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Water deficit in the soybean breeding

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ABSTRACT

The climate unpredictability causes long periods of drought, becoming the main risk factor in soybeans production fields and consequent losses to farmers in Brazil and worldwide. As sessile organisms, plants are constantly challenged by a wide range of environmental stresses, including drought. Growth constraints and stress due to these environmental changes result in reduced yield and significant harvesting losses. The response to abiotic stresses is a very complex phenomenon, since several stages of plant development can be affected by a particular stress and often several stresses affect the plant simultaneously. In order to mitigate the damages caused by the climate, new soybean cultivars adapted to the drought and the diversified climate are necessary, as well as technological advances in the production of soybeans that must advance with the increase of cultivated area. Therefore, the mechanisms underlying tolerance and adaptation to stress have been the focus of intensive research. In this sense, the objective of this review is to provide an overview of the evolution of genetic improvement regarding the search for more drought-tolerant cultivars, as well as to verify which strategies are used in the genetic improvement of soybean in the search of these genotypes.

Keywords: Drought tolerance, genetic breeding, nutritional value, soybean sensitivity, physical and physiological quality, food security.

INTRODUCTION

The soybean (*Glycine max* L. Merrill) is widely inserted in the world economy as one of the main agricultural products. It is considered a key crop for the food safety because it is a source of protein and oil for human and animal consumption, effectively participates in the agro-industrial complex and due to its range of uses, accounting for 56% of total oilseed production in the world ((Food and Agriculture Organization of the United Nations [FAO], 2017); Morando et al., 2014; Bubans et al., 2021; Carvalho et al., 2021; Soares, Sediyama, & Matsuo, 2020). The subtropical region of South America that includes Brazil, Argentina and Paraguay has the largest area sowed with oilseed in the world, with more than 50 million hectares grown every year (FAO, 2017).

Among the economic activities that are worth mentioning for its significant growth in recent decades, is soybean production. This was due to several factors, such as the development of a solid international market interrelated with the trade in soybean agro-industrial products, consolidation of it as an important source of vegetable protein, especially in concern to the growing demands from the sectors involved in the manufacture of animal products. Also, the arrival of technologies that enabled the expansion of new frontiers in diverse regions of the world that were not previously exploited.

The exponential growth in food demand has made it possible for Brazil to enter in the competition for commodity exports and, due to its high nutritional value, is expected to increase about 25% by 2026 (Foyer et al., 2016; O‟Donoghue, Hansen, & Stallings, 2017). However, Brazilian agriculture began to act in a relevant way in the global supplying matter, by evolving with the use of technologies and expansion of farming fields, allowing soybean to scale, placing the country at the level of agricultural potency. As a result, agribusiness became the main economic activity in Brazil, with soybean being its main product, reaching second place in the ranking of the largest producers and first in terms of exports (Rio, Sentelhas, Farias, B., Sibaldelli, & Ferreira, 2016; Battisti et al., 2017).

But all this success is not higher, only due to large variations of climate conditions that have occurred during the growing season, where the soybeans had to face yearly any other abiotic stress affecting their growth in the field, being the lack of water or drought the main adverse factor faced by the crop (Fita, Rodríguez-Burruezo, Boscaiu, Prohens, & Vicente, 2015). Considering the last six crop seasons in Brazil, practically all producing States had a decrease in production of more than 10%, caused mainly by long and severe drought periods during the crop cycle (Hirakuri, 2016).

Extreme climatic phenomenon that can be intensified with global climate change are a recent threat to Brazilian agriculture. In this scenario, drought events may occur more frequently and intensely, which directly impacts grain production, such as soybean (Iizumi & Ramankutty, 2015; Lesk, Rowhani, & Ramankutty, 2016).

Drought or water deficit affects the soybean production regardless of the development stage of the plant, even though the soybean sensitivity is higher in the reproductive phase, the occurrence of water deficit in the vegetative stages can reduce the yield of grains by up to 40%, and in the case of seed production it can reduce its physical and physiological quality (Thao & Tran, 2012; Krishnan, Singh, Verma, Joshi, & Singh, 2014).

In view of this scenario, countries that largely produce grains, such as Brazil, will have to privilege, besides the profitability, the use of cultivars that are more tolerant to abiotic stresses to guarantee the expansion of crop productivity and contribute to food security. Thus, the search for soybean genotypes more drought tolerant has relevant economic, environmental and social importance.

Therefore, the objective of this review is to provide an overview of the evolution of genetic improvement regarding the search for more drought tolerant cultivars, as well verify which strategies are being used in the genetic improvement of soybean in this search.

CHARACTERIZATION OF SPECIES

The soybean has its origin in China. It was lowland and cultivated on the banks of the rivers, being domesticated and probably introduced in the period from 1500 to 1027 BC. About 3000 years later, it spread to Asia, where it began to be used as food (Lee, Crawford, Liu, Sasaki, & Chen, 2011). Commercially, it was only in the twentieth century that it was grown in the United States. With the development of the first commercial cultivated varieties, there was a high increase in the production, becoming the most important oilseed crop in the world nowadays (Santos-Neto, Lucas, Fraga, Oliveira, & Pedroso-Neto, 2013). In Brazil, the first record of soybean cultivation occurred in 1914 in the municipality of Santa Rosa-RS. However, it was from the 1960s that soybean established itself as an economically fundamental crop for the country, mainly in the states of Rio Grande do Sul, Santa Catarina, Paraná and São Paulo, driven by the wheat subsidy policy aimed at self-sufficiency. From there, large areas began to be grown, bringing the country to the second place on the soybean production globally (Hiromoto & Vello, 1986; Companhia Nacional de Abastecimento [CONAB], 2018).

The soybean, species *Glycine max* (L.) Merrill, is self-pollinated plant belonging to Leguminosae family and the Fabaceae subfamily, being a plant Diploid (2n = 40 chromosomes). It is considered one of the most important legumes, due to its composition, 20% oil, 38% protein, 34% carbohydrates, as well as fibers and inorganic constituents (Sediyama, Teixeira, & Reis, 2005; (Empresa Brasileira de Pesquisa Agropecuária [Embrapa], 2011)). It is also considered an important raw material for the production of biodiesel (Oliveira & Coelho, 2016). It is a herbaceous plant with an erect stem and annual production, its height can vary from 80 to 150 centimeters, the legumes measure from 2 to 7 cm and they lodge from 1 to 5 seeds. The growing season is quite diverse, and in Brazil cycles ranging from 100 to 160 days being ranked according to the relative maturity group (RMG) and different types of growth: indeterminate, semi-determined and determined. Brazilian soybean varieties are well adapted to temperatures between 20°C and 30°C; the ideal temperature for its growth and development is around 25°C. The vegetative growth of soybeans is short or null at temperatures less than or equal to 10°C. Temperatures above 40°C have an adverse effect on the growth rate, leading to disturbances in flowering and decreased retention capacity of vegetables. These problems are accentuated by the occurrence of water deficits (Farias, Nepomuceno, & Neumaier, 2007). Soybean is strongly influenced by the genotype x environment interaction (Alipriandini et al., 2009; Centro de Inteligência da Soja [CISOJA], 2018).

ECONOMIC IMPORTANCE

Globally, soybean is among the four most grown crops, ranking first among leguminous, occupying 6% of the farmable fields (Valliyodan et al., 2017). Due to its high world demand, according to Foyer et al. (2016), by 2026 it is expected to increase by 25%. The world soybean production, in the last 50 years, has multiplied by ten to 300 million tons and, according to the FAO (Food and Agriculture Organization), by 2050 the production could double to 515 million tons. China, large soybean importer, doubled its consumption in nine years and projections indicate that by 2021 to 2022 it will be 59% of increase in imports.

According to the FAO, soybeans are a key part of food security, accounting for 56% of total oilseed production in the world, as it is an important source of protein and oil for human and animal nutrition. The overall soybean production for the 2018/2019 crop season is estimated at 369.3 million tons, driven mainly by higher harvests in the United States and China, which partially offset the reduction in projections for Canada, India and Uruguay. A total area of 130.1 million hectares is expected to be seed, surpassing values recorded in previous harvests (United States Department of Agriculture [USDA], 2018).

At about the age of 70, soybeans quickly surpassed the traditional coffee and sugarcane crops in Brazil and had a remarkable development, especially in the last 30 years, becoming the main agricultural asset that drives the economy in all sectors nowadays, with great influence in its complex industry chain. Brazil is, currently, the world's second largest soybean producer, second only to the United States. In the presented figures is shown the evolution of the area (Figure 1a), production (Figure 1b) and productivity (Figure 1c) in the three largest soybean producers in the world, until the 2016 harvest according to FAO. It can be observed from Figure 1 that in the last 20 years, in the three largest soybean producers in the world, the increase in production was mainly due to the increase in farming fields' area, and the yield contribution pertaining to production per unit of area was relatively lower. When analyzing the scenario in Brazil, soybean took 25 years from 1976/77 to 2000/01 to increase its productivity by 66%, from 1500 to 2500 kg ha^{-1}, however, in the last 15 years (2001/02 to 2016/17) exceeded 3000 kg ha^{-1} to give an increase of 24%. It means that over the last 20 years, most of the expansion of domestic production increase was explained by area, as mentioned above.

Brazil has a total area of 850 million hectares. The legal reserve area of the Amazon Rainforest and other natural biomes gather a total of 503 million hectares, while the pastures and crop fields cover 211 and 71 million hectares, respectively. The available area for the agriculture expansion is estimated in about 65 million hectares (Instituto Brasileiro de Geografia e Estatística [IBGE], 2009).

According to CONAB (2018), in the last crop season 2017/18, Brazil grew 35.2 million hectares with an average yield of 3394 kg ha^{-1}, with a total national production of 119.2 million tons, while, the Americans produced 120 million tons. Some institutions of crop season projections put Brazil as early as next season 2018/19 as world's largest producer of soybeans, surpassing the United States.

The largest Brazilian soybean producer is the state of Mato Grosso (production: 30.51 million tons, sowed area: 9.32 million hectares, productivity: 3273 kg ha^{-1}), Paraná (production: 19.52 million tons, sowed area: 5.25 million hectares, productivity: 3714 kg ha^{-1}), Rio Grande do Sul (production: 18.21 million tons, sowed area: 5.70 million hectares, productivity: 2970 kg ha^{-1}) and Goiás (production: 10.82 million tons, sowed area: 3.28 million hectares, production: 3300 kg ha^{-1}) (CONAB, 2018). According to Sentelhas et al., 2015, Rio Grande do Sul has the greatest yield potential; however, what is observed is that this potential is not reached mainly by climatic variations during the year, mainly drought, causing reduction in yield.

Soybean is considered a "*commodity*" and is so named because there is a large-scale production, it is commercialized in the world market and has its price determined by international supply and demand. By definition, commodities are cyclical, that is, production is stimulated or discouraged according to price. If prices are high, producers will feel stimulated to produce, and production will be large, inventories will increase, prices will fall, and most producers will lose interest in producing large quantities, causing a decrease in production in that harvest. As inventories reduce, the price rises again, there is no eternal upward or downward trend, but cycles, because of this, commodities are considered cyclical (Nehmi, 2012).

In this sense, the export-import ratio in Brazil, the so-called "Soybean Complex", which includes grains, bran and oil, is an important component of the Brazilian economy, obtaining in 2017 US$ 30 billion in export revenue (CONAB, 2018; (Ministério da Agricultura, Pecuária e Abastecimento [MAPA], 2018)). Besides the economic importance of this complex, socially it has a very important role, being responsible for generating more than 5 million jobs.

In the 2017/18 crop season, Brazil exported around 76.2 million tons, which brings it to the highest soybean exporter in the world. Considering all the soybeans that are exported to the world, Brazil owns 50% of this total, since, together, Brazil, USA, Argentina, China, Paraguay and others exported 153.1 million tons (USDA, 2018). Regarding to the world soybean consumption in the 2017/18 crop season, China, followed by the United States, Argentina and Brazil are the largest soybean consumers in the world, making 254.3 million tons out of a total of 336.8 million. In the last two decades, world consumption of soybeans grew 3.38% per year, with China, Brazil and Argentina being the main highlights, with respective annual consumption growth rates of 8.84%, 3.45% and 5.10%. As for stocks, Argentina followed by the United States and Brazil have the world's largest stocks, with about 68.1 million tons out of a total of 96.7 million tons (Hirakuri, 2014; USDA, 2018).

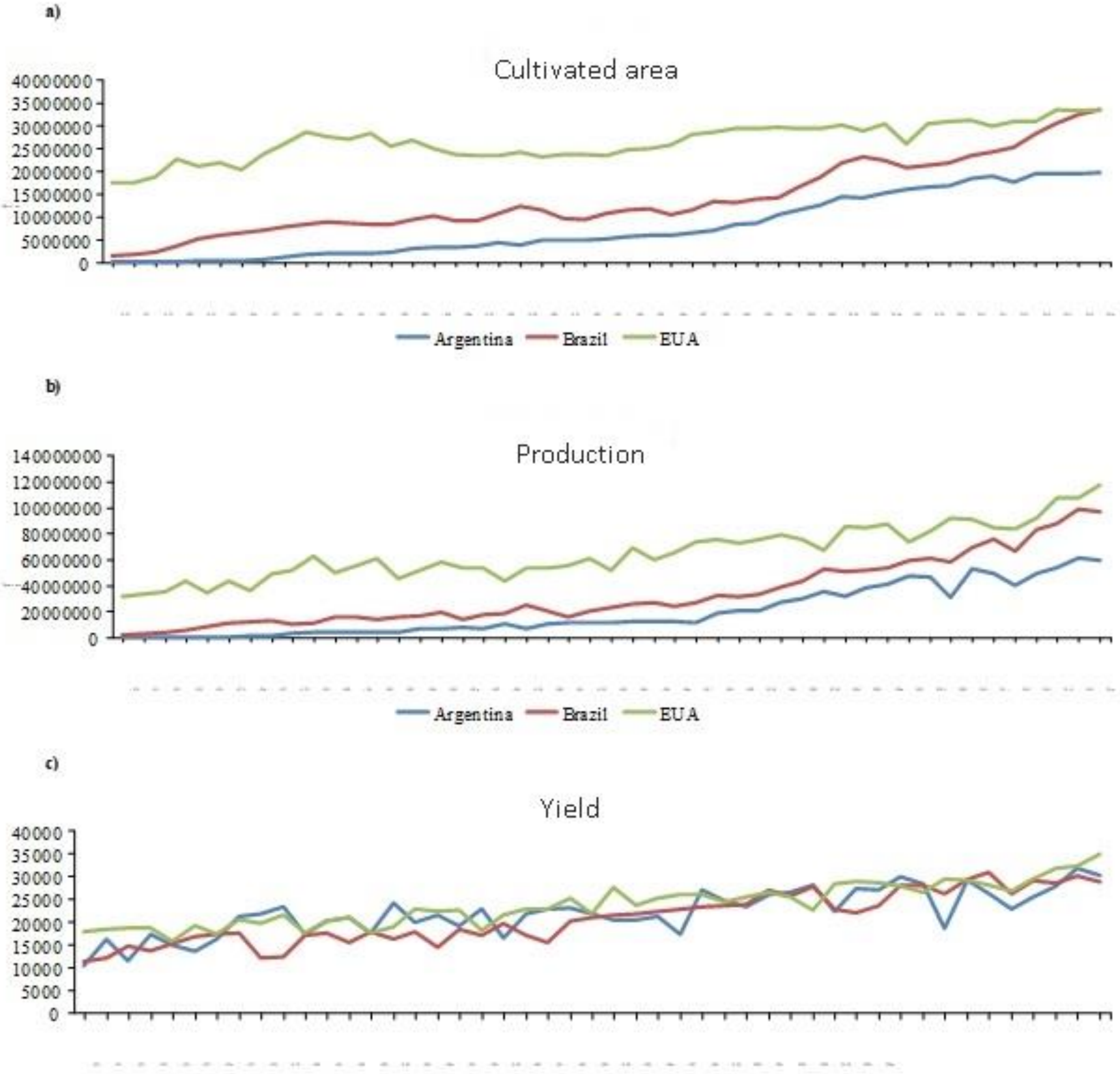

Figure 1. Evolution of cultivated area, production and yield of the three main producers of soybean in the last 46 years.
Source: FAO, 2017.

THE GRAIN USE

Regarding the soybean utilization, 90% of the total amount consumed is sent to the crushing process, generating soybean bran and oil, in an approximate ratio of 80/20, without considering the losses. Soybean bran, with a protein content of 44% to 48% (if the grain is peeled before the oil is extracted), is most often used as a high protein supplement for raising animals. Bran can also be used as fish food in aquaculture, in the production of domestic animal feed and as a substitute for milk for calves. In order to obtain the soybean bran, it is necessary to roast and grind the soybean cake, which remains after the extraction of the oil with solvents (Missão, 2006). Soybean oil is rich in polyunsaturated fatty acids. It can be used domestically as cooking oil and in industries such as pen ink, biodiesel, paint in general, shampoos, soaps, and detergents (Missão, 2006). In the food industry, in the important ingredients of the production of cereals, breads, biscuits, pastas, fine meat products, etc., the textured soybean protein is used as a meat substitute.

DROUGHT

The drought phenomenon is an unpredictable climatic event, however, some interventions and strategies may help the population to be more prepared to live with this phenomenon. Among the promising strategies in some regions in the world are the geographic changes in the crop production systems, drying systems resistant to climatic changes and more efficient irrigation systems (Solh & Ginkel, 2014).

In the case of Brazil, it is necessary to explore these, and other alternatives, within more transversal contexts related to water and soil use issues, in a way connected to climate, and scenarios of climate change. Also, more applied contexts related to plant production, animal production, bioenergy and integrated systems, in order to propose technological solutions appropriate to the Brazilian reality.

Drought (when evapotranspiration exceeds rainfall for a period) is characterized by absence, scarcity and reduced frequency, limited amount and poor distribution of rainfall during rainy seasons. This event can affect a region for a large period and can negatively affect at the most localized level, regionally, or even nationally. The agricultural sector is most harmed when this event happen, propitiating the development and spread of pests and diseases, loss of living beings, as well harming the economy of the country.

Analyzing the data of the annual occurrence of drought in Brazil from 1991 to 2012 (Figure 2), available in the Centro Universitário de Estudos e Pesquisas sobre Desastres (CEPED)(2013), it can be observed that during this period, 19,517 occurrences were recorded, being concentrated in 2002 (1226), 2005 (1874), 2011 (1480), and 2012 (2489) records. The spatial distribution of the drought records can be observed in the period from 1991 to 2012 throughout Brazil. As mentioned previously, drought records total 19,517 occurrences, and this number represents 48% of the total of 39,837 disasters in Brazil during the analyzed period.

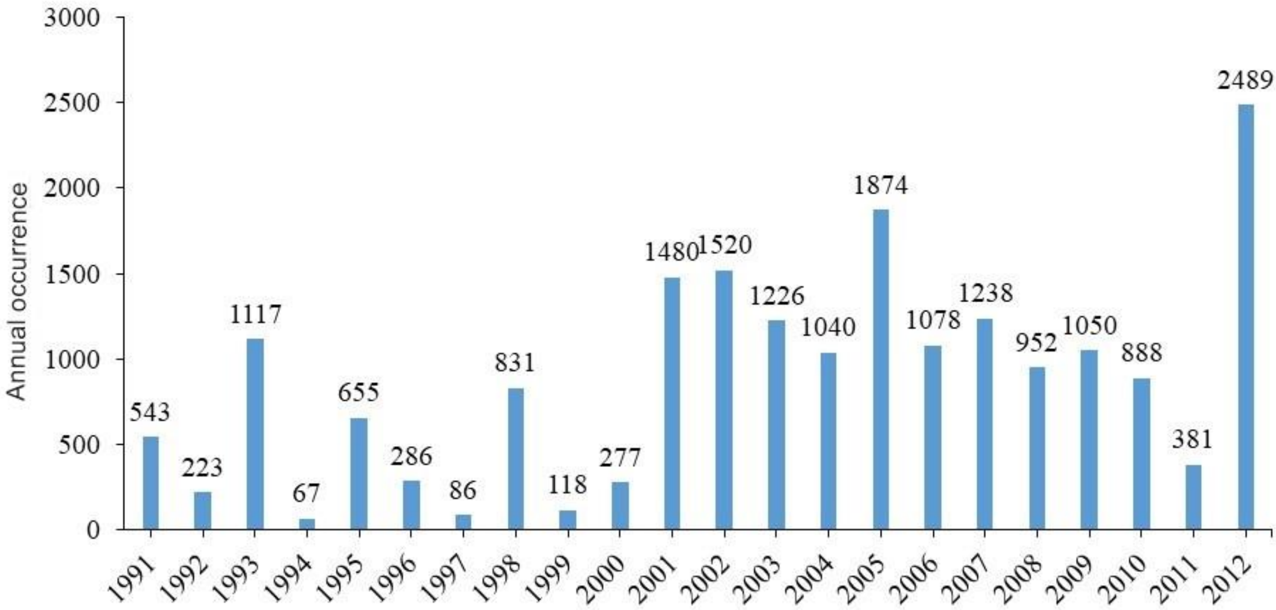

Figure 2. Annual occurrence of drought in Brazil from 1991-2012.
Source: CEPED, 2013.

The increased soybean demand makes it to be responsible for the occupation of unexplored areas in Brazil, mainly in the Cerrado. However, soybean expansion may be affected by limitations due to abiotic factors, including drought, given that the adaptation of different genotypes to certain regions depends on photoperiodic, thermal and water requirements. The increase in yield per area in the coming years will be, still, the main component for a global strategy to guarantee the supply of food and energy, in addition to protecting natural resources and environmental quality for future generations (Lobell, Cassman, & Field, 2009).

Besides Rio Grande Sul being among the largest soybean producers in the country, its productivity is far behind when compared to Mato Grosso and Paraná, for example. This can be partly attributed to the water deficit during the neutral and negative events of South Oscillation of El Niño (ENSO) (Alberto, Streck, Heldwein, Buriol, & Medeiros, 2006), when less rainfall is received in southern Brazil.

In figure 3 it is possible to observe the productivity of these three states over the last 37 years and to perceive this variation due to the drought events, mainly in RS. Among the climatic factors that most affect soybean cultivation the stress due to water deficit is highlighted, because of it, soybean productivity levels in the different growing regions of the country vary substantially, resulting in production gaps of considerable magnitude (Sentelhas et al., 2015). The success of the entire soybean complex is nowadays greatly influenced by climatic conditions (Farias et al., 2009). The amount of water available during the crop cycle has been one of the main factors influencing agricultural productivity. Agricultural production in environments with low water availability is directly affected, where losses are minimized by the plant characteristics that allow maintenance of water amount during soil moisture reduction, being characterized as the form that the crop tends to tolerate drought.

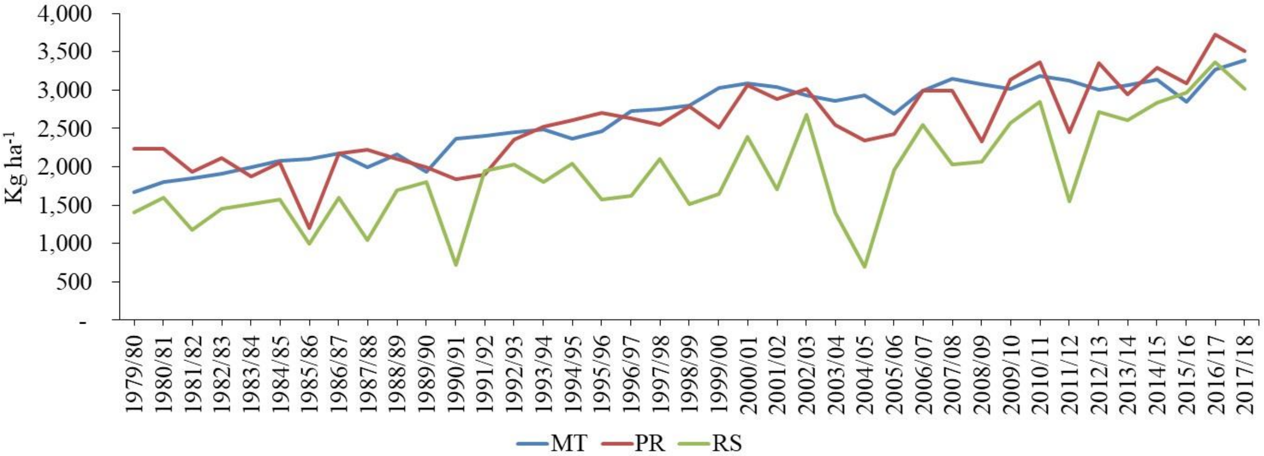

Figure 3. Variation of soybean yield over the last 37 years in the states of Mato Grosso-MT, Paraná-PR and Rio Grande do Sul-RS.
Source: CONAB, 2018

However, it is necessary to consider that the soybean plant consists of approximately 90% of water, and that water acts practically in all physiological and biochemical processes, playing a solvent role, acting in the transport of gases, minerals and other solutes in the plant (Farias et al., 2009). When the plant is submitted to water deficit, there are strategies that minimize the effects of drought using the tolerance mechanism, such as osmotic adjustment, so that the cell absorbs water and maintains the pressure potential at adequate levels.

The reduction of the osmotic potential is one of these strategies in response to the water deficit, which results in a passive concentration of solutes, a consequence of the loss of water from the cell, or the active accumulation of solutes, being considered as osmotic adjustment. The osmotic adjustment capacity of the different crops is variable and, when the crop's ability to withstand drought is measured, this aspect should be considered. In relation to soybean, it is considered a species with low capacity for osmotic adjustment (Oosterhuis & Wullschleger, 1988).

When it comes to soybeans, water availability is important at all growth stages, ranging from germination/emergence to grain filling, the latter being the most sensitive because it directly affects the final yield. During the early stages, the crop stand is directly affected by both the excess and water deficit. The seed needs to absorb at least 50% of its weight in water to ensure germination, and the amount of water in the soil cannot exceed 85% of the maximum available water and not less than 50%. The water requirement of the soybean crop increases with the development of the plant, decreasing during the maturation period (Farias et al., 2007).

The development of drought tolerant genotypes is considered one of the strategies for plants to survive droughts. Tolerant genotypes present gene transcription factors that regulate the expression of several genes related to the defensive response to abiotic stresses, thus mitigating their deleterious effects (EMBRAPA, 2013; Rolla et al., 2013).

Perception and initial answer of soybean plants under drought stress

In order to be viable, soybean production requires a large amount of water, where for every kilogram of dry matter produced through photosynthesis, the plant exudes about 580 kg of water (Câmara, 2009). The total water requirement in soybean cultivation, for maximum yield, ranges from 450 to 800 mm cycle^{-1} depending on climatic conditions and crop management (EMBRAPA, 2010).

Due to its severe effect on crop production, drought is currently the most studied abiotic stress (Zhang et al., 2014). Throughout the evolution of plants species there are specific mechanisms of response (tolerance) to adverse environments, which may include growth inhibition, osmotic regulation and detoxification, among others (Zhu, 2002; Harb, Krishnan, Ambavaram, & Pereira, 2010).

In general, the water deficit primary effects on plants, such as reduction of water potential and cell dehydration, alter the physical and chemical properties of the cells. It triggers secondary effects, such as changes in metabolic activity, ionic cytotoxicity and production of Reactive Oxygen Species that initiate and accelerate the breakdown of cellular integrity and may cause cell death (Taiz & Zeiger, 2013).

The ROS molecules such as singlet oxygen (O_2), hydrogen peroxide (H_2O_2), superoxide ($O_2^{\cdot-}$), and hydroxyl radicals (HO) produced in mitochondria, chloroplasts and peroxisomes are capable of causing oxidative damage to lipids, protein and DNA (Apel & Hirt, 2004; Møller, Jensen, & Hansson, 2007). In order to minimize the cytotoxic effects of ROS, the plants release a complex anti-oxidative system where specific enzymes act to neutralize the action of these radicals, starting with the superoxide dismutase, which dismantles the radical $O2^-$ to H_2O_2. This, in turn, undergoes the action of several enzymes such as: catalase, responsible for the conversion of H_2O_2 to H_2O and O_2, and peroxidases, ascorbate peroxidase and guaiacol peroxidase that reduce H_2O_2 to H_2O (Apel & Hirt, 2004). There is also accumulation of osmoprotective molecules, which aid in the tolerance of plants under low water availability such as sugars (trehalose, sucrose and fructose), amino acids (proline and tryptophan) and ammonium compounds (polyamines and glycyl-betaine) (Hossain, Liu, Qi, Lam, & Zhang, 2014; Devi & Giridhar, 2015).

Some mechanisms are involved in signal transduction processes, in which cations play a fundamental role as hormones, among them abscisic acid (ABA), related to the opening and closing of the stomata that reduces the rates of transpiration, so that the plant can save water (Reddy, Ali, Celesni, & Day, 2011; Lee & Luan, 2012). Thus, water deficit sensitivity represents all water content of a tissue (or cell) below the highest water content exhibited in the state of higher hydration, while "tolerance" is the ability of the plant to cope with the unfavorable environment to the accumulation of compatible solutes or osmolytes, osmoprotective proteins and the antioxidant capacity (Taiz & Zeiger, 2013).

Changes in the transcription of genes of soybean plants as a response to drought conditions

To minimize the effects of drought on crop yield, it is necessary to identify plants that tolerate this stress, as well as identify which mechanisms are involved to improve the efficiency of water use (McAusland, Davey, Kanwal, Baker, & Lawson, 2013). Knowledge of these mechanisms leads to complex metabolic pathways with specific genes expressed in the stress condition. The response of plants to water deficit can represent a series of combinations of molecular events that are activated or deactivated when it perceives stress. This occurs through the alteration in the transcription model of the genes.

Membrane channels can be activated, causing alterations in the conformation and juxtaposition of proteins responsible for the perception of stress or even cause changes in the continuity of the system "cell wall - plasmalemma", consequently triggers another molecular signaling that activates other genes, in response to water deficit (Yamaguchi-Shinozaki et al., 2002). When a water loss occurs through the plant cell, some regulatory processes are initiated by adjusting cellular metabolism to these cellular conditions. Concomitantly, some developmental changes occur which results in additional changes in gene expression (Taiz & Zeiger, 2013).

In order to fight drought, there is a need for the development of molecular strategies that involve the understanding of the functioning of differentially expressed genes, where the products fits into two major groups: functional proteins and regulatory proteins (Shinozaki & Yamaguchi-Shinozaki, 1997).

In a group of proteins that are transcription factors (regulatory) is the family of HD-Zip genes. Some HD-Zip proteins participate in vascular and organ development or meristem maintenance. Others mediate the action of hormones, or are involved in the response to environmental conditions (Ariel, Manavella, Dezar, & Chan, 2007). The expression of genes from the HD-Zip I subfamily is regulated by abiotic factors such as drought, extreme temperatures, osmotic stress, light rate and is specific in different tissues and organs of the plant (Gago, Almoguera, Jordano, Gonzalez, & Chan, 2002; Olsson, Engström, & Söderman, 2004; Rueda, Dezar, Gonzalez, & Chan, 2005).

Two main groups of genes are activate and are linked to the mechanism of tolerance to water deficit. The first group include genes encoding proteins where the function is to protect cells from the effects of water stress. It includes the protein involved in the water channel of the water movement within membranes, the enzymes needed for the biosynthesis of various of osmoprotectants (sugars, Pro and Gly- betaine), protein that can protect macromolecules and membranes (LEA protein, osmotin, antifreeze protein, chaperon and mRNA binding protein), proteases for proteic turnover (thiol proteases, Clp proteases and ubiquitin), detoxification enzymes (glutathione S-transferase, epoxide soluble hydrolase, catalase, superoxide dismutase and ascorbate peroxidase). Some of the genes induced by stress that encodes protein, as a key enzyme for Pro biosynthesis, were overexpressed in transgenic plants to produce a plant phenotype; this indicates that the genetic products properly work on stress tolerance. The second group is responsible for the production of proteins that regulate the transduction of stress signals and modulates the expression of genes (Reis, Lima, & Souza, 2012; Reguera, Peleg, & Blumwald, 2012). This group of proteins contains factors involved in the additional regulation of signal transduction and gene expression that probably work in the response of stress: protein kinases, transcription factors, PLC e 14-3-3 proteins.

The Dehydration Responsive Element Binding Proteins (DREBs) are other gene groups that are extensively studied by genetic engineering, and their use is linked to environmental stress tolerance mechanisms such as drought (Todaka, Nakashima, Shinozaki, & Yamaguchi-Shinozaki, 2012). DREBs are important transcription factors that induce a set of genes responsive to abiotic stresses and contribute to plant responses to these stresses (Lata & Prasad, 2011). Soybean has been genetically modified with the DREB gene by researchers from EMBRAPA / Soybean in order to obtain a drought tolerant variety.

By participating in early stages of the process of perception and signaling, transcription factors regulate the expression of various gene groups, or metabolic pathways (Shinozaki & Yamaguchi-Shinozaki, 1997). This makes interesting the use of transcription factors in genetic engineering works, where it is sought to improve characteristics of drought tolerance, which are polygenic characteristics.

Biochemical modifications occurring in the plant under dry conditions

The water restriction is responsible for serious morphological, physiological and biochemical dysfunctions in plants, causing several changes in their cellular metabolism (Munns, 2011; Filippou, Bouchagier, Skotti, & Fotopoulos, 2014). Water deficit occurs when the water loss exceeds the absorption, acting directly on the water relations in the plants. The intensity and the exposure period will characterize the damages to the plant, and it will promote changes in the cell and in the molecular pathways, as well as accumulation of organic solutes such as carbohydrates and proline (Costa et al., 2008).

The changes that may occur may be linked to osmotic adjustment, due to the effective and rapid increase of the concentration of compatible solutes such as proline, glycine, betaine, trehalose, sucrose, polyamines, mannitol, pinitol in the vacuole or plant cell cytosol (Ashraf & Harris, 2013; Pintó-Marijuan, & Munné-Bosch, 2013). In a study, Lobato et al. (2008) evaluated the biochemical behavior of soybeans submitted to six days of water stress at the beginning of the reproductive phase, and observed an increase in total soluble carbohydrate levels of 40%, 205% for sucrose, 67% for proline and 388,1% for free amino acids, besides the 20% reduction in the total soluble protein level.

Due to the high synthesis of amino acids, derived from the hydrolysis of proteins, there is an increase in the level of free amino acids, in which these are used by plants to minimize the effects of water deficit through the accumulation of organic solute, thus increasing the capacity of water retention. Under drought effects, the free amino acids such as proline and glycine-betaine are strongly affected and consequently rapidly accumulated, as well as in the secondary form there is an increase of aspartate, glutamate and alanine (Ramos, Parsons, & Sprent, 2005). The probable increase of the enzymatic activity in the plants submitted to the water deficit causes reduction of the soluble protein, consequently, this enzyme promotes the breakdown of the proteins, consequently decreasing the amount of protein presented in the plant (Taiz & Zeiger, 2013).

A common response to water stress in plants is related to the accumulation of amino acids, but specifically proline, which plays a role of osmo-protectant, protecting the integrity of protein, enzymes and membranes. Furthermore, it presents role as compatible solute that does not harm enzymes and other macromolecules of the cytoplasm, contributing to the stability of the membranes and subcellular structures. In addition, it acts together with flavonoids and carotenoids, as a non-enzymatic antioxidant that protects the cellular functions of intoxication by reactive oxygen species (Sharma, Jha, Dubey, & Pessarakli, 2012; Kaur & Asthir, 2014).

Thus, increasing the free amino acids level decreases the effects of water deficit by increasing water retention capacity (Morando et al., 2014). Some intrinsic properties of these amino acid molecules explain this occurrence, since both contain the amino portion ($^-NH_2$) and a carboxyl functional group (^-COOH). The proline contains an imino portion (C = NH), which means that it has a carboxyl functional group and a secondary imino group conferring neutrality to the molecule, reporting as an important osmoprotective that acts on the integrity and protection of the plasmatic membrane.

The proline accumulation in the plant may be important in the DNA, membranes and protein complexes stabilization; in addition to providing a source of carbon and nitrogen for plant growth after stress (Szabados & Savouré, 2010; Sharma et al., 2012; Giberti, Funck, & Forlani, 2014).

Drought effects on morphologic and physiologic characters of soybeans

Drought causes a lot of physiological and morphological disorders in the plant, among them, leaf wilting and consequent reduction in leaf area, decreased plant height, fall of flowers and fruits, stomatal closure and osmotic adjustment, which causes reduction of photosynthesis negatively affecting growth, development and grain yield (Farias et al., 2007).

The stomata consist of a pair of guard cells, stomatal pores, and subsidiary cells that surround the guard cells, which help to control the pores. Its opening or closing is controlled by the guard cell turgor, which is related to the concentration of potassium and their counterbalance ions (Taiz & Zeiger, 2013). The potassium acts as the main inorganic osmoregulatory used to establish the osmotic gradients in vegetables (Jákli, Tavakol, Tränkner, Senbayram, & Dittert, 2017). The abscisic acid (ABA) plays an important role in this process. When dehydration of the mesophilic cells begins, the release of ABA that is stored in the chloroplasts to the apoplast occurs, with ABA being redistributed, on the other hand, ABA synthesis occurs, which is accumulated in the apoplast (Taiz & Zeiger, 2013). Therefore, ABA induces stomatal closing to reduce water loss through transpiration and decreased photosynthesis rate to improve water use efficiency in plants.

The stomatal closure, one of the main adaptation mechanisms to drought in plants, causes lowering of the stomatal conductance, inducing a reduction of the internal concentration of CO_2, and therefore decreasing the photosynthetic rate. Before the stress beings, posterior to the development of the leaf area, the plants close the stomata to reduce the loss of water to the environment. When it occurs, as a form of protection of the plant against desiccation, simultaneously, occurs a restriction to the diffusion of atmospheric carbon dioxide causing a decrease in the net assimilation of CO_2, due to the severity and duration of the water deficit.

Moreover, the closure of the stomata reduces the demand for reducing power in the biochemical stage of photosynthesis (Flexas, Bota, Loreto, Cornic, & Sharkey, 2004; Chaves, Flexas, & Pinheiro, 2009; Lauteri, Haworth, Serraj, Monteverdi, & Centritto, 2014). Severe water deficit, occurring in conjunction with high irradiance, may cause a state of super-reduction in the electron transport chain in chloroplasts, due to the excess of excitation energy on the photosystems, which may cause the generation of reactive species of oxygen (ROS) (Dinakar, Djilianov, & Bartels, 2012; Dahal, Martyn, & Vanlerberghe, 2015; Zhang, Liu, Yang, Du, & Yang, 2016).

In soybean, which is a plant of C3 metabolism, the main cause of photosynthesis reduction, when subjected to a moderate to low water stress, is the reduction of the CO_2/O_2 ratio (Pinheiro & Chaves, 2011). This is because plants, when submitted to environmental abiotic restrictions, accumulate reactive oxygen species, which can lead to injury and cell death since in the long term they negatively affect nucleic acids, proteins, and lipids (Atkinson & Urkin, 2012). However, in a short time, ROS play a key role in intracellular communication, which causes the plants to develop a mechanism of acclimatization to unfavorable conditions functioning as a mechanism for the transduction of external signals, triggering important adaptations to stress (Miller, Suzuki, Ciftci-Yilmaz, & Mittler, 2009; Rejeb, Abdelly, & Savouré, 2014).

In soybeans, drought causes a reduction in total leaf area, leaf senescence, reduction in the production of flowers, flower bud abortion, reduction in the number of pods, decrease in productivity, decrease of water use efficiency and other factors (Firmano, Kuwahara, & Souza, 2009; Fioreze, Pivetta, Fano, Machado, & Guimarães, 2011; Fang & Xiong, 2015). The availability of essential nutrients is affected by water deficit, causing productivity to be affected by the reduction of biological nitrogen fixation (BNF), which is essential for the formation of proteins that participate in the composition of soybeans. When this deficit is associated at high temperatures, which is common, it can lead to early flowering stimulating the reduction of the vegetative cycle (Sinclair & Rufty, 2012). Some endogenous phytohormones, such as cytokinin and ethylene can alter the metabolism of plants during drought, however, these responses are highly variable due to cross signaling among these compounds (Peleg & Blumwald, 2011; Daszkowska-Golec & Szarejko, 2013).

The flow of soil water through the plant to the atmosphere is determined by the gradient of soil water potential, plant root, plant vessels, plant leaves and atmosphere (Santos et al., 2013). The soybean plant under conditions of low water availability presents the larger root system, thus confirming the adaptation of the species to the conditions of water stress. The expansion stimulus of the radicular system occurs because of the water deficit, when superficial dry of the soil occurs due to low moisture. (Scalon, Mussury, Euzébio, Kodama, & Kissmann, 2011). Under these conditions the plants invest in the development of the root system, increasing the root length (Fitter & Hay, 1987).

The effective absorption of water by the roots is due to the volume of roots explored, as well as the intimate contact between the surface of the roots and the soil. This contact is potentiated when the plant emits roots, increasing the surface area and the capacity of water absorption. The water deficit stimulates the increase and expansion of the root system for deeper and humid zones of the soil profile in search of moisture, as the water deficit causes soil surface drying (Hoogenbomm et al., 1987).

Drought effect on soybean yield

Independent of the soybean development stage, the water deficit resulting from drought affects growth and productivity. Even though soybean is more sensitive to this stress in the reproductive phase, the occurrence of water deficit during the vegetative stages can negatively affect the yield of grains, and there may be reductions of up to 40% (Thao & Tran, 2012; Krishnan et al., 2014). In addition, prolonged water deficit in the field can cause premature plant death even during vegetative growth and result in total crop loss (Fita et al., 2015).

The mechanisms that make the plant acclimate to dry conditions, usually counteracts the high productivity, since the allocation of resources need to be allocated for both acclimatization to stress, as to its income. Thus, the evaluation of plants at the vegetative stage can be an escape from this competition, allowing the maximum expression of the tolerance character of the genotype.

In a study of water deficit and productivity, Rambo et al. (2003) observed an 18% reduction in soybean yield. According to Zhang et al. (2007), drastic losses occurred in yield, varying from 20 to 46% and, as state by Assad et al. (2007), losses of up to 70% in soybean productivity were found, which confirm the effects.

Mechanisms of response to drought

In recent years, there has been a breakthrough on signaling networks, besides that, plant responses to drought remain fragmented. The vast amount of pathways that are activated under these conditions and the connection that these pathways have with other abiotic stresses make it difficult to uncover the details and mechanisms adjacent to resistance to drought in plants (Nakashima, Yamaguchi-Shinozaki, & Shinozaki 2014; Kooyers, 2015). Plants can acclimatize to drought through a set of physiological, morphological, biochemical, and molecular changes, and these can be combined in escape, avoidance, and tolerance strategies (Salehi-Lisar & Bakhshayeshan-Agdam, 2016).

As for escape, the same occurs with adjustment in the life cycle and growth in the situation in which it develops and reproduces before the environment becomes excessively dry. Thus, escape depends directly on environmental conditions, although the plant genotype may also influence (Akhtar & Nazir, 2013; Kooyers, 2015). When in avoidance, the plant maintains a high water potential and increases the efficiency of water usage (EUA), through reduction of leaf transpiration and root growth, which prevents dehydration of the plant during shorter periods of water deficit in the environment (Blum, 2005; Luo, 2010, Kooyers, 2015). Avoidance can be promoted by abscisic acid phytohormone (ABA) in response to water deficit by inducing rapid stomatal closure. Thus, the excessive loss of water via transpiration is avoided, causing the tissues to remain hydrated, contributing to the greater resistance to drought (Lim, Baek, Jung, Kim, & Lee, 2015).

The tolerance is nothing more than the capacity of the plant has to maintain its physiological activities in operation, even at the lowest level, before a more severe drought (Luo, 2010; Fang & Xiong, 2015). This is done by half of the regulation of physiological processes, metabolic pathways and the expression of protein genes, and defense metabolites, which together act to reduce and repair some damage due to stress (Hu & Xiong, 2014).

These strategies are presented as a constitutive response of the plant, which depends on some alert, such as the water deficit in the soil. Avoidance strategies as well as tolerance strategies are the most common and can be combined in the same plant, however, it depends on the species, the stage of development, and the characteristics of the environment, making the study of this theme even more complex (Varshney et al., 2014; Zhou, An, Wang, Du, & Huang, 2014; Yıldırım & Kaya, 2017).

Improvement strategies for the development of drought tolerant soybean genotypes

Due to the threats that climate change poses to global agriculture, it is necessary to develop more resilient crops (Basu, Ramegowda, Kumar, & Pereira, 2016). One of the main factors that restrict production is the availability of water, even a crop with high productive potential becomes vulnerable if there are limitations in the water supply (Sinclair & Rufty, 2012).

However, the multiplicity of pathways involved in drought tolerance makes it difficult and complex to increase the expression of this characteristic in crops. Some specific genes are expressed during stress conditions, which makes it necessary to know the mechanisms that lead to these complex metabolic pathways.

For decades the genetic improvement of plants has been successful as regards the adaptation of species to hydric stress. Due to this fact, the improvement of the production of crops under conditions of water deficit has been one of their main objectives (Tuberosa, 2012). Due to the multigenic nature involved in drought stress response mechanisms, low heritability, and high genotype x environment interaction, the selection of drought tolerant species becomes a major challenge.

In order to increase the tolerance of soybean to drought, it is necessary to explore the genotype x environment relationship, that is, to identify genotypes that have morphological characteristics of drought tolerance, as well as to identify management conditions in which this genetic tolerance is expressed. Thus, in addition to obtaining individuals more tolerant to water restriction by plant breeding, it is necessary to manage the soil properly, aiming at maximum retention and water availability to the plants, seeking to achieve high levels of productivity. In this perspective, studies aiming to understand the physiological responses of plants concerning soil water availability variation, to create behavioral models capable of estimating the possibilities of management reflexes and water availability on plant metabolism (Chavarria, Durigon, Klei, & Kleber, 2015).

In addition, soybean genotypes submitted to intense water deficit show a different behavior in relation to the morpho-physiological responses. In this sense, soybean yield will depend on both the annual climatic conditions and the development of new genotypes that tolerate drought (Fioreze et al., 2011; Morando et al., 2014).

Most of the research related to drought tolerance in soybean cultivation is performed by comparing genotypes of plants submitted to water deficit under the same conditions. Proline, for instance, is the most studied compatible solute because of its high responsiveness to stress conditions (Ashraf & Harris, 2013). Thus, the measurement of its content provides an important parameter for the selection of tolerant plants, being that the increase in its concentrations attenuates the effects of water stress (Cvikrová, Gemperlová, Martincová, & Vanková, 2013; Filippou et al., 2014).

In this sense, identifying genes that regulate plant tolerance responses to water deficit is important in the generation of soybean cultivars more suitable for these conditions, which guarantees higher crop yield, even in a more unfavorable condition (Abberton et al., 2016; Bateley & Edwards, 2016; Tripathi et al., 2016). Any strategy to develop drought tolerant cultivars should take into account that breeding programs are very dynamic and that new cultivars always bring some adaptation to the new demands or even environmental changes in the region where they will be indicated.

When improving a crop, it is sought to increase grain yield and production stability over favorable and unfavorable environments. These two characteristics describe as heritable and genetically independent are evaluated in field trials involving large numbers of representative environments of the target region and repeated for several years. In soybean, since other restrictive factors such as diseases and pests have been properly controlled, it is common that water deficit be the main determinant of an unfavorable environment.

It is of utmost importance that breeders know the probability of occurrence of water deficit in working with improved plants adapted to these conditions. This is because plant response to stress depends on the combination of stress traits and plant attributes (Fritsche-Neto & Borém, 2011).

In general, two principles are used to obtain cultivars adapted to the water deficit. The first is to breed aiming drought tolerance, which is the ability of the plant to tolerate the decrease in the tissue water potential caused by the cell dehydration without occurring fatal damage on metabolic processes. Alternatively, the breeding for efficiency of water usage, which concerns the effectiveness that the plant has to fix carbon while transpires, since plants require large amounts of water, direct consequence of the absorption of CO_2 for photosynthesis. It is known that the most of the water absorbed by the roots is evaporated from leaf surfaces through transpiration, while small part remains in the plant to meet the growth demands, photosynthesis and other metabolic processes (Flexas et al., 2004; Morando et al., 2014).

Normally, these terms are confused, however, from the physiological point of view, the simultaneous improvement for the two characteristics is contradictory (Fritsche-Neto & Borém, 2011; Bassett, 2013). Among breeding strategies, the knowledge of genetic diversity and its distribution in a species are useful both for the conservation of germplasm and for the identification of genetic material that has characteristics of interest to be included in breeding programs. The selection of plants can be direct, in which plants are under hydric deficit, or indirect, where is not imposed stress, and, may be combined. However, to be useful to selection, the variables need to have high heritability, be of easy measurement and have a high correlation with the plant response to hydric stress.

For selection, may be used physiological characteristics (stomatal conductance, photosynthetic ability, plasmatic membrane composition, stomatal closure); morphologic (leaf area, thickness of the cuticle, central nerve development, stomatal density); or morpho-agronomics (root development, root/shoot ratio), since they meet the above mentioned assumptions, which should be previously evaluated, for each species and stress condition.

The genetic control of both the tolerance to drought as the water use efficiency are quantitative and involve a number locus spread in different regions of the genome. Thus, the choice of the breeding method to be used should consider the heritability and inheritance type of the most important characteristics, which should be studied previously. Among the different classical breeding methods, the most commonly used for adaptation to water deficit is the genealogic method (Fritsche-Neto & Borém, 2011; Bassett, 2013).

However, because drought tolerance is a polygenic characteristic and difficult to work with in classical genetic breeding, few breeding programs have paid attention to these characteristics. As a consequence, few cultivars have been developed with characteristics of drought tolerance. Thus, the timely identification of genes involved in the responses to water deficit, involving molecular biology, will provide in the near future the identification and understanding of metabolic routes that are involved in the physiological responses of the plant to drought. This will allow the use of these genes as molecular probes that seek the identification of genotypes that express metabolic mechanisms to increase tolerance to water deficiency conditions. There is also the possibility through genetic engineering to transfer genes of interest to other genotypes and even between incompatible species.

Another method used are population methods, which are based on recurrent selection and aim to gradually increase the frequency of favorable alleles to quantitative traits through repeated selection cycles without significantly reducing the genetic variability of the population. Recurrent selection can be divided into progenies obtaining, evaluation of progenies in experiments with replicates and recombination of the superior progenies to originate the next generation. Improved populations can be used repeatedly to initiate a new cycle of recurrent selection after recombination of selected and superior progenies (Bernardo, 2002).

Biotechnology is also an important ally of genetic improvement in the development of varieties more adapted to different water deficit conditions. Specifically, with genetic engineering, it has been possible to design molecular strategies that allow plants to tolerate longer periods of the unavailability of water in the soil. The understanding of the function of a specific gene and its interaction with several others has allowed researchers to understand the complex range of responses that plants use to protect themselves from environmental stresses. It is this knowledge that promotes the emergence of new ideas of genetic engineering to change, at the molecular level, the defense mechanisms, aiming to affect the physiological and agronomic responses of crops to the water deficit.

The transgenic method have also been applied in the identification and transfer of genes responsible for drought tolerance or water use efficiency. Genes that are expressed during stress events are identified early in cell tolerance to dehydration, through protective functions in the cytoplasm and cell membrane, alternations to promote water uptake in the cell, control of ion accumulation, and regulation of other genes.

Through genetic manipulation, some researchers from Embrapa Soja have been able to introduce a gene that makes the plant more tolerant to drought. This gene is termed "Y", and is capable of activating and potentiating other genes of natural defense of plants. This causes the plants to withstand shortages of water for longer.

Another tool that has been used is the mapping of Quantitative Trait Loci (QTLs), being important for the improvement through selection assisted by markers. Although there has been progress in QTL identification and cloning capacity, the contributions of assisted selection have not met original expectations, and further efforts to make the use of assisted selection more effective should be encouraged.

FINAL COMMENTS

The new scenario that the world is going on, with global warming, tends to intensify in the coming decades, being that some regions are already experiencing these changes, becoming increasingly dry and warm, making necessary an appropriate use of technology and new genotypes that may mitigate this effect on soybean crop, a crop of great economic and social importance for the country.

The plant's response to this situation is due to the reprogramming of gene expression, which allows for survival under adverse conditions. Therefore, studies on adaptation technologies and acclimatization to environmental stress, that result from integrated events occurring at all levels of the organization, from the anatomical and morphological to the cellular, biochemical and molecular, are crucial to increase the ability to water stress tolerance, considering the use of tolerant genotypes.

Therefore, the characterization of tolerant or drought-sensitive genotypes is a prerequisite for genetic selection and manipulation, and the identification and understanding of drought tolerance mechanisms in plants are crucial in the development of new, more tolerant soybean cultivars.

CONFLICT OF INTEREST

The authors declare that have no conflict of interest.

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