…). Also, different *in vitro* culture techniques can help implement breeding programmes, for example, micropropagation systems, *in vitro* pollination and embryo rescue, somatic hybridisation, somaclonal variation, *in vitro* selection, or double-haploid production by gynogenesis or androgenesis (through anther or isolated microspore cultures). These and other technological advances and their possible application to the (relatively) rapid generation of new cultivars tolerant to high salinity or drought have been covered in several recent reviews (Fita et al., 2015; Boscaiu et al., 2019; Oladosu et al., 2019; Haque et al., 2021). As an example, we can mention the work of Rana Munns' group in wheat. Crossing an ancestral wheat relative (*Triticum monococcum*) with a commercial durum wheat variety (*T. turgidum* ssp. *durum* var. Tamaroi), they were able to introgress the *Nax2* gene, encoding a Na^+ transporter protein, into the durum variety. The Nax2 protein is located in the plasma membrane of root cells surrounding xylem vessels, and its expression reduced Na^+ transport from the roots to the aerial part of the plant, resulting in increased yield under salt stress conditions (Munns et al., 2012). Apart from specific examples, it is relevant to mention that these molecular tools allow designing new strategies to obtain large-scale pre-breeding materials with introgressions from wild relatives into the genetic background of specific crops ('introgressiomics', Prohens et al., 2017). This approach can be used, in principle, to introduce any trait of interest present in the wild species, not only tolerance to drought or salinity, as shown, for example, by the development of eggplant (*Solanum melongena*) lines with introgressions from the wild relative *S. incanum* (Gramazio et al., 2017).

These and many other promising results should make us optimistic that cultivars of the major crops with enhanced tolerance to abiotic stress will be developed within the next few decades, if not years.

GENETIC ENGINEERING

An alternative or rather a complementary approach to classical breeding for generating stress-resistant crop varieties relies on genetic transformation and the new methods of genome editing (CRISPR/Cas9). This, however, requires a deep understanding of the mechanisms of plant stress tolerance to identify and characterise genes involved in the plant responses to drought or salinity. The rationale behind this strategy is based on the assumption that overexpression of those genes in transgenic plants would activate stress response pathways leading to enhance tolerance.

Intensive research over the last decades has allowed elucidating a series of conserved mechanisms activated in response to different abiotic stresses and others specific for a particular stress condition. Those general defence mechanisms basically include osmotic adjustment to compensate for the stress-induced disturbance of cellular osmotic balance and the activation of antioxidant systems to counteract the secondary oxidative stress caused by water deficit, high salinity, too high or too low temperatures, and other abiotic stressors. In addition, several 'protection' proteins are synthesised in response to stress, such as heat shock or LEA (late embryogenic abundant) proteins.

The first group of responses includes the control of ion transport and ion homeostasis at the cellular, organ and whole plant levels; for example, by compartmentalisation of toxic ions in vacuoles with the parallel synthesis and accumulation of 'compatible solutes' or osmolytes - such as proline, glycine betaine, or different soluble sugars and polyalcohols - in the cytosol, to maintain osmotic balance (Alvarez et al., 2022).

The second group of responses is dependent on the activation of antioxidant enzymes - such as superoxide dismutase, catalase, ascorbate peroxidase (and other peroxidases), or glutathione reductase - and the synthesis of antioxidant metabolites, including, for example, phenolic compounds, particularly the subgroup of flavonoids, carotenoids, vitamin C or glutathione (Hasanuzzaman et al., 2020).

A large number of genes encoding proteins involved in all processes mentioned above have been considered as potential 'stress-tolerance' genes and expressed in transgenic plants. Among them, we can mention genes encoding ion transporters, enzymes of osmolyte biosynthesis pathways, antioxidant enzymes, and, obviously, transcription factors involved in the stress-induced change of gene expression patterns. Many specific examples are described in recent reviews (Fita et al., 2015; Wang et al., 2016; Ahanger et al., 2017; Husaini, 2022), but only a few will be cited here. Amongst ion transporters, Na^+/H^+ antiporters of the plasma membrane (SOS1) and the tonoplast (NHX1) seem to play an essential role in decreasing the concentration of the toxic Na^+ in the cytoplasm by transport to the apoplast or the vacuole, respectively. Overexpression of the genes encoding these proteins, isolated from *Arabidopsis thaliana* or other species, enhanced salt tolerance in different transgenic plants (Zhang & Blumwald, 2001; Shi et al., 2003).

A significant improvement in drought and salt tolerance was also observed in tobacco plants overexpressing enzymes involved in Pro biosynthesis, such as pyrroline-5-carboxylate synthetase (P5CS), an effect mediated by the large increase in Pro levels in the transgenics (Kishor et al., 1995).

A slightly different strategy is based on the overexpression of 'stress target' proteins, that is, proteins that are inactivated under stress conditions or involved in cellular processes sensitive to stress. Increasing the levels of these proteins in transgenic plants is expected to counteract, at least partly, the deleterious effects of the stress. Already 20 years ago, we isolated two *Arabidopsis* cDNA clones, encoding splicing factors of the SR-like (Ser/Arg-rich) family, based on the phenotype of salt tolerance conferred by their expression in yeast; then we showed that the expression of these genes in transgenic *A. thaliana* plants also increased their tolerance to salt and water stress (Forment et al., 2002). As shown in Figure 2, plant growth was strongly inhibited in wild type plants in the presence of salt, but to a lesser extent in the transgenic line L7, expressing one of the SR-like proteins. These data support the idea that mRNA processing - or probably RNA metabolism, in general - is inhibited under high salinity and drought conditions and that this process is stimulated by the expression of the splicing factors.

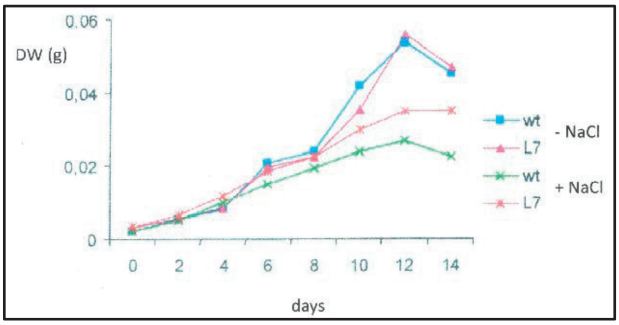

Figure 2. Salt tolerance of *A. thaliana* transgenic plants expressing the splicing factor *C-SRL1*. Dry weight (DW, g) of transgenic line L7 and wild type (wt) plants under control conditions (-NaCl) or treated with 250 mM NaCl (+NaCl) at different times after starting the treatment. The values shown are the average weights of 20 plants. (Bourgon & Vicente, unpublished results)

There are hundreds of reports of laboratory and greenhouse studies showing how the expression of genes involved in the processes mentioned above can enhance salt tolerance in transgenic plants. However, most experiments have been performed using *A. thaliana* and other model plants, focussing on the level of stress resistance and not addressing, in general, possible negative effects of the expression of the transgenes or agronomic traits. Any increase of tolerance accompanied, for example, by developmental abnormalities or substantial yield reductions, would be useless. In any case, up to now, no salt-tolerant biotech varieties have been commercialised.

The development of drought-tolerant transgenic crops has been more successful. Specifically, a maize variety expressing the CspB bacterial protein showed higher yields than the control, non-transgenic cultivar under water deficit conditions (Castiglioni et al., 2008). CspB is an RNA-binding protein that seems to act as a chaperonin, stabilising the RNA under stress conditions, which agrees with the data mentioned above regarding the sensitivity to abiotic stress of processes related to RNA processing and metabolism. This maize cultivar, developed by BASF and Monsanto, has been grown commercially since 2012, performing quite well in some USA states commonly affected by drought. It has also been the basis for generating other improved varieties by traditional breeding and extending their cultivation areas to drought-prone African countries and other regions.

As for classical breeding, it should be expected that genetic transformation and genome editing will allow the development of new salt and drought-tolerant crop cultivars in the near future.

DOMESTICATION OF WILD STRESS-TOLERANT SPECIES

Drought and soil salinity are the stressful environmental conditions that not only cause the most important agricultural losses worldwide but also affect substantially the distribution of wild plants in nature, as wild species are generally sensitive, to a greater or lesser extent, to these abiotic stressors. However, a small percentage of wild taxa are naturally adapted to very harsh environments, such as highly saline soils (halophytes), arid lands (xerophytes), or even to habitats combining both conditions, e.g., saline deserts (xerohalophytes). The domestication and commercial cultivation of some of these species would represent a complementary approach to generating stress-tolerant crop varieties by the strategies mentioned above, classical breeding and genetic engineering. In fact, it is most likely that these wild species will be significantly more tolerant to stress than any newly developed crop variety. Therefore, domesticated halophytes/xerophytes could be the basis of a more efficient 'saline' and/or 'arid' sustainable agriculture (Fita et al., 2015; Ventura et al., 2015; Duarte & Caçador, 2021).

People have traditionally used several of these species as food since ancient times; for example, in salads as raw vegetables or cooked in different ways; also, as forage for animals. They are collected from the wild for self-consumption, grown in backyard gardens or sold in local markets but are not commercially cultivated. Therefore, we already know that the plants are edible and would be readily accepted by consumers. In many cases, they are also very nutritious because of their high content in minerals, vitamins, essential amino acids and fatty acids, and/or antioxidant compounds. Domestication and breeding of these species will be necessary to improve agronomic and commercial traits - e.g., selecting the best genotypes, eliminating toxic or undesirable compounds, uniformity of the harvested product, appropriate market supply, post-harvest characteristics. All these improvements are common objectives of breeding programmes that would be relatively easy to achieve. The critical issue that should be highlighted is that these plants already possess the most challenging trait to be introduced: a high degree of stress tolerance.

There are many examples of halophytes that could be used as food for humans or feed for livestock. Promising candidates are species of the related genera *Salicornia* and *Sarcocornia*. For example, *Salicornia europaea* or *Sarcocornia fruticosa* (Figure 3), which are extremely salt-tolerant (they can be grown with seawater irrigation), have an excellent potential for commercial cultivation as 'gourmet' vegetables for their succulent shoots that can be consumed fresh in salads. Another *Sarlicornia* species, *S. bigelovii*, can be grown as an economically attractive oilseed crop; it provides high seed yields, containing about

30% of high-quality edible oil, rich in healthy polyunsaturated fatty acids, mostly linoleic acid. The seeds are also rich in protein, and, after extraction of the oil, the seed meal can be used as a protein supplement in animal feed, for example, in fish or ruminant farms. Many other salt or drought-tolerant species of different genera (*Inula*, *Limonium*, *Plantago*, *Portulaca*) can be added to the list of candidates for domestication and commercial cultivation as food crops (Fita et al., 2015).


Figure 3. *Sarcocornia fruticosa* plant in a salt marsh near Valencia, SE Spain

Also, we cannot forget to mention quinoa (*Chenopodium quinoa*), an iconic example of this strategy, even though it cannot be considered a 'new' crop. On the contrary, quinoa was probably domesticated 4,000 to 5,000 years ago; however, since its cultivation has been limited to the Andean region and at a relatively small scale, it has not been subjected to contemporary breeding techniques until recently. Quinoa ecotypes show extraordinary resistance to different abiotic stressors, such as high salinity, drought or frost, and are adapted to many different environments, from sea level to high mountains. Quinoa's nutritional properties are well-known: the seeds contain high proportions of starch and proteins, with all essential amino acids and are gluten-free. The straw is also very nutritious and can be harvested to feed livestock. During the last decade, FAO has been promoting and supporting the extension of quinoa cultivation to many different countries outside South America, considering that it can contribute substantially to food security under climate change conditions (Angeli et al., 2020).

The development of 'saline' and 'arid' agriculture provides many other possibilities not directly related to food security. Apart from human or animal consumption, many stress-tolerant species, halophytes and xerophytes, show a great potential to generate economically profitable crops for the production of industrial products: biofuels (biodiesel from seeds' oil and bioethanol from lignocellulosic biomass), pharmacological, nutraceutical, medical or cosmetic compounds. They could also be cultivated as ornamentals, for landscaping, protection against soil erosion, and desalinisation or phytoremediation of saline and contaminated soils.

COMPLEMENTARY APPROACHES

Applying all the strategies briefly described above, we should be confident that new salt and drought-tolerant crops and crop varieties will be developed within the next few decades, contributing to an increase in agricultural yields and, therefore, to food security. In the meantime, some complementary approaches can contribute, even if only modestly, to this goal. They include cultivating traditional, neglected crops and crop varieties, landraces or local cultivars, completely abandoned (recovered from seed banks) or cultivated locally at a small scale. These varieties may be better adapted to abiotic stress and compete under unfavourable environmental conditions with common, generally more productive cultivars.

Other strategies to enhance crop yields could be based on optimising plant nutrition and stress responses, in the frame of sustainable agriculture, by the application of 'new generation' fertilisers and biostimulants, as discussed below.

The plants' dilemma: growing or defending themselves

Constantly faced with limited availability of resources - water, sunlight, nutrients - plants must allocate them to both growth (primary metabolism, biomass accumulation, vegetative and reproductive development) and defence against biotic and abiotic environmental stressors (activation of secondary metabolism and stress responses) (Herms & Mattson, 1992). The proportion of these resources invested in growth and defence is genetically determined. As a result, some species are highly stress-tolerant and grow slowly, whereas others can grow faster, accumulating more biomass but paying the cost of reduced stress resistance (Figure 4). Crop species belong to this latter category, as they have been selected for rapid growth and high yields of the harvested products - vegetative biomass (leaves, tubers, roots), fruits or seeds. This partly explains why cultivated plants are generally more sensitive to pathogens, pests, and abiotic stress conditions than their wild relatives.

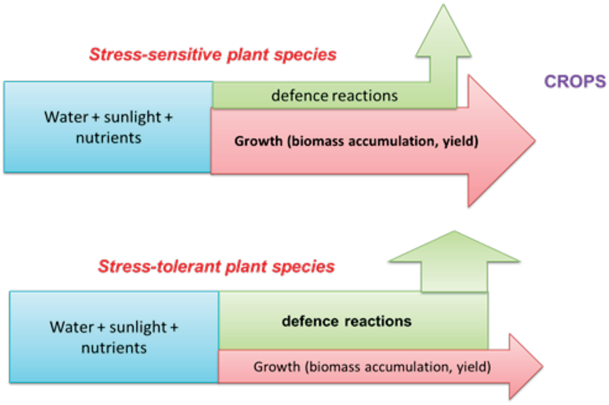

Figure 4. Resource allocation in stress-sensitive and stress-tolerant plant species

Currently, much effort is being invested in optimising plant treatments that could modulate this resource allocation. For example, the application of improved fertilisers and the so-called 'biostimulants' is a growing trend (and an excellent business for the agrochemical sector) as they can enhance the plants' nutritional efficiency, stress resistance and even the product quality, at the same time that yield is also improved or, at least, not reduced.

'New generation' fertilisers

The use by the plants of conventional chemical fertilisers is generally very inefficient. Large amounts of fertilisers are applied to the crop, but only a relatively small proportion is actually taken up by the plants, the excess resulting in soil and water contamination. This is one of the most relevant ecological and sustainability problems of industrial agriculture. Fertiliser companies have been working on the development of 'new generation' slow-release (SRFs) and controlled-release (CRFs) fertilisers designed to overcome this problem.

During the last years, our group has collaborated with Fertinagro Biotech S.L., a Spanish company dedicated to producing and commercialising plant nutrients, on testing the efficiency of a CRF produced by the company, on field trials of three essential cereal crops, wheat, rice and maize. This CRF is a urea-based N fertiliser coated with water-soluble lignosulphonates and enriched with humic acids as biostimulants (see below). Compared with traditional nitrogen fertilisers (ammonium nitrate and non-coated urea), the CRF allowed maintaining yields with a reduction of about 20% in the N dose or slightly increasing them at the same dose. This increase in the fertiliser efficiency may not look spectacular, but the main advantage of the CRF instead refers to its effects on the soil, decreasing the environmental impact of traditional fertilisers due to lower N losses. Also, the CRF polymeric coating is not synthetic but efficiently and economically produced from the waste of paper and wood industries. Therefore, this new fertiliser can be considered 'eco-friendly', contributing to a circular 'green' economy and reducing the agriculture C-footprint (Gil-Ortiz et al., 2021).

Biostimulants

Plant 'biostimulants' are a disparate collection of 'substances' (single compounds and mixtures of compounds, organic and inorganic, natural or synthetic, crude or partly purified extracts of unknown or partially known composition) and microorganisms (bacteria or fungi), defined operationally by their positive effects on plants, when applied at low doses, improving growth, abiotic stress tolerance or even the quality of the harvested product.

Biostimulants can be classified in different, unrelated groups: ***i)*** amino acids and peptide mixtures, generally produced by chemical or enzymatic protein hydrolysis; for example, from agricultural wastes; ***ii)*** seaweed (and microalgae) extracts, generally crude extracts, which could also be enriched in their polysaccharide fraction; ***iii)*** humic and fulvic acids, and other humic substances extracted from the soil organic matter; ***iv)*** biopolymers like chitosan, synthesised industrially or prepared from natural sources; ***v)*** some 'beneficial' chemical elements, such as Se, Si or Co, with biostimulant activity for some plant species; ***vi)*** mycorrhizal and non-mycorrhizal fungi; and ***vii)*** plant growth-promoting rhizobacteria (PGPRs) inhabiting the plant rhizosphere, and other beneficial endosymbiotic bacteria (e.g., *Rhizobium*).

The last years have seen how the interest in biostimulants increased exponentially. They represent a rapidly growing business for agrochemical companies, which sell commercial preparations of single or combined biostimulants to the farmers as a complement to their fertilisers.

Biostimulant selection and application has been made chiefly on an empirical basis, and their mechanisms of action are largely unknown. Therefore, there is also considerable interest in basic research on this topic, reflected on hundreds of articles published during the last few years, including several reviews (da Silva et al., 2021; Fadiji et al., 2022; Monteiro et al., 2022).

As an example of biostimulant effects on stressed plants, we can refer to experiments carried out in our laboratory, using Fertinagro Biotech products on tomato plants. Pre-application of Terrabion® (an amino acid-based biostimulant, patented by the company) or a seaweed extract with the irrigation water partially protected the plants subsequently subjected to a severe water deficit stress for seven days (Figure 5).

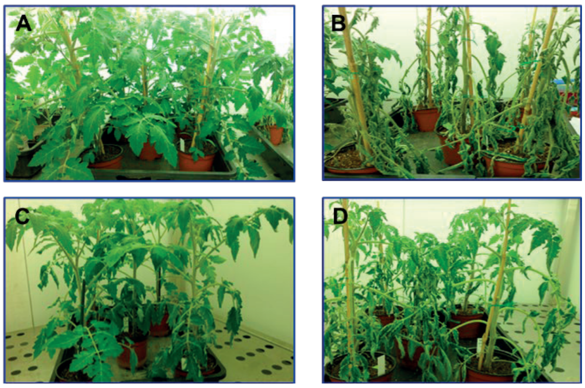

Figure 5. Effect of pre-treatment with biostimulants on cherry tomato plants subjected to seven days of water stress by complete withholding of irrigation. **A)** control, normally watered plants. **B)** water-stressed plants. **C)** water-stressed plants pre-treated for ten days with Terrabion®. **D)** water-stressed plants pre-treated for ten days with a seaweed extract (Gil-Ortiz & Vicente, unpublished results)

Notwithstanding the use of and research on non-microbial biostimulants, beneficial bacteria and fungi are probably attracting more attention. In this sense, we can mention the 'Darwin21' project, focused on the "Establishment of a global knowledge base of desert rhizosphere microbes and their use in re-establishing sustainable agricultural systems in arid lands" (Darwin 21, 2022).

CONCLUSIONS AND PERSPECTIVES

Under the present climate change scenario, the foreseeable increase in food production with our present crop varieties will not be sufficient to cope with population growth, due to the associated increase in environmental stress. Drought and salinity are the major stressors responsible for reducing crop yields worldwide; therefore, the most sensible strategy to increase food production will be developing new, salt and drought-tolerant crop cultivars. As this is the most serious challenge faced at present by agriculture, all possible strategies should be applied to achieve this goal. They include traditional breeding programmes, now supported by a wide array of molecular and tissue culture techniques, and the generation of genetically modified plants. We can also develop a sustainable 'saline' or 'arid' agriculture, based on the domestication of wild species highly tolerant to stress. These 'new' crops will not compete with conventional crop varieties for limited resources, such as fertile land and good-quality irrigation water. They could be grown in farmland abandoned because of secondary salinisation or persistent droughts, or even in marginal areas not cultivated before, and with limited irrigation or using brackish water for irrigation.

Many research lines in progress, which have already delivered some successful examples, support the notion that all approaches mentioned above will result relatively soon in the obtention of the stress-tolerant crop varieties needed to increase food production under climate change conditions. In the meantime, additional strategies may also contribute, even if only modestly, to the same goal of enhancing crop tolerance to abiotic stress and promoting more sustainable agriculture. For example, recovering neglected traditional crops or crop varieties, improving the plants' nutritional efficiency using 'new generation', controlled-release fertilisers, or applying some 'biostimulants', substances or microorganisms with beneficial effects on plant nutrition, crop quality and/or stress defence responses.

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