Pržulj, N., Jovović, Z., Velimirović, A. (2020): Breeding small grain cereals for drought tolerance in a changing climate. Agriculture and Forestry, 66 (2): 109-123.

DOI: 10.17707/AgricultForest.66.2.11

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BREEDING SMALL GRAIN CEREALS FOR DROUGHT TOLERANCE IN A CHANGING CLIMATE

SUMMARY

Climate change, more intense in the 21st century, has and will have a detrimental effect on food production and quality in many parts of the world. The adverse effect of climate change will be the consequence of increased incidence of abiotic stresses, such as high temperatures and water shortages, and increased incidence of biotic stresses, such as pests and diseases. Climate change is expected to cause a decrease in biodiversity, especially in marginal conditions. Drought, as a yield-limiting factor, has become a major threat to food security. Plant responses to drought are affected by various factors including growth conditions, physiology, genotype, development stage, drought severity and duration. Thus, drought tolerance mechanisms involve diverse gene expression patterns and as complex signalling pathways. The complexity of inheriting drought tolerance has limited the progress of small grain breeding by using only the classical breeding methods. To accelerate yield improvement, physiological traits at all levels of integration need to be considered in breeding. Physiological breeding increases the probability of achieving cumulative gene action for yield compared to crossing physiologically uncharacterized genotypes. In practice, it differs from conventional breeding by considering a larger range of traits, including genetically complex physiological characteristics and differs from molecular breeding by encompassing both phenomic and genomic information.

Plant breeding is a complex process related to changing the genotype and phenotype of cultivated plants, as well as their relation to abiotic and biotic stresses. The climate change adaptation strategy, where photoperiod-temperature response of the cultivated plant is used, seeks to synchronize more precisely the dynamics of plant phenology with the dynamics of available water in the soil. This method mainly influences the change in flowering time, which seeks to avoid predictable occurrences of stress at critical periods in crop life cycles. So far, breeding has done the least to alter the roots genetically, making modern high-yielding varieties less effective than their predecessors in absorbing nitrogen

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Paper presented at the GEA (Geo Eco-Eco Agro) International Conference 2020, Podgorica.

Notes: The authors declare that they have no conflicts of interest. Authorship Form signed online.

Received:10/05/2020 *Accepted:21/06/2020*

from the soil. Harvest index is a measure of success in partitioning assimilated photosynthate. An improvement of harvest index means an increase in the economic portion of the plant. In water-limited environments, biomass production is a function of the water used by the crop and the efficiency with which it is converted into biomass. Biomass production can be defined by the amount of radiation intercepted and the radiation-use efficiency, i.e. the efficiency of the conversion of this radiation to dry matter.

Keywords: conventional breeding, physiological approach, flowering time, root, harvest index, grain filling period

INTRODUCTION

Climate change is a global phenomenon of climate transformation that manifests itself in a deviations from the usual climate of an area or planet, and which is especially triggered by human activity. Drought stress in the last two decades has had a negative impact on total agricultural production and also on grain production, indicating the uncertainty of this production and its high dependence on weather conditions (Bindi and Olesen, 2011). Observed globally, climate change has a negative impact on global food production, regardless of the increase in primary production resulting from breeding and improved cultivation technologies (Morgounov et al., 2018). Tripathi et al. (2016) state that since 1980, climate change has reduced global maize and wheat production by 5%.

Water deficiency usually leads to decreased growth, decreased photosynthesis intensity and metabolic disorders. The response of plants to drought is complex because drought stress is most often associated with problems of uptake of nutrients and transport of nutrients and assimilates, which is reflected in the overall metabolism. Thus, a lower water deficiency causes an increase in bound and a decrease in free water in the plant, which leads to a decrease in the intensity of photosynthesis. A higher water deficiency causes drying, and if it continues withering of plant.

Although it is generally accepted that small amounts of precipitation are the most important factor in reducing yields in drought conditions, this may not always be true (Kirkegaard et al., 2008). Other factors, such as disease, poor physical and chemical properties of the soil, problems with soil nutrients, or even flooding at some stage of plant development, can reduce yields (Suresh and Nagesh, 2015). All these factors should be excluded, as far as possible, before the analysis of the physiological traits in drought conditions relevant to yield realization. The intensity of tillering in cereals can also be an indicator of the external conditions or health of the plant (Akram, 2011). Grain cereals belong to the grass family and in favorable conditions, they are tillering intensively, whereas in conditions of severe drought only the main shoot is usually productive and the secondary and tertiary are sterile.

By creating new varieties of cultivated plants whose genotype allows greater tolerance to stress conditions, breeders seek to mitigate the effects of climate change. Over the last 50 years, significant improvements in production and productivity of all major crops have been achieved. Progress has been made mainly through conventional breeding methods, improving the genetic basis for yield and tolerance to abiotic and biotic factors. Despite efforts to produce enough food in recent years, productivity has been reduced in cultivated plants (Slafer and Peltonen-Sainio, 2001). With the aim of more efficient breeding as a complementary method to traditional breeding for yield per se, plant physiology and molecular biology in the identification, characterization and manipulation of genetic variability are used. Some of these methods are presented in this paper.

MECHANISMS OF DROUGHT TOLERANCE

Biological stress is defined as an external factor affecting yield reduction relative to the maximum genetic potential of the genotype (Salisbury and Marineous,1985). Stress tolerance is the capacity of a plant to better adapt to biotic or abiotic stresses, such as drought, high and low temperatures, saline soils, the presence of toxic metals, harmful organisms, and more (Duvick, 1997). Drought is considered to be one of the most significant factors that limit the yield of cultivated plants worldwide. As climate change leads to warmer and drier summers, the impact of drought limiting yield and yield components has increased (Sareen et al., 2018; Mehraban et al., 2019). The use of genetics in improving drought tolerance and ensuring yield stability is an important aspect of stabilizing global crop production (Edmeades et al., 2003).

Drought tolerance consists of resistance to high temperatures and resistance to water scarcity. Genotype tolerance to soil water scarcity is a complex trait and cultivated plants can achieve it through one of the following mechanisms: (1) drought avoidance, (2) dehydration reduction, and (3) dehydration tolerance (Fang and Xiong, 2015).

Early ripening and fruiting is a physiological trait that ensures drought avoidance in many areas (McKay et al., 2003). Early maturity involves timely flowering, which is controlled by major genes that control photoperiod, vernalisation and early maturity per se (Gomez et al., 2014). In breeding of cultivated plants, genotype selection for traits that enable intensive growth and rapid development, such as high stoma conductivity, high photosynthetic activity, high water use efficiency, and early flowering, allow early maturity and drought avoidance (Kereša et al., 2008).

Physiological adaptation of plants to soil water deficiency is achieved by reducing dehydration (McKay et al., 2003). Low metabolic activity, slower growth, and high water potential and turgor in cells during the drought period distinguish genotypes that have a mechanism for reducing dehydration. The basis of this mechanism is the progressive closure of the stoma, leading to a decrease in transpiration as well as photosynthesis. Stoma closure is controlled not only by available water in the soil but also by the interaction of leaf properties and external factors (Medrano et al., 2002). As a reaction to drought, abscisic acid (ABA) is synthesized at the root, which is transported by xylem to the leaf and causes stoma closure (Schachtman and Goodger, 2008). ABA accumulation in plants induced by drought is under the control of the Quantitative Trait locus (QTL) (Quarrie et al., 1994).

Dehydration tolerance is tolerance to the changes caused by drought at the molecule and cell level, which the plant achieves by osmotic regulation or adaptation (Živčák et al., 2009). Osmotic regulation is a decrease in cytosol potential due to the accumulation of osmolytes during reduced water potential in the leaf, which allows the maintenance of positive turgor and continuation of processes that depend on the turgor to a certain level and under stressful conditions. Organic and inorganic substances that allow osmotic regulation are specific to different plant species. Osmotic adjustment is achieved by passive concentration of the solution, trough the process of dehydration. In this way, osmotic potential of root can reach lower values than osmotic potential of the soil, thereby achieving movement of water from the soil in line with concentration gradient (Stanković et al., 2006). The degree of osmotic adaptation to drought conditions varies among plant species and can be used as one of the criteria for selecting dehydration-tolerant species (Chaves et al., 2003). Due to osmotic regulation in tolerant genotypes for drought, the stoma remains open allowing photosynthesis to take place, leaves elongate, although with reduced intensity, the root continues to grow and allows more efficient absorption of water from the soil, delaying leaf wilting, more efficient accumulation of dry matter and higher yield under stress conditions.

Saradadevi et al. (2017) point out that the ability to keep the stoma open in water stress conditions is an agronomic form of drought tolerance. Guo et al. (2019) state that potassium is particularly important inorganic ion in wheat. Accumulation of potassium under stress conditions is controlled by a major locus, located on the short end of chromosome 7A. Regardless of the importance of potassium, organic osmolytes play a major role in osmotic regulation (Ahanger et al., 2014). Organic osmolytes can be divided into two groups: (1) osmolytes containing nitrogen such as free amino acids (e.g. proline) and quaternary ammonium compounds such as betaine, polyamines and proteins and (2) carbohydrate osmolytes such as sugars (mannitol, sorbitol), monosaccharides (fructose, glucose), oligosaccharides (sucrose, trehalose) and polysaccharides (fructan).

THE CONVENTIONAL VS. PHYSIOLOGICAL APPROACH IN BREEDING TO DROUGHT

Breeding for yield in optimal conditions creates genotypes that produce high yield in both favourable and stress conditions (Ceccarelli et al. 2004). Genetic variation in traits contributing to high yield under all agro ecological conditions, such as e.g. high harvest index is higher in optimal conditions, which makes the selection of high yield genotypes more likely. Richards (2006) stated that there was no reason for high yield genotypes not to express their genetic potential under favourable conditions and under less favourable conditions if selection was performed under normal conditions without irrigation. The large number of specific adaptations that may be of particular importance for irrigation-free conditions may also be important for achieving high yield in stress conditions.

Breeding to specific physiological traits that are assumed to provide plants with tolerance to drought conditions is difficult and relatively modest results have been achieved so far (Luo et al., 2019). One of the reasons for these modest results is the difficulty in evaluating these traits, their low heritability, and the fact that breeding has been aimed at increasing productivity and quality. In addition, some traits that provide adaptability to drought are negatively correlated with yield or other traits. For example, early flowering in winter small grain cereals provides partial avoidance of drought in the flowering period and the first half of the grain filling, but leads to a decrease in aboveground biomass and yield, and increases the risk of late spring frosts. Some features may be unsuited in another region.

So far in breeding of small grain cereals, flowering time and plant height have had the greatest influence on yield increase under irrigation conditions (Mirosavljević et al., 2016). Genetic manipulations during flowering time were of the greatest importance in the adaptation of vegetative and reproductive growth and grain formation and filling with respect to available water, low temperatures and evaporation. The decrease in plant height played a key role in increasing the harvest index, which is, increasing the grain share in total aboveground biomass, but without changing the total amount of biomass. Researchers around the world have largely defined morphological and physiological traits that limit yield in drought conditions, which opens up new directions and breeding methods for stress conditions (Pržulj et al., 2004).

Grain yield and quality are the most important traits for breeding of cultivated plants in most breeding programs. Yield continues to increase with breeding, but to a lesser extent than in the past. The increase in yields of cultivated plants under irrigation conditions has been achieved mainly through conventional breeding. The increase in yields is largely the result of improved resistance to stress, which is achieved by combining improved genetics and appropriate agrotechnics. For example over the last 30 years, the continuous increase in maize yields has been the result of more improved stress tolerance than an increase in yield capacity. Increasing stress tolerance did not increase the genetic potential of yield – the genotype of the varieties remained the same, but plant tolerance to stress increased, thus enabling the realization of the genetic potential for yield.

Drought is a limiting factor of intensive production that is permanently, to a greater or lesser extent, constantly present. Since the effect of water scarcity and high temperatures on the growth and development of plants is very complex, it is also extremely complicated to enrich this complex trait. Regardless of the achievements of modern techniques – molecular markers, secondary properties, etc. – direct breeding by conventional methods under certain agro-ecological conditions remains the main method of yield increase, primarily due to genetic adaptation of the genotype, manifested through grain weight, and efficient and reliable field testing (Jonas and Koning, 2013). Particular attention must be paid to the selection of the site for the experiment, the cultivation technology, the size of the plots and the number of repetitions.

As the progress of increasing yields today by applying only conventional breeding methods is more modest than in the second half of the last century, it is expected that the use of other methods, especially the physiological approach, in breeding will be increasingly used (Lee and Tollenaar, 2007). Better knowledge and understanding of the factors that influence plant growth and development under certain agroecological conditions, crop physiology and genotype response to environmental conditions enables a more successful application of a physiological approach to plant breeding. By defining the main limiting factors for realizing the genetic potential for yield and knowing the physiological traits that can change the effect of stress, it will increase the yield of cultivated plants. The physiological approach to breeding can contribute to increasing yields in many ways (Richards, 2006). Breeding should use physiological traits that have high heritability and that contribute to the realization of yield potential more effectively than direct selection for yield. In comparison to direct selection for yield, selection based on physiological traits, especially in the younger generations of separation, can be cheaper, very efficient and more productive in the faster emergence of a variety or hybrid on the market (Richards, 2006).

BASIS FOR DROUGHT BREEDING

Drought management methods are numerous, complex and complementary, but it is certainly that breeding and the creation of genotypes that have the ability to generate yields under conditions of limited water supply is one of the first and effective ways to combat drought. Thanks to new research, the rapid development of new techniques and methods of research and cultivation in recent decades, great progress has been made in drought breeding. However, new knowledge about drought tolerance of cultivated plants is rather limited, especially in answering the following questions: (1) how drought tolerance develops in plants during domestication, (2) how to determine drought resistance genes and evaluate their effectiveness in breeding and (3) how to use the results and findings of theoretical research in practical plant breeding practice (Luo et al., 2019).

Root architecture represents the trait of the plant that provides the most opportunities in generating of drought tolerant genotypes (Wasson et al. 2012; Meister et al. 2014). When studying drought resistance, the problem of accurately assessing the response of many genotypes to drought under field conditions is always raised. Therefore, it is necessary to use modern technologies more suited to the requirements of researchers in the study of drought resistance. Condorelli et al. (2018) proposed a new platform based on which, with the use of the Normalized Difference Vegetation Index (NDVI), in 248 durum wheat genotypes, they determined traits that were closely correlated with drought tolerance. Based on the NDV index data using GWAS (genome-wide association studies) method, QTLs related to drought tolerance were determined, which confirmed the theoretical and breeding significance of the proposed platform.

PHYSIOLOGICAL METHODS OF BREEDING ON DROUGHT STRESS

Flowering time. Studying wheat yield under conditions of water deficit, Passioura (1977) states that yield depends on three factors: (1) the amount of water available, (2) the efficiency of water utilization, that is, the amount of dry matter produced per unit of transpired water, and (3) the harvest index. Since there is no negative interaction between these parameters, increasing one of them also increases the yield. In arid conditions, flowering time is the most significant factor affecting the yield and adaptation to environmental conditions. As cultivation technology changes with climate change, breeding programs focus on genetic changes in flowering time (Langer et al., 2014). Modern mechanization and pesticides allow early sowing, requiring that varieties to be adapted to photoperiod and vernalisation.

WATER USAGE

Morphological characteristics of plants and roots significant for water usage. So far, studies of cultivated plants were least related to root research, so there is essentially no information as to whether the root system of modern varieties is adapted to soil and environmental factors and whether is necessary to make changes trough breeding (Zhu, 2019). A deep root system involves drought tolerance and the ability to absorb more water from the soil. If it is assumed that it is necessary to increase the capacity of the root system, its depth and distribution in the soil, it is easiest to do so by using varieties of a longer vegetative period. This can be achieved relatively easily – early sowing or sowing of late varieties. In addition, selecting varieties with a larger early vigour can result in faster root growth, deeper penetration into the soil, and a more developed system of adventitious roots. In addition to the deep root system and the stronger vigour of the young plant, greater water uptake and more developed root can be regulated by plant phenology, reduced tillering and osmotic regulation (Atta et al., 201). For varieties of reduced tillering, nutrients are not consumed for the development of unproductive stems, but for the development of a stronger root system. However, varieties with lower tillering capacity have a number of negative characteristics, which is why they are not introduced into production (Mitchell et al., 2013).

Lower temperature of canopy or higher stomata conductance is indication of favourable soil water regime and deeper root system (Guo et al., 2019). As these properties are easily measured, they can be used as selection criteria, provided that the soil is absolutely uniform, to avoid misinterpretation due to the variability of the soil. Stay-green leaves, especially in maize, can also be an indicator of the favourable water regime of the soil, and indirectly of the deep root. Maintaining the photosynthetic capacity of the leaves is especially important in conditions when after early dry period in second half of vegetation and grain filling period wetter soil is expected, and, consequently, the photosynthetic activity of the plant (Sarto et al., 2017). Leaf twisting in drought conditions may also be an indicator of the adaptive capacity of the genotype to preserve the photosynthetic ability of the plant, and to continue photosynthesis if later water is available to the root.

Water efficiency. Water deficit during the growing season have a significant limiting effect on achieving high, stable yields and quality. The term water use efficiency (WUE) refers to the relationship between total dry matter and evapotranspiration (Hatfield and Dold, 2019). An increase in transpiration efficiency (TE), that is, the value of the dry matter/transpiration coefficient and/or a decrease in the evaporation of water from the soil leads to an increase in WUE. Both of these factors can be changed by breeding.

Plants of C-3 type of photosynthesis have low net photosynthesis, because parallel to photosynthesis, they also undergo photorespiration (CO_2 release in light), which is often more intense than breathing in the dark (Long et al, 2006). With C-4 plants, the CO_2 release by photorespiration is insignificant, which is a basic reason for much more net photosynthesis.

Transpiration efficiency is an important component of water efficiency. Transpiration is the separation of water from plants in the form of water vapour on surfaces confines to the atmosphere. It mainly occurs through the leaves, through the stomata – stomata transpiration, and much less through the epidermis (cuticle) – cuticular transpiration (Zhang et al., 1998). When the surface of the plant, i.e. the transpiration surface, is higher and the saturation of the atmosphere with water vapour is lower, the suction power of the atmosphere is higher, and the potential for transpiration is higher. Transpiration depends on the ability of the plant to make up for lost water by absorption from the soil, leaf structure, openness of the stoma, etc. Transpiration is not only a physical process of water evaporation but a significant physiological process. Because in many areas of the soil there is insufficient water required for optimal transpiration, plants adapt in various ways to reduce water loss (Turner and Begg, 1981).

There are various ways of increasing the efficiency of transpiration in plants, but the most effective is the growing of genotypes where the period of maximum biomass increase occurs during periods of moderate temperatures, when less water is used for growth (Blum, 2009). By selecting the time of sowing and the appropriate length of the phenophases of the variety, it is possible to adjust the time of maximum biomass synthesis in relation to available soil moisture (Pržulj and Momčilović, 2011; Ochagavía et al., 2018). Due to the large influence of environmental factors and the small effect of individual traits and the difficulty of measuring the influence of individual plant traits on transpiration, it is usually difficult to determine the influence of specific plant traits on the formation of higher biomass and the formation of higher yield (Reynolds et al., 2001). However, sowing varieties of larger vigour develops a larger leaf area that is able to absorb more light in the colder period, leading to more efficient transpiration. Some progress has also been made with the growing of small cereal varieties that have a waxy, blue-whitish coating on the surface of leaves, stems and ears. Field studies have shown that isogenic barley lines with this coating have an increase in grain yield of 7-16% and wheat lines of 7%, without changing the harvest index (Parvathi et al., 2017).

The harvest index. In some crops, such as small grain cereals, significant progress in breeding for higher yields is achieved mainly by increasing the harvest index (HI), or by increasing the plant's capacity to allocate more assimilates to formed reproductive organs (Austin et al., 1980; Calderini et al. 1,9; Mirosavljević et al., 2018). Slafer et al. (2005) found that the physiological maximum of the harvest index in wheat was about 0.62. The maximum harvest index of 0.56, obtained from the English winter wheat variety Consort, was achieved by increasing the mass of the grain with reduce of the mass of the stem and the leaf sheath. Modern varieties have a significantly higher grain yield compared to the varieties grown before the Green Revolution, which is primarily due to the redistribution of aboveground biomass between the vegetative part and the grain in favour of the grain, and an increase in HI, respectively (Unkovich et al., 2010). In one century of breeding, the harvest index for wheat has been increased from 0.30-0.35 to 0.55. (Evans, 1993). Similar progress has been made in barley and rice.

Further increase in grain yield in cereals through a change in harvest index cannot produce significant results, which is why it is necessary to look for alternative ways of increasing yield. Richards (1996), Fischer (2007) and Reynolds et al. (2009; 2011) consider that nowadays is necessary to use modern methods of plant breeding, where increasing above-ground biomass is one of the main breeding goals. Breeding should also be directed at increasing photosynthetic activity and the efficiency of using solar radiation. However, in essence it can be considered that the variation of HI in modern semi-dwarf wheat varieties is largely exploited and that the existing variability is more a result of non-genetic than genetic factors. Aisawi et al. (2010) and Fischer (2011) state that modern plant breeding does not only seek to increase HI but HI and aboveground biomass at the same time, or only biomass.

Drought tolerant harvest index. Properties of plants that contribute to high HI under optimal growing conditions also contribute to high yield under all growing conditions, provided that there is no reduction in total biomass (Richards et al., 2001). This is an advantage of semi-dwarf wheat varieties over tall varieties and the basis of high yield of semi-dwarf varieties under favourable and less favourable conditions. High drought tolerance in certain conditions is a prerequisite for high yield in drought conditions, since it determines the genetic potential under those conditions. Drought tolerant HI is the result of different distribution of dry matter between vegetative and reproductive organs (Araus et al., 2008). Therefore, the selection of wheat genotypes that carry stem height reducer genes and early flowering genes is a simple and effective way of increasing HI, since their effect is manifested in a smaller increase in vegetative mass.

Droughtdependent harvest index. When the HI of a genotype is high only under the conditions of the required amount of water available, in the absence of drought stress, it is a drought-sensitive, drought-dependent harvest index (Richards et al., 2001). Drought sensitiveness depends on water uptake during the grain filling period. If the water uptake during the grain filling period is high, the harvest index will be high. If the amount of water in the soil is limited, stored water before flowering, which can be used during grain filling, will increase HI. In this case, achieving a high grain yield depends on the ratio and growth balance before and after flowering. However, achieving this balance is very difficult. For example, too low growth in the period before flowering will limit the total yield of aboveground dry matter but will maximize HI, while a large growth before flowering will allow high dry matter yield, but this can result in low HI.

The use of water is a function of the evaporation requirement and leaf area (Pržulj et al., 2004). There is little ability to change the evaporation capacity, although breeding can change the onset and duration of individual phenophases. Also, there are a number of traits whose genetic changes can reduce the leaf area, which is positively correlated with transpiration. In this way, the use of water can be regulated and, on the basis of this, effectively increase the HI of cereals (Richards et al., 2001; Pržulj and Momčilović, 2001a; 2001b). In this way, water use can be regulated and, thus, effectively increase the value of drought-sensitive HI. Genotypes that have earlier anthesis will have a higher efficiency of water utilization under conditions where temperatures increase after flowering. Combining early flowering with higher vigour or low temperature resistance may be beneficial in breeding for higher HI and yield.

Due to the smaller number of sterile unproductive ears competing with the fertile ears for water and nutrients, reduced tillering, i.e. reduced number of sterile classes, can contribute to the formation of a higher HI, both in conditions of optimally available water and in conditions of water deficit. Lower tillering also contributes to the formation of higher HI under drought conditions due to the formation of a smaller leaf area before flowering, which contributes to less transpiration and the provision of more water for the grain filling period (Richards et al., 2001).

The narrower water conductive xylem channels in the seminal root also contribute to the formation of higher HI (Richards et al., 2001). In essence, reducing the diameter of the conductive channels is an advantage in drought stress conditions, while in favourable conditions it is of no particular importance, since the nodal secondary root, located in the surface of the soil, provides the plant with the required amount of water. Selection of plants of smaller upper leaves, including flag leaves, or selection for lower stoma conductivity and/or lower night-time leaf conductivity also reduces transpiration before flowering (Magorokosho et al., 2003).

In addition to manipulating the amount of water absorbed before and after flowering, there are other methods of increasing the drought-dependent harvest index. In a large number of cultivated plant species, the excess assimilates, which are synthesized until flowering, accumulates in the form of soluble carbohydrates in the stem (Pržulj and Momčilović, 2001a; 2001b; 2003b). Depending on the plant species and agro-ecological growing conditions, the excess assimilates can be up to 25% of the total aboveground biomass in the flowering phase (Pržulj and Momčilović, 2003b; Mirosavljević et al., 2018). During the irrigation phase, the assimilates are translocated in the grain, and in extremely arid conditions can participate 100% in the final grain mass (Pržulj and Momčilović, 2001b; Gutam 2011). In small grains, large genetic variation in the accumulation and remobilization of assimilates synthesized until flowering was found. Although effective selection techniques based on the accumulation and remobilization of assimilates have not yet been developed, Pržulj and Momčilović (2001b) suggest the use of data on the difference in stem mass between flowering and ripening. Morphological features can also be used to determine the efficiency of assimilate remobilization. Thus, for example, the presence of the tillering inhibitor gene causes the formation of a thicker stem. Variation in the size and anatomy of internode cavities has also been found to be important for the storage of assimilates (Ehdaie et al., 2006).

CONCLUSIONS

In plant breeding for yield and yield stability in drought conditions, a physiological approach can be extremely important support for empirical breeding. The simultaneous application of both breeding methods will produce drought-tolerant genotypes faster and more efficiently than using only one method. In essence, a physiological approach in breeding plants involves a new, more detailed and deeper way of thinking, linking plant development to environmental factors, paying more attention to factors affecting yield, using more diverse germplasm for breeding, and evaluating separation generations more effectively. Like the empirical and physiological breeding program, it requires considerable and long-lasting investment.

ACKNOWLEDGEMENTS

This work is a result of the research within the project Adaptive management of the natural resources of the Republic of Srpska, № 19.032/961-146/19, supported by the Ministry for Scientific and Technological Development, Higher Education and Information Society of the Republic of Srpska.

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