REVIEW

Improved drought tolerance in wheat is required to unlock the production potential of the Brazilian Cerrado

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Abstract: *Improving rainfed wheat cultivation in central Brazil, where the Cerrado biome (Brazilian savanna) is predominant, remains a bottleneck for future increases in domestic wheat production. In the Cerrado, the limited water availability during the wheat-growing season is an obstacle to increase wheat yield. To address this issue, the physiological and molecular drought response of wheat and the environmental conditions of this region must be better understood. In this review, we characterized the impact of drought on rainfed wheat production in the Cerrado. Based on the peculiarities of this environment, we suggest that certain traits should be prioritized in selection. These traits and their molecular basis are important to raise wheat yields in the Cerrado and also to improve food security in Brazil, one of the top wheat-importing countries in the world.*

Keywords: *Triticum aestivum L., tropical wheat, water stress, water deficit.*

INTRODUCTION

The potential area for wheat production in Brazil is estimated at 7.27 million hectares (Mha), including temperate, subtropical and tropical zones (Mingoti et al. 2014). Due to the different climatological/geographical properties throughout this enormous area, four homogeneous regions of adaptation of wheat cultivars (here designated as wheat cultivation regions) were outlined (Figure 1) based on the level of precipitation, temperature and altitude (Scheeren et al. 2008). The three southernmost states in Brazil (Rio Grande do Sul, Santa Catarina and Paraná), which account for more than 90% of the domestic wheat production, belong mostly to region 1 (humid and cold) and region 2 (humid and moderately cold).

In the other two cultivation regions, where the Cerrado biome is predominant, the climate conditions are hot and moderately dry (region 3) or hot and dry (region 4). In these regions, wheat can be cultivated under irrigated or rainfed conditions. However, irrigated cultivation inflates the production costs, mainly because of the increased energy expenditure, and may be affected by environmental restrictions, in particular with regard to water availability and use. Therefore, rainfed wheat cultivation is considered the most environmentally friendly way to significantly increase grain production in the Cerrado. Abiotic factors that restrict wheat production in this region are soil acidity (aluminium toxicity), heat and irregular rainfall distribution, with a drought period after the

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flowering stage (Scheeren et al. 2008). Other authors reported that water stress (dry spells) can also be deleterious in the early stages (until tillering) (Ribeiro Junior et al. 2006). Independent of the developmental stage, drought is one of the stresses most detrimental to crop productivity.

In this context, this review pointed out the importance of drought for rainfed wheat production in Brazil by describing the characteristics of the Cerrado, which is the best-represented biome in wheat cultivation region 4. We highlighted the wheat traits and their molecular basis that should be pursued by breeders to increase rainfed wheat productivity in the Cerrado.

WHY SHOULD WHEAT PRODUCTION IN THE CERRADO BE INCREASED?

Brazil is a major producer and exporter of soybean, poultry, sugar, cellulose, coffee, corn, beef, tobacco, cotton, pork, orange juice and ethanol. On the other hand, Brazil is the one of the largest wheat importers in the world. To compensate for the deficit in internal production, ~6 million tons (Mt) of wheat grain have been imported yearly, which has a significant impact on the trade balance. This impact can be reduced by increasing the area and productivity of wheat cultivation in the four cultivation regions. In central Brazil, an area of ~4 Mha has been estimated as potentially appropriate for wheat in cultivation region 4 (Mingoti et al. 2014), of which 2.7 Mha were classified as adequate for rainfed wheat (Pasinato et al. 2018). However, even when both irrigated and rainfed cultivation are considered, the area in region 4 destined for wheat is only ~120 thousand hectares (CONAB 2017). Based on mean yields of 1.3 to 2.4 tons per hectare for rainfed wheat in region 4 (Scheeren et al. 2008, Condé et al. 2013), an increase in area and productivity of this crop in this region would have a significant effect on reducing the gap between domestic wheat production (~5.5 Mt) and consumption (~10.5 Mt) in Brazil.

A reduction in the heavy dependence on wheat imports is also a major issue of food security in Brazil. Although the rate of Brazilian wheat production is projected to increase (~2.5% per year) more than the consumption (~1.1% per year) until 2026/2027, imports (6.1 Mt) will still be needed to meet nearly half of the estimated demand (12.3 Mt) (MAPA 2017). Projections until 2050 are even worse, showing import needs of around 60% (10.5 Mt) of the Brazilian domestic consumption (17.8 Mt) (Weigand 2011). In this context, the future scenario of global wheat production should also be taken into consideration. Based on the current increase in global mean wheat yield (0.9% per year), the wheat production will have increased only ~38% by 2050, i.e., far below the 60-110% increase in global agricultural production needed to meet the future demands (Ray et al. 2013). Thus, increments in wheat production in the Cerrado will help to protect Brazil from a future scenario in which wheat grain supply might decline.

Other reasons why wheat production in the Cerrado should be increased are: high quality grain (harvest occurs in periods with lower chances of precipitation), grain harvest when supply is low (wheat grain is produced prior to the harvest in the south - main producing region), lower logistics demand/transport costs (important flour mills and consumer markets are not located in the south), improvement in soil quality, reduction in diseases and weeds (wheat is a good option for crop rotation and succession - after summer crops) and improvement in sustainability (wheat biomass - mulch - improves soil fertility and water retention) (Só e Silva et al. 2001, Ribeiro Junior et al. 2006, Pires et al. 2011, Condé et al. 2013).

THE CERRADO

The Cerrado, usually described as Brazilian savanna, is the second largest biome in Brazil. It covers an area of ~204 Mha, at altitudes from sea level to 1,800 m asl, spreading over 22° latitude and across 10 Brazilian states and the Federal District (Sano et al. 2010). It has been proposed that the Brazilian Cerrado should be considered a complex of different biomes. Here, we used the term "Cerrado" (capital first letter) to indicate the entire area that is composed of the different vegetation types (Batalha 2011). The Cerrado is mostly dominated by tropical climate with clearly differentiated wet and dry seasons and average annual temperatures ranging from 18-22 °C to 23-27 °C in the center-south and north of the region, respectively (Silva et al. 2008). Most soils are acidic Oxisols, Ultisols and Entisols, with high aluminum (Al) saturation and phosphorus fixation capacity, but low nutrient availability and water-holding capacity (Lopes 1996).

While more than 50% of the soybean, cotton, beef, and maize and a significant part of coffee and Eucalyptus production of Brazil come from the Cerrado, only ~5% of the wheat is harvested in this biome. Most wheat grain in the Cerrado is produced under irrigation (Mega-Environment 1, according to the Wheat Breeding Mega-Environments defined by CIMMYT) where averages can reach more than 4 tons per hectare. However, rainfed wheat cultivation in this region has a higher potential to increase wheat production in comparison to the irrigated cultivation. Rainfed cultivation is indicated for areas above 800 m asl, where average temperatures rarely exceed 25 °C during crop development. In the Cerrado, rainfed wheat (Mega-Environment 4) is sown in February/March and usually precipitation decreases significantly until the end of the cropping season (Figure 1). Due to the irregular rainfall distribution, which results in a high coefficient of variation, the average rainfall is not a reliable index to precisely estimate the water availability (Assad et al. 1993, Silva et al. 2008). Nevertheless, the annual rainfall in the Cerrado can vary from 464 to 2,234 mm, but is usually between 1,000-1,100 and 1,400-1,600 mm (Lopes 1996, Buol 2009), with an average of ~1,500 mm (Assad et al. 1993). It is estimated that 80-90% of the annual expected rainfall is concentrated in the rainy season (Assad et al. 1993), although dry spells from one to three weeks can occur during this period (Lopes 1996). A precipitation of ~550 mm is expected from sowing (February) to harvest (June/July) but during the major part of the wheat growing season (March - June), long-term data of ~30 years recorded an average of less than 400 mm (Silva et al. 2008, Marcuzzo et al. 2012). This precipitation (<400 mm) is near the lower limit of wheat water requirements of 450-650 mm for higher yields, depending on the climate and duration of the growth period (Doorenbos and Kassan 1979). Shifting the wheat sowing date to a period with higher water availability is not recommended since this change would increase the risk of losses in grain yield/quality, result in competition with summer crops, require a higher heat tolerance and increase the chances of wheat blast occurrence (disease discussed below).

TRAITS AND THEIR MOLECULAR BASIS POTENTIALLY ASSOCIATED WITH DROUGHT TOLERANCE IN WHEAT GROWN IN THE CERRADO

There are reviews focusing on drought tolerance traits in wheat and the underlying molecular mechanisms (for example, Budak et al. 2015, Sheoran et al. 2016, Mohammadi 2018). Here, we do not intend to be repetitive and to exhaustively review these traits and their molecular basis. Rather, we will point out that, among the nearly 50 traits

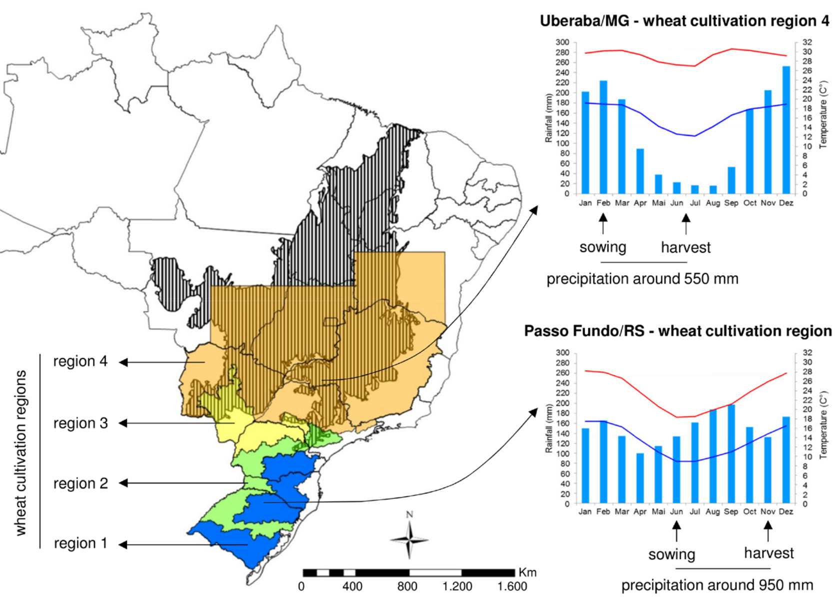

Figure 1. The Cerrado and the four homogeneous regions of adaptation of wheat cultivars (here named as wheat cultivation regions) in Brazil. In the map, the cultivation regions are indicated by different colors and the Cerrado by parallel vertical lines. The graphs show the different climatological properties of two representative cities in regions 1 (Passo Fundo/RS) and 4 (Uberaba/MG). The mean precipitation is represented by blue bars while average maximum and minimum temperatures are indicated by red and blue lines, respectively. The sowing and harvest dates of rainfed wheat, which depend on the cultivar and weather conditions, are indicated by arrows.

associated with drought tolerance in wheat (Mohammadi 2018), breeders can target a shorter list of only the main traits to increase wheat yield in the Cerrado.

The parameters used here to choose core traits related to drought tolerance as primary targets of selection for increased wheat productivity in the Cerrado were based on the components detailed by Passioura (1977). According to this author, under limited water availability, grain yield is determined by the transpired water (water uptake), transpiration efficiency (water use efficiency) and harvest index. A low number of traits was addressed in order to avoid an inefficient use of resources and labor and eliminate controversial and probably irrelevant traits for wheat cultivation in the Cerrado. For instance, a rapid initial growth (early ground cover) is important to minimize water evaporation from the soil surface (Richards et al. 2010, Bellundagi et al. 2013) but it could also increase water use before flowering, which could reduce the water available for grain filling (Richards et al. 2010). As wheat in Brazil is normally grown in no-tillage systems, the crop residues left on the soil surface can contribute to minimize water evaporation. Additionally, although water-soluble carbohydrate (WSC) accumulation and distribution have been reported as important for wheat production under drought, a recent report has shown that WSC concentration and total WSC per area in wheat are strongly affected by genotype × environment interactions and weakly correlated with yield (Ovenden et al. 2017). Based on these studies, neither early ground cover nor WSC accumulation were considered here.

To improve wheat drought tolerance, not only the related traits and their molecular basis should be taken into account. The timing and severity of drought and interactions with the peculiarities of an environment need to be carefully evaluated because, in a particular region, some traits can be more relevant than others. For instance, when 25 elite wheat genotypes were characterized at the experimental station of CIMMYT, the traits associated most closely with drought were canopy temperature and carbon isotope discrimination, related to water uptake and transpiration efficiency, respectively (Reynolds et al. 2007). On the other hand, in experiments under rainfed conditions in India, a positive correlation of grain yield with early ground cover, flag leaf area, relative water content and canopy temperature was observed (Bellundagi et al. 2013). For wheat grown in the Brazilian Cerrado, scientific evidence for the relevance of these traits is rare. Clearly, yield and its components are key traits and deserve careful attention. However, based on the characteristics of the Cerrado, some morpho-physiological traits and their molecular basis, aside from yield components, are promising selection targets with a view to increasing wheat yields. These traits are:

1) Traits associated with water uptake: During first attempts of wheat cultivation in the Cerrado, it was commonly observed that superficial rooting led to water stress during the growth period (Buol 2009). Thus, deeper and more vigorous roots are desirable. Even relatively small amounts of subsoil water can be relevant to stabilize grain yield. For instance, under moderate post-anthesis stress, 10.5 mm of additional subsoil water increased grain yield with an efficiency of 59 kg/ha.mm (Kirkegaard et al. 2007). Increased root vigor around flowering and grain filling that promote higher water uptake can significantly increase grain yield (Passioura 2006) and an intensified investment in deeper-reaching fine roots, with reduced root proliferation in the surface layers, will enable the plant to access to extra resources, resulting in higher yields (King et al. 2003). The root depth can be estimated by measuring the canopy-air temperature difference and several chromosome regions in wheat have significant effects on canopy temperature (Sheoran et al. 2016). In this case, genotypes with a lower canopy temperature are associated with deeper root depth or intensity, enabling access to greater amounts of water (Reynolds et al. 2007). As soils in the Cerrado have acidic subsoils (Lopes 1996), Al-tolerant wheat genotypes could contribute to deeper root growth. In fact, superior alleles of the two most important genes for Al tolerance in wheat (*TaALMT1* and *TaMATE1B*) are found in wheat cultivars recommended for rainfed cropping in the Cerrado (Pereira et al. 2015, Aguilera et al. 2016). These alleles are associated with wheat performance in acid field soils (Aguilera et al. 2016) and the performance in the field is highly correlated with the initial root growth (Pereira 2018). Tracking these alleles during breeding will be an interesting target to eventually improve drought tolerance in central Brazil. Undoubtedly, management practices (lime/gypsum application) also need to be performed to improve root growth in acidic sub-soils, reduce nutritional deficiencies (for instance, calcium deficiency) and ensure higher yields. Osmoregulation (osmotic adjustment) is also a plant mechanism with the function of maintaining water uptake and cell turgor pressure. In a Brazilian wheat cultivar recommended for cultivation in the Cerrado region, starch and sucrose metabolism, associated with osmoregulation, have been named among the most important drought-induced pathways that leaves and roots have in common (Poersch-Bortolon et al. 2016). However, in a large variety of Brazilian wheat cultivars osmoregulation has not been described so far. Another method to evaluate cell turgor and water status in wheat genotypes is the leaf relative water content (RWC), which is correlated with the photosynthetic rate (Siddique et al. 2000).

2) Traits associated with water-use efficiency: Water use efficiency reflects the relationship between photosynthesis and transpiration and is an important indicator of the amount of carbon fixed per unit of water use (biomass/water transpired). In this case, wheat genotypes that reduce water loss through efficient transpiration should be identified and selected. Transpiration efficiency is directly (negatively) associated with carbon isotope discrimination (Δ) and low Δ is being used to select for high wheat yield under rainfed conditions (Condon et al. 2002, 2004). Measurements of Δ are highly reproducible and little affected by genotype × environment interactions (see review in Richards et al. 2010). However, other methods such as canopy temperature depression and near-infrared reflectance may be alternatives to reduce the costs associated with Δ measurements (Richards et al. 2010). Theoretically, wheat genotypes with low Δ could potentially cope better with the environmental conditions of the Cerrado. Water use efficiency is also associated with cuticular wax (waxiness), since the accumulated wax is assumed to contribute to the maintenance of a relatively high water potential by reducing leaf transpiration (Guo et al. 2016). Under water-limited conditions, wax is correlated with water-use efficiency and yield in wheat (see review in Xue et al. 2017). Some QTLs and genes are associated with Δ and cuticular wax (Xue et al 2006, Diab et al. 2008, Rebetzke et al. 2008, Wu et al. 2011, Aprile et al. 2013, Wang et al. 2016). In some cases, QTLs for Δ are associated with variation in heading date (negative correlation) and/or plant height (positive correlation) (Rebetzke et al. 2008). In fact, dwarfing alleles have been shown to reduce Δ in wheat (Richards 1992). Thus, it is essential to know the dwarfing alleles in wheat to breed varieties for the Cerrado.

3) Traits associated with harvest index: Harvest index is an important factor of grain yield. It has been reported that, in areas of the Mediterranean region where wheat plants are exposed to water-shortage in the terminal stage of their development, the heading time of the cultivars was a key component of the harvest index (Kobata et al. 2018). In this way, early flowering can be considered a mechanism of drought avoidance and yield increase in the Cerrado, since plants would be less affected by terminal drought. Among the four cultivars (BR18-Terena, BRS404, MGS1-Aliança and MGS3-Brilhante) exclusively indicated for rainfed cropping in the Brazilian wheat cultivation region 4 (excluding the states of Mato Grosso do Sul and São Paulo), only one (BRS404) has a medium developmental cycle and all others have short cycles (Comissão Brasileira de Pesquisa de Trigo e Triticale 2017). Clearly, as some genomic regions for water-use efficiency (measured by Δ) can be negatively correlated with heading date, any cultivar with very short developmental cycle needs to be properly evaluated to check if the impact on water-use efficiency and yield is as low as possible.

For most of the above morpho-physiological traits, QTL, genes and molecular markers have been reported to underlie these phenotypes. However, this molecular information may vary for each environment and needs to be carefully evaluated. High-throughput sequencing and genotyping, which have become more accurate and affordable in the last years, can improve the analyses of these QTL and markers and also make headway in understanding drought response in wheat. For instance, these high-throughput platforms have increased the number of association mapping studies in wheat, which have revealed markers associated with drought-related traits or yield components under rainfed conditions or different water regimes (Maccaferri et al. 2011, Mora et al. 2015). Markers are also important for genomic selection, a promising approach to increase genetic gains (Bhat et al. 2016). However, the gains obtained so far in terms of raising wheat yields in the Cerrado were still mostly accomplishments of conventional breeding. The reasons are probably related to the fact that breeders need convincing evidences that a specific trait has value for plant performance under field conditions (Rebetzke et al. 2013). It has been shown that molecular markers associated with drought-related traits are not commonly used in wheat breeding programs (Gupta et al. 2010). Clearly, with the progress of the knowledge related to the molecular plant response to drought, more tools can be developed and used in breeding programs. One of these tools is developing genetically modified or genome edited plants. Transgenic wheat plants with better drought tolerance were bred by the overexpression of different genes, most commonly transcription factors, although osmoprotectant genes and LEA proteins were also evaluated (see review in Budak et al. 2015). The phenotypes of transgenic wheat plants were analyzed by different methods, most commonly under greenhouse conditions, after withholding water supply for a different number of days. The preferred method to demonstrate the difference in performance is to compare transgenic lines with the conventional genotypes used for transformation, whereas comparisons with conventional drought-resistant genotypes are rare. When evaluating these transgenic lines, proper diagnostic methods must be used to assess the benefits since important components such as wheat biomass and leaf development in the early growth stages appear to be weakly correlated with final biomass and grain yield (Kovalchuk et al. 2017). Only few studies have analyzed genetically modified wheat plants under both controlled and field conditions. In those cases, improved phenotypes of transgenic plants with good performance under greenhouse conditions (Sivamani et al. 2000, Pellegrineschi et al. 2004) were not clearly and stably maintained in the field (Bahieldin et al. 2005, Saint Pierre et al. 2012). Theoretically, the use of genes not necessarily directly associated with plant drought response can also increase the plant ability to maintain growth during periods of short water supply. For instance, the transgenic wheat lines over-expressing *TaALMT1*, the major gene controlling Al-tolerance in wheat, have longer roots in acidic nutrient solution and soil (Pereira et al. 2010). Although these Al-tolerant transgenic lines have not been evaluated in the field, they might have a larger root system when grown in the Cerrado, indicating a putative better performance under drought.

FORESEEABLE FUTURE: CLIMATE CHANGE AND OTHER STRESSES

Significant impacts of climate change on agriculture have been predicted by different models since, in a number of regions, water stress will most likely increase. In Brazil, changes in precipitation profiles are uncertain and studies show different trends for some regions, although increased rain in the south and reduced precipitation and increasing frequency/intensity of consecutive dry days in the eastern Amazon and Northeast seem to be reliable forecasts (Marengo 2014). Additionally, temperature is very likely to rise throughout South America, with the highest warming projected for the southern Amazon (Marengo 2014). However, climate change scenarios usually do not only predict a likely change in rainfall and temperature rises, but also an elevated CO_2 level. When a combined effect of elevated CO_2 and small temperature increases (2 °C) is evaluated, total biomass and grain yield in wheat could actually improve, regardless of whether the crop is irrigated or affected by drought in the final stages of the development (Oliveira et al. 2013). However, temperature increases of 4 °C and 6 °C above the ambient temperature would not improve but rather tend to decrease wheat biomass and grain yield, indicating no advantage of the CO_2 fertilization effect under these conditions (Oliveira et al. 2013). For Brazil, an analysis of different climate change scenarios indicated that temperature increases of > 3 °C would reverse the positive effects of increased CO_2 levels on wheat yield (Streck and Alberto 2006). Clearly, the future scenario is concerning and efforts to develop cultivars with better climate adaption and the implementation of improved management practices are required.

Aside from drought, two other abiotic stresses (soil acidity/Al toxicity and heat) and one biotic stress (wheat blast) must also be addressed in order to increase wheat production in the Brazilian Cerrado. As discussed earlier in this review, the combination of lime/gypsum application and use of Al-tolerant germplasm must be considered to achieve higher crop yields in central Brazil. The other important abiotic stress, heat, can cause irreversible damage to the crop, affecting plant growth and yield. One of the most common heat-related problems in crops is the reduced fertility caused by high temperatures during meiosis and fertilization (see review in Driedonks et al. 2016). In the Cerrado, average maximum temperatures during the wheat cultivation season can reach 25-29 °C. The response to heat stress of the wheat cultivars recommended for the Brazilian Cerrado is varied (Souza and Pimentel 2013), however, the mechanisms underlying this response have not been studied. Lastly, an important biotic stress, wheat blast, caused by *Magnaporthe oryzae* (*Triticum* haplotype), threatens wheat production in the Cerrado. So far, no resistant wheat genotypes have been detected, not even of synthetic wheat (Cruz et al. 2009). In this context, when breeding for higher wheat yields in the Cerrado, drought tolerance has to be considered along with a better performance against the said other stresses.

FINAL CONSIDERATIONS

The world population is predicted to reach nearly 10 billion by 2050 and, in most countries, life expectancy is expected to increase (United Nations 2015). This larger and wealthier world population will need more food. However, high wheat import levels will still be necessary in Brazil by 2050 (Weigand 2011). In this context, increases in wheat production in Brazil are imperative. In the Cerrado, a drought-prone environment that represents most of the wheat cultivation region 4, overcoming the difficulties of rainfed cultivation under the regional conditions is considered to be the next frontier to increase domestic wheat production. In wheat breeding, Brazilian researchers should focus on the key drought-related traits discussed in this review that may contribute to higher yields in the wheat cultivation region 4. Undoubtedly, a better understanding of the physiology of wheat adapted to the Cerrado can provide new and other targets for breeders than those listed here. However, so far, little is known about the phenotypic variability of the drought tolerant traits in Brazilian wheat. In the analysis of drought-related traits in wheat, whether based on molecular or physiological studies, the specific environmental characteristics of the Cerrado have to be taken into consideration. Ideally, research in multi-environmental trials, representing the environmental conditions of the Cerrado, should be undertaken to test the adaptability of wheat lines, whether having been introduced from other countries or bred in Brazilian institutions. The key drought-related traits need to be accurately measured and exploited in breeding. To the extent that this type of information is incorporated into breeding programs, the development of wheat cultivars adapted to rainfed cropping in the Cerrado can be accelerated.

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