Physiological and Molecular Bases of Drought and Heat Tolerance in Pearl Millet

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Abstract

Pearl millet is one of the most important sources of nutrition for millions of people in arid and semi-arid areas in Africa and Asia. Farmers have had, throughout its domestication, to select cultivars adapted to their environments. So, pearl millet appears as an interesting crop model to study drought adaptation. However,

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current and future climatic changes pose challenges to its cropping sustainability. Drought and heat are the main factors of climate change. To accelerate pearl millet adaptation and improve its productivity to cope with climate change, its mechanisms of adaptation must be dissected. Here, we review the state of research on the physiological and molecular bases of pearl millet adaptation to drought and heat. However, pearl millet remains a neglected crop, and progress in research remains to be made.

10.1 Climate Change

Climate change is a major threat to agriculture and food security (Kang et al. 2009; Godfray et al. 2010; Wang et al. 2018). The most conspicuous climate changes in recent times are the increase in atmospheric temperatures due to increasing levels of greenhouse gases (Solomon et al. 2007; Stott et al. 2010; Christidis et al. 2012; Wang et al. 2018) and associated changes in the water cycle (Bates et al. 2008; Collins et al. 2013; Jung et al. 2002; Balling and Cerveny 2003; Fauchereau et al. 2003; Trenberth et al. 2007). A continued rise in global temperature is predicted if greenhouse gas (GHG) emissions continue unabated, according to the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC). The frequency of warm days, warm nights, and heat waves have increased, while the frequency of cold days and cold nights has decreased (Sillmann et al. 2013). Based on emission scenarios, the IPCC predicts a temperature increase between 0.3 and 0.7 °C by 2035 with a medium degree of confidence (Kirtman et al. 2013). In a study assessing long-term projections of climate change, Collins et al. (2013) showed that increase in global mean surface temperatures for 2081–2100, relative to 1986–2005, will likely be in the 5–95% range of CMIP5 (Coupled Model Intercomparison Project Phase 5) models; 0.3–1.7 °C (Representative Concentration Pathway 2.6 or RCP2.6), 1.1–2.6 °C (RCP4.5), 1.4–3.1 °C (RCP6.0), 2.6–4.8 °C (RCP8.5). As a result, an increase in temperature from 0.3 to 4.8 °C is expected by the end of the twenty-first century. This increase in mean temperatures is expected to be greater in the tropics and subtropics than in the mid-latitudes (high confidence; Kirtman et al. 2013).

Along with the increase in temperature, global warming is associated with changes in the intensity/uncertainties of precipitation. Future climate projections show that precipitation could increase or decrease depending on the latitude of the area. These results corroborate those of Bates et al. (2008), who reported that over the past century, precipitation has mainly increased over northern high-latitude lands, while notable decreases have occurred in recent years from 10°S to 30°N. This observed effect is expected to continue in the coming years as climate model simulations predict an increase in precipitation in high latitudes and parts of the

tropics and decreases in some subtropics and lower mid-latitudes by the end of the twenty-first century (Collins et al. 2013).

Arid and semi-arid areas, especially those in Asia and Africa, are very vulnerable to climate change. Temperature and precipitation variability is expected to increase in these areas. In Africa, it is predicted that the temperature will rise faster compared to the rest of the world. This increase could exceed 2 °C by the middle of the twenty-first century and 4 °C by the end of the twenty-first century (Niang et al. 2014; Adhikari et al. 2015; Djanaguiraman et al. 2018) and will lead to reduced crop yields (Fischer et al. 2005a, b; Howden et al. 2007; Liu et al. 2016). Regarding rainfall, significant negative trends are observed in West Africa and the Sahel. The Sahelian region of West Africa experienced a decrease in rainfall between the late 1950s and the late 1980s (Dai et al. 2004). Recently, Sultan and Gaetani (2016) predicted an increase in extreme events and increased variability in precipitation from year to year. Precipitation projections for the twenty-first century are not spatially homogeneous in West Africa. As a result, there is a large dispersion in the representation of rainfall from one regional model to another, both on a seasonal and intra-seasonal scale (Salack et al. 2012b). Beyond the changes in the total amount of rain, precipitation patterns are also predicted to change in the Sahelian area. For instance, Salack et al. (2011) identified two agro-climatic zones where rainfall breaks frequently occur at the start and end of the rainy season (Salack et al. 2012a). These rainfall breaks accompanied by heat stress are likely to affect crop yield. These factors constitute a major agronomic problem that contributes to severe yield losses of up to 10% for pearl millet in arid and semi-arid areas (South Asia and Africa) (Knox et al. 2012). It is therefore urgent to better understand heat and drought stress mechanisms in pearl millet to develop new agricultural practices and varieties adapted to these stresses and ensure food and nutritional security in sub-Saharan Africa.

10.2 Effects of Drought and Heat on Pearl Millet and Annual Plant Growth and Development

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is an important food crop grown under hot and dry conditions in arid and semi-arid regions of Africa and Asia (Arya and Yadav 2009; Ullah et al. 2017). Since these areas are characterized by low and irregular rainfall, high temperatures, and low soil fertility, they constitute the main constraints for its production. These stresses often occur simultaneously, making it very difficult to separate the effects of each on plants. However, the combined stresses have a negative impact on plant growth and productivity, which is more pronounced than the individual impacts (Craufurd and Peacock 1993; Prasad et al. 2008; Dreesen et al. 2012).

10.2.1 Drought Effects

Drought stress is one of the major constraints limiting crop production worldwide (Forster et al. 2004; Khan et al. 2010). Drought can be defined as a deficit of adequate moisture necessary for normal plant growth in the complete life cycle (Zhu 2002). Plants are subject to drought when the stock of water in the soil is limited, and the vapor pressure deficit is very low (Anjum et al. 2011b). It has a considerable influence on plant growth and development. Pearl millet is sensitive to drought stress at the vegetative and reproductive stages (Vadez et al. 2012). The effects of drought stress depend on the degree, duration, stage of crop development, and tolerance level of the species. Drought stress during the growth phase affects cell division and elongation, the main processes involved in plant growth. Due to the reduction in turgor pressure, cell elongation appears to be one of the most drought-sensitive processes. Even though cell division is less sensitive than cell elongation, it can be affected by mild drought stress. Tardieu et al. (2000) reported that soil moisture deficit resulted in a reduction in the length of the cell division zone and the relative division rate. According to Alves and Setter (2004), the reduction in leaf area was caused largely by development delay and a reduction in cell division in the youngest meristematic leaves.

However, the effects of drought on the leaves depend on the intensity of the stress. A slight drought causes a reduction in the rate of expansion, number, and size of leaves, while severe stress decreases the rate of leaf elongation, which can even cause leaf growth to stop. The most common negative effect of drought stress on crop plants is the reduction in growth. This has been reported in pearl millet by many authors (Muchow 1989; Winkel et al. 1997; Aparna et al. 2014; Kholová et al. 2016). Drought reduces leaf size, stem extension, and root proliferation, disrupts plant–water relationships, and reduces water use efficiency (Farooq et al. 2009; Anjum et al. 2011b). These results agree with those of Khan et al. (2001) and Anjum et al. (2011a), who reported a significant decrease in the growth of maize under drought in terms of plant height, stem diameter, leaf area, and plant biomass.

In addition, drought has been shown to alter physiological processes (Radhouane 2008, 2013; Pinheiro and Chaves 2010; Anjum et al. 2011a; Ghatak et al. 2016). Photosynthesis, transpiration rate, stomatal conductance, water use efficiency, intrinsic water use efficiency, and intercellular CO_2 have been reduced by drought (Anjum et al. 2011a). In millet, severe drought stress leads to a reduction in photosynthesis (Ashraf et al. 2001; Golombek 2003; Radhouane 2009). This reduction has also been reported in C4 cereals such as maize (Boyer and Westgate 2004) and sorghum (Ogbaga et al. 2014). One or more steps in the photosynthetic process can be affected by water deficit, such as the diffusion of CO_2 through the stomata and into intercellular spaces (Flexas et al. 2006). For Slatyer (1973), almost all the decrease in photosynthesis must be attributed to stomatal closure. On the other hand, according to Bois (1993) and Golombek (2003), the decrease in photosynthesis of pearl millet is due jointly to stomatal resistance and non-stomatal changes. The imposition of drought stress also resulted in a decrease in chlorophyll content (Ghatak et al. 2021),

which could be related to the increase in the activity of the enzyme chlorophyllase (Ashraf et al. 1994).

In terms of production, drought stress strongly affects yield during the grain-filling period (Aparna et al. 2014). In sorghum, the yield can be reduced by more than 36% and 55% when water stress occurs in the vegetative and reproductive phases respectively (Assefa et al. 2010). Stress reduces grain size and weight, resulting in a reduction in grain yield (Arya et al. 2010). Many studies corroborate this result (Barnabás et al. 2008; Alqudah et al. 2011; Aparna et al. 2014; Debieu et al. 2018). A severe reduction in panicle filling occurs under drought (Winkel et al. 2001) due to a reduction in the assimilate partitioning and activities of sucrose and starch synthesis enzymes (Farooq et al. 2009; Anjum et al. 2011b). However, according to Aparna et al. (2014), the decrease in grain yield depends more on the number than the size of the seeds. Therefore, it is due to the combined effect of a reduction in the number of panicles (productive tillers) and seeds. In pearl millet, a strong correlation was found between grain yield and grain number (Bidinger and Raju 2000). In wheat, drought stress reduced yield following tiller abortion and a lower grain number per spike (Izanloo et al. 2008). Thus, drought most often occurs during the vegetative and reproductive stages of pearl millet, causing drastic effects on growth and productivity.

10.2.2 Heat Effects

Heat stress (increase in air temperatures above the optimum) is an agricultural problem in many parts of the world (Wahid et al. 2007). It is a key determinant of crop growth and productivity (Al-Khatib and Paulsen 1999), whose adverse effects on cereals vary with the timing, duration, and intensity (sternness) of stress (Barnabás et al. 2008; Fahad et al. 2016a). In Africa and India, soil temperatures generally exceed 45 °C and sometimes reach 60 °C (Yadav et al. 2010). This explains the important place occupied by pearl millet cultivation in these areas because the optimum temperature for its development fluctuates between 33 and 34 °C (Ashraf and Hafeez 2004).

Indeed, pearl millet is the most heat-tolerant cereal crop and needs high temperatures to grow. This has been illustrated by numerous works showing that the growth of pearl millet is optimal up to a temperature of 35 °C (Arya et al. 2014), but beyond that, inhibition of the normal growth process is noted (Ashraf and Hafeez 2004; Yadav et al. 2010, 2016; Arya et al. 2014; Djanaguiraman et al. 2018).

A temperature above the optimum can delay or prevent germination. This germination delay was reported in pearl millet cultivars subjected to supra-optimal temperatures compared to controls (Khalifa and Ong 1990). In pearl millet and maize, heat stress has been reported to cause a decrease in the final percentage of germinated seeds and the germination rate (Ashraf and Hafeez 2004). Yadav et al. (2016) showed that increasing the temperature can decrease the germination rate or even inhibit germination depending on the tolerance of the genotype, which agrees with the results of Wahid et al. (2007).

In later stages, heat stress can also negatively affect the vegetative growth of plants. It induces a reduction in shoot dry mass, relative growth rate, and net assimilation rate (Ashraf and Hafeez 2004; Wahid 2007). On the roots, temperatures above optimal lead to a decrease in primary root length, number of lateral roots, and their angle of emergence (Calleja-Cabrera et al. 2020). In addition, it causes a decrease in shoots or root's water status, root's hydraulic conductivity, or leaf stomatal conductance, which only occurs when the stress is prolonged (Heckathorn et al. 2013).

Reduction in photosynthetic activities by higher temperature has been reported by numerous studies (Al-Khatib and Paulsen 1999; Crafts-Brandner and Salvucci 2000, 2002; Prasad et al. 2004; Fahad et al. 2016b; Yadav et al. 2016). This reduction in photosynthesis was attributed to the damage to chlorophyll pigments, a decline in leaf nitrogen contents, blockage of PSII reaction center and electron flow decreased quantum efficiency (Fv/Fm), and down-regulation of PSII photochemistry (Fahad et al. 2016b, 2017). Heat stress decreases the activation and activity of Rubisco (Prasad et al. 2004) by inhibiting the activity of the enzyme Rubisco activase (Crafts-Brandner and Salvucci 2000, 2002). Heat also reduces the photochemical efficiency of photosystem II (PSII), which appears to be the most heat-sensitive photosynthetic component (Al-Khatib and Paulsen 1999).

On the other hand, despite the multiple negative effects of heat stress at the vegetative stage, plants appear more sensitive at the reproductive stages (Farooq et al. 2011; Prasad et al. 2017). Recently, much work has been done on cereals to identify the growth stage(s) most sensitive to heat stress during reproductive development (Prasad and Djanaguiraman 2014; Prasad et al. 2015; Djanaguiraman et al. 2018). Two periods were identified, ranging from 10 to 12 days and 2 to 0 days before anthesis in pearl millet (Djanaguiraman et al. 2018), 8 to 6 days and 2 to 0 days before anthesis in wheat (Prasad and Djanaguiraman 2014), 10 to 5 days before anthesis and 5 days before and 5 days after anthesis in sorghum (Prasad et al. 2015). During these periods, heat stress causes maximum decreases in pollen germination percentage, seed number (Djanaguiraman et al. 2018), and floret fertility (Prasad and Djanaguiraman 2014; Prasad et al. 2015).

In pearl millet, high temperatures (>40 °C) often coincide with the flowering and grain-filling stages (Gupta et al. 2015). Heat stress during these stages leads to a decrease in grain number and weight, leading to poor crop yield and quality (Bita and Gerats 2013; Djanaguiraman et al. 2018). According to Sultan et al. (2013), raising the temperature to 6 °C would lead to a 41% reduction in pearl millet yield. Several studies have reported a decrease in the yield of pearl millet and other cereals under heat stress (Gupta et al. 2015; Prasad et al. 2017; Djanaguiraman et al. 2018; Qaseem et al. 2019; Jagadish 2020).

According to Fahad et al. (2016a, b), the decrease in pollen germination mainly results from the retention of pollen in dehiscent anthers. However, an increase in the content of reactive oxygen species and a decrease in the activity of antioxidant enzymes in pollen and pistils have been reported in millet (Djanaguiraman et al. 2018). Pistils were more sensitive than pollen grains because they had relatively higher reactive oxygen species and lower antioxidant enzyme activity. Increased

production of reactive oxygen species under these conditions may be responsible for decreased germination and pollen viability in sorghum (Prasad and Djanaguiraman 2011).

Heat stress also causes a decrease in spikelet fertility due to a decrease in the production and number of pollens on the stigma (Prasad et al. 2006a) and inhibition of panicle emergence (Prasad et al. 2006b). This decrease in spikelet fertility resulted in fewer filled grains, lower grain weight per panicle, and lower harvest index. According to Gupta et al. (2015), heat stress causes reproductive sterility in pearl millet leading to a drastic reduction in grain yield. In addition, the increase in temperature promotes a higher rate of evapotranspiration, which ultimately reduces soil moisture and available water needed to fill the grains.

10.2.3 Heat and Drought Combined Effects

In arid and semi-arid areas, drought and heat stress often occur simultaneously (Shah and Paulsen 2003; Barnabás et al. 2008). This effect occurs because of a negative correlation between temperature and precipitation on inter-annual scales because dry conditions favor more sunshine and less evaporative cooling (Trenberth and Shea 2005; Zscheischler and Seneviratne 2017). However, few studies examining the impact of the combined effects of both stresses on crops, let alone pearl millet, have been carried out. The few studies carried out on this subject have shown that the combined effects on growth and productivity considerably exceed the simple effects (Savin and Nicolas 1996; Prasad et al. 2008; Dreesen et al. 2012; Qaseem et al. 2019).

Drought and heat stresses, by their intensity and duration, can influence the growth and development of plants. At the leaf scale, the distribution of the relative elongation rate was independently affected by these stresses, which had quasi-additive effects (Tardieu et al. 2000). Additionally, leaf elongation rates were positively correlated with leaf temperatures and negatively with vapor pressure deficit and pre-dawn leaf water potential (Welcker et al. 2007). This shows the strong relationship that exists between leaf elongation rates and various physiological components that can be indicative of drought and heat stress. In terms of growth, drought, and heat affect stem growth and plant height (Katerji et al. 1994; Winkel et al. 1997; Prasad et al. 2006b).

Similarly, these stresses can also impact the transition and duration of the developmental stage. Cooper et al. (2009) reported a reduction in the length of the growing period of plants in dry tropical regions. This reduction is the result of both the rapid development of the leaf canopy and an increase in the overall growth rate of the crop stimulated by heat stress. Higher temperature results in faster development, and therefore shorter, growth phase duration.

Heat stress combined with drought can cause stomatal closure leading to an increase in leaf temperature (Rizhsky et al. 2002), unlike the simple effect of heat stress, which promotes the opening of the stomata, thus leading to cooling of the leaves by transpiration. Consequently, the water status of the plant is partly linked to

the temperature, which affects several parameters of the plant. According to Shah and Paulsen (2003), the interactions between stresses were pronounced, and the consequences of drought were more severe at high temperatures than at low temperatures on all physiological parameters. Barnabás et al. (2008) confirm these statements by asserting that the synchronization of the two results in even greater severity of drought stress. Thus, heat increases the intensity of the drought by causing the soil to dry faster. This effect results from the increase in the vapor pressure deficit of the air, which favors a greater demand for evapotranspiration. In addition to warming, the indirect effect of heat on water evapotranspiration from the soil can have a great impact on plants.

On the other hand, antagonistic interactions between heat and drought have been reported on net photosynthesis. In wheat, Lu and Zhang (1999) asserted that drought stress increases the tolerance of PSII to heat stress. However, many authors have argued that drought tends to dramatically exacerbate the effects of heat stress on plant growth and photosynthesis (Shah and Paulsen 2003; Xu and Zhou 2005a, b, 2006).

The effect of drought and heat stresses on root growth depends on the intensity of the stress. Moderate stress results in greater root growth due to increased distribution of carbohydrates to the roots and greater exploration of the soil caused by drought and heat stress, respectively. On the other hand, severe stress leads to a reduction in the number, length, and diameter of the roots, which becomes more important when drought and heat stress are associated (Prasad et al. 2008).

When these constraints occur during grain development, they cause significant yield losses in cereals (Chaves et al. 2003; Bai et al. 2004; Prasad et al. 2008). Knowing that starch represents a major part of the dry weight of cereals, this reduction is due to a decrease in its accumulation. On the other hand, data on the possible variation of this trait in pearl millet are limited.

10.2.3.1 Mechanisms of Adaptation to Climate Variability (Drought and Heat) in Pearl Millet

Faced with environmental constraints, plants must be able to react and adapt to increase their chance of survival. Thus, they are developing different strategies to adapt and resist drought and heat stresses. These strategies are characterized by a strong ability to set up biochemical, molecular, and physiological responses which influence various cellular processes in the plant. Drought survival mechanisms of plants are like those used to cope with heat stress (Wu et al. 2018). Escape, avoidance, and tolerance mechanisms have long been considered important strategies for drought adaptation (Chaves et al. 2003). These mechanisms have also been reported by Kooyers (2015) and Li et al. (2017).

Drought escape allows some plants to cope with stress by completing their full development cycle before the water deficit sets in the soil (Annerose 1990). Drought avoidance, on the other hand, is the ability of plants to maintain high levels of water potential in their tissues by reducing water loss or improving water uptake (Ludlow and Muchow 1990). Escape and avoidance strategies may be the most effective for survival and reproduction when drought stress is mild-tomoderate (Kooyers 2015).

Mechanisms of dehydration avoidance include morphological and functional modifications such as leaf area size, leaf rolling, stomatal conductance, and osmotic adjustment (Blum 2011; Kadioglu et al. 2012). However, when drought stress becomes severe, plants must be able to rely on tolerance strategies to avoid desiccation. Thus, drought tolerance appears to be the capacity of plants to resist water deficit while maintaining appropriate physiological activities (Xiong et al. 2006). Therefore, the response of plants to drought depends on the species, duration of the drought as well as the timing of application (Sanchez et al. 2002; Pinheiro and Chaves 2011).

Due to its drought and heat tolerance (Arya et al. 2010), pearl millet is an ideal model for studying the heat and drought resistance mechanism of cereal crops.

Leaf Rolling and Stomatal Conductance

In plants, many changes occur in the leaf, both in structure and morphology, in response to drought and heat stress. Leaf rolling is an abiotic stress avoidance mechanism (Kadioglu and Terzi 2007; Kadioglu et al. 2012). It occurs when plants are under stress and is caused by folding in the midrib of upper leaves and changes in their leaf's orientations (Kusaka et al. 2005b). This leads to a reduction in leaf temperature via a decrease in incident radiation (O'toole et al. 1979; Heckathorn and DeLucia 1991) and thus offers protection against the effects of excessive radiation (Kadioglu and Terzi 2007). Leaf rolling effectively reduces light interception, transpiration, and leaf dehydration (Kadioglu and Terzi 2007).

However, reduced transpiration has often been associated with leaf senescence which results in an efficient and rapid decrease in leaf area. It can extend the duration of soil water availability by reducing the plant's water requirements and losses. According to Wallace et al. (1993) and Soegaard and Boegh (1995), senescence constitutes the main mechanism responsible for the reduction of transpiration. However, it can be a limiting factor for the accumulation of crop biomass and hence grain yield due to its irreversible effect. Unlike senescence, the reversible nature of leaf rolling provides flexibility when drought is temporary and intermittent.

However, sorghum and pearl millet studies have shown that leaf rolling did not occur until after stomatal closure (Blum and Sullivan 1986; Ludlow and Muchow 1990). Therefore, the immediate response of plants under drought stress is the stomatal closure to prevent water loss through transpiration (Cornic and Massacci 1996; Assmann et al. 2000; Ghatak et al. 2016; Buckley 2019). Through the transpiration stream, drought induces root-to-leaf signaling promoted by soil drying, which causes stomatal closure (Farooq et al. 2009; Anjum et al. 2011b). This stomatal closure is higher and faster in tolerant genotypes (Ghatak et al. 2021) and appears to be more effective in reducing water loss than leaf rolling. It has been reported that the decrease in water use by stomata is greater pre-anthesis than post-anthesis because of the ontogenetic decline in the range of stomatal conductance (Winkel et al. 2001).

Under drought conditions, plants tend to have lower stomatal conductance, which decreases as drought stress increases (Ghatak et al. 2021). This decrease in conductance allows the plant to conserve water and maintain an adequate water status of the

leaves, hence the close relationship between them. A significant correlation between stomatal conductance and leaf xylem water potential has been reported by Matsuura et al. (1996). However, a low stomatal conductance could be partly related to a difference in stomatal density. According to Slama (2002), the increase in the number of stomata per unit area could be one of the factors of resistance to water deficit in cereals if accompanied by appropriate photosynthesis activity. It can decrease water loss and increase the net uptake of CO_2, which allows the plant to maintain photosynthesis. Increased stomatal density can also affect crop yield. The variety of durum wheat with the highest yield and the largest kernels has a higher stomatal density at the beard and flag leaf (Slama 2002). On the other hand, according to Kholová et al. (2010), stomatal regulation is more important than stomatal density in regulating the loss of water in pearl millet. Nevertheless, stomatal conductance and leaf rolling have been shown to be reliable physiological indicators of drought tolerance in plants (Kadioglu and Terzi 2007).

Heat stress, often associated with a high vapor pressure deficit (VPD), also causes leaf rolling in plants (Omarova et al. 1995) and stomatal closure (Maroco et al. 1997). It causes a change in the temperature of the leaves, which can be an important factor in controlling the leaf water status under stress. The study by Kadioglu and Terzi (2007) showed that leaf rolling was linearly correlated with osmotic potential and leaf temperature. Thus, the physiological role of leaf rolling was reported as the maintenance of adaptive potential by increasing the efficiency of water metabolism in wheat flag leaves under heat stress (Sarieva et al. 2010). In fact, this is consistent with the fact that leaf rolling results in more efficient use of water during photosynthesis (Kadioglu and Terzi 2007). In addition, a reduction in leaf area was noted in pearl millet and sorghum under high VPD (Choudhary et al. 2020). According to Choudhary et al. (2020), water conservation when increasing VPD depends primarily on reduced leaf area and somewhat on transpiration restriction in these two crops. This restriction of transpiration has also been reported by Kholová et al. (2010). However, partial stomatal closure is achieved by limiting the transpiration rate under conditions of high VPD. Stomatal sensitivity to VPD was correlated with the hydraulic conductance of leaves relative to the total leaf area (Ocheltree et al. 2014). However, reducing the transpiration of pearl millet under a high vapor pressure deficit has been proposed to be beneficial for crop yield under such conditions (Kholová et al. 2010).

Root Characteristics

Pearl millet is one of the most abiotic stress-tolerant cereal crops in part due to its strong root system. Rapid root growth at depth can offer a chance for survival in harsh conditions as water uptake requests deep roots because of the quick water drainage of the sandy soils where millet is usually grown. The advantage of deeper root systems was demonstrated in pearl millet (Faye et al. 2019), sorghum (Chopart et al. 2008b), wheat (Kirkegaard et al. 2007; Christopher et al. 2008), maize (Sinclair and Muchow 2001; Hund et al. 2009), and rice (Manschadi et al. 2010; Wasson et al. 2012). In pearl millet, the root system is made up of several types of roots, namely the primary root (emerges from the seed and the mesocotyl connecting the seed and

the base of the stem), crown roots (emerges from the base of the stem), lateral roots (appear on primary or crown roots), and secondary roots (ramifications of lateral roots) (Passot et al. 2016). Crown roots form most of the root system, even though the primary root characterizes the root system at the start of pearl millet growth. This primary root will regress from 1 month after sowing (within 2 months after germination) (Maiti and Bidinger 1981; Passot 2016). Passot et al. (2016) showed that the number of central metaxylem vessels constitutes the major difference between the different root types.

Different lateral root types have been reported in pearl millet, rice, and maize (Passot et al. 2016, 2018; Hochholdinger and Tuberosa 2009; Rebouillat et al. 2009). The different types of lateral roots in cereals have been identified through anatomical studies of roots, often based on traits such as root diameters and vascularization (Varney et al. 1991; Watt et al. 2008; Henry et al. 2016; Passot et al. 2016). Recently, Passot et al. (2018) were able to classify roots based on their growth rate profiles. The study found three types of lateral roots with similar characteristics in pearl millet and maize. This revealed three types of lateral roots with similar characteristics in pearl millet and maize.

Under drought stress, pearl millet root growth is reoriented toward deeper soil layers that retain more water. Several studies have argued that root growth orientation was only dependent on soil depth (Chopart and Siband 1999; Chopart et al. 2008a, b; Faye et al. 2019). This dependence differed between thick roots and fine roots. Thick root growth was horizontal in shallow soils and became more and more vertical with increased depth, unlike the growth orientation of fine roots, which was only marginally dependent on soil depth (Faye et al. 2019). This result agrees with those found in sugarcane and sorghum (Chopart et al. 2008a, b). They claimed that fine roots appeared isotropic when thick roots were horizontal near the surface and gradually became vertical in deeper horizons. According to Passot et al. (2016), the thick roots correspond to the seminal or crown roots, while the fine ones probably correspond to the different types of laterals.

Increasing water uptake is a way of avoiding stress. It takes place via the roots, and its transport from the soil to the xylem vessels uses two pathways: the apoplastic pathway and the cell-to-cell pathway, which summarizes the transcellular and the symplastic pathways (Steudle 2001). The type of path depends mainly on environmental conditions. Water flows through the apoplastic path under non-stressful conditions due to hydrostatic forces while it flows through the cell-to-cell path under stressful conditions due to osmotic forces. Aquaporins, water channels present in cell membranes, enable cell-to-cell water transport (Prado and Maurel 2013; Chaumont and Tyerman 2014). They are involved in the physiology of plant growth (Maurel et al. 2015), thus influencing the hydraulics, transpiration, and water conservation of the soil. Their importance has been demonstrated in pearl millet where they contribute up to 84% to the hydraulic conductivity of roots (Grondin et al. 2020). Interestingly, aquaporins contribution was higher in root hydraulic conductivity for a pearl millet line with lower water use efficiency (Grondin et al. 2020). Aquaporins are also well known for their response to drought stress (Alexandersson et al. 2005; Aroca et al. 2012; Grondin et al. 2016). Several types

of aquaporin families have been identified with different functions. Many of them are involved in the regulation of water uptake by roots under drought conditions (Aroca et al. 2012).

On the other hand, root length is an important trait for tolerance to drought stress. Root length increased in all genotypes under drought stress (Ghatak et al. 2021). This increase in the root system has been reported by many authors (Kusaka et al. 2005a; Ghatak et al. 2016). It has been reported in cereals that a deep root system allows water uptake from deep layers of the soil in drought-stressed environments (Kondo et al. 2000; Kashiwagi et al. 2006; Manschadi et al. 2010; Wasson et al. 2012; Steele et al. 2013; Wasaya et al. 2018; Faye et al. 2019). In sorghum and pearl millet, there is a positive correlation between drought tolerance and root length (Matsuura et al. 1996), even though the roots of pearl millet were found to be longer than those of sorghum (Rostamza et al. 2013). In addition to length, root density can be a factor in drought tolerance. In a study on maize, Zhan et al. (2015) argue that reduced lateral root density improves drought tolerance. This reduction in density is associated with deeper rooting resulting in lower root length density for thick roots than for fine roots (Chopart et al. 2008b).

Therefore, fine root diameter, specific root length, specific root surface area, root angle, and root length density are considered useful traits for improving plant productivity under drought conditions (Wasaya et al. 2018). Increased root airspaces (aerenchyma) and root xylem diameter have also been linked with greater yield under drought conditions in maize (Chimungu et al. 2015) and the conservation of water resources to laid grain filling in wheat (Richards and Passioura 1989) respectively. Increased root growth can also be helpful for heat stress conditions. It allows plants to maintain their water potential despite significant transpiration. Under these conditions, plants develop strategies to restrict water loss. The reduction of transpiration in pearl millet under high vapor pressure deficit (VPD) was associated with aquaporins function (Reddy et al. 2017b). VPD-insensitive genotypes increased their transpiration rate, which may be since they used more symplastically mediated water transport (aquaporins) pathways than VPD-sensitive genotypes (Reddy et al. 2017b). Thus, water uptake in warmer soil appears to be positively correlated with aquaporin activity in wheat (Carvajal et al. 1996). In mature maize plants, increasing temperature slows lateral root growth to promote the development of long axial roots to reach water in deeper soil layers (Hund et al. 2008). Therefore, leaf and roots hydraulic conductance plays an important role in the response of plants to evaporative demand (Ocheltree et al. 2014).

Osmotic Adjustment

Osmotic adjustment is considered a major drought adaptation mechanism (Kusaka et al. 2005b; Izanloo et al. 2008; Sanders and Arndt 2012; Blum 2017). It allows the maintenance of water absorption and cell turgor pressure thanks to the accumulation of solutes. As a result, increasing the number of osmotically active substances in the cell leads to a more negative osmotic potential, which can improve the degree of cell hydration, maintaining turgor in leaf tissue and other metabolically active cells (Sanders and Arndt 2012). Osmotically active substances can be either organic

solutes (amino acids, glycerol, sugars, and other low molecular weight metabolites) or inorganic ions (Na^+, K^+, Ca^{2+}, and Cl^-). Several studies have reported the important role of these solutes in tolerance to abiotic stresses (Chaves and Oliveira 2004; Ashraf and Foolad 2007; Chen and Jiang 2010; Verslues and Sharma 2010). Depending on the adjustment capacity, the types of solutes accumulated, and their relative contribution to lowering osmotic potential, the osmotic adjustment may vary between species and genotypes (Chen and Jiang 2010).

Variation in the osmotic adjustment of cultivars in response to drought has been reported in many crop plants, including pearl millet. Local varieties from more arid areas exhibited a greater capacity for osmotic adjustment (Blum and Sullivan 1986). However, the latter depends not only on the stage of development of the plant (Chimenti et al. 2006) but also on the degree and duration of the water deficit (Shangguan et al. 1999; Kusaka et al. 2005a, b; Nio et al. 2011). Kusaka et al. (2005b) studied the contribution of several solutes to the osmotic adjustment of two pearl millet cultivars, one susceptible (IP8949) and the other tolerant (IP8210) to drought stress. They reported that, for both accessions, the stem exhibited higher osmotic adjustment than the younger and expanded leaves, while their decrease in relative water content was different. In addition, an increase in the concentration of organic components (sucrose, glucose, proline, and QAC) was noted in both accessions in response to drought stress. This has also been reported in durum wheat, where drought stress increased sugar and proline concentrations and decreased nitrate levels (Bajji et al. 2001). Sugars were the main solutes that contributed to osmotic adjustment, especially in growing leaves, followed by proline and quaternary ammonium compounds (Bajji et al. 2001). However, in pearl millet, accumulation of proline was greater (more than four times) in young leaves of the tolerant genotype than in the susceptible genotype (Kusaka et al. 2005b). This increase has also been reported in maize up to 10 days after stress application and declines when stress becomes severe (Anjum et al. 2011a). A strong accumulation of proline increases the cell solute concentration, resulting in increased water potential in the tissues and decreased cellular damage. As a result, it constitutes the first response of plants exposed to drought stress and contributes to the immediate recovery of plants after stress.

In addition to proline, glycine betaine, and soluble sugars contribute to osmotic adjustment and stress adaptation in pearl millet. However, the accumulation of organic components remained lower than that of K^+ and NO_3^- (Kusaka et al. 2005b). The concentration of K^+ increased both in the cell sap of the leaves and the stems of the two accessions at the onset of stress. The accumulation of K^+ in the cell sap reached a very high level and was relative to decreasing relative water content. This proves the role of inorganic compounds in contradiction to the conclusion of Bajji et al. (2001). Fischer et al. (2005a, b) found a positive correlation between osmotic adjustment and grain yield under moisture deficit. Likewise, in a critical review examining 26 published studies in which osmotic adjustment and yield were measured under drought stress in variable genotypes from 12 crops, Blum (2017) reported a positive and significant association between osmotic adjustment and performance in 24 published studies. In pearl millet, drought tolerance was more

correlated with osmotic adjustment capacity than total root length under severe drought stress (Kusaka et al. 2005a).

Like drought stress, heat stress also leads to changes in the accumulation of compatible osmolytes (Sakamoto and Murata 2002). The early synthesis of these osmolytes (proline, glycine betaine, or soluble sugars) compensates for the effect of the decrease in leaf water potential, which appears as an immediate response to heat. By maintaining the cell water balance and membrane stability and buffering the cellular redox potential, the accumulation of osmolytes regulates osmotic activities and protects cellular structures from high temperatures (Farooq et al. 2008). The role of glycine betaine in photosynthesis in plants under heat stress has been reported by Allakhverdiev et al. (2008). The activation of Rubisco is maintained by the production of glycine betaine in the chloroplasts by sequestering Rubisco activase near thylakoids and preventing its thermal inactivation (Allakhverdiev et al. 2008). However, there is a difference between species in their ability to synthesize glycine betaine under heat-stress conditions (Ashraf and Foolad 2007). In maize and sugarcane, a strong accumulation of glycine betaine has been reported in response to elevated temperatures (Quan et al. 2004; Wahid and Close 2007). At the same time, the increase in temperatures causes the accumulation of proline and soluble carbohydrates in wheat while the levels of valuable proteins are reduced (Qaseem et al. 2019). Thus, despite the lack of studies on pearl millet, work on other crops has shown the role of osmotic adjustment in tolerance to heat stress.

Transpiration Efficiency

In times of stress, plants need to develop mechanisms to conserve soil water or maximize their water use efficiency to alleviate the effect of stress. Several studies have been carried out in recent years to determine the water use efficiency of crops (Vadez et al. 2011, 2013a, 2014, 2021; Schittenhelm and Schroetter 2014; van Oosterom et al. 2021). Water use efficiency appears to be an important criterion for evaluating the water supply. It provides a simple and quick measure of how the available water can be converted into biomass and grain (Sekhon et al. 2010). Defined as the accumulation of biomass per unit of water transpired (Xin et al. 2009), transpiration efficiency can also be understood at the leaf level as the intrinsic water-use efficiency. It is the ratio of the instantaneous rates of CO_2 assimilation and transpiration at the level of the stomata (Condon et al. 2002). Thus, increased biomass or photosynthesis, decreased transpiration, or a combination of both can result in reduced water use reflecting higher water use efficiency of plants. However, Xin et al. (2009) reported that transpiration efficiency based on biomass production was strongly correlated with increased biomass accumulation rather than reduced water use.

In a recent study comparing the transpiration efficiency of C4 cereals, Vadez et al. (2021) found that transpiration efficiency in maize was higher than in millet and somewhat higher than in sorghum (Fig. 1.12). This difference between species could be explained by differences in the ability to restrict transpiration under high VPD (Vadez et al. 2014). Likewise, Choudhary et al. (2020) reported that maize conserves water by limiting transpiration during increased VPD and under higher soil moisture

than sorghum and pearl millet. In addition, the transpiration efficiency seems to depend on the type of soil. It was higher in high clay than in sandy soil under a high VPD (Vadez et al. 2021), while the differences in transpiration efficiency between maize and sorghum were not visible in Alfisol and sandy soil.

However, there is variation in transpiration efficiency within species that has been demonstrated for C4 plant species (Mortlock and Hammer 2000; Xin et al. 2009; Vadez et al. 2011, 2014, 2021). Transpiration efficiency was higher under stress conditions (Mortlock and Hammer 2000). Sorghum genotypes with low internal CO_2 concentration and improved photosynthetic capacity may be a factor explaining the high transpiration efficiency in some lines (Xin et al. 2009). Under water deficit conditions, water use efficiency was also increased in sweet sorghum, while for maize, it was reduced (Zegada-Lizarazu et al. 2012). Bhattarai et al. (2020) confirm this result by stating that the water use efficiency was highest for sorghum cultivars, followed by millet and maize. According to Blum (2005), water use efficiency is often associated with drought tolerance and improved crop yields under stress conditions. Thus, genotypes with higher water use efficiency have greater survivability.

However, water extraction also seems to play an important role during grain filling. Differences in yield under terminal drought in sorghum have been reported to be determined by TE, followed by water extraction (Vadez et al. 2013b). Although the amount of water extracted by tolerant and susceptible genotypes was similar under drought stress, tolerant genotypes extracted less water before anthesis and more water after anthesis. This explains the lower yield of sensitive genotypes than that of tolerant lines under drought stress (Vadez et al. 2013a). Thus, the early conservation of water during pre-anthesis increases the yield of pearl millet during terminal drought (Kholová and Vadez 2013; Kholová et al. 2010). The drought tolerance of pearl millet is explained by the higher water use efficiency. Therefore, improving transpiration efficiency can effectively increase pearl millet yield in arid and semi-arid regions.

10.3   Molecular Basis of Stress Tolerance

Pearl millet is an important model for studying the physiological and molecular mechanisms of drought tolerance. Yet, compared to other cereals, the molecular mechanisms of drought stress tolerance in pearl millet remain elusive. Recently, genome-wide association studies (GWAS) have detected some genes associated with the domestication and differentiation of local millet varieties that have adapted to climatic conditions. These genes are related to heading date and plant height (Lakis et al. 2012), flowering time, morphological character, and yield (Saïdou et al. 2009; Vigouroux et al. 2011; Clotault et al. 2012; Diack et al. 2020), fitness under irregular climatic conditions (Ousseini et al. 2017), biomass and stay green (Debieu et al. 2018). Molecular responses involve a set of genes and signal transduction pathways that are highly regulated. The tolerance mechanisms begin with the

detection of the stress, which causes a series of signal molecules transported in the leaves via the xylem.

Among the signals, abscisic acid (ABA) is a very important drought response pathway. It is a key root-to-shoot signal of drought stress (Xu et al. 2010) even though it is variable among species (Zhang et al. 2005; Jia and Zhang 2008). However, how the root cells detect the moisture state of the soil remains a mystery. Root tissues synthesize ABA upon detection of stress, which induces stomatal closure, thereby reducing transpiration and photosynthesis and allowing plant adaptation to drought conditions (De Ollas et al. 2013). ABA is also involved in regulating aquaporin activity, which contributes to the maintenance of the favorable water status of the plant (Parent et al. 2009; Reddy et al. 2017a). The ABA-dependent signaling response to stress involves different genes and transcription factors (Tuteja 2007). These genes and transcription factors are either involved in ABA biosynthesis or induced by the presence of ABA. For example, under drought conditions, strong expression of the 9-*cis*-epoxycarotenoid dioxygenase gene (NCED) is the first step in ABA biosynthesis (Qin and Zeevaart 1999; Behnam et al. 2013), provides evidence of ABA accumulation. In addition, several transcripts such as the WRKY transcription family (Jaiswal et al. 2018; Chanwala et al. 2020), PYL/PYR, PP2C SnRK2, ABRF DREB2A/2B, AREB1, RD22BP1, NAC, and MYC/MYB family (Tuteja 2007; Bhargava and Sawant 2013; Dudhate et al. 2018; Zhang et al. 2021) are known for their role in phytohormone signaling and response to abiotic stresses in plants. Furthermore, during drought stress, reactive oxygen species (ROS) accumulation increases considerably (Farooq et al. 2009; Alam et al. 2010). ROS form a natural by-product of normal oxygen metabolism and plays an important role in cell signaling. ROS include oxygen ions, free radicals, and peroxides, whose common characteristic is their ability to cause oxidative damage to proteins, DNA, and lipids (Apel and Hirt 2004). They target various organelles, including chloroplasts, mitochondria, and peroxisomes, resulting in premature leaf senescence or plant death (Ma et al. 2013). However, a versatile and cooperative antioxidant system tightly controls improved ROS production. It modulates the intracellular concentration of ROS and defines the redox status of the cell. Superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), ascorbate peroxidase (APX), and guaiacol peroxidase (GPOX) constitute the main mechanisms of entrapment (Cruz de Carvalho 2008, Takayuki et al. 2013). An increase in the levels of these antioxidant enzymes (AOX) has been noted in pearl millet in water-deficit stress conditions (Vijayalakshmi et al. 2012). On the other hand, prolonged drought stress leads to the ineffectiveness of the antioxidant system causing cell damage and death. Many genes conferring tolerance to drought stress have been identified in plants. These genes were presented in the study by Kumar et al. (2018) and classified into two groups (Bray 1997; Yamaguchi-Shinozaki and Shinozaki 2005; Kumar et al. 2018). The first group includes functional genes encoding proteins whose catalytic activities are responsible for the protection of cells and organs against stress, regulatory genes encoding proteins necessary for signal transduction and the regulation of expression of genes. The second group comprises several genes and transcription factors responsive to drought, such as the binding gene to elements

sensitive to dehydration, aquaporin, abundant proteins of late embryogenesis, and dehydrins (Farooq et al. 2009).

In pearl millet seeds, Ghatak et al. (2016) also identified heat shock proteins (HSP), molecular chaperones, storage proteins, and abundant late embryogenesis (LEA) with increased levels. These proteins help stabilize the folding and conformation of structural proteins and the functionality of enzymes (Wang et al. 2004), hence their protective function.

In recent years, proteomic studies have become increasingly important as proteins are the main drivers of all cellular events. At the proteomic level, several studies have been carried out to understand the effect of drought stress on cereals such as millet (Ghatak et al. 2016, 2021), maize (Riccardi et al. 2004), and wheat (Ford et al. 2011; Komatsu et al. 2014; Ghatak et al. 2021). In pearl millet, a shotgun proteomics approach was used to study protein signatures from different tissues under drought and control conditions (Ghatak et al. 2016). Proteins have been identified and quantified in the root, leaf, and seed tissues. However, there is a pronounced change in the proteome of stressed plants compared to control conditions. Putative drought-sensitive proteins have also been identified in the root (271 proteins), seed (159 proteins), and leaf (292 proteins). Leaf tissue showed the most significant changes, followed by roots and seeds.

A high temperature also triggers important molecular changes in plants. Many transcripts and proteins alter their expression and levels to prevent or reverse the effects of heat on proteins. Under stress, plants synthesize (induce) a set of heat shock proteins (HSPs), unlike in normal conditions where they are almost absent. Based on their molecular weight, HSPs are divided into different families with distinct functions. Numerous studies have shown the role of HSP families in thermotolerance (Gurley 2000; Queitsch et al. 2000; Sun et al. 2002; Hu et al. 2010; Reddy et al. 2010; Nitnavare et al. 2016). Heat stress transcription factors (Hsfs) are the main regulators of heat stress response gene expression (Baniwal et al. 2004; Kotak et al. 2007; Schramm et al. 2008). Since protein aggregation is irreversible, HSPs appear important in the thermo-tolerance reaction and act as molecular chaperones to prevent the denaturation or aggregation of target proteins and facilitate protein refolding (Ahuja et al. 2010; Scharf et al. 2012). In addition, they lead to an improvement in physiological parameters and membrane stability or hydration of cellular structures (Camejo et al. 2005; Ahn and Zimmerman 2006; Wahid and Close 2007). These improvements promote adequate plant growth and development under heat stress. Thus, it has been reported that the expression of genes inducing HSPs may be an important mechanism for increasing tolerance to heat stress (Wahid et al. 2007).

The plant cuticle is a protective layer made of lipids and waxes present on the surface of aerial organs. It forms a barrier against pathogen infection and limits water losses through transpiration. A similar hydrophobic barrier, the Casparian strip, is formed at the periphery of the endodermis's root vascular bundle and is thought to contribute to the limitation of water loss. Recent results suggest that these lipid-made barriers are important components of water potential and heat stress tolerance in pearl millet. Indeed, sequencing of the pearl millet genome revealed an expansion of

gene families involved in the biosynthesis and transport of cut-in, suberin, and wax components of the cuticle and Casparian strip (Varshney et al. 2017; Debieu et al. 2017). Moreover, an association genetics study for tolerance to water stress at the vegetative stage in pearl millet led to the identification of four genetic loci associated with increased biomass production under early drought stress. One of these associations contained a gene encoding an enzyme (3-ketoacyl-CoA synthase or KCS) catalyzes the elongation of C24 fatty acids during wax and suberin biosynthesis (Debieu et al. 2018). Altogether, this suggests that wax and fatty acids biosynthesis could be targeted to increase water and heat stress tolerance in dryland cereals.

10.4 Breeding Pearl Millet for Drought and Heat Tolerance

Current climate models' prediction showed that more inter- and intra-annual variability in rainfall and temperature are expected in sub-Saharan Africa (Brown and Lall 2006; Sultan and Gaetani 2016). This situation will increasingly threaten pearl millet production in this part of the world, where this cereal is one of the most important sources of nutrition for more than 90 million people (Anuradha et al. 2017). Therefore, breeders should develop efficient breeding strategies to accelerate the development of improved varieties with better tolerance to drought and heat stresses. During the last decades, several attempts to improve phenotypic screening methods, study the genetic variation in breeding lines, and develop high-yielding and tolerant pearl millet varieties to heat and drought stress using conventional and molecular breeding methods have been accomplished.

Drought is considered the primary abiotic constraint for pearl millet production and is caused by the low and erratic rainfall distribution. In breeding, progress has been made in the development of screening techniques, identification of sources of tolerance, development of early maturing varieties, and identification of QTL linked to drought tolerance (Yadav et al. 2017). Screening of 21 genotypes for osmotic stress tolerance (as a proxy for drought) using PEG 6000 revealed three genotypes (TNBH 0538, TNBH 0642, and ICVM 221) tolerant to moisture stress at germination and early growth stages (Govindaraj et al. 2010). However, pearl millet grain yield is more affected by post-flowering and terminal drought stresses (Kholová and Vadez 2013). To overcome these stresses, drought escape mechanisms have been successfully exploited by targeting early maturity (Yadav and Rai 2013). It has been demonstrated that early flowering pearl millet genotypes with low biomass, few basal tillers and high harvest index can tolerate terminal drought stress (Bidinger et al. 2005). Across West African countries, several landraces characterized by earliness, high grain yield, bold grain, and compact and conical panicles have contributed to the development of pearl millet cultivars adapted to drought-prone areas, including ICTP-8203 and GB-8735 (Wilson et al. 2008). These varieties flower within 40–45 days and mature within less than 75 days, making them suitable cultivars for arid zones. Interestingly, recurrent drought in the 1980s led to selection by farmers in Niger for earlier flowering pearl millet varieties (Vigouroux et al. 2011).

Another important research strategy was using molecular markers to identify genomic regions associated with drought tolerance in pearl millet. Several major QTLs with significant effects on pearl millet grain in terminal drought stress environments were identified and successfully used in marker-assisted selection to improve drought-sensitive pearl millet lines (Yadav et al. 2002, 2004; Serraj et al. 2005; Bidinger et al. 2005). Similarly, potential QTLs for tolerance to water stress during the vegetative phase were identified (Debieu et al. 2018).

For heat tolerance, a good amount of work has been accomplished in breeding. Both field and greenhouse heat tolerance screening techniques have been developed and improved at ICRISAT for pearl millet (Gupta et al. 2015). These techniques were widely used in assessing the effect of heat on a large number of hybrid parental lines, germplasm accessions, and improved varieties across several field locations in India for four consecutive years. The field screenings led to the identification of five hybrid parental lines and a germplasm accession as new sources of resistance to heat tolerance that has been used to develop a high-yielding and heat-tolerant composite variety (Gupta et al. 2016).

10.5   Conclusion

Climate change in arid and semi-arid areas is led by heat and drought, often intermittent or terminal. Drought is due to soil water and vapor pressure deficits. The climate models predicted an increase in climate change effects in the near or long term. Heat and drought are distinctive stresses but often occur simultaneously on crops. They are studied separately or jointly to understand their effects on the plant better. Dry spells and heat stress are the factors constituting major agronomic problems that cause severe yield losses for pearl millet in arid and semi-arid areas. Their effects on pearl millet depend on intensity, phase of occurrence, and duration. However, the flowering period is more vulnerable for pearl millet. Drought and heat affect aerial and root development and physiological and molecular performance. This results in a proportional decrease in pearl millet yield.

In general, drought survival mechanisms of plants are similar to those used to cope with heat stress. Escape, avoidance and tolerance mechanisms have long been considered important strategies for drought adaptation. Due to its drought and heat tolerance, pearl millet is an ideal model for studying the heat and drought resistance mechanism of cereal crops. The avoidance mechanism is commonly used by pearl millet. It responds to water deficit with leaf rolling, senescence, and stomatal conductance, leading to reduced water loss when water soil stock becomes limiting. Also, transpiration restriction under high vapor pressure deficit reducing the transpiration of pearl millet is beneficial for crop yield under terminal drought. Increasing water uptake by root morphological and functional modifications reinforces pearl millet avoidance of heat and drought. Few studies on pearl millet mention osmotic adjustment, the leading mechanism of heat and drought tolerance. These tolerance mechanisms led to changes in the accumulation of compatible osmolytes. The water use efficiency also explains the drought tolerance of pearl millet.

The molecular mechanisms of drought stress tolerance in pearl millet remain elusive. However, gene discovery is ongoing with the detection of genes associated with domestication, genes conferring tolerance to drought stress like gene families involved in the biosynthesis and transport of antioxidant and constitutive molecules. The role of these genes has to be precise and validated to be useful for pearl millet improvement. Progress in pearl millet breeding is based essentially on drought escape mechanisms, with the development of early flowering and maturing varieties. However, molecular breeding started to use QTLs to improve terminal drought-sensitive pearl millet. Heat-tolerant varietal sources are also identified and used in pearl millet improvement.

Progress is made in understanding the molecular bases of pearl millet adaptation to drought and heat. However, pearl millet in research is still far from other major cereals and remains a neglected crop. So, it is urgent to address drought and heat adaptation mechanisms to breed pearl millet varieties for the benefit of the dry-land farmers.

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