Chapter 8
Effects of Abiotic Stress in Crop Production

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Contents

Abstract Crops respond to stress includes, from molecular to the morphological level. Responses at the whole crop level integrate processes taking place at all the underlying levels. For this reason, their quantitative assessment is not always straight forward. Abiotic stresses already represent one of the key factors limiting worldwide crop production. In poor countries, where agriculture is still practiced at a subsistence level, the livelihood of a large share of the population is constantly challenged by abiotic stress factors and their interactions with biotic stress factors. Climate change is likely to aggravate this situation. Taking into account the expected growth in world population and food demand, finding ways to improve crop tolerance with respect to abiotic stress factors will be essential to further improve agricultural production and enhance food security.

Keywords Biotic and abiotic stress • Crop production • Food security • Sensitivity and stress resistance

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M. Ahmed, C.O. Stockle (eds.), *Quantification of Climate Variability, Adaptation and Mitigation for Agricultural Sustainability*,
DOI 10.1007/978-3-319-32059-5_8

8.1 Introduction

Owing to advances in breeding, the introduction of improved farming technologies and, at least in developed countries, relatively cheap access to water, fertilizers and crop protection products, crop yields have risen considerably since the 1950s (Edgerton 2009). While this increase extends to worldwide crop production (World Bank 2015), in many areas progress has not been sufficient to close the gap between actual yields and their climatic potentials (Licker et al. 2010). Various reasons contribute to this state of affairs. Pests and diseases play a role (Oerke 2006), but probably more important has been the impact of abiotic stress factors (Boyer 1982; Bonhert 2007; Devine 2009). Crops experience abiotic stress when environmental conditions depart too strongly from the optimum range for growth and reproduction (Larcher 2003). According to Levitt (1980a) biological stress can be defined as "any environmental factor capable of inducing a potentially injurious strain in living organisms".

In turn, biological strain can defined as either a physical or a chemical change induced by stress on a living organism. As opposed to physical strain, biological strain is therefore "not necessarily [only] a change in dimension" (Levitt 1980a). Various factors can lead to stress in crops (Fig. 8.1). Not all of them are directly linked to climate. In practice, however, the emergence of abiotic stresses is often triggered by anomalous climatic conditions, such critical low and high temperatures, persistent absence of rain, extreme precipitation intensities, or high radiation

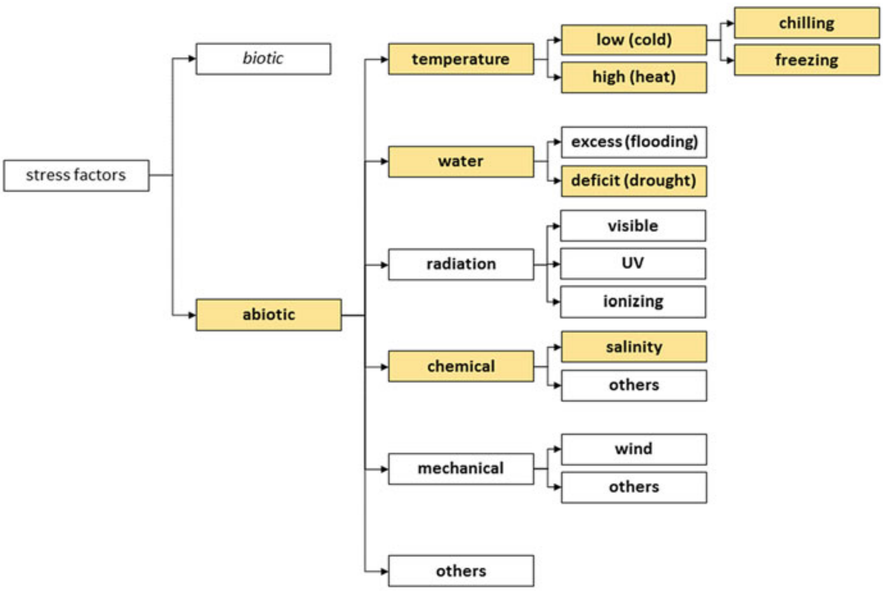

Fig. 8.1 Abiotic stress factors. *Coloured fields* denote those factors often addressed in impact assessments (Modified after Levitt (1980a) and Beck and Lüttge (1990))

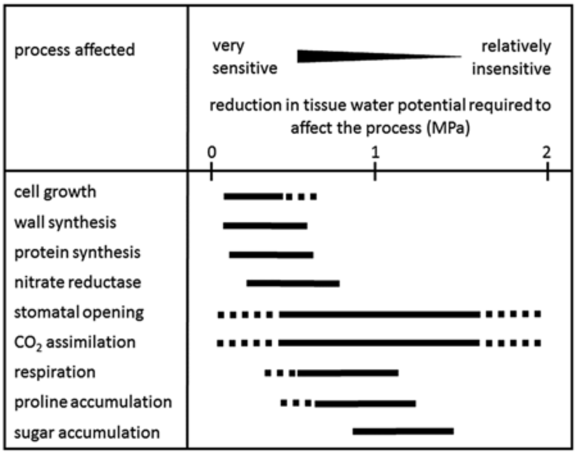

Fig. 8.2 Generalized sensitivity of plant processes to water stress and sequence of processes triggered by decreasing water potential in plant tissues (Modified after Hsiao (1973))

intensities. Problems caused by high salinity are common in arid or semiarid environments (Abrol et al. 1998), where rainfall is too low to prevent accumulations of ions in the soil (Qadir et al. 2014) and where irrigation is the cause of secondary salinization (Ghassemi et al. 1995).

Crops respond to stress at various levels, from the molecular to the morphological (Bonhert 2007). Depending on the process involved, responses to a given stress factor display different sensitivities with respect to the imposed stress signal (Fig. 8.2). Responses at the whole crop level integrate processes taking place at all the underlying levels. For this reason, their quantitative assessment is not always straightforward (Blum 1996).[1]

What happens during stress is essentially determined by the intensity and duration of the factor causing strain. Yet equally important for crops is the timing of stress in relation to development, as crop sensitivities to various stress factors vary according to phenology (Feller and Vaseva 2014). With sorghum exposed to drought, for instance, the largest reduction in grain yield is to be expected when water stress occurs during booting and flowering (Craufurd and Peacock 1993). It is also well known that wheat is particularly sensitive to high temperatures during flowering (Porter and Gawith 1999; Barlow et al. 2015) and that heat stress occurring during the reproductive phase is more harmful than during the vegetative phase (Stone and Nicolas 1995; Farooq et al. 2011).

[1] More information concerning specific responses to various types of abiotic stress can be found elsewhere in the literature and are no further treated here. As a starting point for extending the present discussion one can recommend the textbooks by Levitt (1980a, b), Larcher (2003), various chapters in the book edited by Boote et al. (1994), and several review articles (e.g. Beck and Lüttge 1990; Lichtenthaler 1996; Bonhert 2007; Mittler 2006; Feller and Vaseva 2014; and, Suzuki et al. 2014).

8.2 Resistance to Stress

As with wild plants, crops can, to some extent, resist stress. Stress resistance consists of two components: stress avoidance, i.e. the ability to prevent stress from causing a strain, and stress tolerance, i.e. the ability to cope with a reversible or even irreversible response already triggered by stress (Levitt 1980a, b). The terms "hardiness" and "acclimation" are sometimes used as synonyms to "stress resistance", in particular when discussing the ability of some crops to better survive extreme cold (Snyder and De Melo-Abreu 2005), heat (Paulsen 1994) or drought (Levitt 1980b). For the same reason, the term "hardening" is employed to denote the development of improved tolerance. Acclimation can take place very rapidly. On a hot afternoon, for example, plants are able to shift to higher limiting temperatures within hours (Larcher 2003). In other circumstances, acclimation may require an entire season, as is the case for the development of freezing tolerance in winter cereals (e.g. Pomeroy et al. 1975) and forage grasses (e.g. Larsen 1994). Moreover, the ability to resist adverse environmental conditions is not an enduring feature and can be lost when favourable conditions return. In winter cereals and forage grasses that already underwent acclimation to freezing temperatures, de-hardening can be prompted by a few days of relatively mild temperatures. The consequence is a much higher risk of crop failure from late frosts.

Sensitivity and resistance to stress vary considerably across crops and cultivars (Bray et al. 2000). In cereal crops, resistance to freezing is highest in rye and lowest in oats and durum wheat (Snyder and De Melo-Abreu 2005). When hardening is completed, rye can survive temperatures as low as −40 to −45 °C, whereas the limit is at about −10 °C for durum wheat (Lecomte 1993). This is equivalent to a 30 °C difference in cold tolerance. Likewise, critical temperatures that can impair grain formation during reproductive development barely exceed 30 °C in bean but can reach almost 40 °C in soybean, with intermediate values of about 35 °C in wheat, maize, sorghum, cotton and rice (Hatfield et al. 2011). Different sensitivities also exist with respect to water stress. According to data compiled by Soltani and Sinclair (2012), growth development in sorghum, soybean and maize continues until the fraction of transpirable water in the root zone has dropped to about 0.25, but the development of rice ceases as soon as the fraction of transpirable water in the root zone falls below about 0.6.

8.3 Multiple Stresses

A single abiotic stress seldom befalls a crop. More frequent are situations in which crop development is compromised by the simultaneous occurrence of more than one stress factor (Mittler 2006; Suzuki et al. 2014). In open fields, for example, strong radiation, exceedingly high temperatures, low air humidity and water deficit tend to occur in combination. Common co- occurrences are high salinity in combination with drought, or of high ozone levels in combination with extreme heat. As abiotic stresses have the potential to weaken the defence mechanisms of crops against pathogen and herbivore pests, abiotic stresses are often also precursors of biotic stresses (Suzuki et al. 2014). In many circumstances, crop responses to multiple stresses are unique and cannot be simply inferred by extrapolating responses to individual stress factors. This has clearly been shown concerning molecular responses to heat and drought in tobacco and *Arabidopsis* (Rizhsky et al. 2002, 2004), but similar conclusions hold true also regarding other combinations of stresses (see literature review in Suzuki et al. 2014). When the combined effects of two stress factors are additive, multiple stresses have a higher damaging potential than one would estimate from the sum of the strains induced by the individual factors. This is the case with drought and heat, drought and exceedingly high UV intensities, drought and salinity, heat and ozone, or heat and salinity (Mittler 2006; Suzuki et al. 2014).

Stress enhancement can result even when two (or more) factors act on the same physiological mechanism, if they prompt responses in opposite directions (Feller and Vaseva 2014). Under drought and heat, for instance, a crop initially subjected to high temperatures will open its stomates to increase transpiration and promote cooling. This results in a faster depletion of soil water reserves and onset of water stress. Conversely, a crop subjected to water stress will initially react by closing its stomates, a process that reduces cooling through transpiration and leads to higher foliage temperatures. When compensatory mechanisms exists, the effects of multiple stresses are not cumulative and the overall impact is usually less harmful than the sum of the individual strains (Suzuki et al. 2014). Reduced stomatal conductance in crops suffering from water stress, for example, can enhance the tolerance to ozone stress, and therefore reduce the impact of high ozone doses, which tend to occur with high temperatures during the summer season (Pääkkönen et al. 1998).

8.4 Crop Production and Drought

Drought represents without doubt one of the major threats to worldwide crop production, even in countries where agriculture is highly industrialized (Fig. 8.3). Failure to meet expected production levels can have severe repercussions on prices of agricultural commodities and hence have implications for global food security (IPCC 2014). Also, in poor countries drought has tremendous impacts on livelihood and household economy (Dilley et al. 2005; Sivakumar 2005; Miyan 2015). Especially in Africa, drought has been the reason for food crises and famines.

Often, crops suffering from drought also suffer from heat stress (see discussion in the previous section) which was the case during the drought that affected U.S. agriculture in 2012. Indeed, climatic data reveal that this event was not only exceptional because of the persistence of drought over a large fraction of the cropland (Fig. 8.4) but also because temperatures were higher than normal during most of the summer season, particularly during July (Fig. 8.5c) (GISTEMP Team 2015; EIA 2015).

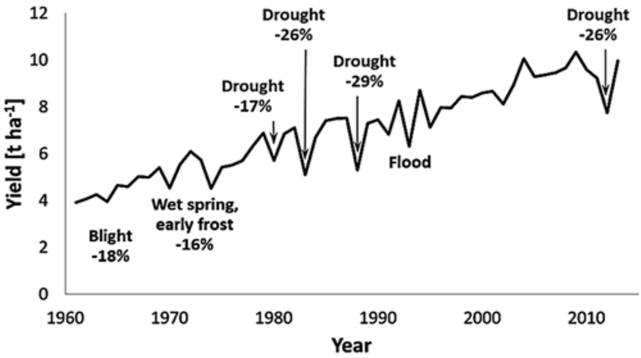

Fig. 8.3 Impact of extreme weather events on maize yields in the US (Adapted from Karl et al. (2009) based on the newest compilation of yields available from FAOSTAT (FAO 2015). The relative loss for 2012 was computed by comparing the actual yield to an estimated potential of ~11 t ha^{-1})

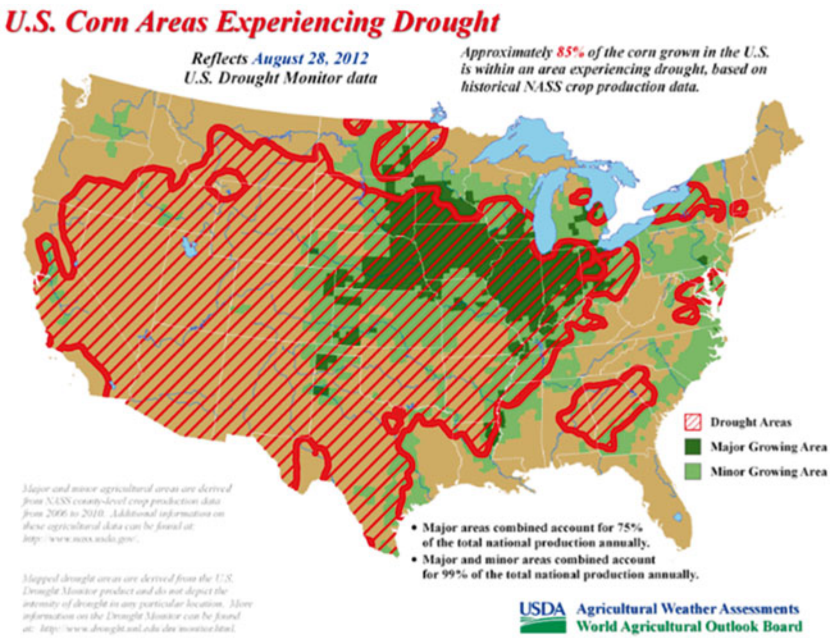

Fig. 8.4 U.S. Corn area in drought at the end of August 2012 (Analysis courtesy of the U.S. Department of Agriculture (EIA 2015))

Thus, the 2012 drought is remembered as "the most extensive drought to affect the U.S. since the 1930s resulting in widespread harvest failure for corn, sorghum and soybean crops, among others, Initial expectations at planting time had suggested [corn] yields averaging a record 166 bushels per acre, but deteriorating growing conditions throughout the summer led USDA to reduce yield expectations. The

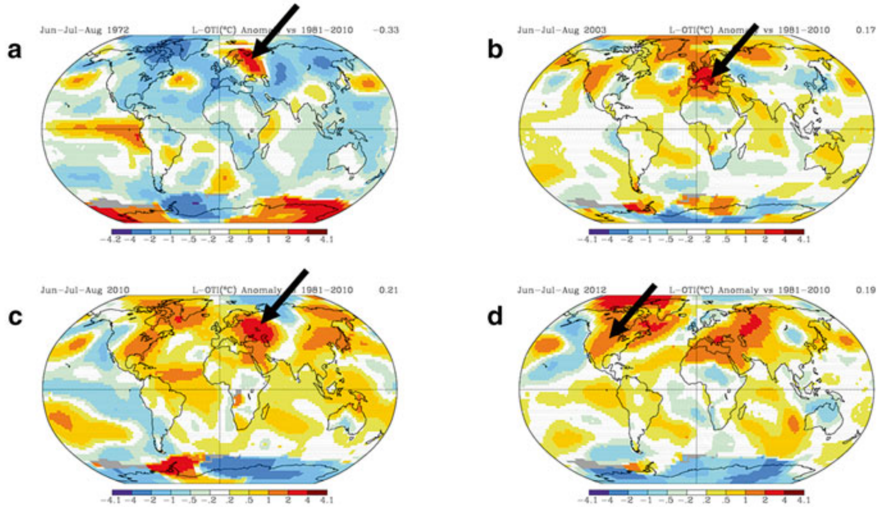

Fig. 8.5 Global temperature anomaly maps for (**a**) 1972, (**b**) 2003, (**c**) 2010 and (**d**) 2012. Courtesy of the National Aeronautics and Space Administration (NASA), Goddard Institute for Space Studies (Hansen et al. 2010; GISTEMP Team 2015). Shown here are the mean anomalies relative to a 1981–2010 baseline for the Northern-Hemisphere summer (June, July and August). Key areas discussed in the text (in the order Ukraine, Western Europe, Russia and the U.S) are indicated with an *arrow*

final 2012 yield estimate was set at 123.4 bushels per acre, the lowest since 1995" (USDA 2015).

As seen in Fig. 8.5, the occurrence of anomalously high temperatures has also been a characteristic of many drought events of relevance for global crop production, e.g. the 1972 event in the Ukraine and, more recently, the two heat waves that struck Western Europe in 2003 and Russia in 2010[2] (Battisti and Naylor 2009; Wegren 2011; Anyamba et al. 2014).

8.4.1 Crop Exposure to Heat Stress: Recent Trends

Global temperatures have risen by about 0.8 °C since 1975 (Hartmann et al. 2013). According to IPCC (2014) "negative impacts of climate change on crop yields have been more common than positive impacts (high confidence). The smaller number

[2] The large-scale circulation patterns responsible for the 2010 Russian heatwave eventually led to catastrophic floods in Pakistan. This event affected more than 20 million people (Kirsch et al. 2012) and negatively affected agriculture to an unprecedented scale (FAO 2010; WFP 2010). Undoubtedly, there is an abiotic stress contribution to the damages caused by these floods to crops. Overall, however, the effects of these floods and similar events extend beyond what can be considered as abiotic stress component.

of studies showing positive impacts relate mainly to high-latitude regions, though it is not yet clear whether the balance of impacts has been negative or positive in these regions (high confidence). Climate change has negatively affected wheat and maize yields for many regions and in the global aggregate (medium confidence). Effects on rice and soybean yield have been smaller in major production regions and globally, with a median change of zero across all available data, which are fewer for soy compared to the other crops. Observed impacts relate mainly to production aspects of food security rather than access or other components of food security. Since AR4 [IPCC Fourth Assessment Report], several periods of rapid food and cereal price increases following climate extremes in key producing regions indicate a sensitivity of current markets to climate extremes among other factors (medium confidence)".

The increase in mean growing season temperatures alone has been shown to have had a negative impact on the recent upward trend in crop yields, effectively reducing maize and wheat production by roughly 4 and 6 %, respectively, below what could have potentially been achieved without global warming (Lobell et al. 2011).[3]

In many areas of the world, notably Europe, Asia, Africa and South America, the rise in global mean temperature has been accompanied by an increase in both nighttime minimum as well as daytime maximum temperatures, and by an increase in the frequency of extremely warm conditions (Vose et al. 2005; Donat et al. 2013). The result has been a decrease in exposure to low temperature but an increase in exposure to critically high temperatures and heat stress, in recent decades. Past increase of crop exposure to heat stress during reproductive growth has been confirmed by Gourdji et al. (2013), although the correspondence to trends in growing season mean temperatures has, so far, been weak.[4] According to their analysis, about 10 (soybean and rice) to 30 % (wheat and maize) of the crop area has been exposed to more than 0.1 °C/decade increase in critical high temperatures.

The geographic distribution of crop areas currently at risk of heat stress during reproductive development are easily identified in the maps presented by Gourdji et al. (2013, their Figs. 8.1 and 8.2) and similar maps presented by Teixeira et al. (2013, their Figs. 8.2 and 8.4). For wheat, hot spots are concentrated in southern Russia, Kazakhstan, Pakistan and India; for maize, hot spots are spread across the globe, including Europe (Iberian Peninsula and the Southeast), Africa, and North, Central and South America. These are the regions where the risk of incurring heat stress is expected to further increase in the near future.

[3] According to the analysis of Lobell et al. (2011), for maize and wheat, trends in precipitation have worsened the situation, with an additional relative impact of about −0.5 to −1 %.

[4] This is because temperatures have been for the most part below crop critical thresholds and therefore the increase in temperature has yet to be reflected in a significant increase in exceedance probabilities

8.4.2 Global Warming, Heat Stress and Drought

There is little doubt that global change will further alter the conditions for crop production (Lobell and Gourdji 2012). Global climate model simulations suggest that global temperatures will continue to rise during the coming decades (Collins et al. 2013). Depending on which emission scenarios and experiments are being evaluated, the increase in global surface temperature relative to 1986–2005 is expected to reach between +0.3 °C and +4.8 °C by the end of the century. Changes in the shape of the temperature distribution would come on top of the trends in annual or seasonal averages. As a result, by the end of the century growing season temperatures in the tropics and subtropics are expected to exceed current extreme temperatures, and present exceptional temperatures in the temperate zones, such as those recorded during the 2003 heat wave in Western Europe, are expected to become the norm (Battisti and Naylor 2009).

In more detail, daily maximum temperatures are projected to increase by +1.5 to +5.5 °C until the end of the century (Collins et al. 2013; Sillmann et al. 2013). Exposure to critically high temperatures during the reproductive period is expected, therefore, to be more common in the future. Without adaptation, there could be an increase in the fraction of the total harvested area exposed to heat stress (Gourdji et al. 2013). For maize, for instance, this fraction could triple by 2050 as compared to today, with serious implications for global production. Changes in land utilization and management could reduce the global exposure to heat stress. Critical high temperatures in wheat production could e.g. be avoided by shifting sowing dates (Teixeira et al. 2013).

Less certain is the future exposure of cropland to agricultural droughts. In fact, projected changes in total precipitation amounts, seasonality of precipitation, and duration of wet and dry spells vary considerably depending on model and emission scenario (Collins et al. 2013). The question of whether changes in the atmospheric branch of the hydrological cycle will be dominated by thermodynamics (intensification reflecting a higher energy content of the lower atmosphere) or shifts in the circulation patterns, including possible shifts in global teleconnection patterns such as the El Niño-Southern Oscillation, is also not settled.

According to Collins et al. (2013), there is nevertheless some confidence that some of the current agricultural areas will experience a decrease in soil moisture. In the words of Trenberth et al. (2014), "the contrast in precipitation between wet and dry regions and between wet and dry seasons will probably increase, although there may be regional exceptions. Climate change is adding heat to the climate system and on land much of that heat goes into drying. A natural drought should therefore set in quicker, become more intense, and may last longer. Droughts may be more extensive as a result. Climate change may not manufacture droughts, but it could exacerbate them and it will probably expand their domain in the subtropical dry zone."

8.4.3 Effects of Elevated CO_2 Concentrations

For the discussion of abiotic stresses under future climatic conditions, it is important to bear in mind that the positive effects of elevated atmospheric CO2 concentrations (Körner 2006; Lobell and Gourdji 2012) could partially offset the negative effects of higher temperatures and decreased water availability. Results of so-called Free-Air CO_2 Enrichment (FACE) experiments have shown that higher CO_2 levels stimulate photosynthesis and net primary production (along with dark respiration, though), improve nitrogen use efficiency and decrease water use at both the leaf and canopy scale (Leakey et al. 2009).[5]

Increased water use efficiency under high CO_2 levels would result from a reduction in stomatal conductance (Bunce 2004) and transpiration (Vanuytrecht et al. 2012),[6] which should potentially lead to decreased incidence of water stress under future climatic conditions. Reduced evapotranspiration would also help control the salinity problem since reduced transpiration would improve the water status of the soil and limit the necessity for irrigation.

However, as indicated earlier, changes in stomatal conductance also affect the thermal balance of crops, and reduced stomatal conductance could therefore lead to higher heat stress if water is insufficient to maintain transpiration for a longer time at an adequate level. Clearly, the consequences of elevated CO_2 for crop exposure to multiple stresses need to be more systematically examined (cf. Lobell 2014).

An additional pathway by which elevated CO_2 concentrations could alter the sensitivity of crops to water shortage is by increasing the root: shoot ratio (Vanuytrecht et al. 2012). The processes by which assimilates would be preferentially allocated to the roots are not fully understood (Passioura 1994), but undoubtedly a relative increase in root biomass would improve the ability of crops to exploit soil water and nutrients alike, which could help reduce the susceptibility of crops to nutrient stress.

8.5 Adaptation

Given that the probability of extreme climatic conditions is likely to increase under climate change, options to cope with a higher incidence of some abiotic stress factors are necessary to maintain or even increase crop productivity (IPCC 2014). There are various options by which the impact of abiotic stress can be reduced. With regard to heat stress, changes in field calendars (e.g. earlier sowing dates), the use of early-ripening cultivars, or the replacement of sensitive with less sensitive crops

[5] Because of the different photosynthetic pathways, overall responses to high levels of CO_2 in C3 and C4 crops are expected to differ, though perhaps not as distinctly as the direct effect of CO_2 on assimilation (Vanuytrecht et al. 2012).

[6] Note that in grasslands water savings are almost fully responsible for the observed biomass responses to elevated CO_2 (Körner 2006).

are among those most often addressed in impact assessments when considering the farm scale (e.g. Trnka et al. 2014). Some of these options are not without side effects, though. An example is the cultivation of early-ripening varieties. On the one hand, this would help reduce exposure to critical temperatures during summer. On the other hand, it would entail an overall shortening of the growing season and could eventually lead to lower yields.

Improved soil management can also help cope with abiotic stresses, as shown by the outcomes of an experiment conducted in Switzerland during the record-breaking heatwave of 2003 (Feller and Vaseva 2014). In this experiment, leaf temperature and stomatal conductance in sugar beet were monitored during sunny days on till and no-till plots. Under conventional tillage, midday temperatures in leaves were 2 to 3 °C higher than under conservation soil management, whereas stomatal conductance was reduced by roughly a factor of two.

The impact of abiotic stresses can also be reduced by improving stress tolerance. This is a primary goal of ongoing breeding programs. The reader is referred to e.g. Vinocur and Altman (2005); Witcombe et al. (2008) or Devine (2009) for good overviews, and to e.g. Tardieu (2003); Tardieu and Tuberosa (2010) and Semenov et al. (2014) for an appreciation of how breeding efforts can be supported by mathematical modelling. So far, experiences indicate that there is potential for breeding to improve heat and low temperaturetolerance, as well as tolerance to multiple stresses (Devine 2009). Breeding for drought and salinity tolerance appears to be more difficult, but not without possibilities (Witcombe et al. 2008). It has been shown that breeding could help adapt crops to low nutrient levels while retaining the ability to respond to fertilization (Witcombe et al. 2008).

Concerning drought, changes in the hydrological cycle and a reduction in global water availability for the agricultural sector (Milly et al. 2005; Strzepek and Boehlert 2010) leave little doubt that in many areas of the world the need for irrigation is going to increase in the future (Vörösmarty et al. 2000). Even though in some areas sustained irrigation could be possible without unintended consequences, consideration of the environmental impacts of irrigation is necessary. Salinization of agricultural soils is a problem that already has reached critical levels (Ghassemi et al. 1995) and that needs to be solved to make crop production sustainable. Depletion of groundwater is a problem in major crop production areas in the U.S., Europe, China and India and the Middle East (Wada et al. 2010). Again, options to limit groundwater extractions are required to limit the impacts of agriculture on the global environment.

8.6 Concluding Remarks

Abiotic stresses already represent one of the key factors limiting worldwide crop production. In poor countries, where agriculture is still practiced at a subsistence level, the livelihood of a large share of the population is constantly challenged by abiotic stress factors and their interactions with biotic stress factors. Climate change is likely to aggravate this situation. Taking into account the expected growth in world population and food demand, finding ways to improve crop tolerance with respect to abiotic stress factors will be essential to further improve agricultural production and enhance food security. Various options are currently being explored, some of them showing promising results. A proper assessment of the net effects of such measures can deliver the basis for an objective discussion (Lobell 2014).

Acknowledgements The preparation of this contribution has been facilitated by the author's participation in the project "Modelling vegetation response to EXTREM Events" (MODEXTREME, http://modextreme.org), which has received funding from the European Community's Seventh Framework Programme – FP7 (KBBE.2013.1.4-09) under Grant Agreement No. 613817, 2013–2016.

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