



Adaptive strategies to drought stress in grasses of the poaceae family under climate change: Physiological, genetic and molecular perspectives: A review

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ABSTRACT

Drought stress is one of the most critical abiotic factors which negatively impacts on growth, productivity, and survival of plants. Grass species have an important role in the sustainable intensification of cropping systems. This review focus on the specific drought tolerance characteristics in grass species and application of prevalent classical and molecular methods for genetic improvement of them to drought stress. Generally, grass species adapt to drought stress by utilizing more than one strategy including of changes in the root growth, photosynthetic pigments, activation of antioxidant enzymes, and accumulation of compatible osmolytes. They also have other specific characteristics consisted of summer dormancy, drought recovery, and persistence, which lead to drought adaptation after prolonged drought. Studies on different grasses, indicated that most of above mentioned traits usually have positive correlation with drought tolerance. Also, high heritability has been reported for most of them in different grasses. Therefore, an effective index might be considering in identification of drought tolerance genotypes. Recently, high-throughput imaging phenotyping and advanced molecular techniques such as genotyping-by-sequencing (GBS), RNA sequencing, genome-wide association study, and genome editing help conventional breeding methods to increase the accuracy, selection efficiency, genetic gains, and speed of breeding programs for developing drought tolerant cultivars.

1. Introduction

Global warming is an alarming situation all over the world, having significant effects on both cropping and livestock activities, through the changes in temperature and water availability (IPCC, 2021; Leisner, 2020). According to the predicted scenarios of climate change, greenhouse gases may increase the mean annual temperature between 1.5 and 2 °C which in turn will lead to more often and longer periods of drought in most of the crop growing regions in the world (IPCC, 2021). And in addition to the direct effect the climate change brings to agriculture, there will be socio-economic consequences, such as lower profitability, loss of employment and will increase instability within and among the countries (Leisner, 2020).

It is predicted that climate change will increase occurrence of drought in many areas of the world (Hail et al., 2020; IPCC, 2021;

Vaghefi et al., 2019). Drought stress is one of the main abiotic environmental stresses, negatively impacting plant growth, development, and ultimately yield production (Blum, 2011). Plants response to drought stress by changing their morphological, physiological, metabolic, biochemical, and molecular mechanisms (Akinroluyo et al., 2021; Farooq et al., 2009; Ilyas et al., 2021). Recently, breeders are looking for decreasing the negative effects of climate change and drought stress on agricultural productivity using agronomic management of crops and improvement of plant genetic through the classical and molecular methods (Qu et al., 2021; Wang and Brummer, 2012).

Grasslands cover about 70% of the world's agricultural land and thus are important components of ecological communities, playing an important role in climate regulation, carbon sequestration, protection and enrichment of the soil, forage production for animal farming, greenbelt, and preservation of biodiversity (Mara, 2012). The

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sustainability of both native and sown grasslands has been exposed to environmental fluctuations due to climate change (Bellocchi and Picon-Cochard, 2021). Drought stress as one of the most significant environmental constraints, reduces the photosynthetic pigments, stomatal conductance, biomass, growth, persistence, survival, and finally the forage yield and its components in grass species (Bao et al., 2013; Saeidnia et al., 2020). Therefore, understanding those mechanisms and using the knowledge gained in plant breeding programs is very important as it would help to improve plant adaptability to drought stress and thus increase or sustain plant productivity. Researchers report that grasses respond and adapt to drought stress with a variety of escape, avoidance, tolerance, and drought recovery mechanisms, thus making it a complex phenomenon (Pirnajmedin et al., 2015; Shaimi et al., 2009a and b; Wang and Huang, 2004). Drought escape is the ability of a plant to survive drought stress by becoming dormant during drought (perennial grasses) or completing and finishing its life cycle prior to drought occurrence (annual grasses) (Farooq et al., 2009). Drought avoidance can be achieved by maintaining internal water status by reducing water loss from plant canopy or increasing water uptake from the soil via roots and thus surviving or sustaining growth during drought (Farooq et al., 2009; Ilyas et al., 2021). Drought tolerance is the ability of plants to resist dehydration by maintaining metabolic processes such as osmotic adjustment even under decreased cellular water content, which allows plants to endure prolonged drought stress. The strategies are not mutually exclusive and are often combined consecutively or simultaneously, since the adapted plant species may utilize more than one strategy during drought stress period (DaCosta and Huang, 2007; Farooq et al., 2009; Ilyas et al., 2021). Resistance or adaptation to drought are the results of a complex combination of many variables, control by multiple genes and have quantitative inheritance. Hence, in breeding for drought tolerance, only one specific trait cannot be used as an effective factor in the selection of drought tolerant genotype but a set of traits should be considered as a selection criterion for detecting the desired genotypes and developing drought tolerant cultivars. In forage grass breeding programs, maintaining yield performance or producing high yield relative to other genotypes under drought stress conditions are criteria for being considered drought tolerance (Ebrahimiyan et al., 2012; Pirnajmedin et al., 2021). However, in turf species, low forage production, high extensive root system, recovery potential, and survival would be considered as drought tolerance criteria (Carrow and Duncan, 2003; Kanapeckas et al., 2008; Karcher et al., 2008). To achieve this goal and selecting drought tolerant genotypes, knowledge about the extent and nature genetic variation, heritability of drought tolerance related traits, and their association would be necessary (Annicchiarico et al., 2015; Pirnajmedin et al., 2017a).

This review encompasses an overview and discussion of the works reported on mechanisms and specific drought tolerance characteristics in grass species (generally from the poaceae family), along with application of most important and prevalent classical and molecular methods for genetic improvement of grass species to drought stress.

2. Important drought tolerance characteristics in grass species

Grass species response and adapt to water deficit by different changes in morphological, physiological, and biochemical characteristics such as root growth, water content, photosynthetic pigments, activation of antioxidant enzymes, and accumulation of compatible osmolytes (Ebrahimiyan et al., 2013; Fariaszewska et al., 2020; Pirnajmedin et al., 2015; Zhou et al., 2013). Grasses also have other specific characteristics, which lead to drought adaptation after prolonged drought stresses. These characteristics are including of summer dormancy, recovery after drought stress, and persistence (Kallida et al., 2016; Norton et al., 2008; Pirnajmedin et al., 2018).

2.1. Summer dormancy

Summer dormancy is acknowledged as an important drought resistance trait in some perennial grass species, controlled by endogenous processes leading to cessation of leaf growth, senescence, and reduction of biomass while keeping the plant meristems alive (Norton et al., 2008). This trait is expressed under subsequent long photoperiods and high temperatures in summer under full irrigation conditions and is regulated by circadian clock genes (Ding and Missaoui, 2017; Norton et al., 2006a, b; Salome et al., 2008). Summer dormancy indices have been recommended based on comparison with control cultivars with a known level of summer dormancy in order to identify the level of dormancy in plants (Norton et al., 2008; Shaimi et al., 2009a). However, it is more important for plants growing in the Mediterranean climate than the continental condition. Two groups of summer dormancy including complete or incomplete recognized in grass species (Norton et al., 2016; Volaire et al., 2001). Under complete summer dormancy, plants senescence and cease their growth for at least four weeks during summer regardless of soil moisture availability (Shaimi et al., 2009b). Under incomplete summer dormancy, plants exhibit moderate levels of senescence and significant reduction in growth without dehydration of leaf bases (Norton et al., 2006a,b). In both types, resumed growth occurs in autumn when the temperatures decrease and continues through late spring. The dormancy when plants reallocate energy resources and as a result inhibit meristematic activity and water use followed by the senescence of aboveground parts enables them to survive at higher rates severe and repeated summer drought and regrow afterwards (Annicchiarico et al., 2011; Ding and Missaoui, 2017; Shaimi et al., 2009b; Norton et al., 2008; Volaire et al., 2001). The studies on *F. arundinacea*, *D. glomerata*, and *B. inermis* has shown that summer dormancy type genotypes had slower growth rates and lower yield production during summer than during autumn and spring despite irrigation. Moreover, they had higher survival and recover rates under extended hot and dry conditions (Norton et al., 2016; Pirnajmedin et al., 2017b; Saeidnia et al., 2017b, 2018).

Therefore, breeding for drought tolerant of forage type varieties would need trading off between high yield, moderate level of summer dormancy, recovery, and survival after prolonged drought stress. While turf type grass breeding aims at slow growth and thus low forage production, extensive root system, survival, and recovery leading to high levels of summer dormancy and recovery after unfavorable conditions (Kanapeckas et al., 2008; Pirnajmedin et al., 2021).

Moderate to high value of narrow sense heritability reported for summer dormancy index in orchardgrass (0.64), indicating phenotypic recurrent selection would be effective for it (Pirnajmedin et al., 2018). However, there is a lack of available literature on the inheritance of summer dormancy in different perennial grass species thus more investigation is needed.

2.2. Post drought recovery

Post drought recovery is an important though complex strategy in survival and drought tolerance of grasses in the areas with limited rainfall and irrigation. Thus taking into consideration the mechanisms underlying plant survival and rapid recovery after long drought condition and upon re-watering or rainfall is very important (Couchoud et al., 2020; Pirnajmedin et al., 2018). This trait is related to preservation of growing points during prolonged water deficit, compensatory growth in surviving tissue, and the regeneration of new tissue from crowns, stolons, and rhizomes of grass plants (Chai et al., 2010; He et al., 2017). For evaluation of this trait in perennial grass species under field conditions in Iran, as an arid region, usually irrigation is withholding for a long time (between 30 and 60 days) to impose a severe drought until 90%–95% desiccation of foliage. Then, weekly irrigation was implemented (during 30–60 days) to allow for recovery from drought stress (Pirnajmedin et al., 2017b). After re-watering, based on the genetic variation in

each germplasm different levels of recovery (dead, no survival, low recovery, moderate recovery, and high recovery) were observed between genotypes (Abdollahi et al., 2019; Monje-Jimenez et al., 2019; Pirnajmedin et al., 2017b; Saeidnia et al., 2019).

Chai et al. (2010) compared post drought recovery of two C3 perennial grass species, *P. pratensis* and *L. perenne* in growth chamber. They indicated that *P. pratensis* had higher drought tolerance and recovery potential than *L. perenne*, which was due to the higher osmotic adjustment, cell wall elasticity, cell membrane stability, accumulation of carbohydrates in leaves, rhizomes growth during drought stress, and new root production after re-watering in this species. Xu et al. (2011) and Carrizo et al. (2020) introduced enhanced antioxidant enzymatic activities (e.g. CAT, POD, and APX) and relative water content (RWC) associated with rapidly post drought recovery in *Cenchrus ciliaris* L. and *P. pratensis* species. Other researchers found a high positive correlation between recovery after prolonged drought stress with total aerial biomass, persistence, winter growth vigor, extensive root system, and some morphological traits (e.g. plant height and crown diameter) in several perennial grass species, which can be predicted through developing an index (Abdollahi et al., 2019; Nie et al., 2008; Pirnajmedin et al., 2016; Saeidnia et al., 2019). Saeidnia et al. (2020a,b) reported that breeding system (self and open pollination) did not have significant effect on post drought recovery of *D. glomerata* and *B. inermis*. However, they indicated that *D. glomerata* had higher drought tolerance and post drought recovery potential than *B. inermis*, which is probably due to higher extensive root system in this species. Based on this study the values of heritability for post drought recovery was 0.20 and 0.30 in open pollinated and selfed populations of *D. glomerata*, respectively (Saeidnia et al., 2020a). Pirnajmedin et al. (2021) reported moderate narrow sense heritability value (0.44) for post drought recovery in half-sib families of *F. arundinacea*.

2.3. Persistence

Sustainable production and persistence over the years are other desirable traits in forage grasses, especially in arid and semi-arid regions of the world (Culvenor and Simpson, 2014; Jayasinghe et al., 2019). Persistence is affected by plant genotype, species, environmental factors, such as soil characteristics, temperature, precipitation and light, as well as genotype \times environment interaction effect and management consisting of irrigation, fertilization, soil management, pest, disease, and weed control, and etc. (Pirnajmedin et al., 2018; Nie et al., 2008; Woodward et al., 2019). This trait is defined as the plant ability to maintain a viable crown at the soil surface from which growth can regenerate and to survive over several growing seasons (Norton et al., 2016; Duchini Paulo et al., 2018). Persistence of the crops in the field is measured as the percentage of living plants in each plot over the years or as a measurement of plant viability, vitality, and fitness at the end of the seasonal growth and is assumed to be linked with survive through consecutive summer droughts (Norton et al., 2016; Poirier et al., 2012). However, on a single plant level, persistence of perennial grasses is usually considered as yield stability after successive years and mainly determined by the difference in performance of each genotype throughout the years (Pirnajmedin et al., 2017b; Saeidnia et al., 2019; Taleb et al., 2021). Recently, image analysis has also been used to evaluate the persistence of perennial ryegrass under field conditions providing canopy related information such as size, shape, texture, pattern, shadow, site, ground coverage, association between these characteristics, and finally persistence and dry matter yield (Jayasinghe et al., 2019). Studies indicated that summer dormancy and recovery after severe drought are positively associated with persistence in perennial grasses (Nie et al., 2008; Shaimi et al., 2009b). Also, positive correlation between various root traits, plant height, crown diameter, and number of stems per plant with persistence and drought tolerance have been reported in different grass species (Pirnajmedin et al., 2017b; Saeidnia et al., 2019). However, studies on the relation between

flowering time and persistence are controversial. Abdollahi et al. (2019) found a negative correlation between days to flowering with recovery and persistence in *D. glomerata* under drought condition, while Pirnajmedin et al. (2017b) reported a positive correlation between flowering and recovery and persistence in *F. arundinacea* under water deficit, which was possibly due to their high extensive root system, plant size, and crown diameter. The studies on *F. arundinacea*, *D. glomerata*, *B. inermis*, and *Panicum maximum* Jacq. revealed that water deficit significantly decreased persistence and drought tolerance of genotypes, resulting in decrement of crown diameter, plant height, growing points, and number of stems per plant (Abdollahi et al., 2019; Njarui et al., 2015; Pirnajmedin et al., 2018; Poirier et al., 2012; Saeidnia et al., 2017a). Saeidnia et al. (2020a, 2020b) documented that open pollination improved persistence in *B. inermis*, where heritability ranged from 19.26 to 16.76 in selfed and from 17.87 to 19.60 in open pollinated populations under normal and drought stress conditions, respectively. However, that was not the case for *D. glomerata* plants. Pirnajmedin et al. (2018) reported the moderate narrow sense heritability values (0.54 and 0.49 under normal and drought stress, respectively) in half-sib families of *D. glomerata* derived from polycrosses. This suggests that selection of abovementioned traits could help improving perennial grass persistence and thus developing superior varieties.

2.4. Root system

Plant roots play a major role in plant growth and biomass accumulation by exploiting soil resources via the uptake of water and nutrients and is the first organ that perceives and responds to water deficit (Wasaya et al., 2018). Hence, improving the root system for increasing the plant's ability in water and nutrient acquisition is very important and is known as a new green revolution in plant breeding programs (Herder et al., 2010). However, little information is still available on root growth and its genetic control in plants because it is underground organ thus studying it is inherently time-consuming, technically demanding and costly (Maeght et al., 2013). There are destructive and non-destructive methodologies for evaluation root characteristic of plants. Most of the studies have been using destructive method but recently, De Carvalho et al. (2020) used non-destructive method to evaluate the growth and distribution characteristics of the root system in perennial grass *Paspalum millegrana* Schrad. This methodology allows evaluation of root development in the soil profile using Digital Imaging Processing (DIP) and modeling (De Carvalho et al., 2020). High-throughput imaging phenotyping techniques, including visual and infrared thermal imaging, imaging chlorophyll fluorescence, and imaging hyperspectral spectroscopy, recently have been used to image morphological, physiological, and biochemical traits related to plant growth, yield, and adaptation to abiotic stresses of plants at different scales of organization (Biswas et al., 2020; Dao et al., 2021).

The root system architecture (RSA) is determined by crop species, soil type, soil temperature, moisture, fertility, and other environmental variables. Hence, there are different reports on the distribution patterns of roots in the vertical and horizontal, and amount root penetration in the soil profile under drought stress conditions (Panke-Buisse et al., 2020; Wasson et al., 2012). Studies revealed that drought stress reduces root characteristics such as root area, root length, root volume, and biomass but increases root to shoot ratio in most grass species (Abtahi et al., 2019; Pirnajmedin et al., 2016; Vries et al., 2016). Pirnajmedin et al. (2015) and Huang and Gao (2000) reported that intense drought stress significantly reduced root traits (such as root area, root volume, and root length) in *F. arundinacea* at the first layers of the soil (0–20 cm and 20–40 cm depths of the root zone), while increased them at the downer layers (40–60 depths). Increased root traits at deeper soil layers during drought stress has been considered as an important adaptation mechanism to improve the efficiency of water and nutrient uptake and drought tolerance in plants (Farre and Faci, 2009; Hanslin et al., 2019). Most of the studies revealed that root characteristics have been

associated with above ground growth and biomass formation, while the decline in biomass could be due to the decrease of root traits (Karcher et al., 2008; Pirnajmedin et al., 2017a; Taleb et al., 2021). Also, positive correlations were found between some of root traits such as root length, root area, root volume, and root to shoot ratio with drought tolerance index, persistence, and recovery in some grass species. This indicated that root traits can be used as an appropriate selection index for identifying preferable genotypes in the arid and semi-arid regions (Culvenor and Simpson, 2014; Karcher et al., 2008; Pirnajmedin et al., 2016; Taleb et al., 2021). In addition, when selecting for the genotypes with extensive root system the indirect outcome of this selection might be superior drought tolerant and persistent genotypes. Perlikowski et al. (2020) indicated that just long roots are not sufficient to perfectly avoid drought damage in *F. arundinacea* and the metabolic performance of roots is as crucial as its architecture for coping with drought stress via avoidance, tolerance, and regeneration strategies. The positive correlations between various root traits with proline, ascorbate peroxidase (APX), and peroxidase (POX) has been reported in *F. arundinacea* under drought stress conditions (Pirnajmedin et al., 2015). Still, little literature is available on the relationships of root traits with biochemical traits and metabolic performance of roots in grass species, which needs more investigation.

The range of narrow sense heritability for root traits is varies depending on experimental design and biometrical methods. The values of narrow sense heritability for different root traits in various populations of some studied grass species was shown in Table 1. It is notable that in most of these studies yield performance had lower heritability than root traits, indicating that indirect selection through root traits could be more efficient than direct selection for yield performance.

2.5. Physiological and biochemical characteristics

It has been demonstrated that physiological and biochemical characteristics through drought avoidance and drought tolerance mechanisms alleviated the detrimental effects of abiotic stresses such as drought (Farooq et al., 2009; Zhang et al., 2020). Therefore, investigation on these underlying mechanisms or traits contributing to drought tolerance would be beneficial for selecting superior genotypes and increasing the efficiency of breeding programs (Blum, 2018; Pirnajmedin et al., 2017b). However, the effects of drought stress on these traits are various and depend on the grass species, duration and intensity of drought.

Chlorophyll (*Chl*) is one of the major chloroplast components and an important factor in determining the photosynthesis capacity. Under drought stress, chloroplast ultrastructures are the first target to be damaged at the cellular level since they constitute the major site of reactive oxygen species (ROS) production (Farooq et al., 2009; Guan et al., 2015). Therefore, the decrease of chlorophyll content under drought stress has been considered a typical symptom of oxidative stress and may be the result of pigment photo-oxidation, chlorophyll degradation, and diminishing chlorophyll biosynthesis which can disrupt carbon stabilization and finally decrease plant growth and performance (Farooq et al., 2009; Liang et al., 2019). The decrease of chlorophyll *a*, *b*,

and total chlorophyll and increase of the *Chl a/b* ratio and carotenoids during drought stress has been reported in many grass species (Abtahi et al., 2019; Fariaszewska et al., 2020; Guan et al., 2015; Pirnajmedin et al., 2015). Carotenoids act as a non-enzymatic antioxidant and play a key role in stabilizing photosynthetic complexes, light harvesting and scavenging ROS caused by drought (Nisar et al., 2015). Therefore, selection of genotypes with high and stable chlorophyll content and carotenoids under drought stress may lead to prevention of yield loss and improve drought tolerance (Fariaszewska et al., 2020; Zhou et al., 2013). In some grass species, moderately to high narrow sense heritability has been reported for chlorophyll content and carotenoids under drought stress condition, indicating additive gene action play a major role in genetic control of these traits. Higher ratio of additive variance compared to other gene effects (such as dominance) indicated that phenotypic selection can be successful to achieve genetic progress (Abtahi et al., 2019; Pirnajmedin et al., 2017a; Saeidnia et al., 2018).

Osmotic adjustment (OA) is a biochemical mechanism that through accumulation of compatible solutes such as proline and carbohydrates can help plants to mitigate the drought stress (Marimuthu and Murali, 2018). These components can improve drought stress tolerance in plants by maintaining osmotic balance, decreasing the loss of water, preserving membrane structure, activating the antioxidant system, and reducing ROS (Blum, 2017; Pirnajmedin et al., 2015). Proline and carbohydrates contents known as important compounds and their increase during drought can help improving yield performance, drought tolerance, and survival (Aalipour et al., 2019; Ebrahimiyan et al., 2013; Fariaszewska et al., 2020). Pirnajmedin et al. (2017a) and Abtahi et al. (2019) reported high narrow sense heritability (more than 0.60) for proline content under drought stress in *F. arundinacea* and *B. inermis*, respectively. However, little information is still available on the inheritance of carbohydrates content in most of the grass species.

The ROS induces lipid peroxidation causing irreversible damage to membrane structural and its functional integrity as well as increase production of malondialdehyde (MDA) and electrolyte leakage in plant cells therefore can be use as valuable parameters for identification of stress tolerant genotypes in crops (Alam et al., 2018; Dias et al., 2018; Nisar et al., 2015). The antioxidant defense mechanism of plants protects them against damage caused by drought stress through scavenging ROS, maintaining a steady state of electrolyte leakage in cell fluid, and reducing lipid peroxidation (Nisar et al., 2015). Significant negative correlation was observed between MDA with antioxidative enzymes activities such as catalase (CAT), peroxidase (POX), and ascorbate peroxidase (APX), confirming the role of antioxidant enzymes in oxidative scavenging and finally association of antioxidative mechanism with drought tolerance in grass species (Aalipour et al., 2019; Alam et al., 2018; DaCosta and Huang, 2007). Nevertheless, the inheritance of antioxidant enzymes is poorly understood in grass species.

The perceived stress signal is converted to increased levels of abscisic acid (ABA) production and accumulation in stomatal guard cells which regulate transpiration through stomata closure and thus conserve water in tissues (Pardo et al., 2020; Sun et al., 2021). Hence, increasing of ABA negatively affects the photosynthetic activity and aboveground biomass accumulation, but at the same time positively affects the growth and

Table 1

The range of narrow sense heritability for root traits in various populations of some grass species.

Grass species	Studied population	Root traits	Range of narrow sense-heritability	References
<i>Lolium perenne</i>	Half-sib families derived from open pollination	Root mass, root growth, and root to shoot ratio	0.29 to 0.35	Crush et al. (2006)
<i>Agrostis palustris</i>	Parent-offspring regression method	Root number, root area, and root length	0.61 to 0.82	Lehman and Engelke (1991)
<i>Festuca arundinacea</i>	Half-sib families derived from polycross	Root length, root volume, root area, root weight, and root to shoot ratio	0.42 to 0.84	Pirnajmedin et al. (2017a)
<i>Dactylis glomerata</i>	Half-sib families derived from polycrosses	Root length, root volume, root area, root weight, and root to shoot ratio	0.45 to 0.61	Abtahi et al. (2017)

development of roots that largely help to overcome stress (Chen et al., 2019; Sun et al., 2021). ABA also plays an important role in inducing the protective role of dehydrins (DHNs). DHNs, subfamily of group 2 LEA (Late Embryogenesis Abundant) proteins, accumulate typically in maturing seeds or are induced in vegetative tissues following salinity, dehydration, cold and freezing stresses (Liu et al., 2017). It has been reported that DHNs play a fundamental role adaptation to abiotic stresses through binding and protection of membranes and DNA, scavenging ROS and oxidative modification in grass species such as bermudagrass, Kentucky blugrass, and fescue wild grass (Fan et al., 2017; Hu et al., 2010; Qiu et al., 2021). However, little information is still available on the inheritance of these traits in grass species.

Relative water content (RWC) is one of the well-known physiological responses to drought stress thus can be used as an indicator of plant water status for determining homeostasis and water relation in plants when breeding for drought tolerance (Soltys-Kalina et al., 2016; Wang et al., 2019). Usually, drought tolerant genotypes had higher values of RWC than susceptible genotypes under drought stress condition, which can be due to their higher potential to absorb water or loss less water through the stomata (Anjum et al., 2011). Research studies in different grass species such as *Festuca arundinacea* L., *Dactylis glomerata* L., *Bromus inermis* L., *Poa pratensis* L., *Lolium perenne* L., and *Cynodon dactylon* L. indicated that drought stress causes reduction in RWC, resulting in reduction of photosynthesis and leading to lower yield (Aalipour et al., 2019; Abtahi et al., 2019; Alam et al., 2018; Fu, 2003; Pirnajmedin et al., 2015; Zhou et al., 2013). The range of narrow sense heritability for this trait was reported from 0.53 to 0.59 in *B. inermis*, from 0.56 to 0.50 in *D. glomerata*, and from 0.30 to 0.59 in *F. arundinacea* under normal and intense drought stress conditions, respectively (Abtahi et al., 2019; Pirnajmedin et al., 2017a; Saeidnia et al., 2018).

3. Conventional breeding method of grass species

The best and nearly most sustainable way to deal with climate change and its effects such as drought stress is developing breeding varieties with better adaptation to changes in seasonal pattern and increased variation of precipitation, temperature, and length of the growing seasons (Gary et al., 2017). Most of the grass species are open-pollinated, polyploids, and have large and highly heterozygous genome (Talukder and Saha, 2017). Hence, breeding outcrossing grass species is very difficult due to their high degree of self-incompatibility, cleistogamous flowers, and complexity of genome (Buckner, 1960). In this kind of grasses, the general breeding goal has so far been focused on developing improved synthetic varieties (Nguyen and Sleper, 1983; Welu, 2016). For this purpose, half-sib mating including open-pollination, topcross, and polycross are common and cost effective breeding procedures for evaluating general combining ability (GCA) of parental clones for development of synthetic variety, creating a basic pool of genetic variation in recurrent selection programs, and obtain quantitative genetic information (Aastveit and Aastveit, 1990; Sam-poux et al., 2020). Generally, in polycross breeding procedure, a relatively large number of superior genotypes inter cross in such a way to promote random pollination and create a various genetic combination in the progenies. Then, seeds from crossed genotypes are often harvested separately from individual genotype to produced half-sib families in order to preserve maternal parent, whereas paternal parent is usually unknown. These half-sib progenies are used for further evaluation, determining the GCA, and selection of best parents. These superior parents serve as base population that with inter-crosses during one to two generation can constitutes the synthetic cultivar (Fig. 1) (Riday et al., 2013; Rognli et al., 2021; Qu et al., 2021). Since genetic variance among half-sib families created by polycross or open-pollination is essentially quarter of the additive genetic variance ($\sigma_F^2 = 1/4 \sigma_A^2$), estimation of genetic parameter based on half-sib family evaluation gives a good prediction of narrow-sense heritability (Kearse and Pooni, 1996; Sleper and Poehlman, 2006). The genetic information and heritabilities

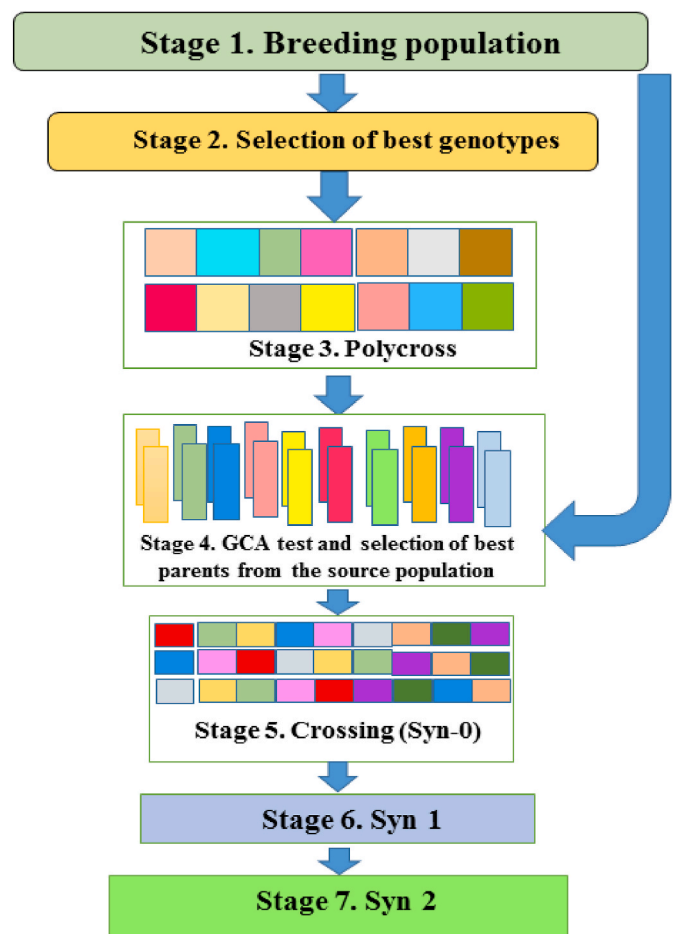


Fig. 1. Overview of developing synthetic varieties in grass species. Step 1: Breeding population which is including of collection of varied genotypes from different regions. Step 2: selection of best genotypes as parental genotypes based on the field experiment and visual evaluation. Step 3: polycross is inter cross between relatively large number of superior genotypes in such a way to promote random pollination and create a various genetic combination in the progenies. Step 4: Sowing polycross progenies in replicated experiment and doing the general combining ability (GCA) test, then selection of best parental genotypes (clones) from the source population. Step 5: Syn-0 is intercross between the selected best parental genotypes. Step 6: Equal amount of seed harvested from each clone and mixed the seeds. The harvested seeds name Syn1. Step 7: Open pollinate to form Syn2.

of different agro-morphological traits have been estimated in some species including of *D. glomerata*, *F. arundinacea*, *B. inermis*, and *Bromus riparius* Rehm. using half-sib families derived from polycross and open pollination breeding methods. Most of these studies reported low to a moderate value of heritability for forage yield and moderate to high values for yield-related traits such as plant height, crown diameter, and the number of stems per plant (Amini et al., 2013; Araghi et al., 2014; Araujo et al., 2002; Pirnajmedin et al., 2017a; Qu et al., 2021; Saeidnia et al., 2019; Shaimi et al., 2009a).

However, classical or conventional breeding methods in grass species are useful, but are time consuming for crossing, selection, and progeny testing and can take one or two decades to create new variety (Ahmar et al., 2020). Therefore, use of molecular techniques and tools along with conventional breeding methods in grasses can increase the accuracy and speed of the breeding programs for developing tolerant cultivars.

4. Molecular achievements in breeding of grasses

Conventional breeding techniques are still the most practical and efficient methodologies but are not sufficient to cope with the increasing demand for both feed and food. Plant breeding, combined with molecular genetic tools and biotechnology, which revolutionized in the 21st century, increased the accuracy and genetic gains of breeding practices, gene scope and expression, and speeded up the development of new varieties for future climate conditions (Akinroluyo et al., 2019, 2020; Rauf et al., 2021; Talukder and Saha, 2017).

4.1. Genotyping by sequencing and genome-wide association study

In general, whole genome sequencing of most of grass species is not available due to their complex genomes, which make a little difficult the molecular studies in these grasses. Until now, perennial ryegrass and *L. multiflorum* draft genome sequences are available and genome sequencing of intermediate wheatgrass is underway (Byrne et al., 2015; Dorn, 2017a, 2017b). However, molecular characterization of un-sequenced plant species such as *D. glomerata*, *P. pratensis*, *F. arundinacea*, and *Agrostis* spp. is now possible by genotyping-by-sequencing (GBS) using recent next generation sequencing technologies or *de novo* assembly of the whole genome using other sequenced C3 grasses. This method can provide identification of genome-wide variations, millions of SNPs, candidate genes or useful markers for increasing selection efficiency and genetic gains in breeding plans (Baral et al., 2018; Talukder and Saha, 2017). Recently with advancing in genotyping technologies, association or linkage disequilibrium (LD) mapping using a genome-wide association study (GWAS) became an approach for unraveling the molecular genetic basis underlying the natural phenotypic variation (Jaskune et al., 2020). For performing a successful GWAS experiment three important stages, namely phenotyping, genotyping, and combining phenotyping and genotyping data using appropriate software are necessary (Fig. 2) (Alqudah et al., 2020). The GWAS methodology has been used to identify candidate

genes significantly associated with winter survival and spring regrowth in *L. perenne* and identify association between agronomic traits with SSR markers in *F. arundinacea* (Yu et al., 2015; Lou et al., 2015). Using GWAS technology, Jaskune et al. (2020) could discover single nucleotide polymorphism (SNP) markers, which were adjacent to genes predicted to encode phytochrome B (*PhyB*) and a *MYB41* transcription factor in *L. perenne*. They indicated that expression of *PhyB* and *MYB41* genes were associated with leaf growth and yield productivity in *L. perenne* through modulating drought stress response, so identified SNP markers can serve as a valuable resource in future breeding programs for enhanced biomass formation under drought stress conditions (Jaskune et al., 2020). Saeidnia et al. (2021) utilized association analysis to identify the association of 626 SRAP markers with important agronomic traits and drought tolerance indices in *B. inermis*. They reported that Me1/Em5–11, Me1/Em3–15, and Me5/Em4–7 markers were associated with drought tolerance and can be used for marker assisted selection (MAS) in the future breeding programs of *B. inermis*. For the first time, mapping QTL for summer dormancy and its related traits has been done through bi-parental crosses (pseudo testcross population) in *F. arundinacea* by Talukder Shyamal et al. (2020). In this study, seven QTL associated with summer dormancy and its related traits such as plant height, tiller number, plant moisture content, and dry yield were identified, suggesting they can be valuable resources to the *F. arundinacea* breeders for initiating marker-assisted breeding and developing cultivar with adequate summer dormancy (Talukder Shyamal et al., 2020). In another research in *F. arundinacea*, association between summer dormancy with 23 various candidate genes involved in seasonal dormancy, meristem determinacy and growth, flowering time, heat shock proteins, and ABA synthesis has been investigated (Ding and Missaoui, 2017). The results of this study indicated that some of the heat shocks proteins and meristem determinacy and growth genes were involved in summer dormancy in *F. arundinacea* (Ding and Missaoui, 2017). Detection of quantitative trait loci (QTLs) for physiological and biochemical characteristics is also very important basis for identifying the genetic mechanisms of drought tolerance. Several QTLs for

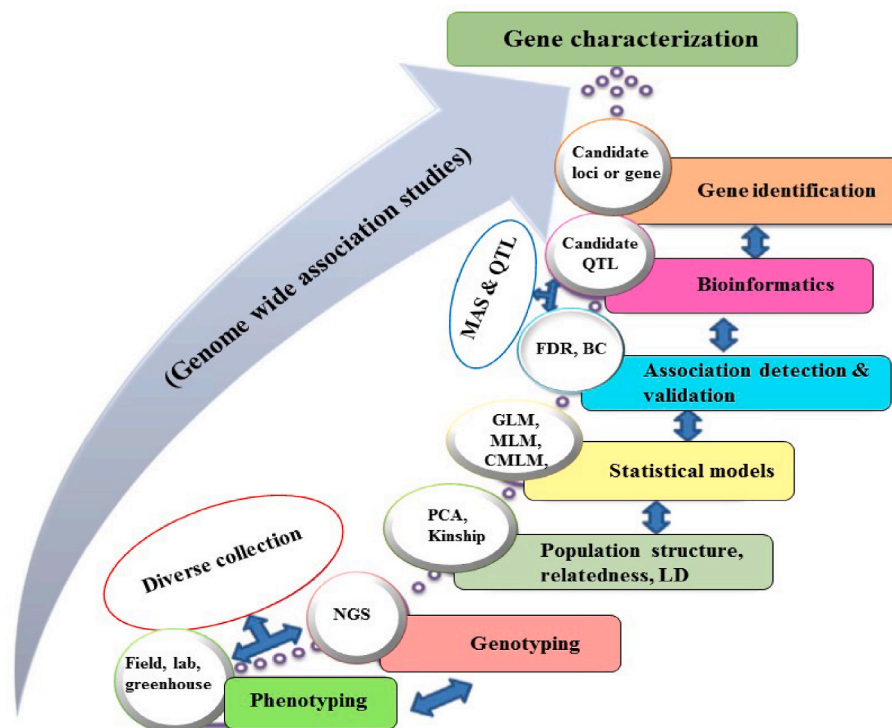


Fig. 2. Overview of three important stages of genome wide association studies (GWAS), including of phenotyping, genotyping, and combining phenotyping and genotyping data using appropriate software.

chlorophyll content and relative water content were detected in different grass species, which were associated with drought tolerance (Des Marais et al., 2016; Jiang et al., 2017; Merewitz et al., 2014).

4.2. RNA-sequencing

Another useful method for genome study of un-sequenced plant species is whole genome next-generation transcriptome sequencing or RNA sequencing (RNA-seq), which is easier than GBS in grasses with complex polyploidy genomes (Grabherr et al., 2011). The RNA-seq method has been used to capture differential gene expression, study alternative splicing, determine exon/intron boundaries, identify SNP markers and simple sequence repeats (SSRs), study transcription factors, microRNA, ribosomal RNA, transfer RNA, and small nuclear RNA (Kukurba and Montgomery, 2015; Talukder et al., 2015). Talukder et al. (2015) performed transcriptome profiling in drought tolerant and susceptible genotypes of *F. arundinacea* to unravel the genetic regulatory mechanism of drought stress responses. This study led to identification of SSRs and SNPs markers, genes and transcription factors related to drought stress in *F. arundinacea* and facilitation marker-assisted breeding in this plant (Talukder et al., 2015). Zhang et al. (2019) could also identify genes and transcriptional factors related to drought tolerance such as *FaAAO1*, *FaZEP*, and *FaNCD3* (involvement in ABA synthesis under drought stress), *FaHSP17*, *FaHSP70*, *FaHSP90* (heat shock proteins), *FaMPK3* (involvement in kinase activities), *FaDREB2A* (involvement in ABA synthesis under drought stress), and *FaHsfA2C*, *FaMYB2*, and *FaMYC4* (effective transcriptional factors in response to salt and drought stresses) using RNA sequencing in *F. arundinacea*. Zhang et al. (2018) evaluated the molecular responses of *Panicum virgatum* L. to dehydration stress through RNA-seq and identified that transcriptional factor *MYB* and genes *NCED* (involvement in ABA synthesis), *P5CS* (involvement in proline synthesis) are involved to drought tolerance of this plant. Recently, several researchers used RNA-seq method to determine the molecular mechanism of metabolic responses of grasses under drought stress conditions and to identify a large quantity of differentially expressed genes (DEGs) associated with drought stress response e.g. in *Pennisetum Giganteum*, *Psammochloa villosa*, and *Lolium multiflorum* (Akinroluyo et al., 2021; Cheng et al., 2022; Liu et al., 2022; Zhou et al., 2021). The results of these studies, provide not only insights into the genomics of adapting drought tolerance in grasses, but also candidate genetic resources involved in drought tolerance research. Akinroluyo et al. (2021) assessed the expression pattern of drought related genes between diploid and tetraploid lines of *Lolium multiflorum* using RNA-seq method. They demonstrated that tetraploid lines of *L. multiflorum* had higher drought tolerance and survival than diploid lines, due to the higher expression level of genes encoding functional proteins and dehydrin (*Dh3*) in tetraploid lines. Zhou et al. (2021) reported that the expression of DEGs (a total of 16,726 and 46,492 after 7 and 14 days of drought stress, respectively) and the identification of the hub gene encoding β -glucosidase can help elucidate the response mechanism, rehydration recovery, and physiological indices of *P. Giganteum* during drought stress condition. Using full-length isoform sequencing and *de novo* assembly from short reads Liu et al. (2022) obtained 119,005 unigenes representing the transcriptome of *P. villosa* under drought stress and, identified 3089 DEGs and 1484 transcription factors. According to this study, the relative expression of eight genes were involved in the mitigation of radical oxygen species (ROS), DNA repairing, and transmembrane transporter activity in *P. villosa*. The results of this study demonstrated that *P. villosa* improves its drought resistance through various pathways, including regulation of calcium-dependent protein kinase, malate dehydrogenase, photosynthesis, and drought-induced protein (*Di19*) (Liu et al., 2022). For the first time, comprehensive and comparative analyses of physiology and transcriptomic changes in the roots of *L. multiflorum* under drought stress was done by Cheng et al. (2022) to elucidate the molecular mechanism of root drought resistance. Based on this research, 8588

DEGs related to drought tolerance in root were identified, which were mainly enriched in oxidation-reduction process, carbohydrate, apoplast, metabolic process, arginine and proline metabolism, and phenylpropanoid biosynthesis pathways. Genes related to sucrose and starch synthesis, root development (*XTH* gene involvement in root structure, root vigor, and ABA signal regulation), osmotic adjustment, and specifically up-regulated transcription factor genes such as *WRKY41*, *WRKY51*, *ERF7*, *ERF109*, *ERF110*, *NAC43*, *NAC68*, *bHLH162*, and *bHLH148* were discovered that are involved in drought tolerance responses (Cheng et al., 2022).

4.3. Genome editing

The application of modern gene editing techniques especially clustered regularly interspaced short palindromic repeats (CRISPR) allows addressing several challenges caused by climate change and abiotic stresses for developing forage grass cultivars with improved adaptation to the future climatic conditions. Genome editing has several advantages over the transgenic techniques including precision, lower number of off-target effects, more streamlined production, multiplex possibility, as well as potential for modification of many more different traits (Sustek-Sánchez et al., 2023). However, application of these approaches in grasses of the poaceae family has been much slower pace than for other crops in particular wheat, barley, rice, maize, and etc., due to the reproductive and genetic characteristics of them which are difficult to work with (Li and Iqbal, 2024; Sustek-Sánchez et al., 2023). Genome editing in grasses of the poaceae family is in its early stages and generally the first attempts of it has been done in *Lolium multiflorum*, *Lolium perenne*, *Panicum virgatum*, and *Lolium arundinaceum* with CRISPR-Cas tools (Liu et al., 2020; Zhang et al., 2020, 2021).

5. Summary and future prospective

Drought stress is one of the most common stresses encountered by grasses and other plants and leads to significant growth, productivity, quality, and survival losses. Plants can adapt to drought stress in many different ways by changing morphological, physiological, biochemical, and molecular processes. Therefore, having deeper understanding about plant response mechanisms against drought stress is very crucial to mitigate the effects of drought stress on plants. In grass species, characteristics associated with drought tolerance are very varied and sometimes specific to these plants. The most important of these traits are summer dormancy, post drought recovery, persistence, extensive root system, physiological, and biochemical characteristics effective in reducing ROS, regulating leaf water potential, osmotic adjustment, and reducing yield loss (e.g., accumulation of compatible osmolytes, antioxidant enzymes, and photosynthetic pigments). In grass breeding programs, only one specific trait cannot be used as an effective factor in the selection of drought tolerant genotype, and based on the breeding purpose an index of traits should be considered as a selection criterion for selecting the desired genotypes and ultimately producing drought tolerant cultivars.

Studies indicated that in most grass species, genotypes with high extensive root system, osmotic potential, and photosynthetic pigments having the high ability of persistence, recovery, and drought tolerance. Also, it has been reported that summer dormancy leads to decreasing of forage yield during hot and dry summer, while increasing of recovery and survival of grasses after long drought stress period. In several grass species, most of root characteristics and physiological traits having high narrow sense heritability than dry forage yield, suggest that these traits are mainly under additive genetic control and recurrent selection may be effective to achieve genetic progress. On the other hand, these traits could be used in an appropriate selection index to enhance forage yield, persistence, and recovery potential of grasses and identify preferable genotypes in the arid and semi-arid regions. Actually, in forage grass species the breeding purpose is having genotypes with preferable

performance, recovery and survival after long drought stress condition. Therefore, for selecting suitable genotypes, it would be necessary to tradeoff between preferable performance, extensive root system, moderate level of summer dormancy, and high level of recovery, and survival after prolonged drought stress. However, in turf grass species the main breeding purpose is increasing of plant survival and recovery; therefore, selection based on the extensive root system and high level of summer dormancy and recovery would be suitable. Recently, the use of molecular techniques and tools (e.g., genotyping-by-sequencing RNA sequencing and genome-wide association study) along with conventional breeding methods in grasses increased the accuracy and speed of breeding programs for producing drought tolerant cultivars. In grasses, these techniques have been instrumental in assessing genetic diversity, molecular identification of paternal parent in open pollination populations, determining the gene loci, genome sequencing, and identification of genes associated with drought tolerance, which could increase selection efficiency and genetic gains in breeding programs.

Some of research scopes has been less investigated in grass species and should be more consider in the future studies, since can provide a much richer information about drought stress tolerance strategies in grasses. For example, study of microbial functional capacity (such as inoculation with fungi, bacteria, viruses, and several bacterial elements) will help identify specific activities that are enriched or depleted under drought and how such shifts contribute to observed community abundance trends (Shaffique et al., 2022). In addition, research to identify the effect of microbes on root system, persistence, recovery, and different physiological and biochemical characteristics grasses under drought stress condition is needed. These kind of research can provide this facility to identify the most appropriate and effective microbes, dealing with the evaluating potential organisms in the field for microbial formulations to improve plant performance under drought stress and significantly lower yield losses in drought-affected areas.

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Declaration of competing interest

The authors declare that there is no conflict of interest.

Data availability

No data was used for the research described in the article.

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