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Responses of Plants to Soil Flooding

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Preface

The growth of plants is greatly affected by both excesses and deficiencies in water. Environmental conservation, such as the greening of deserts, has previously received a large amount of research attention, including investigations related to drought stress. However, in comparison, relatively little attention has been paid to the study of plants experiencing excessive water stress. Temporary or permanent flooding is widespread in the world, and the importance of understanding this condition is increasing with the development of global warming. The two main types of flooding stress are waterlogging, in which roots are exposed to excessive water, and submergence, in which roots are flooded to the top of the shoots. Among the many physical and chemical changes, oxygen deprivation is the main factor inhibiting plant growth because of flooding. However, most previous studies on the responses of plants to flooding have focused on seed germination and soil water retention for the ease of experimental systems. In recent years, remarkable discoveries and developments have been recognized in the fields of molecular biology, plant physiology, and plant morphology in relation to submerged and waterlogged environments. The purpose of this book *Responses of Plants to Soil Flooding* is to introduce the latest research on flood-induced anaerobic responses to improve the availability and accessibility of this work for future research and general interest.

When rice plants are flooded, they grow taller and expand their leaves above the water surface. This is a survival strategy to escape the anaerobic environment and maintain aerobic energy metabolism and photosynthesis, by expanding their leaves above the water surface. In water, the solubility of gases such as oxygen and carbon dioxide are low and their diffusion rate is 10^4 times slower than in the atmosphere. Therefore, in flooded conditions where the water surface is stagnant, the oxygen concentration in the water becomes low due to the respiration of green algae, especially at night, and the hypoxia affects the energy metabolism of rice. Under such hypoxic conditions, rice undergoes anaerobic metabolism to obtain energy. However, anaerobic metabolism produces only two moles of ATP from one molecule of glucose, which is much less energy efficient than the 38 moles of ATP produced by aerobic metabolism. Therefore, if the anaerobic environment is prolonged, carbohydrates will be depleted, and the rice plant will not be able to survive. In addition, the supply of carbohydrates by photosynthesis in the water is also reduced due to the inhibition of light penetration and the decrease in carbon dioxide concentrations in the plant. By quickly escaping this flooding stress environment and expanding the leaves above the water surface, it is possible for the plant to take in oxygen and carbon dioxide from the atmosphere and improve the photosynthetic capacity of the leaf blade. The most important features of this work are to analyze the mechanisms of these types of physiological plant responses to anoxia and hypoxia under flooding conditions. Specifically, the importance of photosynthetic functions, chlorophyll injury, photosynthetic product translocation, root plasticity, and respiration in plants under anaerobic conditions.

In this book, leading researchers from this field plan to systematically explain the latest research results on anaerobic responses in plants. The book is characterized by its in-depth coverage of the tolerance functions of plants under hypoxic conditions from a variety of perspectives, with a particular focus on research areas related to molecular biology, physiology, and genetics. Although drought responses have dominated water stress research in the past, recent floods and attempts to introduce new cropping systems have made it necessary to take measures against excessive water stress injury, and systematic research is needed for this purpose. From this point of view, the approach taken in this book is new and interesting in that it covers basic research and adaptation technologies in the field and can be applied to various different situations. Avoiding the effects of global warming, which are expected to increase in the future, and improving the adaptability of plants to the environment are two extremely important and current issues. The focus of this book is how plants can adapt to poor environments and improve productivity under the conditions of soil hypoxia caused by excess water, such as heavy rains and typhoons. From this point of view, the reader will be able to understand the various adaptations of plants to climate change, which will clarify the future directions of research and show the possibility of applying the knowledge and techniques gained in this book to the field.

The Sixth Report of the Intergovernmental Panel on Climate Change (2021) warns that global warming will proceed faster than previously assumed and that all regions of the world will face increasing changes. “Climate Resilient Development” has been proposed as a key phrase to combat global warming, and it is important to identify the adaptive capacity of plants and improve it where possible. In this regard, the publication of this book, which includes ideas for mitigating flood damage caused by global warming, is extremely important, timely, and rational. A portion of our book may be suitable for undergraduate courses, but our audience is primarily scholars. Writing on the narrow topic of plant anaerobiosis for a well-defined audience will help our book resonate more strongly with its readers and increase the impact of this book.

Kagoshima, Japan Jun-Ichi Sakagami
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Part I

Impacts of Climate Changes on Plant Adaptation

Chapter 1
Abiotic Factors Affect Plant Growth

Tohru Kobata

1.1 Increased Impacts of Abiotic Factors Such as Flooding, Drought, High Temperature and Soil Deterioration on Crop Production Under Climate Change

Crop plants suffer from flooding, drought, high temperature, and soil degradation, such as soil compaction, salinity, acidification, and metal pollution, and these abiotic factors seriously inhibit crop production (Loomis and Connor 1992). Climate change has modified the total rainfall and distribution of precipitation in seasonal rainfall, resulting in water availability extremes, including drought and flooding in agricultural regions of the world in the past 50 years (Bailey-Serres et al. 2012; Shortridge 2019; Kaur et al. 2020). The model estimations show that areas of hyper-arid, arid, semiarid, and/or dry subhumid are expanding with generally greater aridity at a global scale, but at regional and local scales, the outcomes may vary, with dryland areas decreasing in some temperate regions and expanding in tropical and subtropical regions (Hermans and McLeman 2021). Furthermore, models suggest a worst world scenario in which small floods for farm water supplies are decreasing but large flood events that pose a risk to life and infrastructure are increasing (Wasko et al. 2021). Therefore, the instability of rainfall as one of the critical abiotic factors for crop production has increased, and soil water conditions could become unfavorable to maintain crop growth in the future. As one of the most typical phenomena of climate change, the ranges of elevated temperature in the future differ depending on the scenario; the average global temperatures in 2100 may be 1.7–4.8 °C warmer than those in 2000 (Hermans and McLeman 2021). These changes in rainfall and temperature could also have an impact on soil fertility and the physical and

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chemical conditions of soils: heavy rain reaches soil nutrients, a decrease in rainfall under arid and semiarid areas accelerates soil salinity by reducing salt reaching and upward groundwater containing salt under uncontrolled irrigation, and high temperature increases soil nutrient consumption by stimulating plant growth and decomposition of soil organic matter (Loomis and Connor 1992; Hiell 2003; Kaur et al. 2020). Therefore, the negative effects of abiotic factors on crop production could compound and become complicated under climate change.

1.2 Water Balance Causing Flooding and Drought in Crop Fields

Water is one of the most important abiotic factors. Flooding and drought that give serious impacts to crop production occur from an imbalance between supplied water and the output of water to soils in crop fields. The supplied water consists of rainfall (W_R), irrigation (W_I), and upward water supply from the groundwater table (W_G) (Fig. 1.1). Part of the supplied water ($W_R + W_I$) seeps or overflows (W_S), and the remaining water ($W_R + W_I - W_S + W_G$) gradually soaks into the soil sections at different depths. The soil section is a bulk soil with roots. Soil sections are regarded as a pool of water (W_{POOL}), which consists of plant available water (sometimes, it is defined as a fraction of transpirable soil water, FTSW) (Ray and Sinclair 1998) plus unavailable water fixed in soils (water content lower than wilting point) (Hiell 2003). The amount of W_{POOL} changes depending on the soil water-holding capacity determined by the soil physical properties and organic matter content (Hiell 2003). Water over the water-holding capacity is infiltrated out of the W_{POOL} (W_{IF}). Water in the soil sections is absorbed by plant roots as transpiration (T) and evaporated from

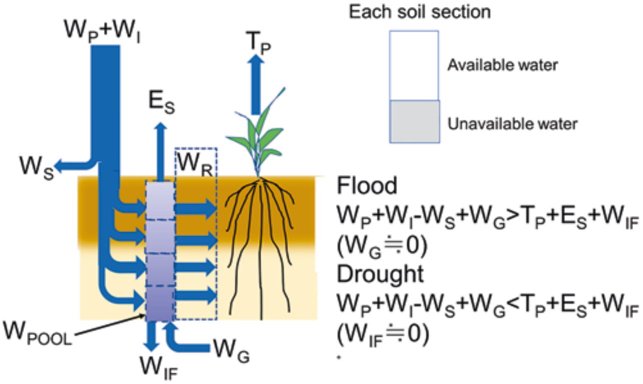

Fig. 1.1 Water balance of crop fields. W_P precipitation, W_I irrigation, W_S seeping or overflow, E_S soil evaporation, T transpiration, W_R root absorption, W_{IF} infiltration, W_G supply from ground water, W_{POOL} water pool of soil sections. Each soil section consists of available and unavailable water for plants. Cases of water balance during flooding and drought are shown

soil surfaces (T_S). Water absorbed by plant roots (W_R) equals transpiration (T) when absorbed, and transpired water is maintained in a steady state, while W_R temporarily differ from T (under high T, $T > W_R$ and under low T, $T < W_R$ by the buffer of water stored in the plant body).

Soil saturation and flooded soils occur when the water supply to crop fields ($W_P + W_I - W_S + W_G$) is over the maximum potential of $W_{POOL,}$ as the water use of the fields ($T_P + E_S - W_{IF}$) is less than W_{POOL}. When $W_P + W_I$ continuously increases and W_S reduces, air spaces in soils are filled by water, and furthermore, crop plants are submerged. Meanwhile, drought is the opposite case in which $W_P + W_I - W_S + W_G$ is below $T + E_S - W_{IF}$. W_G under flooding and W_{IF} under drought can be ignored because upper water flow under flooding conditions would be scarce, and under drought conditions, water movements would be small due to the high resistance of water flux in soils unless a high water table continuously supplies water (Hiell 2003).

Climate change could alter these water economies due to an increase or decrease in the amounts of rainfall (W_P) and evapotranspiration ($T + E_S$) related to radiation and humidity (Loomis and Connor 1992) and W_{POOL} related to soil physical properties influenced by the contents of organic matter (Hiell 2003).

1.3 Determination Factors for Crop Yield

Crop yield (Y) is indicated by

$$Y = \mathrm{BY} \times \mathrm{HI} \tag{1.1}$$

where BY is the biomass yield and HI is the harvest index (Passioura 1977; Unkovich et al. 2010). From the equation, yield is determined by two factors, BY and HI. In crops with harvested biomass such as sugarcane, BY nearly equals Y. The effect of abiotic factors such as flooding, drought, high temperature, and soil degradation on Y can be reviewed from the effects on BY and HI.

1.4 Effects of a Single Abiotic Factor on Crop Production

1.4.1 Flooding

Flooding causes water saturation of soils and submergence of plants; water saturation of soils removes oxygen in soil pores and directly inhibits root respiration; and furthermore, submerged water prohibits leaf gas exchange, decreasing plant growth and causing plant death, while the timing and length of flooding change plant damage (Bailey-Serres et al. 2012; Kaur et al. 2020). The negative effects of water submergence and saturation of soil pores on gas exchanges such as photosynthesis and respiration depend on a much lower diffusion rate of CO_2 and O_2 in water than in air, in which these gases are 1/10,000th and the flux of O_2 into soils is approximately 320,000 times less in water-filled soil pores than in gas-filled soil pores (Kaur et al. 2020).

The effect of flooding on yields in wheat and soybean under variable terms at different growth stages is summarized by Kaur et al. (2020), and these data are shown in figures (Fig. 1.2). Yield loss (flood/control) in wheat tends to increase around the flowering stage in the reproductive stage, although in the vegetative stage, the extension of flooding terms increases the effect. In soybean, of which the reproductive stage (R1-) starts from the early growth season, yield loss occurs across the whole growing season, while fluctuations in the loss are observed. In rice plants that can grow under flooded conditions, clear yield loss is not observed except in cases of heavy submergence of aboveground plants (Suge 1987; Sakagami et al. 2012). The high adaptation of rice plants to flooded soils comes from the development of aerenchyma in roots that supplies O_2 to root systems (Arikado 1955). Aerenchyma development is one type of the flood resistance methods often observed in crop plants (Bailey-Serres et al. 2012). Aerenchyma tissue composed of low-resistance gas conduits in roots and stems enables diffusion and exchange of oxygen and carbon dioxide from near the root apex to the uppermost submerged region of the root and into the stem (Jackson and Armstrong 1999). Adventitious roots that emerge from stem tissue under conditions of partial to complete submergence can replace compromised roots and provide efficient aerenchymatous connections between aerial shoot tissues and submerged organs (Bailey-Serres et al. 2012). In upland crops such as wheat and soybean, the development of aerenchyma after flooding has been observed, although it could be insufficient for growth maintenance (Arashi and Nitta 1955; Arikado 1955; Bailey-Serres et al. 2012). Plants can

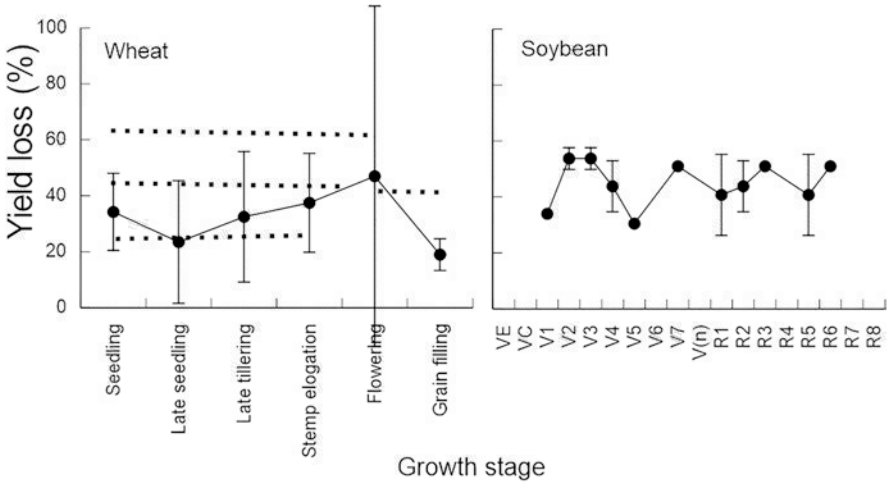

Fig. 1.2 The effect of flooding on yield loss in different growth stages in wheat and soybean. Data are the average of the loss under variable terms of flooding treatments (1–60 days in wheat and 1–14 days in soybean) and vertical bars are standard deviations of observed data derived from Kaul et al. (2020)

escape the submergence of the whole plant by stem elongation, such as deep water and flooded rice (Bailey-Serres et al. 2012), and local rice cultivars in lowland areas along a river in Japan which often suffer from flooding have a high capacity for stem elongation (Suge 1987).

Under flooding conditions, leaf area, branching, plant height, and carbohydrate contents generally decrease in diverse crops (Kaur et al. 2020), and hence, these effects of flooding could have a strong impact on BY. In rice, submergence and flooding reduce plant height and tiller number related to BY but have less influence after heading (Sakagami et al. 2012). The higher yield loss around flowering in wheat suggests that the HI reduces Y due to the inhibition of fertilization (Olgun et al. 2008). These results suggest that flooding mainly reduces Y due to the effect on BY, although a low HI due to low fertilization and fewer flower organs influences Y.

An increase in W_S and W_{IF} under flooding increases the reaching of nitrogen (Kaur et al. 2020); approximately 10–40% of applied N can be lost through leaching depending upon the application time, fertilizer source, and the crop being fertilized (Legg and Meisinger 1982; Kaur et al. 2020). Furthermore, ammonia (NH_3) volatilization increases due to changes in soil microbial communities under flooding (RafaelSánchez-Rodríguez et al. 2019). These nutrient losses immediately lower BP related to Y loss. Flooding effects on crop yields can be lightened by cultivation manipulations such as draining and raised beds (high ridges) to increase the W_{IF} and nitrogen application (Kaur et al. 2020).

1.4.2 Drought

Drought has been a dominant limiting factor for crop production not only in arid and semiarid areas (Turner 1996) but also in humid zones where rainfall has a seasonal bias (Tazaki et al. 1980). The physiological mechanisms, genotypic differences, and genetic background of drought in crop plants have been precisely analyzed and reviewed (Hsiao 1973; Begg and Turner 1976; Turner 1986; Dietz et al. 2021; Panda et al. 2021). The drought resistance of crop plants is conceptually divided into drought tolerance, avoidance, and escape (Begg and Turner 1976); these three traits contribute to maintaining BY and/or assimilating the location into harvest plant organs based on the HI.

Water use can be related to BY by

$$\mathrm{WUE} = \mathrm{BY} / \left(T / \mathrm{VD} \right)$$

where WUE is the water use efficiency and VD is the vapor water deficit of air (Sinclair et al. 1984). From the equation,

$$\mathrm{BY} = \mathrm{WUE} \times \left(T / \mathrm{VD} \right) \tag{1.2}$$

This equation indicates that higher WUE and/or T/VD can maintain BY. Higher WUE is an effective trait for increasing BY under limited water supply. However, improvements in transpiration efficiency of a single leaf (photosynthesis rate/transpiration rate), as the water use efficiency of a leaf-level base correlates well with carbon discrimination, do not always translate into higher WUE of the whole plant base or yield in wheat (Condon et al. 2004). Furthermore, high shoot dry matter increases in rice cultivars under terminated irrigation highly depended not on the superiority of WUE but on the plant water use (T), and the higher T was supported by higher root distribution into moist soil layers (Kobata et al. 1996; Kobata and Palta 2018). In fact, the variation in WUE among genotypes was not larger than that in T/VD. Therefore, in crop plants, there is controversy over whether WUE can contribute to the maintenance of BY (Blum 2005). T/VD is high, if T is higher and/or VD is lower. A lower VD is realized under high humidity conditions and low absolute humidity under cool temperatures. Hence, the planting season is important for escaping from high VD, while the terminal crop season is sometimes under high-temperature and low-humidity conditions, such as wheat in the Mediterranean zone and summer crops (Tazaki et al. 1980: Sadras and McDonald 2012). Higher T results from maintaining leaf area and leaf stomatal conductance under drought; maintenance of leaf expansion, green leaf area, and stomatal apparatuses under desiccated soils is needed. Escape from plant dehydration under drought is one of the most effective traits for maintaining these plant growth processes related with higher T (drought avoidance) (Begg and Turner 1976; Blum 2005), although osmotic adjustment as a capacity of plant adaptation can maintain these processes of dehydrated plants (Turner 1996; Turner et al. 2014), and partial soil desiccation around roots makes it possible to close stomata by hormonal signals even in nondehydrated leaves (Turner 1996). High root accesses of roots with extensive W_{POOL} can increase T. A large difference in root distribution in deep soil layers was observed among cultivars in rice (O'Toole and Bland 1987) and wheat (Mian et al. 1994); the distribution was one of the most important key factors for maintaining T to escape from plant water deficit in crops (Turner 1996; Kobata et al. 1996; Kobata and Palta 2018; Kobata et al. 2018b).

How does soil desiccation under drought conditions relate to T? The relative T (T/T_0, where T_0 is transpiration in the well-irrigated control) is well fitted by the equation for FTSW (Ray and Sinclair 1998).

$$T / T_0 = f\left(\mathrm{FTSW}\right) \tag{1.3}$$

$$\mathrm{FTSW} = \left(\mathrm{SW} - \mathrm{SW_W}\right) / \left(\mathrm{SW_F} - \mathrm{SW_W}\right)$$

where SW is the observed soil water content, SW_F is the upper limit of water absorption (field capacity), and SW_W is the lower limitation (wilting point), while SW_F and SW_W are not physically defined but empirical (Hiell 2003). Eq. (1.3) was not influenced by root size in soybean and maize (Ray and Sinclair 1998). A case in several rice plants for the relationship between T/T_0 and FTSW has been shown (Kobata, unpublished data) (Fig. 1.2). In the relationship, T/T_0 started to decrease at similar

FTSWs in diverse cultivars and different soil types (volcanic and sandy soil). From Eqs. (1.2) and (1.3), the higher FTSW contributes to the maintenance of T related to BY. The higher FTSW can be maintained by a deep root system distributed into large wet bulk soils (larger W_{POOL}).

Suppression of E_{S} saves water in W_{POOL} and can reserve soil water for T. Covering the soil surface by the rapid expansion of leaves suppresses E_{S} (Kobata et al. 1996, 1998). However, the trait for the reduction of E_{S} and high WUE seems to not be compatible (Condon et al. 2004).

Drought at pollen development and the flowering stage strongly decreases fertility in many crops (Nagato 1949; Kobata et al. 1994; Sadras and McDonald 2012), and sterility profoundly decreases the HI by reducing grain number. Furthermore, a lack of assimilates during the grain-filling period under water shortage conditions decreases the HI due to inadequate grain filling (Kobata et al. 2018b). In crops suffering from terminal season drought, such as a typical case in the Mediterranean zone (Turner et al. 2014; Kobata et al. 2018b), the effect of a decrease in the HI on Y would become stronger (Figs. 1.4 and 1.5).

1.4.3 High Temperature

Temperature is a main factor that determines plant growth and development rates; phenological development is indicated by the developmental index (DVI) calculated by summing the developmental rate (DVR), in which DVR is a function of daily mean temperature with a day length (Horie et al. 1995). Elevated temperature shortens the vegetative and reproductive stages, resulting in inadequate BY and a small sink size of the yield portion, and furthermore, extreme high temperature injures plant organs such as leaves and flowers. The most serious effect of high temperature on Y is damage to pollens around the flowering stage, resulting in reductions in the HI; sterility occurs at temperatures over 35 °C in rice (Matsui and Hasegawa 2019) and soybean (Djanaguiraman et al. 2019) and 32 °C in wheat (Nuttall et al. 2018).

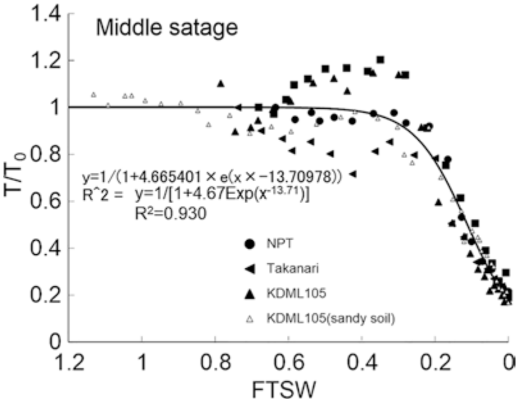

Fig. 1.3 Relative transpiration (T/T_0) and fraction of transpirable soil water (FTSW) in different rice cultivars when watering was terminated. T_0 is the transpiration of the well-watered control. Plants were grown in pots containing volcanic soil (Andosol), and one cultivar did in pots contained sandy soil (Unpublished data)

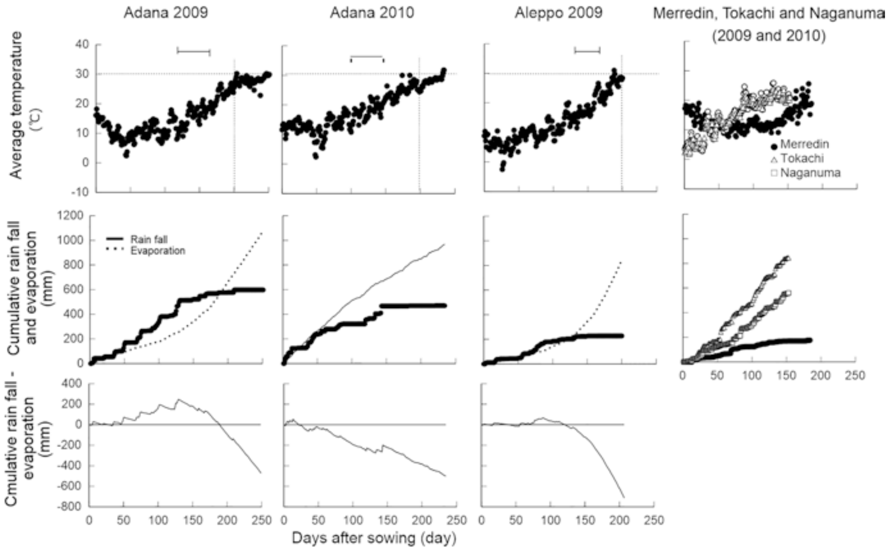

Fig. 1.4 Average temperature, cumulative rainfall, pan evaporation, and cumulative rainfall minus pan evaporation of the day after sowing in Adana, Turkey (2009 and 2010), and Aleppo, Syria (2010), in the wheat-growing season (Kobata et al. 2018b). Additionally, the average temperature and cumulative rainfall in 2009 and 2010 in Merredin, Western Australia, as a case of low temperature and rainfall, and in Obihiro and Naganuma, Hokkaido, Japan, as a case of slightly lower temperature to and high rainfall in wheat-growing areas, are shown

Hence, high-temperature tolerance for fertility or escape from high temperature at flowering would be important traits for high-temperature resistance (Ishimaru et al. 2022). The high-temperature resistance across the whole growth period would be even more important for crop yield because of recent temperature elevation events during the whole growth season (Hermans and McLeman 2021).

1.4.4 *Other Abiotic Factors*

The elevated CO_2 that is one of the causes of climate change increased BY and *Y* in 186 independent studies of 18 C_3 crops based on free-air CO_2 enrichment (FACE) experiments (Ainsworth and Long 2021), although acclimation of plants was possible to reduce the effect of elevation on BY in the long term (Tausz-Posch et al. 2020). Under elevated CO_2, Eq. (1.3) did not clearly differ from that under ambient conditions in spring wheat (Kobata 2006).

Other abiotic factors, such as soil compaction and nutrient, chemical, biological, and physical properties that impact crop production, are affected not only by regional soil characteristics but also by climate conditions such as rainfall and by cultivation procedures such as tillering and irrigation (Loomis and Connor 1992;

Hiell 2003). Therefore, under climate change, the effect of these factors on crop plants could be integrated and intensified.

1.5 Combined Effects of Abiotic Factors on Crop Production

Crops suffer from multiple abiotic stresses under climate change (Hermans and McLeman 2021). Temperature is a widespread factor that acts simultaneously with other abiotic factors; hence, the combined effects of high temperature with flooding and drought on crop production are addressed.

High temperature accelerates plant damage under flooding as a decrease in plant survival in corn plants (Nielsen 2015) and grain yield in winter wheat (Wu et al. 2014) and soybean (Wuebker et al. 2001). These negative effects of temperature elevation result from a reduction in soil oxygen due to an increase in the respiration of microorganisms and plants (Kaur et al. 2020). Furthermore, under higher temperature conditions, flooding induced a rapid release of nutrients and resulted in changes of soil microbial biomass and microbial community structure to influence soil fertility and physical properties related to water holding (RafaelSánchez-Rodríguez et al. 2019; Tisdall 1994). Therefore, high temperature intensifies the negative impacts on crop productivity under flooded conditions. Fertilizer manipulations, such as nitrogen application, cultivated operations such as draining and high-ridge cultivation, and genetic improvements, would be highly required to lessen flooding damage under climate change.

The integrated effect of high temperature and drought on wheat production is suggested in a case in the Mediterranean zone in which rainfall terminated under high-temperature conditions. In southwestern Turkey (Adana) and northern Syria (Aleppo), low rainfall, high evaporation, and high temperature start in the middle growing season, and wheat suffered from severe terminal drought and high temperature (Fig. 1.5) (Kobata et al. 2018b). High temperature increased evaporation due to an increase in VD and accelerated the soil water deficit. The severe high temperature and low rainfall in these two areas were proven to be typical from a comparison with other main wheat-growing areas, Merredin in the Mediterranean zone in western Australia (Bureau of Meteorology 2022), where rainfall was similarly low but temperature was lower, and Obihiro and Naganuma in the subarctic zone in Hokkaido, Japan (JMA 2022), where temperature was slightly lower but rainfall was much higher. In Adana and Aleppo, three different types of wheat, bread wheat (*Triticum aestivum* L.), durum wheat (*T. durum*), and emmer wheat (*T. dicoccum*), which were selected according to their localities, origins, and genetic diversity, were grown under rainfed conditions. The grain yield was closely correlated with the HI across different types of wheat in each location but was not correlated with BY (Fig. 1.5), and hence, *Y* was significantly determined by the partitioning of assimilates into the grain. The *Y* in bread wheat had a higher HI than the others. The HI was negatively correlated with heading days after sowing (Fig. 1.6). Delay of day of heading after sowing increased both average temperature