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# Environment-oriented selection criteria to overcome controversies in breeding for drought resistance in wheat

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## Abstract

Wheat is one of the most important cereal crops, representing a fundamental source of calories and protein for the global human population. Drought stress (DS) is a widespread phenomenon, already affecting large wheat-growing areas worldwide, and a major threat for cereal productivity, resulting in consistent losses in average grain yield (GY). Climate change is projected to exacerbate DS incidence and severity by increasing temperatures and changing rainfall patterns. Estimating that wheat production has to substantially increase to guarantee food security to a demographically expanding human population, the need for breeding programs focused on improving wheat drought resistance is manifest. Drought occurrence, in terms of time of appearance, duration, frequency, and severity, along the plant's life cycle varies significantly among different environments and different agricultural years, making it difficult to identify reliable phenological, morphological, and functional traits to be used as effective breeding tools. The situation is further complicated by the presence of confounding factors, e.g., other concomitant abiotic stresses, in an open-field context. Consequently, the relationship between morpho-functional traits and GY under water deficit is often contradictory; moreover, controversies have emerged not only on which traits are to be preferred, but also on how one specific trait should be desired. In this review, we attempt to identify the possible causes of these disputes and propose the most suitable selection criteria in different target environments and, thus, the best trait combinations for breeders in different drought contexts. In fact, an environment-oriented approach could be a valuable solution to overcome controversies in identifying the proper selection criteria for improving wheat drought resistance.

**Keywords:** Climate change, phenotyping, morphological and functional traits, target environment, grain yield

- 1 **List of abbreviations**
- 2 Chlorophyll-a (Chl a)
- 3 Chlorophyll-a singlet state (1Chl\*)
- 4 Chlorophyll-a triplet state (3Chl\*)
- 5 Critical Temperature (Tcrit)
- 6 Drought Stress (DS)
- 7 Drought Susceptibility Index (DSI)
- 8 Dry Weight (DW)
- 9 Fresh Weight (FW)
- 10 Full Turgor Weight (TW)
- 11 Genome Wide Association Study (GWAS)
- 12 Genotype x Environment (GxE)
- 13 Geometric Mean Productivity (GMP)
- 14 Gibberellic Acid (GA)
- 15 Grain Filling (GF)
- 16 Grain Yield (GY)
- 17 Harmonic Mean (HARM)
- 18 Harvest Index (HI)
- 19 Heat Stress (HS)
- 20 Internal CO<sub>2</sub> Concentration (Ci)
- 21 Leaf Area Index (LAI)
- 22 Leaf Rolling (LR)
- 23 Marker Assisted Selection (MAS)
- 24 Maximum quantum efficiency of photosystem II (Fv/Fm)
- 25 Minimal Chl a fluorescence (F<sub>0</sub>)
- 26 Mean Productivity (MP)
- 27 Net Photosynthesis (Pn)
- 28 Non-Photochemical Quenching (NPQ)
- 29 Peduncle Length (PL)
- 30 PhotoSystem II (PSII)
- 31 Plant Height (PH)
- 32 Polyethylene Glycol (PEG)
- 33 Quantitative Trait Loci (QTLs)
- 34 Reactive Oxygen Species (ROS)
- 35 Relative Water Content (RWC)
- 36 Ribulose 1,5-BisPhosphate (RuBP)
- 37 Stomatal Conductance (g<sub>s</sub>)
- 38 Stress Susceptibility Index (SSI)
- 39 Stress Tolerance Index (STI)
- 40 Thousand Kernel Weight (TKW)
- 41 Tolerance Index (TOL)
- 42 Transpiration (E)
- 43 Vapour Pressure Deficit (VPD)
- 44 Water Use Efficiency (WUE)
- 45 Yield Index (YI)
- 46 Yield Stability Index (YSI)
- 47

## 1 **Wheat worldwide relevance and drought threat**

2 Wheat is one of the most important cereal crops worldwide. It ranks first for global harvested area  
3 (219 Mha in 2020), and second in terms of global production (761 Mt in 2020) behind corn  
4 (FAOSTAT dedicated website, visited 04/26/2022), thereby representing a fundamental agricultural  
5 source of calories and protein for the human population, and an essential source of income for millions  
6 of farmers (Pena-Bautista et al., 2017). Drought stress (DS) is one of the major and widespread threats  
7 for cereal productivity, resulting in consistent losses in average grain yield (GY), affecting large areas  
8 of Europe, Africa, Asia, Australia, South America, Central America, and North America (Daryanto  
9 et al., 2016; Hazaymeh et Hassan, 2016, Zampieri et al., 2017). Climate change is projected to  
10 exacerbate DS incidence and severity by increasing temperatures and changing rainfall patterns.  
11 Extreme meteorological events, e.g. heat waves and drought spells, which have already increased in  
12 many regions, are projected to intensify, both in intensity and duration, in most parts of the world,  
13 including many wheat-growing regions that are naturally prone to drought, such as Mediterranean  
14 climatic zones and semi-arid tropics (Berger et al., 2016; Jia et al., 2019). Estimating that wheat  
15 production has to increase by about 70% by 2050 to guarantee food security to a demographically  
16 expanding human population (CIMMYT, 2014; Mylonas et al., 2020), the need for breeding programs  
17 which focus on the development of wheat cultivars with improved drought resistance is  
18 unquestionable (Merchuk-Ovnat et al., 2016). Increasing wheat drought resistance is thus a key goal  
19 and involves not only bread wheat (*Triticum aestivum* L.), but also durum wheat (*Triticum turgidum*  
20 L. ssp. *durum*). The latter, despite representing only 8% of total wheat production (Sukumaran et al.,  
21 2018; Igrejas et al., 2020), is typically grown in semiarid countries of the Mediterranean basin  
22 (Southern Europe, North Africa, and the Middle East) (Del Moral et al., 2003), where it is a  
23 fundamental staple food. This area, where about 60% of global durum wheat is cultivated, mainly as  
24 a rainfed crop (Giraldo et al., 2016), is already prone to low and erratic precipitation profiles and is  
25 severely threatened by climate change, as climatic projections foresee a rise in temperatures and a  
26 simultaneous reduction in precipitation for this region, with important yield losses expected (Flato et  
27 al., 2013).

28

## 29 **Difficulties in breeding for drought resistance**

30 Drought resistance can be defined as the capacity of a crop to successfully produce a satisfactory  
31 yield in water shortage conditions (Luo et al., 2010). It is a complex quantitative trait, resulting from  
32 numerous mechanisms adopted by plants to cope with water scarcity, comprising a broad spectrum  
33 of morphological, physiological, biochemical and molecular processes activated at different  
34 phenological stages (Rampino et al., 2006; Nezhadahmadi et al., 2013). All these adaptations can  
35 confer drought resistance through drought escape (ability to complete the life cycle before stressful  
36 conditions appears), avoidance (ability to maintain a good water status in a drought context) or  
37 tolerance (ability to withstand dehydration) (Ludlow, 1989 – cited by Kooyers, 2015). The highly  
38 significant Genotype x Environment (GxE) interactions consistently reduce yield heritability in  
39 drought contexts (Farooq et al., 2014), making genetic improvement very challenging for breeders.  
40 Differences in drought occurrence along the wheat life cycle, in terms of time of appearance, duration,  
41 frequency and severity, are highly significant among different environments (Reynolds et al., 2005).  
42 Moreover, in rainfed conditions, weather fluctuations in terms of temperature and precipitation  
43 distribution in the cropping season produce a consistent genotype x year interaction, further  
44 complicating the direct or indirect selection for yield in an open-field environment (Ahmadizadeh et  
45 al., 2012; Budak et al., 2013; Mohammadi et al., 2019). The concomitancy with other abiotic stresses

1 must also be taken into consideration (see section 2.5). In this review, we report first on the direct  
2 selection for yield and highlight strengths and weaknesses of this approach. Phenological,  
3 morphological, and functional traits associated with GY in drought conditions, commonly used in the  
4 indirect selection for yield, are then dissected, highlighting the controversies that have emerged  
5 regarding their reliability as effective breeding tools. In fact, morpho-functional traits related to wheat  
6 drought resistance are well-known and documented, as reviewed by Khadka et al. (2020), but  
7 evidence is still contradictory regarding the reliability of such traits as indirect selection criteria for  
8 final GY. Disputes remain over which of these traits are most desirable (e.g., tall vs short genotypes),  
9 as a consequence of the high variability of drought scenarios in terms of duration, timing and severity.  
10 In an attempt to overcome these controversies, here we analyze the available literature, identify the  
11 possible causes of these disputes and, finally, offer a proposal for the most suitable selection criteria,  
12 and thus the best trait combinations, for breeders in different drought contexts.

13

## 14 **1. Direct selection for yield**

15 Despite all the above-mentioned difficulties, the selection for yield (commonly referred to as “direct  
16 selection”) is still considered a valuable strategy, precisely because of the general lack of  
17 understanding of physiological and molecular processes underlying DS response in wheat (Dugasa et  
18 al., 2019; Patel et al., 2019). In an attempt to overcome the discrepancies arising from differences in  
19 drought frequency, duration, and/or severity, several researchers have suggested selection criteria  
20 based only on yield in non-stress conditions, where the low GxE interaction should permit the full  
21 expression of a genotype’s yield potential (Rajaram et Van Ginkle, 2001 - cited by Patel et al. 2019).  
22 The main limitation of this approach is that genotypes with high potential yield under non-stress  
23 conditions may not necessarily result in high yield under drought (Patel et al. 2019). Similarly,  
24 genotypes with satisfactory yield under stress conditions may not be the best choice in favorable  
25 agronomic years because of a low yield potential (Mohammadi et al., 2010). A possible solution is to  
26 prefer genotypes with high yield potential in mild-stress environments, and to prefer highly resistant  
27 ones with low yield potential in severe stress contexts (Voltas et al., 1999 – cited by Mohammadi et  
28 al., 2010). Instead of this dichotomous selection, authors currently prefer a mid-point solution that  
29 considers yield in both stress and non-stress conditions, aiming to a more exhaustive, comprehensive  
30 and efficient selection, especially under unpredictable yearly drought scenarios in rainfed  
31 environments (Mohammadi et al., 2010; Patel et al., 2019). For this purpose, multiple indices have  
32 been proposed in the past (Fischer & Maurer, 1978; Rosielle and Hamblin, 1981; Bouslama and  
33 Schapaugh, 1984; Fernandez, 1992; Schneider et al., 1997; Gavuzzi et al., 1997), as reported in Table  
34 1.

35 Several authors have conducted experiments to identify the most suitable indices for successful  
36 breeding (Golabadi et al., 2006; Mohammadi et al., 2010; Mohammadi et a., 2011; Ahmadizadeh et  
37 al., 2012; Patel et al., 2019). Based on their findings, it is advisable to conduct the selection process  
38 under mild stress conditions. This is due to the fact that severe stress causes massive yield reduction  
39 for most genotypes, thus reducing phenotypic variability. Moreover, different indices provide  
40 different information. SSI, TOL, and YSI allow identifying genotypes with satisfactory yield in  
41 stressful environments, but with low yield potential in favorable ones. On the contrary, STI, GMP,  
42 MP, YI, and HARM identify high-yielding genotypes both in stress and non-stress contexts.  
43 Therefore, the most suitable index for screening of drought-resistant genotypes mainly depends on  
44 the environment, in particular by taking into account how frequently and severely drought years occur  
45 compared to favorable ones (Table 1).

1 Direct selection, in general, allows breeders to bypass the understanding of the complex morpho-  
2 functional and biochemical processes regulating the overall phenomenon of drought resistance.  
3 However, this approach is very expensive in terms of time and resources, and is largely affected by  
4 the inevitable fluctuation of agricultural years.

5 Modern Marker Assisted Selection (MAS) strategies can represent a valid solution to improve the  
6 efficiency of direct selection. Wheat landraces and wild progenitors carry an interesting allelic  
7 repertoire for abiotic stresses resistance (Budak et al., 2013; Lopes et al., 2015). Typically, these  
8 genotypes are characterized by satisfactory stable yields in harsh environments, but low yields in  
9 high-input unstressed conditions. Differently, elite modern wheat cultivars are highly responsive in  
10 terms of GY in high-input management, but in case of stress occurrence and adverse conditions their  
11 yield benefit is not so obvious (Rebetzke et al., 2011). MAS can be used to transfer from wild relatives  
12 to modern cultivars genes/Quantitative Trait Loci (QTLs) conferring tolerance to several biotic and  
13 abiotic stresses (Merchuk-Ovnat et al., 2016). Molero et al. (2022) performed a Genome Wide  
14 Association Study (GWAS) on 149 spring wheat lines, identifying promising exotic alleles for heat  
15 stress (HS) tolerance in *Aegilops tauschii* (the ancestral donor of the D genome). Similarly, Merchuk-  
16 Ovnat et al. (2016), used a recombinant inbred line population derived from a cross between durum  
17 wheat and wild emmer, to map QTLs conferring drought resistance. These studies demonstrate that  
18 breeding programs based on the introgression of QTL alleles from wheat wild progenitors could  
19 represent a valuable strategy to produce high yielding modern wheat cultivars, resistant to the effects  
20 of abiotic stresses (including drought), but at the same time with no yield penalties under favorable  
21 conditions.

22

## 23 **2. Indirect selection for yield**

24 GY is the result of complex interactions with the environment and is determined not only by drought  
25 conditions, but also by a wide range of other biotic and abiotic factors (Reynolds et al., 2005). For  
26 this reason, a different approach is the so-called “physiological breeding”, meaning an indirect  
27 selection for yield, based on various traits associated with GY (Sukumaran et al., 2018). This  
28 comprehensive approach is still evolving in knowledge and its applicability is often hindered by  
29 contradictory information regarding several traits. For example, the relative importance of a given  
30 trait in determining GY is often unclear, making it difficult to identify the most desirable single trait  
31 associated with drought resistance. As a consequence, there is a lack of simple and reliable  
32 combinations of selection criteria to be used as screening tools and the issue is still debated (Merah  
33 et al., 2001; Habash et al., 2009; Sukumaran et al., 2018).

34 In this review, we report on controversies that emerge from the literature regarding the main  
35 parameters used in screening methods, based on phenology, morphology, and physiology, so as to  
36 offer a state-of-the-art overview and to propose selection criteria combinations to be adopted in  
37 different target environments.

38

### 39 **2.1 Phenology**

40 DS during different plant phenophases impacts GY in different ways: in the early phases, going from  
41 germination to the double ridge stage, compromises correct crop establishment and Leaf Area Index  
42 (LAI); from double ridge to anthesis impacts negatively on spikelet number and number of kernels

1 per spike; at anthesis, it reduces spikelet number and fertility; from anthesis to maturity, drought  
2 compromises Grain Filling (GF), thereby lowering Thousand Kernel Weight (TKW) (Giunta et al.,  
3 1993; Acevedo et al., 2002; Del Moral et al., 2003). The relative importance of each of these phases  
4 in terms of final yield is not absolute, but depends strongly on the environment and, therefore, on  
5 when, how severely, and for how long the stress occurs. Consequently, conflicting information  
6 regarding the most sensitive phases to DS can be found in the literature. For example, with respect to  
7 GY, Del Moral et al. (2003), citing several authors, reports that the most sensitive period to drought  
8 in durum wheat goes from the double ridge stage to anthesis, as it has negative effects on spikelet  
9 number and kernels per spike. On the contrary, DS from anthesis to maturity might not have such  
10 negative effects on final yield, since the duration and rate of GF can be maintained relatively stable  
11 thanks to the remobilization of stored pre-flowering assimilates. On the contrary, Mohammadi et al.  
12 (2019), while recognizing the possible yield loss linked to early drought because of disturbance in  
13 spike development, states that durum wheat yield reduction during GF is typically more strongly  
14 affected, since most of wheat grain carbohydrates derive from post-anthesis photosynthesis. This  
15 apparent contradiction could be largely explained by the severity of the stress, other than obviously  
16 its timing in the target environment. In fact, it is widely understood that in case of severe stress, durum  
17 wheat yield reduction is mainly due to a drop in spikelet number and number of kernels per spike;  
18 conversely, in the case of mild stress, yield loss is mainly due to lower TKW (Giunta et al. 1993).  
19 Phenology is a plastic and flexible trait, meaning that it can be hastened or slowed down (Van Andel  
20 and Jager, 1981). Figure 1 summarizes phenological alterations due to drought observed in wheat.  
21 Simane et al. (1993) found that early DS (at tillering) increases the time necessary for durum wheat  
22 to reach both anthesis and maturity. They also found that mid (flowering) and late (GF) DS did not  
23 affect time to flowering, but significantly shortened GF duration. Ihsan et al. (2016), studying drought  
24 effects on phenology in bread wheat, observed different results. Imposing the stress immediately after  
25 crop establishment (2 weeks after sowing), DS accelerated bread wheat phenological development  
26 already from tillering, pushing all the genotypes involved in the experimentation to early maturity. In  
27 particular, days to complete 50% heading and crop physiological maturity were the most reduced  
28 compared to the other phenological stages. So, they concluded that both booting and GF are  
29 significantly accelerated by early drought. Qaseem et al. (2019) found that also stress imposed from  
30 heading reduces bread wheat days to anthesis and days to maturity.

31 The different genetic background of the cultivars examined might, at least in part, explain the  
32 apparently contradictory results. Different genotypes can in fact undertake different strategies to cope  
33 with water scarcity, either drought escape or drought avoidance (Shavrukov et al., 2017). It is quite  
34 well established that terminal drought reduces GF duration, as a consequence of accelerated leaf  
35 senescence, reduced photosynthesis, downregulation of enzyme activities, and sink limitation  
36 (Farooq et al., 2014; Ihsan et al., 2016; Pour-Aboughadareh et al., 2020a), with a negative impact on  
37 TKW. Terminal drought is typical in Mediterranean-climate regions, comprising the Mediterranean  
38 Basin (North Africa, southern Europe, and the Middle East), California, central Chile, the Cape region  
39 in South Africa, and SW Australia, where hot and dry summers follow wet and temperate winters  
40 (Acevedo et al, 1999; Shavrukov et al., 2017; Del Pozo et al., 2019). In these areas, wheat is rainfed,  
41 so DS typically emerges in spring, around anthesis, and progressively increases throughout GF  
42 (Simane et al., 1993; del Moral et al., 2003; Mohammadi et al., 2019). The semi-arid tropics, where  
43 wheat cropping relies on stored soil moisture, also experience terminal drought, thereby limiting GY  
44 during the grain development stages (Berger et al., 2016). In contexts like these, early heading and  
45 early maturity genotypes are preferable, since they avoid exposure to terminal drought by escape  
46 strategies (Simane et al., 1993; Mohammadi et al, 2019; Yashavanthakumar et al., 2021). Early  
47 heading and maturity should be accompanied in resistant genotypes by a longer GF period, in the



1 attempt to limit stress effects on grain starch accumulation (Yashavanthakumar et al., 2021; Ihsan et  
2 al., 2016; Simane et al., 1993). Therefore, in Mediterranean-type climate areas and in semi-arid  
3 tropical zones, genotypes characterized by early maturity, i.e. short pre-heading phase and increased  
4 GF duration, should be preferred. This combination of traits minimizes exposure to terminal drought,  
5 while assuring grain starch accumulation via prolonged photosynthesis (retarded leaf senescence) and  
6 remobilization of prestored assimilates (strategy 1 in Table 2). An alternative solution to preserve  
7 high GY by avoiding terminal drought is to prefer genotypes that can reach early maturity by  
8 combining a longer pre-heading phase, and a short (but highly efficient) GF period; this maximizes  
9 earlier-forming yield components (such as tiller number or spike number per plant) and  
10 photosynthetic production, while GF influences only TKW (Al-Karaki 2012; Singh et al. 2014). This  
11 solution (strategy 2 in Table 2) derives from evidence highlighting that a reduced pre-heading phase  
12 (and therefore early flowering) could reduce yield potential; it has, however, been experimentally  
13 demonstrated that it is possible to obtain genotypes with early flowering, yet having a high yield  
14 potential (Shavrukov et al. 2017). As flowering time has a strong genetic component, this trait has  
15 been widely exploited in the last century by breeders operating in terminal drought contexts. The  
16 predominant breeding strategy is, therefore, to allow wheat to escape terminal DS by selecting for  
17 “short-cycle” genotypes, with early flowering and early maturity, while favoring GF duration  
18 (Shavrukov et al., 2017; Mohammadi et al., 2019) (strategy 1 in Table 2). In such genotypes, drought  
19 escape requires that the crop complete its short life cycle before the stress appears by a rapid and  
20 active metabolism. Therefore, the “short cycle” trait does not *per se* imply that the genotype is  
21 sensitive or tolerant to drought. Hence, phenological traits which are desirable for one environment,  
22 may be inappropriate for another (Simane et al., 1993).

23

## 24 **2.2 Morphological traits**

25 DS is known to cause morphological changes in wheat (Nezhadahmadi et al., 2013). The simplest,  
26 and most widely used morphological traits to phenotype wheat on a large scale, are plant height (PH),  
27 peduncle length (PL), and leaf rolling (LR). Reduction in PH and PL as a consequence of drought is  
28 well documented (Ihsan et al., 2016; Kamrani, 2015; Nezhadahmadi et al., 2013), mostly due to the  
29 dehydration of the protoplasm, leading to turgor loss and reduced cell expansion and division  
30 (Saleem, 2003). Leaf rolling (LR) instead is caused by loss of turgor and poor osmotic adjustment in  
31 leaf tissues (Monneveux et al., 2004). The attention of breeders has focused on these traits in order to  
32 understand if, in addition to their simple application, they could represent a reliable screening  
33 strategy. Recent evidence and controversies regarding these morphological traits are reported.

### 34 **2.2.1 Plant height (PH)**

35 Reduction in wheat PH has been an essential trait for breeding in the last century, and contributed to  
36 the huge yield increase gained during the so-called Green Revolution. Reduction in plant size led in  
37 fact to new varieties less prone to lodging, and with a boosted resource portioning directed to the  
38 spike, thus maximizing the Harvest Index (HI) (Matthews et al., 2006; De Vita et al., 2007; Rebetzke  
39 et al., 2011; Monneveux et al., 2012). The selection of semi-dwarf high performing wheats was  
40 accelerated by the identification of specific dwarfing alleles (*Rht-B1b* and *Rht-D1b*), so that already  
41 at the end of the 1990s, about 70% of the varieties on the market contained at least one dwarfing allele  
42 (Hedden, 2003; Evans, 1998). This process of intense genetic selection has however led to a notable  
43 genetic erosion in the new cultivated varieties, losing many alleles of interest, related also to tolerance  
44 to abiotic stresses. A source of allelic repertoire of drought resistance is represented by tall-size wheat

1 landraces and wild emmer wheat, left behind by the bottleneck produced by twentieth century  
2 breeding (Budak et al., 2013; Lopes et al., 2015; Merchuk-Ovnat et al., 2016). In general, semi-dwarf  
3 modern wheats are considered to be highly performing in high-input well-managed environments,  
4 while in harsh environments, characterized by stress occurrence and low-input management, yield  
5 benefits are not so obvious, in comparison with tall-size landraces, which display better yield stability  
6 in adverse conditions (Rebetzke et al., 2011; Blum et Sullivan, 1997). There are, however,  
7 contradictory indications. If some authors indicate a positive relationship between PH and drought  
8 resistance (Acevedo et al, 2002; Gao et al., 2020), or a positive correlation between PH and yield  
9 parameters in drought contexts, such as fertile spikes and TKW (Bennani et al., 2016; El-Rawy et al.,  
10 2014), other authors find opposite relationships, and recommend the selection of small-size plants as  
11 a breeding strategy for increasing drought resistance (Mohammadi et al., 2019). Finally, some authors  
12 did not observe any correlation between PH and drought tolerance indices in rainfed conditions  
13 (Kamrani, 2015). Again, these controversies are ascribable to differences in DS intensity, duration,  
14 and moment of appearance in the different experimental conditions. Jatayev et al. (2020),  
15 summarizing many research results obtained all over the world in recent years, reports that in a  
16 context of strong and prolonged DS, such as in the very dry areas of Pakistan, China or Iran, breeders  
17 always found a positive correlation between yield and PH, favoring tall wheats with wild-haplotypes  
18 (i.e., *Rht-B1a-RhtD1a*). In the case of severe and lasting drought, stress appears already during crop  
19 establishment and vegetative growth stage, and then exacerbates during the season. In such  
20 conditions, semi-dwarf genotypes are clearly adversely affected. In fact, semi-dwarf *Rht-B1b* and  
21 *Rht-D1b* wheats have reduced coleoptile length and seedling vigor, requesting a shallow sowing,  
22 exposing young seedlings to higher risk of DS in case of low moisture of the very first centimeters of  
23 soil, resulting in poor early growth and seedling emergence (Rebetzke et al., 2001a; Rebetzke et al.,  
24 2011; Wang et al., 2015a). Moreover, early drought exacerbates the phenotype of semi-dwarf wheats,  
25 further reducing their size, resulting in smaller biomass and LAI as well as fewer tillers and spikes,  
26 ultimately causing reduced yield via shrunken and small grains (Jatayev et al., 2020). On the contrary,  
27 in these contexts, tall wheats can faster produce more biomass, LAI and tillers, passing favorably to  
28 the reproductive stage, and having more assimilates to be re-mobilized successively to the spike  
29 (Butler et al., 2005; Jatayev et al., 2020). In the case of terminal drought, typical of the Mediterranean  
30 climate, with short exposure to stress, semi-dwarf wheats have an advantage over tall genotypes,  
31 being able to express their high yield potential without being thwarted by prolonged stress, especially  
32 if dwarfing alleles are accompanied by early heading and early maturity traits, enabling drought  
33 escape (Pour-Aboughadareh et al., 2020a; Mohammadi et al., 2019; Jatayev et al., 2020).

34 In summary, traditional tall-size wheats show a productive advantage in case of early, severe and  
35 prolonged DS. On the contrary, semi-dwarf wheats are preferable in contexts of mild stress and / or  
36 terminal stress, which allows them to express their high yield potential. Several *Rht* genes responsive  
37 to gibberellic acid (GA) have been identified, different from *Rht-B1b* and *Rht-D1b* that are GA-  
38 insensitive; these (e.g., *Rht8* and *Rht13*) are responsible for greater coleoptile growth and seedling  
39 vigor, thus favoring crop establishment in water deficit conditions. In fact, greater coleoptile length  
40 and seedling vigor allow deeper sowing, assuring germinating seeds to reach soil moisture in deeper  
41 layers, without compromising a good emergence (Rebetzke et al., 2007). Furthermore, some *Rht*  
42 genotypes show a less pronounced reduction in stature (such as *Rht-B1b<sub>E529K</sub>*, *Rht24* and *Rht 25*).  
43 These *Rht* genes could pave the way towards new wheat ideotypes for drought contexts, combining  
44 the productive advantages of semi-dwarf genotypes in mild-stress and well-watered environments,  
45 and a lower susceptibility in case of early and severe stress (Rebetzke et al., 2011; Wang et al., 2014;  
46 Wang et al., 2015a; Jatayev et al., 2020; Mo et al., 2018a; Mo et al., 2018b; Tian et al., 2017).

### 1 2.2.2 Peduncle length (PL)

2 Like PH, also PL, typically shortened by water deficiency, has received great attention. The peduncle  
3 is the last internode of the main stem, located immediately below the initial tip of the spike. The  
4 importance of the peduncle in supporting the GF process, via remobilization of pre-stored  
5 assimilates, especially in contexts of DS in which the contribution of late photosynthesis to GF is  
6 reduced, is well known (Yang and Zang, 2006; Vosoghi Rad et al., 2022). Some authors have  
7 suggested that the peduncle could also play an active non-negligible role in late photosynthesis by  
8 having anatomical and physiological advantages over the flag leaf, e.g., higher stomatal density  
9 (Kong et al., 2010). Nevertheless, the relationship between PL and yield under DS conditions remains  
10 controversial, and depends on the different environments in which the studies are conducted. Authors  
11 observing the highest PL reduction, and the highest positive correlation between PL and GY in  
12 drought conditions, impose water shortage quite early in the life cycle (Bogale et al., 2011; Soares et  
13 al., 2020; Ahmad et al., 2020). When water shortage appears later, no significant correlation emerges  
14 between PL and GY (Villegas et al., 2007; Pour-Aboughadareh et al., 2020a; Vosoghi Rad et al.,  
15 2022), and significant PL reduction due to DS is not always observed, as the peduncle reaches its  
16 maximum length within 5 – 10 days after anthesis (Vosoghi Rad et al., 2022). No significant  
17 correlation between PL and tolerance indexes emerges comparing neither rainfed nor irrigated wheat  
18 in Iran (Kamrani et al. 2015). Peduncle dry matter translocation to the spike, and its efficiency, under  
19 DS conditions, might not be related to PL, but to its specific weight (given by the ratio between  
20 peduncle weight and length). Furthermore, the lower internodes seem to provide the most significant  
21 contribution in terms of dry matter remobilization to the spike (Vosoghi Rad et al. 2022). While  
22 Vosoghi Rad et al. (2022) reported a positive correlation between peduncle specific weight and yield  
23 in drought conditions, Villegas et al. (2007) found the opposite relationship. They identified a positive  
24 correlation between peduncle weight and drought susceptibility index (DSI), suggesting that a lighter  
25 peduncle could be an indicator of drought resistance, insofar as a heavier peduncle would be  
26 characterized by a higher proportion of structural carbohydrates over water-soluble ones that can be  
27 translocated to the spike. A further complexity is given by the fact that PL reduction is also an effect  
28 of *Rht* genes (Rebetzke et al., 2011), and in general PL gives the highest contribution to PH (Vosoghi  
29 Rad et al., 2022), whose complicated relationship with yield in arid and semi-arid contexts has been  
30 treated above.

### 31 2.2.3 Leaf rolling (LR)

32 Another morphological trait, commonly taken into consideration in cereals for the selection of  
33 drought resistant genotypes, is LR, phenomenon that allows wheat to reduce the leaf surface exposed  
34 to solar radiation by about 41%-48% (Clarke, 1986), consequently reducing leaf temperature and  
35 transpiration (E). Furthermore, rolling creates a microclimatic condition of greater humidity around  
36 the leaf surface, allowing the stomata to remain open, thus favoring photosynthesis (Kadioglu and  
37 Terzi, 2007), as well as enabling the interception of atmospheric water via foliar water uptake (Ali et  
38 al., 2022). While LR is recognized as an important drought avoidance mechanism (O'Toole et al.  
39 1979; Clarke, 1986; Kadioglu and Terzi, 2007), its contribution to yield is not much investigated in  
40 wheat, and the results are not always univocal. Bogale et al. (2011) found a positive and significant  
41 correlation between LR and GY in durum wheat grown in pots under water deficit during anthesis.  
42 On the contrary, Monneveux et al. (2004) highlights no significant impact of LR on GY, when bread  
43 wheat in open-field experiments is subjected to mild long-lasting DS after anthesis. Moreover, several  
44 authors report that the degree of LR poorly correlates with leaf water potential and leaf water loss  
45 rate in both bread and durum wheat (Clarke et al., 1986; Yang et al., 1991), with LR starting only  
46 after consistent water loss, probably due to a good capacity for osmotic adjustment, which delays the

1 phenomenon (Clarke et al., 1986; Schonfeld et al., 1988). The contradictory reliability of LR as an  
2 effective breeding tool is confirmed by genomic prediction analysis that produced an estimated  
3 breeding value of 0.16 for the trait, which is much lower, for example, compared to the estimated  
4 value obtained for PL (0.72) (Alemu et al., 2021). However, some genotypic variations in LR have  
5 been reported (Rebetzke et al., 2001b – cited by Sirault et al., 2015), and QTLs are starting to emerge  
6 (Peleg et al., 2009; Alemu et al., 2021). LR is usually phenotyped with a visual score, which assigns  
7 to each leaf a value on a scale of 1-3 or 1-5 (Bogale et al., 2011; Olivares-Villegas et al., 2007).  
8 Therefore, the operator's subjectivity can strongly influence the assigned score, making objective  
9 phenotyping difficult; the task is further complicated by the possibility of a strong intra-genotypic  
10 variability in open-field plots (Clarke et al., 1986). Recently, new objective, quantitative, and  
11 repeatable protocols to compare genotypic differences in LR have been proposed (Sirault et al., 2015),  
12 based on computer vision analysis of transverse leaf sections. Up to date, LR, which occurs only after  
13 strong dehydration when other strategies have failed (e.g., osmotic adjustment), does not appear as a  
14 solid breeding tool when stress appears suddenly, and/or is mild and long-lasting (Clarke et al. 1986).  
15 Nevertheless, LR could be an interesting selection criterion in case of severe progressive drought. Its  
16 genetic basis still remains to be investigated, but there is the possibility that the importance of this  
17 trait may grow in the future, given the opportunities supplied by new objective phenotyping  
18 approaches.

19

## 20 **2.3 Early vigor parameters**

21 Early drought is critical as it can jeopardize proper crop establishment, the first essential component  
22 in the expression of yield potential. Satisfactory seed germination and seedling growth, ensuring a  
23 successful crop establishment, define together the early vigor. Seed water absorption, germination  
24 percentage, seedling vigor index (calculated as the product of shoot length and germination  
25 percentage, divided by 100), root length, and coleoptile length are the main early vigor traits that can  
26 be inhibited under water deficit conditions (Acevedo et al., 2002; Almaghrabi et al., 2012; Ahmad et  
27 al., 2018). All these parameters, which are quick, easy, and cheap to phenotype, have attracted the  
28 attention of breeders as tools for improving wheat drought resistance. Since the 1960s, selection for  
29 these traits is generally carried out in germinating seeds using polyethylene glycol (PEG) (Parmar et  
30 Moore, 1966). PEG simulates drought by inducing a uniform and controlled osmotic stress, with no  
31 direct physiological damage as it is inert, non-ionic, and impermeable to cell membranes, thus  
32 influencing osmotic potential without entering the apoplast (Hohl and Schopfer, 1991). In order for  
33 PEG to mimic drought without altering plant hydraulic properties (therefore without being directly  
34 absorbed by the plant) it is essential to use a high-molecular-weight (> 6000) PEG (Kaufmann et  
35 Eckard, 1971). For these reasons, the use of PEG-6000 to simulate water deficit has been sustained  
36 by several authors (Almaghrabi et al., 2012; Van den Berg et al., 2006; Tuberosa, 2012). Significant  
37 differences among wheat genotypes for the aforementioned traits emerged in different studies,  
38 suggesting the existence of genetic variability to be exploited for obtaining breeding gains (Pour-  
39 Aboughadareh et al., 2020b; Almaghrabi et al., 2012; Moayedi et al., 2009; Dhanda et al., 2004).  
40 Despite representing an interesting tool for targeting early vigorous genotypes, the main drawback of  
41 many PEG-6000 screenings is that they stop at the seedling stage, without considering the rest of the  
42 life cycle. Consequently, promising genotypes identified as “drought resistant”, and recommended as  
43 suitable for cultivation under water deficit conditions, may not show such features if drought appears  
44 later in the life cycle. Even though some evidence of an interesting correlation between seedling  
45 growth under DS and adult plant drought resistance is starting to emerge (Dodig et al., 2015), future

1 research requires further validation of preliminary seedling screening results via pot or open-field  
2 experiments. At any rate, early vigor remains a trait of interest to ensure successful crop establishment  
3 and early drought resistance, and preserve final yield. In addition, regardless of early drought  
4 conditions, a quick canopy cover reduces water loss from the ground, thereby preserving soil water  
5 content for the future crop, i.e., improving water use efficiency in the crop cycle (Blum 2009;  
6 Rebetzke et al., 2011; Tuberosa, 2012).

7

### 8 *2.3.1 Number of tillers*

9 Early-season drought reduces the number of productive tillers (Acevedo et al., 2002; Sarto et al.,  
10 2017), thus reducing the spike number and, ultimately, GY (Khadka et al., 2020). In the case of early  
11 drought, selecting for this trait is a valuable strategy, as it allows to preserve the above-mentioned  
12 early-forming yield components. However, to select for a high tiller number may not always be  
13 advantageous. In fact, this approach might not be advisable under terminal drought scenarios as the  
14 total number of non-productive tillers could be higher. This would increase crop water consumption  
15 before anthesis, limiting the amount of stored available water in the soil during terminal drought  
16 (Elhani et al., 2007; Ribot et al., 2012). Having fewer tillers is also a typical characteristic of semi-  
17 dwarf high-yield genotypes (Jatayev et al., 2020), as limiting the number of tillers allows the plant to  
18 invest fewer resources on structural carbohydrates, maximizing the HI. As mentioned before, the  
19 high-yield potential of these genotypes is maintained in the event of mild drought, but is typically  
20 compromised in case of severe stress. In these scenarios of strong drought, taller genotypes with a  
21 higher number of tillers have an advantage, preserving the ability to successfully produce GY. In fact,  
22 Wasaya et al. (2021), evaluating 14 wheat genotypes, observed no correlation between PH and GY,  
23 and between tiller number and GY, in the case of mild drought; on the contrary, both these  
24 correlations were positive and highly significant under severe drought. Consequently, the number of  
25 tillers could represent a valuable breeding tool in early, long-lasting, and severe water deficit  
26 conditions.

## 27 **2.4 Physiological traits**

28 Functional and biochemical responses to DS are well documented in wheat and mainly involve  
29 stomata closure to prevent excessive water loss. As a consequence, internal CO<sub>2</sub> concentration (C<sub>i</sub>)  
30 drops causing net photosynthesis (P<sub>n</sub>) inhibition and production of Reactive Oxygen Species (ROS)  
31 leading to oxidative damage, so that plant growth and productive performance are strongly  
32 compromised (Nezhadahmadi et al., 2013; Ahmad et al., 2018). A valuable breeding target is,  
33 therefore, to select for varieties able to maintain a good water status in drought contexts.

### 34 *2.4.1 Relative Water Content (RWC)*

35 Different authors have proposed leaf Relative Water Content (RWC) as a better indicator of leaf water  
36 status compared to leaf water potential for wheat. RWC is easy to measure and calculate, by simply  
37 weighing fresh leaf tissue after excision (FW), at full turgor (TW) and after drying (DW), following  
38 the formula (Merah et al., 2001):

$$39 \text{RWC(\%)} = [(FW - DW)/(TW - DW)] \times 100$$

40 By closely reflecting the balance between leaf water supply and E rate, it highlights significant genetic  
41 variation with high heritability, and is informative at different stages of the plant's life cycle.  
42 Moreover, it has proven to positively correlate with E and photosynthetic rate, HI, and GY in both

1 durum and bread wheat (Merah et al., 2001; Moayedi et al., 2011; Mohammadi et al., 2019; Ahmad  
2 et al., 2018). RWC is considered a reliable tool for cereal breeding (Teulat et al., 2003; Rampino et  
3 al., 2006). In fact, as long as the crop can maintain a high leaf RWC, plant physiology is unaffected  
4 by stressful environmental conditions, allowing good productive performances (Beltrano et al., 2006).  
5 On the contrary, when leaf RWC drops, plant water balance is disrupted, affecting normal physiology  
6 and, ultimately, yield (Ahmad et al., 2018). If RWC drops, wheat implements a set of biochemical  
7 and functional responses; some of them are extensively treated in the literature, but their relative  
8 importance as breeding tools is still unclear.

9

#### 10 2.4.2 Osmotic adjustment

11 Osmotic adjustment is a typical mechanism implemented by wheat under DS conditions, in the  
12 attempt to avoid dehydration effects (Nezhadahmadi et al., 2013). The amino acid proline is the main  
13 osmoregulator accumulated, especially in leaves (Ahmad et al., 2018). It stabilizes membranes,  
14 prevents enzyme inactivation and represents a source of rapidly available nitrogen after stress relief  
15 (Dib et al., 1994; Rampino et al., 2006; Ahmad et al., 2018). Thus, high proline levels are generally  
16 considered an indicator of drought tolerance (Nezhadahmadi et al., 2013). Nevertheless, the effective  
17 role of proline accumulation in enhancing DS resistance and its reliability as an effective screening  
18 tool in wheat breeding programs, is still unclear and controversial (Moayedi et al., 2011; Hong-Bo et  
19 al., 2006; Rampino et al., 2006). For example, imposing DS to 10-days-old *Triticum durum* and  
20 *Aegilops* seedlings, Rampino et al. (2006) concluded that increasing proline parallels RWC decrease,  
21 as a consequence of dehydration perception by the plant. Accordingly, proline accumulation was  
22 higher and faster in sensitive genotypes, which had lower RWC. On the contrary, several authors  
23 found a positive correlation between the ability of a genotype to maintain a high RWC and proline  
24 accumulation, both at seedling and later growth stages, concluding that osmotic adjustment mediated  
25 by proline has a key role in reducing cell water loss in drought conditions. These data suggest that  
26 targeting high-proline drought-resistant genotypes is a valuable breeding tool (Hong-Bo et al., 2006;  
27 Bayoumi et al., 2008; Moayedi et al., 2011). Saeedipour et al. (2013), comparing tolerant vs sensitive  
28 genotypes, imposed stress after anthesis and observed higher and faster proline accumulation in the  
29 tolerant ones, thus reaching opposite conclusions as compared to Rampino et al. (2006). Moreover,  
30 Chandrasekar et al. (2000), comparing durum and bread wheat genotypes, observed lower RWC  
31 reduction under DS in durum wheat, but higher proline accumulation in bread wheat, concluding that  
32 proline accumulation does not contribute to the higher level of drought tolerance of tetraploid relative  
33 to hexaploid wheat. Finally, if some authors indicate a significant positive correlation between proline  
34 accumulation and GY in stress conditions (Dib et al., 1994; Bayoumi et al., 2008), other authors find  
35 that this correlation is weak and non-significant (Mwadzingeni et al., 2016a). These contradictory  
36 indications are due to the fact that many studies on proline are carried out in early stages of the life  
37 cycle, without taking into consideration repeated measurements in the most critical phases of  
38 phenological development and often without taking into account final GY. Furthermore, there is a  
39 lack of comprehensive studies based on systematic screening of a large germplasm pool. As a result,  
40 information about proline's relationship with yield and other stress-related physiological parameters  
41 in critical growth stages is scarce and controversial. Mwadzingeni et al. (2016a) aimed to solve this  
42 problem by conducting a study on 96 wheat genotypes, both in the greenhouse and open field, in two  
43 agronomic seasons and by imposing terminal DS (after 50% heading). They found that proline content  
44 had a non-significant correlation with GY, yield components (except for a negative correlation with  
45 TKW), and other agronomic traits. Thus, using proline content as a biochemical marker of breeding  
46 interest is not supported. However, while free proline accumulation does not represent a valuable

1 breeding tool *per se*, its contribution to drought resistance ought to be considered in conjunction with  
2 other fundamental traits of functional adaptation, which could depend on the genotype, the presence  
3 of other stressing factors, and the phase of the life cycle.

#### 4 *2.4.3 Stomatal conductance, transpiration and Water Use Efficiency (WUE).*

5 Since the flag leaf is traditionally recognized as a main contributor to GY formation (Evans et al.,  
6 1970; Sylvester-Bradley et al., 1990), water deficit effects on its physiology and biochemistry have  
7 aroused great interest over time, in the attempt to find reliable breeding tools. DS is known to cause  
8 stomata closure, leading to a drop in stomatal conductance ( $g_s$ ) thereby reducing both E and Pn  
9 (Subrahmanyam et al., 2006; Nezhadahmadi et al., 2013; Ahmad et al., 2018). The decline in  $g_s$  limits  
10 leaf tissue water loss, but at the same time inhibits CO<sub>2</sub> uptake, hence photosynthesis and eventually  
11 dry matter accumulation (Sallam et al., 2019). Thus, while reduced  $g_s$  helps to preserve leaf water  
12 status via reduced E (Farooq et al., 2009), on the other hand high  $g_s$  positively correlates with GY  
13 (Bahar et al., 2009). Therefore, drought-resistant genotypes must be able to maintain high  $g_s$  in  
14 drought conditions, while maintaining high Pn and, ultimately, yield (Saeidi et al., 2015; Wasaya et  
15 al., 2021). Once again, the solution to this dilemma relies on the environment. Stomatal closure is, in  
16 fact, a drought avoidance mechanism; as such, it is more closely linked to a plant's ability to survive,  
17 than to produce, thus limiting yield potential. Li et al. (2021), conducting a meta-analysis on wheat  
18 drought adaptation mechanisms, concluded that in severely water stressed environments, drought  
19 avoidance mechanisms (such as stomatal closure) confer an advantage in terms of GY production,  
20 while avoidance strategies are not effective in the case of moderate or mild stress. Thus,  $g_s$  inhibition  
21 may be a target trait in harsh environments to ensure plant survival and preserve GY, while genotypes  
22 able to maintain high  $g_s$  may have higher yield potential in mildly stressful contexts.

23 Also,  $g_s$  is strictly connected to the concept of Water Use Efficiency (WUE), namely the ratio between  
24 plant total biomass and volume of consumed water. In fact, reduced  $g_s$  means reduced E, hence lower  
25 water consumption by the plant. For decades, breeders have focused on improving WUE, considering  
26 it synonymous of high yield performance with lower water use in drought stressed environments  
27 (Blum, 2009). However, concerns about this strategy have emerged, mainly because WUE genotypic  
28 variability is driven more by differences in water consumption than biomass production (Blum, 2005;  
29 Blum, 2009). Consequently, excluding severe DS conditions in which stomatal closure is a necessary  
30 drought avoidance strategy for plant survival, selecting for genotypes with higher WUE means  
31 selecting for genotypes that are affected by low soil moisture level, leading to stomatal closure and  
32 reduced dry matter accumulation, rather than genotypes able to extract more water from the soil  
33 (Blum, 2009; Tuberosa, 2012).

34 Further complexity derives from those plant water losses not linked to CO<sub>2</sub> fixation, i.e., non-stomatal  
35 E and nocturnal  $g_s$ . Non-stomatal E refers to water loss via evaporation through the leaf cuticle, which  
36 accounts for up to 30% of leaf water loss in stressful conditions (Hasanuzzaman et al., 2018).  
37 Nocturnal E is also not negligible, representing 14-55% of daytime water losses for wheat (Schoppach  
38 et al., 2014; Schoppach et al., 2020; McAusland et al., 2021). In conclusion,  $g_s$  is a trait of interest to  
39 improve wheat drought resistance. Selection should be oriented to genotypes with low  $g_s$  only in a  
40 context of severe water shortage. In moderate to mild drought scenarios, genotypes able to extract  
41 more water from the soil and thus able to maintain high  $g_s$  to sustain CO<sub>2</sub> fixation and GY should be  
42 preferred. In parallel, attention should be shifted from WUE to the maximization of stomatal E while  
43 minimizing water losses not related to CO<sub>2</sub> assimilation (non-stomatal E and nocturnal  $g_s$ ). Non-  
44 stomatal water loss reduction can be achieved by increasing leaf epicuticular waxiness (Richards et

1 al., 1996; Acevedo et al., 2002), and evidence of genotypic variation to exploit nocturnal stomatal E  
2 in wheat is starting to emerge (Schoppach et al., 2020; McAusland et al., 2021).

3 Finally, the use of  $g_s$  as a breeding tool in open-field or greenhouse conditions is complicated by the  
4 fact that environmental conditions interacting with stomatal opening/closure can change rapidly and  
5 several times during the day (depending on cloud cover, solar radiation, and relative humidity),  
6 making it difficult to measure this parameter reliably and, therefore, to perform unbiased  
7 comparisons on a large number of genotypes and in multiple replicate (Tuberosa, 2012 ; Monneveux  
8 et al., 2012). In fact,  $g_s$  does not depend exclusively on drought but is regulated also in response to  
9 Vapour Pressure Deficit (VPD), defined as the difference between the saturation (i.e. the maximum  
10 amount of water vapor that the air can hold) and actual vapor pressure in the atmosphere (Grossiord  
11 et al., 2020). Higher VPD determines a higher evapo-transpirative demand of the atmosphere,  
12 increasing E. So, as VPD increases, E increases till the plant is unable to satisfy the request, and  
13 closes the stomata (Franks and Farquhar, 1999).

14 So, independently of water availability in the root zone, if leaf -to-air VPD increases too much (for  
15 example in case of high temperature or wind speed), plants respond by closing the stomata to prevent  
16 excessive water loss (limiting E). This happens when atmospheric evapotranspirative demand is too  
17 high and cannot be counterbalanced by water absorption and transport towards the leaf. This limit  
18 value varies from species to species, and depends mainly on the hydraulic conductivity characteristics  
19 of the xylem (Franks and Farquhar, 1999). There is no unanimous consensus on the specific  
20 mechanisms driving stomatal closure in response to changes in VPD. It could involve active sensing  
21 of the water status in the leaf or in the stomatal guard-cells, likely mediated by hormonal signals like  
22 abscisic acid (Grossiord et al., 2020). When there is no soil water shortage, but still the crop  
23 experiences stomatal closure in response to high VPD, decreased stomatal sensitivity to VPD has  
24 been proposed as a possible contributor to the relationship between  $g_s$  and yield in grain crops  
25 (Richards, 2000).

26 Schoppach et al. (2012) revealed significant phenotypic diversity across wheat genotypes for  $g_s$  and  
27 E sensitivity to VPD. The researchers concluded that genotypes with early stomata closure in response  
28 to both atmospheric or edaphic induced water stress can store more water in the soil and utilize it  
29 more sparingly during drought episodes. On the contrary, the drought tolerance of  $g_s$  insensitive  
30 genotypes to soil drying and/or increasing VPD may represent a different strategy, favoring CO<sub>2</sub>  
31 fixations over water conservation. Those findings are consistent with the idea that drought resistance  
32 is highly dependent on drought scenarios, with conservative and insensitive genotypes preferable in  
33 case of severe or mild-moderate stress, respectively. Therefore, as noted by Medrano et al. (2002),  $g_s$   
34 is responsive to all factors related to leaf water status, thus representing an integrative breeding trait for  
35 the overall effects of plant water stress.

36

37

#### 38 2.4.4 Flag leaf net photosynthesis ( $P_n$ )

39 Flag leaf  $P_n$  is considered a major contributor to GY, mostly during the GF stage, when other leaves  
40 start to senesce (Evans et al., 1970; Sylvester-Bradley et al., 1990; Loss et Siddique, 1994). As  
41 drought causes a drop in RWC and  $g_s$ ,  $P_n$  is inhibited. Selection for genotypes able to maintain high  
42  $P_n$  rates under water deficit is thus a clear target for wheat breeders, especially in post-anthesis (Inoue  
43 et al., 2004). If decreased  $P_n$  depended solely on decreased  $g_s$ , selecting and phenotyping for both



1 traits would be redundant. However, in several cases, no significant correlation was found between  
2  $g_s$  and Pn in drought-stressed wheat, and reduced  $g_s$  was not considered the main cause of Pn decrease  
3 for both bread and durum wheat exposed to drought (Bogale et al., 2011; Siddique et al., 1999). Other  
4 authors instead indicate a strong correlation between Pn and  $g_s$  drop in wheat under drought (Mu et  
5 al., 2021; Sikder et al., 2015; Wang et al., 2015b). This is due to the fact that in C3 plants drought can  
6 cause non-stomatal Pn limitations, related to impaired ATP synthesis and ribulose 1,5-bisphosphate  
7 (RuBP) regeneration, altered leaf photochemistry, decreased Rubisco activity, and permanent  
8 photoinhibition, as reported in Medrano et al. (2002) and Flexas et Medrano (2002). The prevalence  
9 of stomatal or non-stomatal limitations to Pn depend on stress severity and duration, as well as on the  
10 contextual presence of other stress sources. For example, in a Mediterranean climate, terminal  
11 drought is typically accompanied by HS (Li et al., 2013). Terminal HS in wheat is known to inhibit  
12 Pn due to increased photorespiration, as Rubisco kinetics is affected (Farooq et al., 2011). Some  
13 studies suggest that Pn inhibition is mainly driven by stomatal closure in mild stress - even if  
14 impairment in ATP synthesis and RuBP regeneration have been demonstrated too - while  
15 photosynthetic limitation to Pn is predominant under severe drought (Ashraf et al., 2013; Athar, 2005;  
16 Flexas et Medrano, 2002). Regardless of stomatal or non-stomatal limitation, the fact that some  
17 authors find a significant correlation between flag leaf Pn and GY under drought, or between flag leaf  
18 Pn and stress resistance (Zheng et al., 2011; Inoue et al., 2004) while others do not (Bogale et al.,  
19 2011; Guóth et al., 2009) raises some doubts about the use of Pn as a breeding target. One must  
20 consider that GY, as well as Pn and other gas exchange parameters, are highly integrative traits,  
21 strongly dependent on micro-climatic conditions during sampling. Moreover, the contribution of flag  
22 leaf Pn to GY may vary among genotypes and during the life cycle, depending on other assimilates  
23 sources (e.g., remobilization from reserves, ear photosynthesis, etc.) (Asseng et Van Herwaarden,  
24 2003; Li et al., 2017; Ding et al., 2018). Maintaining high photosynthetic capacity in the flag leaf is  
25 clearly an interesting and desirable trait to select for. Nevertheless, it is not easy to phenotype (given  
26 the high plasticity of the trait during the day and/or over time) and should be selected in combination  
27 with other favorable traits to maximize the positive impact on GY.

28

#### 29 *2.4.5 Chlorophyll performance parameters*

30 When Chlorophyll-a (Chl a) is excited to the singlet state ( $^1\text{Chl}^*$ ) as a result of light absorption, under  
31  $\text{CO}_2$ -limiting conditions (e.g. stomata closure) the amount of harvested light energy and generated  
32 reducing power can easily exceed the rate of its consumption by the photosynthetic machinery.  
33 Therefore, the plant can employ several mechanisms to dissipate the excess of excitation energy, i.e.  
34 emission of fluorescence and heat. Both thermal dissipation and photochemistry mechanisms reduce  
35 the amount of emitted fluorescence, and non-photochemical processes that quench chlorophyll  
36 fluorescence are collectively called Non-Photochemical Quenching (NPQ). Otherwise, energy can be  
37 dissipated via the triplet state ( $^3\text{Chl}^*$ ), a significant valve for excess excitation that can however  
38 generate ROS, extremely damaging to the photosynthetic apparatus (Müller et al., 2001; Grieco et  
39 al., 2020). Altered leaf photochemistry and energy flow in Photosystem II (PSII), the most vulnerable  
40 part of the photosynthetic apparatus (Sherstneva et al., 2022), have received great attention, thanks to  
41 the possibility to easily assess the downregulation of photosynthesis in living plants, measuring  
42 chlorophyll fluorescence parameters by specialized equipment and easy-to-use instruments. In  
43 particular,  $F_v/F_m$ , i.e., maximum quantum efficiency PSII, is indicated by several authors as a  
44 selection criterion to improve wheat drought tolerance and/or GY in drought contexts (Flagella et al.,  
45 1995; Araus et al., 1998; Almeselmani et al., 2011; Farshadfar et al., 2014; Mohammadi et al., 2019).

1 This is based on evidence that a decrease in Fv/Fm measured on dark-adapted leaves is related to  
2 down- regulation of photosynthesis and photoinhibition (Maxwell and Johnson, 2000). Nevertheless,  
3 some authors argue that PSII primary photochemistry, and thus Fv/Fm, is quite insensitive to DS (Lu  
4 et Zhang, 1999; Subrahmanyam et al. 2006). This is supported by studies that do not find a significant  
5 correlation between chlorophyll fluorescence parameters and GY in drought-stressed wheat,  
6 concluding that these are not proper tools to phenotype wheat genotypes for drought resistance  
7 (Bogale et al., 2011; Pour-Aboughadareh et al., 2020a). These contradictory conclusions may be  
8 explained by differences in stress severity and by the presence of other stressing factors that inhibit  
9 wheat PSII maximum quantum efficiency, e.g. HS and high radiation intensity (Sharma et al., 2012;  
10 Sharma et al., 2015). In fact, Fv/Fm seems to be compromised by DS only in cases of severe  
11 dehydration (Živčák et al., 2008). Thus, when assessing its suitability as a screening tool for wheat  
12 drought tolerance, misleading results may be due to the concomitant presence of confounding factors,  
13 such as intense solar radiation and high temperature. On the other hand, field conditions of terminal  
14 drought accompanied by high temperature and solar radiation are typical of the Mediterranean  
15 climate, making Fv/Fm an interesting breeding tool for this type of context.

16 Another widely used Chl *a* fluorescence metrics to measure PSII damage in case of HS, is the critical  
17 temperature ( $T_{crit}$ ) above which minimal Chl *a* fluorescence ( $F_0$ ) rises rapidly, indicating incipient  
18 damage to PSII (Húve et al., 2011). Being  $T_{crit}$  associated with increased thylakoid membrane fluidity  
19 and disruption of the light-harvesting antennae (Geange et al., 2021), it has been used to examine the  
20 vulnerability to HS across plant species (Sharma et al., 2020). So, as for Fv/Fm,  $T_{crit}$  can represent an  
21 interesting breeding tool for wheat, in those contexts where drought is accompanied by high  
22 temperature and high solar radiation, leading to excessive leaf temperature. Posch et al. (2022)  
23 combining data from both field trials and controlled-environment, and meta-analysis on previously  
24 published data, highlighted that leaf  $T_{crit}$  varies widely among wheat species and genotypes (by up to  
25 20 °C). Moreover,  $T_{crit}$  also shows a significant genotype by phenology interaction, mainly due to an  
26 increasing trend in  $T_{crit}$  as plants progressed from heading to anthesis and GF. Genotypes with  
27 enhanced thermal safety margins, thus increased  $T_{crit}$ , could be particularly important in heat stressed  
28 water-limited environments, considering that the concomitant presence of both stresses highly limit  
29  $g_s$  and transpirational cooling, resulting in increased leaf temperature (refer to 2.5 section).

30 Exploring more complex photosynthetic performance parameters than fluorescence alone, such as  
31 NPQ, may allow to better discriminate drought resistant wheat genotypes. However, most of the  
32 studies on NPQ variations in response to drought were carried out in controlled environments, on a  
33 small number of genotypes. According to the experimental conditions, i.e. phenological phase of  
34 stress onset and drought duration and severity, NPQ can increase (Subrahmanyam et al., 2006; Zlatev  
35 2009; Guóth et al., 2009; Zivcak et al., 2014; Yaghoubi Khanghahi et al., 2020; Zhu et al., 2020;  
36 Grieco et al., 2020), decrease (Shangguan et al., 2000; Sherstneva et al., 2021) or not vary (Yudina et  
37 al., 2020), making it difficult at the state of the art to determine the potentiality of this trait for high-  
38 throughput screening. Moreover, NPQ might respond differently to DS and HS (Zhu et al., 2020),  
39 complicating the analysis in those environments where drought is frequently accompanied by heat  
40 waves. Recently, Grieco et al. (2020) provided a base for developing wheat phenotyping for DS  
41 tolerance based on NPQ. This study represents a breakpoint, since the majority of previous studies  
42 emphasize photodamage as the only cause of the downregulation of photosynthesis in case of harsh  
43 DS conditions, while Grieco et al. (2020) monitored NPQ kinetics in slowly increasing levels of DS  
44 in wheat, as it usually occurs in the field. Authors noted that NPQ values started to increase 13–17  
45 days after increasing drought imposition, when soil substrate reached 30% of field capacity, with no

1 detectable change in Fv/Fm. Subsequently, after 18-24 days of increasing DS (substrate at 20% of  
2 field capacity), both NPQ and Fv/Fm increased, indicating PSII damage. However, Grieco et al.  
3 (2020) limited their investigation on DS at early phenological stages (BBCH 23 – 33), thus at the  
4 moment not giving information on NPQ suitability as a breeding tool in case of terminal drought.

5

6

## 7 **2.5 Combined heat and drought stress**

8 Several concomitant environmental factors may have a non-negligible role on the opportunity to use  
9 a specific indicator as a proxy to effectively address DS resistance. In the climate change scenario,  
10 HS is the main environmental constraint that typically affects wheat simultaneously with drought,  
11 especially during reproductive and GF stages (Barnabas et al., 2008; Li et al., 2013; Hlaváčová et al.,  
12 2018). GF is affected by short periods (few days) of temperatures higher than  $34 \pm 2$  °C (the so-called  
13 heat-shock), or by prolonged periods of daily maximum temperature up to 32°C (chronic heat stress)  
14 (Al-Khatib and Paulsen, 1984; Yang et al., 2002; Farooq et al., 2011). So, heat shock conditions are  
15 those typically occurring during heat waves (3-7 days), while chronic HS is produced by the general  
16 rise in temperatures during reproductive and GF stages.

17 Heat and drought impacts on wheat physiology are largely overlapping. In fact, HS induces higher  
18 evapotranspiration, RWC decreases, and stomata closure, leading to reduced  $g_s$ , E and Pn (Farooq et  
19 al., 2011). HS causes a reduction in Pn also as a consequence of increased Rubisco oxygenase activity  
20 at high temperatures (photorespiration). Moreover, Pn drop due to high temperatures is attributed also  
21 to NPQ, disruption in the structure of chloroplasts, and proteins/enzymes degradation/inactivation  
22 due to oxidative damages (Farooq et al., 2011). So, both HS and DS affect Pn directly (stomata  
23 closure) and indirectly (downregulation of photosynthetic metabolism), as well as both stress lead to  
24 oxidative damage, i.e. lipid peroxidation, membrane disruption, protein degradation and enzymes  
25 inactivation, reducing the functionality of leaves (Hlaváčová et al., 2018).

26 Studying the effects of single and combined DS and heat-shock on wheat physiology at anthesis,  
27 Wang et al. (2010) observed that the stress combination resulted in a greater decrease in Pn,  $g_s$  and E  
28 of flag leaves than drought or heat-shock alone. Similarly, Hlaváčová et al. (2018) observed that heat-  
29 shock during anthesis and GF significantly increased the negative impact of drought on CO<sub>2</sub>  
30 assimilation rate. Combined terminal drought and chronic HS resulted in more severe consequences  
31 on Pn and  $g_s$ , considerably reducing growth and yield traits (Shah and Paulsen, 2003; Prasad et al.,  
32 2011).

33 Therefore, the aforementioned physiological parameters remain valid breeding tools for drought  
34 resistance even in case of concomitant HS. Indeed, in mild terminal drought conditions, genotypes  
35 able to extract more water from the soil, thus maintaining higher  $g_s$  to sustain Pn, should be preferred  
36 also if drought is accompanied by HS, as this strategy would ensure more CO<sub>2</sub> fixation, higher E  
37 (leading to tissue temperature regulation), less oxidative damage (linked to lower ROS formation),  
38 thus limiting also the negative effects of HS. Similarly, the indications about phenological breeding  
39 strategies remain valid if DS is accompanied by HS, as they both increase ovule and pollen sterility,  
40 reduce spikelet number, accelerate plant senescence, and reduce GF duration, enhancing the reduction  
41 in TKW (Barnabás et al., 2008; Ji et al., 2010; Farooq et al., 2011; Prasad et al., 2011). So, in the  
42 context of terminal drought, even when accompanied by terminal HS, early heading and early

1 maturity genotypes can be considered preferable, avoiding exposure to terminal stressful conditions  
2 by escape strategies. As exposed in section 2.1, a short cycle could be obtained by the combination  
3 of a short pre-heading phase with an increased GF duration, or by a longer pre-heading phase, and a  
4 short (but highly efficient) GF period.

5 On the contrary, proline accumulation and PSII inhibition could become more relevant breeding tools  
6 when drought is accompanied by HS, due to the synergic effect of DS and HS on proline accumulation  
7 and PSII inhibition via increased thylakoid membrane fluidity and loss of electron-transport  
8 dependent integrity. Wang et al. (2010), studying the effects induced by drought, heat and their  
9 combination in wheat flag leaves, observed the sharpest increase in proline accumulation and osmotic  
10 adjustment in case of stress combination, while Prasad et al. (2011), observed a synergism of the  
11 combined stresses on chlorophyll content decline. Also Urban et al. (2018), imposing single and  
12 combined DS and HS for two weeks after anthesis, observed that Fv/Fm showed a significant  
13 interactions with temperature and water availability, resulting in an amplified decline of this  
14 parameter under the combined influence of drought and heat (temperature above 35 °C). So,  
15 chlorophyll fluorescence parameters and osmotic adjustment are indicators of HS tolerance in wheat,  
16 with strong correlation with GY (Ullah et al., 2022), thus representing a possible criterion for future  
17 breeding under combined HS and DS.

18 In conclusion, breeding strategies based on improving drought resistance, could be useful also in case  
19 of simultaneous HS. However, despite it is known that a large number of physiological, biochemical  
20 and growth processes are affected by interactions between DS and HS, there is still a limited  
21 knowledge in terms of a precise quantification of the effects of these combined stresses on production  
22 parameters, that would be crucial for reliable predictions of climate change impacts on wheat  
23 (Barnabás et al., 2008; Hlaváčová et al., 2018). Acknowledging the complexity in understanding the  
24 contributions of each stress, especially under field conditions (Farooq et al., 2011; Prasad et al., 2011),  
25 precise information on combined heat and drought would be precious, not only for addressing  
26 successful breeding programs, but also for the improvement of crop models, assessing simultaneous  
27 stresses impacts on growth and yield (Hlaváčová et al., 2018).

28

## 29 **2.6 Concluding remarks**

30 Breeding improvements for drought resistance in both bread and durum wheat can be obtained via  
31 direct or indirect selection for yield. Direct selection for yield is hampered by its low heritability, GY  
32 being a highly integrative trait, dependent on a wide range of biotic and abiotic interactions. For this  
33 reason, physiological breeding, i.e., the selection of morpho-functional traits associated with yield  
34 performance in water-stressed environments, attracts most attention. The main obstacle to  
35 physiological breeding is deciding which traits should be preferred as a reliable set of selection  
36 criteria, given the broad spectrum of drought affected environments in which timing, duration, and  
37 severity of the stress vary greatly. In fact, literature shows many conflicting results regarding the  
38 correlation between various morpho-functional traits and GY under water-limiting conditions. In this  
39 review, we offer an insight into the reasons for these controversies, while discussing the ease of use  
40 of each trait. Moreover, we provide an interpretation of how selection criteria should be combined  
41 for selection in different target environments, characterized by different drought scenarios. Table 3  
42 summarizes our conclusions. Thus, this review does not intend to be an exhaustive treatment of all  
43 phenotypic traits associated with DS, nor of the modern high-throughput phenotyping strategies and  
44 genomic approaches available. For example, root architecture traits are extremely important for DS

1 resistance (Manschadi et al., 2006), as well as imaging spectroscopy can be applied in remote sensing  
2 to evaluate numerous traits associated with abiotic stress tolerance (Jangra et al., 2021). New rising  
3 high-throughput phenotyping platforms, providing precise measurements of desired traits among  
4 thousands of field-grown plants, associated with genomic technologies, will accelerate breeding  
5 programs (Mwadingeni et al., 2016b; Jangra et al., 2021). The purpose of this review is to highlight  
6 the contradictions found in the literature for different morpho-physiological and phenological traits,  
7 and to provide an environment-oriented perspective to overcome them.

8 For example, in the Mediterranean climate type contexts, characterized by mild terminal drought,  
9 selection should be oriented to semi-dwarf early maturing genotypes, able to rapidly complete the life  
10 cycle, minimizing the temporal exposure to drought, expressing their high yield potential, with  
11 prompted  $g_s$  and  $P_n$ , as to maximize assimilates accumulation, increasing the efficiency of GF  
12 process, hampered by the terminal stress. On the other hand, where DS appears early in the life cycle,  
13 and progressively increase its severity, early vigorous, tall genotypes, with high tillers number should  
14 be preferred, able to successfully germinate in stressful condition, quickly covering bare soil  
15 (reducing water loss from the ground) and producing more photosynthetic biomass, meaning more  
16 assimilates to be re-mobilized successively to the spike. Moreover, in contexts like these, drought  
17 avoidance features, such as LR, could be considered.

18 In conclusion, climate change makes the risk of water stress more frequent, jeopardizing wheat yields  
19 more often in areas where it is grown in rainfed conditions. For this reason, it is essential to work on  
20 the selection of new varieties of wheat, both bread and durum, capable of giving good yields even in  
21 the presence of periods of drought. This is a rather complicated challenge, as wheat can be affected  
22 by drought at various stages of its life cycle. This makes the combination of phenology, water stress  
23 and physiological characteristics a complex system. It is therefore essential that the selection criteria  
24 are environment-oriented, in order to overcome controversies in breeding for drought resistance in  
25 wheat.

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## References

- 1
- 2 Acevedo, E. H., Silva, P. C., Silva, H. R., Solar, B. R., 1999. Wheat production in Mediterranean  
3 environments, in: Satorre, E.H. and Slafer, G.A. (Eds.), *Wheat Ecology and Physiology of Yield*  
4 *Determination*. Food Products Press, New York, pp. 295- 323.
- 5 Acevedo, E., Silva, P., Silva, H., 2002. Wheat growth and physiology. Bread wheat improvement and  
6 production. FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS,  
7 Rome. <https://www.fao.org/3/y4011e/y4011e06.htm#bm06>
- 8 Ahmad, Z., Waraich, E. A., Akhtar, S., Anjum, S., Ahmad, T., Mahboob, W., ... & Rizwan, M., 2018.  
9 Physiological responses of wheat to drought stress and its mitigation approaches. *Acta Physiol.*  
10 *Plant.* 40(4), 1-13. . <https://doi.org/10.1007/s11738-018-2651-6>
- 11 Ahmad, M. Q., Naseer, M. F., Qayyum, A., Malik, W., Khan, S. H., Noor, E., Sajjad, M., 2020.  
12 Agronomic, physiological and molecular characterization of spring wheat (*Triticum aestivum* L.)  
13 accessions for drought tolerance. *Bangladesh J. B.* 49(1), 29-38.  
14 <https://doi.org/10.3329/bjb.v49i1.49088>
- 15 Ahmadzadeh, M., Valizadeh, M., Shahbazi, H., Nori, A., 2012. Behavior of durum wheat genotypes  
16 under normal irrigation and drought stress conditions in the greenhouse. *Afr. J. Biotechnol.* 11(8),  
17 1912-1923. DOI: 10.5897/AJB11.2370
- 18 Al-Karaki Ghazi, N., 2012. Phenological Development-Yield Relationships in Durum Wheat  
19 Cultivars under Late-Season High-Temperature Stress in a Semiarid Environment. *International*  
20 *Scholarly Research Network ISRN Agronomy* Volume 2012, Article ID 456856, 7 pages.  
21 [doi:10.5402/2012/456856](https://doi.org/10.5402/2012/456856)
- 22 Al-Khatib, K., Paulsen, G. M., 1984. Mode of high-temperature injury to wheat during grain  
23 development. *Physiol. Plant.* 61, 363–368. <https://doi.org/10.1111/j.1399-3054.1984.tb06341.x>
- 24 Alemu, A., Suliman, S., Hagra, A., Thabet, S., Al-Abdallat, A., Abdelmula, A. A., Tadesse, W.,  
25 2021. Multi-model genome-wide association and genomic prediction analysis of 16 agronomic,  
26 physiological and quality related traits in ICARDA spring wheat. *Euphytica.* 217(11), 1-22.  
27 <https://doi.org/10.1007/s10681-021-02933-6>
- 28 Ali, Z., Merrium, S., Habib-ur-Rahman, M., Hakeem, S., Saddique, M. A. B., Sher, M. A., 2022.  
29 Wetting mechanism and morphological adaptation; leaf rolling enhancing atmospheric water  
30 acquisition in wheat crop—A review. *Environ. Sci. Pollut. Res.* 1-19.  
31 <https://doi.org/10.1007/s11356-022-18846-3>
- 32 Almaghrabi, O. A., 2012. Impact of drought stress on germination and seedling growth parameters  
33 of some wheat cultivars. *Life Sci. J.* 9(1), 590-598.
- 34 Almeselmani, M., Abdullah, F., Hareri, F., Naaesan, M., Ammar, M. A., ZuherKanbar, O., 2011.  
35 Effect of drought on different physiological characters and yield component in different varieties  
36 of Syrian durum wheat. *J. Agric. Sci.* 3(3), 127. . [doi:10.5539/jas.v3n3p127](https://doi.org/10.5539/jas.v3n3p127)
- 37 Araus, J. L., Amaro, T., Voltas, J., Nakkoul, H., Nachit, M. M., 1998. Chlorophyll fluorescence as a  
38 selection criterion for grain yield in durum wheat under Mediterranean conditions. *Field Crops*  
39 *Res.* 55(3), 209-223. [https://doi.org/10.1016/S0378-4290\(97\)00079-8](https://doi.org/10.1016/S0378-4290(97)00079-8)
- 40 Ashraf, M. H. P. J. C., Harris, P. J., 2013. Photosynthesis under stressful environments: an overview.  
41 *Photosynthetica.* 51(2), 163-190. DOI: 10.1007/s11099-013-0021-6
- 42 Asseng, S., Van Herwaarden, A. F., 2003. Analysis of the benefits to wheat yield from assimilates  
43 stored prior to grain filling in a range of environments. *Plant and Soil.* 256(1), 217-229.  
44 <https://doi.org/10.1023/A:1026231904221>

- 1 Athar, H. U. R., Ashraf, M., 2005. Photosynthesis under drought stress, in: Pessaraki, M., (Eds.),  
2 Handbook of photosynthesis, CRC Press, Taylor and Francis Group, New York, NY, 2005, pp.  
3 793-809
- 4 Bahar, B., Yildirim, M., Barutcular, C., 2009. Relationships between stomatal conductance and yield  
5 components in spring durum wheat under Mediterranean conditions. *Not. Bot. Horti Agrobot.*  
6 *Cluj-Napoca.* 37(2), 45-48. <https://doi.org/10.15835/nbha3723084>
- 7 Bayoumi, T. Y., Eid, M. H., Metwali, E. M., 2008. Application of physiological and biochemical  
8 indices as a screening technique for drought tolerance in wheat genotypes. *Afr. J. Biotech.* 7(14).  
9 <http://www.academicjournals.org/AJB>
- 10 Barnabás, B., Jäger, K., Fehér, A., 2008. The effect of drought and heat stress on reproductive  
11 processes in cereals. *Plant Cell Environ.* 31(1), 11-38. <https://doi.org/10.1111/j.1365-3040.2007.01727.x>
- 13 Beltrano, J., Ronco, M.G., Arango, A.C., 2006. Soil drying and rewatering applied at three grain  
14 developmental stages affect differentially growth and grain protein deposition in wheat (*Triticum*  
15 *aestivum* L.). *Braz. J. Plant Physiol* Vol. 18 no 2. <https://doi.org/10.1590/S1677-04202006000200011>
- 17 Bennani, S., Nsarellah, N. A., Ouabbou, H., Tadesse, W., 2016. Effective selection criteria for  
18 screening drought tolerant and high yielding bread wheat genotypes. *Univers. J. Agric. Res.* 4,  
19 134–142. [doi:10.13189/ujar.2016.040404](https://doi.org/10.13189/ujar.2016.040404)
- 20 Berger, J., Palta, J., Vadez, V., 2016. Review: an integrated framework for crop adaptation to dry  
21 environments: responses to transient and terminal drought. *Plant Sci.* 253, 58-67.  
22 <http://dx.doi.org/10.1016/j.plantsci.2016.09.007>
- 23 Blum, A., Sullivan, C.Y., 1997. The Effect of Plant Size on Wheat Response to Agents of Drought  
24 Stress. I. Root Drying. *Aust. J. Plant Physiol.* 24, 35-41. <https://doi.org/10.1071/PP96022>
- 25 Blum, A., 2005. Drought resistance, water-use efficiency, and yield potential—are they compatible,  
26 dissonant, or mutually exclusive?. *Aust. J. Agric. Res.* 56(11), 1159-1168.  
27 <https://doi.org/10.1071/AR05069>
- 28 Blum, A., 2009. Effective use of water (EUW) and not water-use efficiency (WUE) is the target of  
29 crop yield improvement under drought stress. *Field Crops Res.* 112(2-3), 119-123.  
30 <https://doi.org/10.1016/j.fcr.2009.03.009>
- 31 Bogale, A., Tesfaye, K., Geleto, T., 2011. Morphological and physiological attributes associated to  
32 drought tolerance of Ethiopian durum wheat genotypes under water deficit condition. *J. Biodiv.*  
33 *Environ. Sci.* 1(2), 22-36. <http://www.innspub.net/>
- 34 Bouslama, M., Schapaugh, W.T., 1984. Stress tolerance in soybean. Part 1: evaluation of three  
35 screening techniques for heat and drought tolerance. *Crop Sci.* 24: 933-937.  
36 <https://doi.org/10.2135/cropsci1984.0011183X002400050026x>
- 37 Budak, H., Kantar, M., Kurtoglu, K. Y., 2013. Drought Tolerance in Modern and Wild Wheat. *The*  
38 *Scientific World Journal* Volume 2013, Article ID 548246, 16 pages  
39 <http://dx.doi.org/10.1155/2013/548246>
- 40 Butler, J.D., Byrne, P.F., Mohammadi, V., Chapman, P.L., Haley, S.D., 2005. Agronomic  
41 performance of Rht alleles in a spring wheat population across a range of moisture levels. *Crop*  
42 *Sci.* 45. 939–947. <https://doi.org/10.2135/cropsci2004.0323>
- 43 Chandrasekar, V. K., Sairam, R., Srivastava, G. C., 2000. Physiological and biochemical responses  
44 of hexaploid and tetraploid wheat to drought stress. *J. Agron. Crop Sci.* 185(4), 219-227.  
45 <https://doi.org/10.1046/j.1439-037x.2000.00430.x>

- 1 CIMMYT (International Maize and Wheat Improvement Center), 2014. Wheat Improvement e The  
2 Mandate of CIMMYT's Global Wheat Program [2014-11-12]. [http://www.cimmyt.org/en/what-](http://www.cimmyt.org/en/what-we-do/wheat-research/item/wheat-improvementthe-mandate-of-cimmyt-s-global-wheatprogram)  
3 [we-do/wheat-research/item/wheat-improvementthe-mandate-of-cimmyt-s-global-wheatprogram](http://www.cimmyt.org/en/what-we-do/wheat-research/item/wheat-improvementthe-mandate-of-cimmyt-s-global-wheatprogram).
- 4 Clarke, J. M., 1986. Effect of leaf rolling on leaf water loss in *Triticum* spp. *Canad. J. Pl. Sci.* 66,  
5 885-891.
- 6 Daryanto, S., Wang, L., Jacinthe, P. A., 2016. Global synthesis of drought effects on maize and wheat  
7 production. *PloS one*, 11(5), e0156362. <https://doi.org/10.1371/journal.pone.0156362>
- 8 De Vita, P., O., Li Destri Nicosia, F. Nigro, C. Platani, C. Riefolo et al., 2007. Breeding progress  
9 in morpho-physiological, agronomical and qualitative traits of durum wheat cultivars released in  
10 Italy during the 20th century. *Eur. J. Agron.* 26, 39–53. <https://doi.org/10.1016/j.eja.2006.08.009>
- 11 Del Moral, L. G., Rharrabti, Y., Villegas, D., Royo, C., 2003. Evaluation of grain yield and its  
12 components in durum wheat under Mediterranean conditions: an ontogenic approach. *Agron. J.*  
13 95(2), 266-274. <https://doi.org/10.2134/agronj2003.2660>
- 14 Del Pozo, A., Brunel-Saldias, N., Engler, A., Ortega-Farias, S., Acevedo-Opazo, C., Lobos, G. A., ...  
15 & Molina-Montenegro, M. A., 2019. Climate change impacts and adaptation strategies of  
16 agriculture in Mediterranean-climate regions (MCRs). *Sustainability.* 11(10), 2769.  
17 <https://doi.org/10.3390/su11102769>
- 18 Dhanda, S. S., Sethi, G. S., Behl, R. K., 2004. Indices of drought tolerance in wheat genotypes at  
19 early stages of plant growth. *J. Agron. Crop Sci.* 190(1), 6-12. [https://doi.org/10.1111/j.1439-](https://doi.org/10.1111/j.1439-037X.2004.00592.x)  
20 [037X.2004.00592.x](https://doi.org/10.1111/j.1439-037X.2004.00592.x)
- 21 Dib, T. A., Monneveux, P. H., Acevedo, E., Nachit, M. M., 1994. Evaluation of proline analysis and  
22 chlorophyll fluorescence quenching measurements as drought tolerance indicators in durum wheat  
23 (*Triticum turgidum* L. var. durum). *Euphytica.* 79(1), 65-73. <https://doi.org/10.1007/BF00023577>
- 24 Ding, H., Liu, D., Liu, X., Li, Y., Kang, J., Lv, J., Wang, G., 2018. Photosynthetic and stomatal traits  
25 of spike and flag leaf of winter wheat (*Triticum aestivum* L.) under water deficit. *Photosynthetica.*  
26 56(2), 687-697. [DOI: 10.1007/s11099-017-0718-z](https://doi.org/10.1007/s11099-017-0718-z)
- 27 Dodig, D., Zoriæ, M., Joviæ, M., Kandia, V., Stanisavljeviæ, R., and ŠurlanMomiroviæ, G., 2015.  
28 Wheat seedlings growth response to water deficiency and how it correlates with adult plant  
29 tolerance to drought. *J. Agric. Sci.* 153, 466–480. [doi:10.1017/S002185961400029X](https://doi.org/10.1017/S002185961400029X)
- 30 Dugasa, M.T., Cao, F., Ibrahim, W., Wu, F., 2019. Differences in physiological and biochemical  
31 characteristics in response to single and combined drought and salinity stresses between wheat  
32 genotypes differing in salt tolerance. *Physiol Plant.* 165, 134– 143. [doi:10.1111/ppl.12743](https://doi.org/10.1111/ppl.12743)
- 33 Elhani, S., Martos, V., Rharrabti, Y., Royo, C., del Moral, L. G., 2007. Contribution of main stem  
34 and tillers to durum wheat (*Triticum turgidum* L. var. durum) grain yield and its components grown  
35 in Mediterranean environments. *Field Crops Res.* 103(1), 25-35.  
36 <https://doi.org/10.1016/j.fcr.2007.05.008>
- 37 El-Rawy, M.A., Hassan, M.I., 2014. Effectiveness of drought tolerance indices to identify tolerant  
38 genotypes in bread wheat (*Triticum aestivum* L.). *J. Crop Sci. Biotech.* 17, 255-266.  
39 <https://doi.org/10.1007/s12892-014-0080-7>
- 40 Evans, L.T., Rawson, H.M., 1970. Photosynthesis and respiration by the flag leaf and components of  
41 the ear during grain development in wheat. *Aust. J. Biol. Sci.* 23, 245–254.  
42 <https://doi.org/10.1071/BI9700245>
- 43 Evans, L.T., 1998. Feeding the Ten Billion. *Plant and Population Growth.* Cambridge University  
44 Press.



- 1 FAO STAT, <https://www.fao.org/faostat/en/#data> (visited 04/26/2022)
- 2 Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., Basra, S., 2009. Plant drought stress: Effects,  
3 mechanisms and management. *Sust. Agri.* 153-188. <https://doi.org/10.1051/agro:2008021>
- 4 Farooq, M., Bramley, H., Palta, J. A., Siddique, K. H., 2011. Heat stress in wheat during reproductive  
5 and grain-filling phases. *Crit. Rev. Plant Sci.* 30(6), 491-507.  
6 <https://doi.org/10.1080/07352689.2011.615687>
- 7 Farooq, M., Hussain, M., Siddique, K. H., 2014. Drought stress in wheat during flowering and grain-  
8 filling periods. *Crit. Rev. Plant Sci.* 33(4), 331-349.  
9 <https://doi.org/10.1080/07352689.2014.875291>
- 10 Farshadfar, E., Ghasemi, M., Rafii, F., 2014. Evaluation of physiological parameters as a screening  
11 technique for drought tolerance in bread wheat. *J. Biodiv. Environ. Sci.* 4, 175-186.  
12 <http://www.innspub.net/>
- 13 Fischer, R.A., Maurer, R., 1978. Drought resistance in spring wheat cultivars. I. Grain yield response.  
14 *Aust. J. Agric. Res.* 29, 897-912. <https://doi.org/10.1071/AR9780897>
- 15 Fernandez, G.C.J., 1992. Effective selection criteria for assessing plant stress tolerance, in: Kuo, C.G.,  
16 (Eds), *Adaptation of Food Crops to Temperature and Water Stress*. Shanhua: Asian Vegetable  
17 Research and Development Center. Taiwan Publication. 93(410), 257.
- 18 Flagella, Z., Pastore, D., Campanile, R. G., Di Fonzo, N., 1995. The quantum yield of photosynthetic  
19 electron transport evaluated by chlorophyll fluorescence as an indicator of drought tolerance in  
20 durum wheat. *J. Agric. Sci.* 125(3), 325-329. [doi:10.1017/S0021859600084823](https://doi.org/10.1017/S0021859600084823)
- 21 Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S. C., Collins, W. J., & Rummukainen,  
22 M., 2014. Evaluation of climate models, in: Stocker, T. F., Qin, D., Plattner, G.K., Tignor, M.,  
23 Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P. M. (Eds.), *Climate Change*  
24 *2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment*  
25 *Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, pp. 741–  
26 866.
- 27 Flexas, J., Medrano, H., 2002. Drought-inhibition of photosynthesis in C3 plants: stomatal and non-  
28 stomatal limitations revisited. *Ann. Bot.* 89(2), 183-189. <https://doi.org/10.1093/aob/mcf027>
- 29 Franks, P.J., Farquhar, G.D., 1999. A relationship between humidity response, growth form and  
30 photosynthetic operating point in C3 plants. *Plant Cell Environ.* 22, 1337–1349.  
31 <https://doi.org/10.1046/j.1365-3040.1999.00494.x>
- 32 Gao, Z.X., Wang, Y.X., Tian, G.Y., Zhao, Y.K., Li, C.H., Cao, Q., Han, R., Shi, Z.L., He, M.Q.,  
33 2020. Plant height and its relationship with yield in wheat under different irrigation regime. *Irrig*  
34 *Sci.* 38, 365–371. <https://doi.org/10.1007/s00271-020-00678-z>
- 35 Gavuzzi, P., Rizza, F., Palumbo, M., Campalino, R.G., Ricciardi, G.L., Borghi, B., 1997. Evaluation  
36 of field and laboratory predictors of drought and heat tolerance in winter cereals. *Can J. Plant Sci.*  
37 77, 523-531. <https://doi.org/10.4141/P96-130>
- 38 Geange, S. R., Arnold, P. A., Catling, A. A., Coast, O., Cook, A. M., Gowland, K. M., ... & Nicotra,  
39 A. B., 2021. The thermal tolerance of photosynthetic tissues: a global systematic review and  
40 agenda for future research. *New Phytol.* 229(5), 2497-2513. doi: 10.1111/nph.17052
- 41 Giraldo, P., Royo, C., González, M., Carrillo, J.M., Ruiz, M., 2016. Genetic Diversity and  
42 Association Mapping for Agromorphological and Grain Quality Traits of a Structured Collection  
43 of Durum Wheat Landraces Including subsp. durum, turgidum and diccocon. *PLoS ONE* 11(11),  
44 e0166577. [doi:10.1371/journal.pone.0166577](https://doi.org/10.1371/journal.pone.0166577)

- 1 Giunta, F., Motzo R., Deidda M., 1993. Effect of drought on and yield and yield components of durum  
2 wheat and triticale in a Mediterranean environment. *Field Crops Res.* 33,399–409.  
3 [https://doi.org/10.1016/0378-4290\(93\)90161-F](https://doi.org/10.1016/0378-4290(93)90161-F)
- 4 Golabadi, M., Arzani, A. S. A. M., Maibody, S. M., 2006. Assessment of drought tolerance in  
5 segregating populations in durum wheat. *Afr. J. Agr. Res.* 1(5), 162-171.
- 6 Grieco, M., Roustan, V., Dermendjiev, G., Rantala, S., Jain, A., Leonardelli, M., ... & Teige, M.,  
7 2020. Adjustment of photosynthetic activity to drought and fluctuating light in wheat. *Plant Cell*  
8 *Environ.* 43(6), 1484-1500. doi: 10.1111/pce.13756
- 9 Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Siegwolf, R. T., ... &  
10 McDowell, N. G., 2020. Plant responses to rising vapor pressure deficit. *New Phytol.* 226(6),  
11 1550-1566. <https://doi.org/10.1111/nph.16485>
- 12 Guóth, A., Tari, I., Gallé, Á., Csiszár, J., Pécsváradi, A., Cseuz, L., Erdei, L., 2009. Comparison of  
13 the drought stress responses of tolerant and sensitive wheat cultivars during grain filling: changes  
14 in flag leaf photosynthetic activity, ABA levels, and grain yield. *J. Plant Growth Reg.* 28(2), 167-  
15 176. <https://doi.org/10.1007/s00344-009-9085-8>
- 16 Habash, D. Z., Kehel, Z., Nachit, M., 2009. Genomic approaches for designing durum wheat ready  
17 for climate change with a focus on drought. *J. Exp. Bot.* 60, 2805–2815. doi: 10.1093/jxb/erp211
- 18 Hasanuzzaman, M. D., Shabala, L., Zhou, M., Brodribb, T. J., Corkrey, R., Shabala, S., 2018. Factors  
19 determining stomatal and non-stomatal (residual) transpiration and their contribution towards  
20 salinity tolerance in contrasting barley genotypes. *Environ. Exp. Bot.* 153, 10-20.  
21 <https://doi.org/10.1016/j.envexpbot.2018.05.002>
- 22 Hazaymeh, K., Hassan, Q. K., 2016. Remote sensing of agricultural drought monitoring: A state of  
23 art review. *Aims Environ. Sci.* 3(4), 604-630. DOI: 10.3934/environsci.2016.4.604
- 24 Hedden, P., 2003. The genes of the green revolution. *Trends Genet.* 19, 5–9.  
25 [https://doi.org/10.1016/S0168-9525\(02\)00009-4](https://doi.org/10.1016/S0168-9525(02)00009-4)
- 26 Hlaváčová, M., Klem, K., Rapantová, B., Novotná, K., Urban, O., Hlavinka, P., ... & Trnka, M.,  
27 2018. Interactive effects of high temperature and drought stress during stem elongation, anthesis  
28 and early grain filling on the yield formation and photosynthesis of winter wheat. *Field Crops Res.*  
29 221, 182-195. <https://doi.org/10.1016/j.fcr.2018.02.022>
- 30 Hohl, M., Schopfer, P., 1991. Water relations of growing maize coleoptiles: comparison between  
31 mannitol and polyethylene glycol 6000 as external osmotica for adjusting turgor pressure. *Plant*  
32 *Physiol.* 95(3), 716-722. <https://doi.org/10.1104/pp.95.3.71>
- 33 Hong-Bo, S., Xiao-Yan, C., Li-Ye, C., Xi-Ning, Z., Gang, W., Yong-Bing, Y., ... & Zan-Min, H.,  
34 2006. Investigation on the relationship of proline with wheat anti-drought under soil water deficits.  
35 *Colloids Surf. B: Biointerfaces.* 53(1), 113-119. <https://doi.org/10.1016/j.colsurfb.2006.08.008>
- 36 Húve, K., Bichele, I., Rasulov, B., Niinemets, Ü. L. O., 2011. When it is too hot for photosynthesis:  
37 heat-induced instability of photosynthesis in relation to respiratory burst, cell permeability changes  
38 and H<sub>2</sub>O<sub>2</sub> formation. *Plant Cell Environ.* 34(1), 113-126. doi: 10.1111/j.1365-3040.2010.02229.x
- 39 Igrejas, G., Ikeda, T.M., Guzmán, C. (Eds.) *Wheat Quality for Improving Processing and Human*  
40 *Health*; Springer: Berlin/Heidelberg, Germany, 2020; p. 542. ISBN 978-3-030-34162-6
- 41 Ihsan, M.Z., El-Nakhlawy, F.S., Ismail, S.M., Fahad, S., Daur, I., 2016. Wheat Phenological  
42 Development and Growth Studies As Affected by Drought and Late Season High Temperature  
43 Stress under Arid Environment. *Front. Plant Sci.* 7,795. doi: 10.3389/fpls.2016.00795

- 1 Inoue, T., Inanaga, S., Sugimoto, Y., An, P., Eneji, A. E., 2004. Effect of drought on ear and flag leaf  
2 photosynthesis of two wheat cultivars differing in drought resistance. *Photosynthetica*. 42(4), 559-  
3 565. <https://doi.org/10.1007/S11099-005-0013-2>
- 4 Jangra, S., Chaudhary, V., Yadav, R. C., Yadav, N. R., 2021. High-Throughput Phenotyping: A  
5 Platform to Accelerate Crop Improvement. *Phenomics*. 1(2), 31-53.  
6 <https://doi.org/10.1007/s43657-020-00007-6>
- 7 Jatayev, S., Sukhikh, I., Vavilova, V., Smolenskaya, S.E., Goncharov, N. P., Kurishbayev, A.,  
8 Zotova, L., Absattarova, A., Serikbay, D., Hu, Y.-G., Borisjuk, N., Gupta, N. K., Jacobs, B., de  
9 Groot, S., Koekemoer, F., Alharthi, B., Lethola, K., Cu, D.T., Schramm, C., Anderson, P., Jenkins,  
10 C. L. D., Soole, K. L., Shavrukov, Y., Langridge, P., 2020. Green revolution ‘stumbles’ in a dry  
11 environment: dwarf wheat with Rht genes fails to produce higher grain yield than taller plants  
12 under drought. *Plant, Cell Environ.* 43 (10), 2355–2364. <https://doi.org/10.1111/pce.13819>
- 13 Ji, X., Shiran, B., Wan, J., Lewis, D. C., Jenkins, C. L., Condon, A. G., ... & Dolferus, R., 2010.  
14 Importance of pre-anthesis anther sink strength for maintenance of grain number during  
15 reproductive stage water stress in wheat. *Plant Cell Environ.* 33(6), 926-942.  
16 <https://doi.org/10.1111/j.1365-3040.2010.02130.x>
- 17 Jia, G., Shevliakova, E., Artaxo, P., De Noblet-Ducoudré, N., Houghton, R., House, J., ... & Verchot,  
18 L., 2019. Land–climate interactions, in: Shukla, P.R., Skea, J., Calvo Buendia, E., Masson-  
19 Delmotte, V., Pörtner, H.-O., Roberts, D.C., Zhai, P., Slade, R., Connors, S., van Diemen, R.,  
20 Ferrat, M., Haughey, E., Luz, S., Neogi, S., Pathak, M., Petzold, J., Portugal Pereira, J., Vyas, P.,  
21 Huntley, E., Kissick, K., Belkacemi, M., Malley, J. (Eds.), *Climate Change and Land: an IPCC  
22 special report on climate change, desertification, land degradation, sustainable land management,  
23 food security, and greenhouse gas fluxes in terrestrial ecosystems* . In press
- 24 Kadioglu, A., Terzi, R., 2007. A dehydration avoidance mechanism: leaf rolling. *Bot. Rev.* 73(4),  
25 290-302. . [https://doi.org/10.1663/0006-8101\(2007\)73\[290:ADAMLR\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2007)73[290:ADAMLR]2.0.CO;2)
- 26 Kamrani, M., 2015. Relationship among agro-morphological traits in bread wheat (*Triticum aestivum*  
27 L.) genotypes under irrigated and rain-fed conditions. *J. Agron.* 14, 254–263. DOI :  
28 [10.3923/ja.2015.254.263](https://doi.org/10.3923/ja.2015.254.263)
- 29 Kaufmann, M. R., Eckard, A. N., 1971. Evaluation of water stress control with polyethylene glycols  
30 by analysis of guttation. *Plant Physiol.* 47(4), 453-456. <https://doi.org/10.1104/pp.47.4.453>
- 31 Khadka, K., Earl, H. J., Raizada, M. N., Navabi, A., 2020. A physio-morphological trait-based  
32 approach for breeding drought tolerant wheat. *Front. Plant Sci.* 11, 715.  
33 <https://doi.org/10.3389/fpls.2020.00715>
- 34 Kong, L., Wang, F., Feng, B., Li, S., Si, J., Zhang, B., (2010). The structural and photosynthetic  
35 characteristics of the exposed peduncle of wheat (*Triticum aestivum* L.): an important  
36 photosynthate source for grain-filling. *BMC Plant Biol.* 10(1), 1-10. [https://doi.org/10.1186/1471-  
37 2229-10-141](https://doi.org/10.1186/1471-2229-10-141)
- 38 Kooyers, N. J., 2015. The evolution of drought escape and avoidance in natural herbaceous  
39 populations. *Plant Sci.* 234, 155-162. <https://doi.org/10.1016/j.plantsci.2015.02.012>
- 40 Li, Y. F., Wu, Y., Hernandez-Espinosa, N., Peña, R. J., 2013. Heat and drought stress on durum  
41 wheat: Responses of genotypes, yield, and quality parameters. *J. Cereal Sci.* 57(3), 398-404.  
42 <https://doi.org/10.1016/j.jcs.2013.01.005>
- 43 Li, Y., Li, H., Li, Y., & Zhang, S. (2017). Improving water-use efficiency by decreasing stomatal  
44 conductance and transpiration rate to maintain higher ear photosynthetic rate in drought-resistant  
45 wheat. *Crop J.*, 5(3), 231-239. <http://dx.doi.org/10.1016/j.cj.2017.01.001>

- 1 Li, P., Ma, B., Palta, J. A., Ding, T., Cheng, Z., Lv, G., Xiong, Y., 2021. Wheat breeding highlights  
2 drought tolerance while ignores the advantages of drought avoidance: A meta-analysis. *Eur. J.*  
3 *Agron.* 122, 126196. <https://doi.org/10.1016/j.eja.2020.126196>
- 4 Lu, C., Zhang, J., 1999. Effects of water stress on photosystem II photochemistry and its  
5 thermostability in wheat plants. *J. Exp. Bot.* 50(336). 1199-1206.  
6 <https://doi.org/10.1093/jxb/50.336.1199>
- 7 Ludlow, M. M., 1989. Strategies of response to water stress, in: Kreeb, K.H., Richter, H., Hinckley,  
8 T.M. (Eds.), *Structural and Functional Responses to Environmental Stresses*, SPB Academic, The  
9 Hague, pp. 269-281
- 10 Luo, L. J., 2010. Breeding for water-saving and drought-resistance rice (WDR) in China. *J. Exp.*  
11 *Bot.* 61(13), 3509-3517. [doi:10.1093/jxb/erq185](https://doi.org/10.1093/jxb/erq185)
- 12 Lopes, M. S., El-Basyoni, I., Baenziger, P. S., Singh, S., Royo, C., Ozbek, K., ... & Vikram, P., 2015.  
13 Exploiting genetic diversity from landraces in wheat breeding for adaptation to climate change. *J.*  
14 *Exp. Bot.* 66(12), 3477-3486. <https://doi.org/10.1093/jxb/erv122>
- 15 Loss, S. P., Siddique, K. H. M., 1994. Morphological and physiological traits associated with wheat  
16 yield increases in Mediterranean environments. *Adv. Agron.* 52, 229-276.  
17 [https://doi.org/10.1016/S0065-2113\(08\)60625-2](https://doi.org/10.1016/S0065-2113(08)60625-2)
- 18 Manschadi, A. M., Christopher, J., deVoil, P., Hammer, G. L., 2006. The role of root architectural  
19 traits in adaptation of wheat to water-limited environments. *Funct. Plant Biol.* 33(9), 823-837.  
20 <https://doi.org/10.1071/FP06055>
- 21 Mathews, K.L., Chapman, S.C., Trethowan, R., Singh, R.P., Crossa, J., Pfeiffer, W., van Ginkel, M.,  
22 DeLacy, I., 2006. Global adaptation of spring bread and durum wheat lines near-isogenic for major  
23 reduced height genes. *Crop Sci.* 46, 603–613. <https://doi.org/10.2135/cropsci2005.05-0056>
- 24 Maxwell, K., Johnson, G. N., 2000. Chlorophyll fluorescence—a practical guide. *J. Exp. Bot.*  
25 51(345), 659-668. <https://doi.org/10.1093/jexbot/51.345.659>
- 26 McAusland, L., Smith, K. E., Williams, A., Molero, G., Murchie, E. H., 2021. Nocturnal stomatal  
27 conductance in wheat is growth-stage specific and shows genotypic variation. *New Phytol.* 232(1),  
28 162-175. <https://doi.org/10.1111/nph.17563>
- 29 Medrano, H., Escalona, J. M., Bota, J., Gulías, J., Flexas, J., 2002. Regulation of photosynthesis of  
30 C3 plants in response to progressive drought: stomatal conductance as a reference parameter. *Ann.*  
31 *Bot.* 89(7), 895-905. <https://doi.org/10.1093/aob/mcf079>
- 32 Merah, O., 2001. Potential importance of water status traits for durum wheat improvement under  
33 Mediterranean conditions. *J. Agric. Sci.* 137, 139–145.  
34 <https://doi.org/10.1017/S0021859601001253>
- 35 Merchuk-Ovnat, L., Barak, V., Fahima, T., Ordon, F., Lidzbarsky, G. A., Krugman, T., Saranga, Y.,  
36 2016. Ancestral QTL alleles from wild emmer wheat improve drought resistance and productivity  
37 in modern wheat cultivars. *Front. Plant Sci.* 7, 452. [doi: 10.3389/fpls.2016.00452](https://doi.org/10.3389/fpls.2016.00452)
- 38 Mo, Y., Pearce, S., Dubcovsky, J., 2018a. Phenotypic and transcriptomic characterization of a wheat  
39 tall mutant carrying an induced mutation in the C-terminal PFYRE motif of RHT-B1b. *BMC Plant*  
40 *Biol.* 18, 253. <https://doi.org/10.1186/s12870-018-1465-4>
- 41 Mo, Y., Vanzetti, L. S., Hale, I., Spagnolo, E. J., Guidobaldi, F., Al-Oboudi, J., ... & Dubcovsky, J.,  
42 2018b. Identification and characterization of Rht25, a locus on chromosome arm 6AS affecting  
43 wheat plant height, heading time, and spike development. *Theor. Appl. Genet.* 131, 2021–2035.  
44 <https://doi.org/10.1007/s00122-018-3130-6>

- 1 Moayedi, A. A., Boyce, A. N., Barakbah, S. S., 2009. Study on osmotic stress tolerance in promising  
2 durum wheat genotypes using drought stress indices. *Res. J. Agric. Biol. Sci.* 5(5), 603-607.
- 3 Moayedi, A. A., Nasrulhaq-Boyce, A., Tavakoli, H., 2011. Application of physiological and  
4 biochemical indices for screening and assessment of drought tolerance in durum wheat genotypes.  
5 *Aust. J. Crop Sci.* 5(8), 1014-1018.  
6 <https://search.informit.org/doi/10.3316/informit.707601011925289>
- 7 Mohammadi, R., Armion, M., Kahrizi, D., Amri, A., 2010. Efficiency of screening techniques for  
8 evaluating durum wheat genotypes under mild drought conditions. *Internat. J. Plant Product.* 4(1),  
9 11-24.
- 10 Mohammadi, M., Karimizadeh, R., Abdipour, M., 2011. Evaluation of drought tolerance in bread  
11 wheat genotypes under dryland and supplemental irrigation conditions. *AJCS.* 5(4), 487-493.  
12 <https://search.informit.org/doi/10.3316/informit.281651288962837>
- 13 Mohammadi, R., Etminan, A., Shoshtari, L., 2019. Agro-physiological characterization of durum  
14 wheat genotypes under drought conditions. *Exp. Agric.* 55(3), 484-499.  
15 <https://doi.org/10.1017/S0014479718000133>
- 16 Molero, G., Coombes, B., Joynson, R., Pinto, F., Piñera-Chávez, F. J., Rivera-Amado, C., ... &  
17 Reynolds, M. P., 2022. Exotic alleles contribute to heat tolerance in wheat under field conditions.  
18 *bioRxiv.* <https://doi.org/10.1101/2022.02.09.479695>
- 19 Monneveux, P., Reynolds, M. P., González-Santoyo, H., Pena, R. J., Mayr, L., Zapata, F., 2004.  
20 Relationships between grain yield, flag leaf morphology, carbon isotope discrimination and ash  
21 content in irrigated wheat. *J. Agron. Crop Sci.* 190(6), 395-401. <https://doi.org/10.1111/j.1439-037X.2004.00116.x>
- 22
- 23 Monneveux, P., Jing, R., Misra, S.C., 2012. Phenotyping for drought adaptation in wheat using  
24 physiological traits. *Front. Physiol.* 3, 429. doi: 10.3389/fphys.2012.00429.  
25 <https://doi.org/10.3389/fphys.2012.00429>
- 26 Mu, Q., Dong, M., Xu, J., Cao, Y., Ding, Y., Sun, S., Cai, H., 2021. Photosynthesis of winter wheat  
27 effectively reflected multiple physiological responses under short-term drought-rewatering  
28 conditions. *J. Sci. Food Agric.* 102(6), 2472-2483. <https://doi.org/10.1002/jsfa.11587>
- 29 Müller, P., Li, X. P., Niyogi, K. K., 2001. Non-photochemical quenching. A response to excess light  
30 energy. *Plant Physiol.* 125(4), 1558-1566. doi: 10.1104/pp.125.4.1558
- 31 Mwadzingeni, L., Shimelis, H., Tesfay, S., Tsilo, T. J., 2016a. Screening of bread wheat genotypes  
32 for drought tolerance using phenotypic and proline analyses. *Front. Plant Sci.* 7, 1276.  
33 <https://doi.org/10.3389/fpls.2016.01276>
- 34 Mwadzingeni, L., Shimelis, H., Dube, E., Laing, M. D., Tsilo, T. J., 2016b. Breeding wheat for  
35 drought tolerance: Progress and technologies. *J. Integr. Agric.* 15(5), 935-943.  
36 [https://doi.org/10.1016/S2095-3119\(15\)61102-9](https://doi.org/10.1016/S2095-3119(15)61102-9)
- 37 Mylonas, I., Stavrakoudis, D., Katsantonis, D., Korpetis, E., 2020. Better farming practices to combat  
38 climate change, in: *Climate change and food security with emphasis on wheat*, Academic Press,  
39 pp. 1-29. <https://doi.org/10.1016/B978-0-12-819527-7.00001-7>
- 40 Nezhadahmadi, A., Prodhon, Z.H., Faruq, G., 2013. Drought tolerance in wheat. *Sci World J.* 2013,  
41 1-12. <https://doi.org/10.1155/2013/610721>
- 42 O'toole, J. C., Cruz, R. T., Singh, T. N., 1979. Leaf rolling and transpiration. *Plant Sci. Lett.* 16(1),  
43 111-114. [https://doi.org/10.1016/0304-4211\(79\)90015-4](https://doi.org/10.1016/0304-4211(79)90015-4)

- 1 Olivares-Villegas, J. J., Reynolds, M. P., McDonald, G. K., 2007. Drought-adaptive attributes in the  
2 Seri/Babax hexaploid wheat population. *Funct. Plant Biol.* 34(3), 189-203.  
3 <https://doi.org/10.1071/FP06148>
- 4 Parmar, M. T., Moore, R. P., 1966. Effects of Simulated Drought by Polyethylene Glycol Solutions  
5 on Corn (*Zea mays* L.) Germination and Seedling Development 1. *Agron. J.* 58(4), 391-392.  
6 <https://doi.org/10.2134/agronj1966.00021962005800040007x>
- 7 Patel, J., Patel, A., Patel, C., Mamrutha, H., Pradeep, S., Pachchigar, K.P., 2019. Evaluation of  
8 selection indices in screening durum wheat genotypes combining drought tolerance and high yield  
9 potential. *Int. J. Curr. Microbiol. App. Sci.* 8, 1165–1178.  
10 <https://doi.org/10.20546/ijcmas.2019.804.134>
- 11 Peleg, Z. V. I., Fahima, T., Krugman, T., Abbo, S., Yakir, D. A. N., Korol, A. B., Saranga, Y., 2009.  
12 Genomic dissection of drought resistance in durum wheat × wild emmer wheat recombinant  
13 inbred line population. *Plant Cell Environ.* 32(7), 758-779. doi: 10.1111/j.1365-  
14 3040.2009.01956.x
- 15 Pena-Bautista, R.J., Hernandez-Espinosa, N., Jones, J.M., Guzman, C., Braun, H.J., 2017. CIMMYT  
16 series on carbohydrates, wheat, grains, and health: wheat-based foods: their global and regional  
17 importance in the food supply, nutrition, and health. *Cereal Food World.* 62(5), 231–249.  
18 <http://dx.doi.org/10.1094/CFW-62-5-0231>
- 19 Posch, B. C., Hammer, J., Atkin, O. K., Bramley, H., Ruan, Y. L., Trethowan, R., Coast, O., 2022.  
20 Wheat photosystem II heat tolerance responds dynamically to short-and long-term warming. *J.*  
21 *Exp. Bot.* 73(10), 3268-3282. doi: 10.1093/jxb/erac039
- 22 Pour-Aboughadareh, A., Mohammadi, R., Etminan, A., Shooshtari, L., Maleki-Tabrizi, N., Poczai,  
23 P., 2020a. Effects of drought stress on some agronomic and morpho-physiological traits in durum  
24 wheat genotypes. *Sustainability.* 12,5610. doi: 10.3390/su12145610
- 25 Pour-Aboughadareh, A., Etminan, A., Abdelrahman, M., Siddique, K. H., Tran, L. S. P., 2020b.  
26 Assessment of biochemical and physiological parameters of durum wheat genotypes at the  
27 seedling stage during polyethylene glycol-induced water stress. *Plant Growth Regul.* 92(1), 81-93.  
28 <https://doi.org/10.1007/s10725-020-00621-4>
- 29 Prasad, P. V. V., Pisipati, S. R., Momčilović, I., Ristic, Z., 2011. Independent and combined effects  
30 of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu  
31 expression in spring wheat. *J. Agron. Crop Sci.* 197(6), 430-441. <https://doi.org/10.1111/j.1439-037X.2011.00477.x>
- 33 Qaseem, M. F., Qureshi, R., Shaheen, H., 2019. Effects of pre-anthesis drought, heat and their  
34 combination on the growth, yield and physiology of diverse wheat (*Triticum aestivum* L.)  
35 genotypes varying in sensitivity to heat and drought stress. *Sci. Rep.* 9, 1–12.  
36 <https://doi.org/10.1038/s41598-019-43477-z>
- 37 Rajaram, S., Van Ginkle, M., 2001. Mexico, 50 years of international wheat breeding, in: Bonjean.,  
38 A.P., Angus, W.J., (Eds.), *The world wheat book: A history of wheat breeding.* Lavoisier  
39 Publishing, Paris, France, pp. 579–604.
- 40 Rampino, P., Pataleo, S., Gerardi, C., Mita, G., Perrotta, C., 2006. Drought stress response in wheat:  
41 physiological and molecular analysis of resistant and sensitive genotypes. *Plant. Cell. Environ.* 29,  
42 2143–2152. <https://doi.org/10.1111/j.1365-3040.2006.01588.x>
- 43 Rebetzke, G.J., Appels, R., Morrison, A., Richards, R.A., McDonald, G., Ellis, M.H., Spielmeier,  
44 W., Bonnett, D.G., 2001. Quantitative trait loci on chromosome 4B for coleoptile length and early  
45 vigour in wheat (*Triticum aestivum* L.). *Aust. J. Agric. Res.* 52, 1221–1234.  
46 <https://doi.org/10.1071/AR01042>

- 1 Rebetzke, G.J., Morrison, A.D., Richard, R.A., Bonnett, D.G., Moore, C., 2001b. Genotypic variation  
2 for leaf rolling in wheat. Wheat breeding society of Australia (Eds), Mildura, pp. 172–174
- 3 Rebetzke, G. J., Richards, R. A., Fettell, N. A., Long, M., Condon, A. G., Forrester, R. I., Botwright,  
4 T. L., 2007. Genotypic increases in coleoptile length improves stand establishment, vigour and  
5 grain yield of deep-sown wheat. *Field Crops Res.* 100(1), 10-23.  
6 <https://doi.org/10.1016/j.fcr.2006.05.001>
- 7 Rebetzke, G. J., Ellis, M. H., Bonnett, D. G., Condon, A. G., Falk, D., Richards, R. A., 2011. The  
8 Rht13 dwarfing gene reduces peduncle length and plant height to increase grain number and yield  
9 of wheat. *Field Crop Res.* 124, 323–331. <https://doi.org/10.1016/j.fcr.2011.06.022>
- 10 Reynolds, M. P., Mujeeb-Kazi, A., Sawkins, M., 2005. Prospects for utilising plant-adaptive  
11 mechanisms to improve wheat and other crops in drought-and salinity-prone environments. *Ann.*  
12 *Appl. Biol.* 146(2), 239-259. <https://doi.org/10.1111/j.1744-7348.2005.040058.x>
- 13 Ribot, G. G., Silva, P., Acevedo, E., 2012. Morphological and physiological traits of assistance in the  
14 selection of high yielding varieties of durum wheat (*Triticum turgidum* L. spp. Durum) for the  
15 rainfed Mediterranean environments of central Chile. *Am. J. Plant Sci.* 3,1809-1819.  
16 <http://www.scirp.org/journal/PaperInformation.aspx?PaperID=25993>
- 17 Richards, R. A., 1996. Defining selection criteria to improve yield under drought. *Plant Growth*  
18 *Regul.* 20(2), 157-166. <https://doi.org/10.1007/BF00024012>
- 19 Richards, R. A., 2000. Selectable traits to increase crop photosynthesis and yield of grain crops. *J.*  
20 *Exp. Bot.* 51(suppl\_1), 447-458. [https://doi.org/10.1093/jexbot/51.suppl\\_1.447](https://doi.org/10.1093/jexbot/51.suppl_1.447)
- 21 Rosielle, A.A., Hamblin, J., 1981. Theoretical aspects of selection for yield in stress and non-stress  
22 environment. *Crop Sci.* 21, 943-946.  
23 <https://doi.org/10.2135/cropsci1981.0011183X002100060033x>
- 24 Saeedipour, S., 2013. Relationship of grain yield, ABA and proline accumulation in tolerant and  
25 sensitive wheat cultivars as affected by water stress. *Proc. Natl. Acad. Sci., India Section B:*  
26 *Biological Sciences.* 83(3), 311-315. <https://doi.org/10.1007/s40011-012-0147-5>
- 27 Saeidi, M., Abdoli, M., 2015. Effect of drought stress during grain filling on yield and its components,  
28 gas exchange variables, and some physiological traits of wheat cultivars. *J. Agric. Sci. Technol.*  
29 17(4), 885-898. <http://jast.modares.ac.ir/article-23-6741-en.html>
- 30 Saleem, M., 2003. Response of durum and bread wheat genotypes to drought stress: biomass and  
31 yield components. *Asian J. Plant Sci.* 2, 290– 293.
- 32 Sallam, A., Alqudah, A. M., Dawood, M. F., Baenziger, P. S., Börner, A., 2019. Drought stress  
33 tolerance in wheat and barley: advances in physiology, breeding and genetics research. *Int. J. Mol.*  
34 *Sci.* 20(13), 3137. <https://doi.org/10.3390/ijms20133137>
- 35 Sarto, M. V. M., Sarto, J. R. W., Rampim, L., Rosset, J. S., Bassegio, D., da Costa, P. F., Inagaki, A.  
36 M., 2017. Wheat phenology and yield under drought: a review. *Aust. J. Crop. Sci.* 11, 941-946.  
37 [doi: 10.21475/ajcs.17.11.08.pne351](https://doi.org/10.21475/ajcs.17.11.08.pne351)
- 38 Schneider, K. A., Rosales-Serna, R., Ibarra-Perez, F., Cazares-Enriquez, B., Acosta-Gallegos, J. A.,  
39 Ramirez-Vallejo, P., ... & Kelly, J. D., 1997. Improving common bean performance under drought  
40 stress. *Crop Sci.* 37(1), 43-50. <https://doi.org/10.2135/cropsci1997.0011183X003700010007x>
- 41 Schonfeld, M. A., Johnson, R. C., Carver, B. F., Mornhinweg, D. W.. 1988. Water relations in winter  
42 wheat as drought resistance indicators. *Crop Sci.* 28(3), 526-531.  
43 <https://doi.org/10.2135/cropsci1988.0011183X002800030021x>

- 1 Schoppach, R., Sadok, W., 2012. Differential sensitivities of transpiration to evaporative demand and  
2 soil water deficit among wheat elite cultivars indicate different strategies for drought tolerance.  
3 *Environ. Exp. Bot.* 84, 1-10. <https://doi.org/10.1016/j.envexpbot.2012.04.016>
- 4 Schoppach, R., Claverie, E., Sadok, W., 2014. Genotype-dependent influence of night-time vapour  
5 pressure deficit on night-time transpiration and daytime gas exchange in wheat. *Funct. Plant Biol.*  
6 41(9), 963-971. <https://doi.org/10.1071/FP14067>
- 7 Schoppach, R., Sinclair, T. R., Sadok, W., 2020. Sleep tight and wake-up early: nocturnal  
8 transpiration traits to increase wheat drought tolerance in a Mediterranean environment. *Funct.*  
9 *Plant Biol.* 47(12), 1117-1127. <https://doi.org/10.1071/FP20044>
- 10 Shah, N. H., Paulsen, G. M., 2003. Interaction of drought and high temperature on photosynthesis  
11 and grain-filling of wheat. *Plant and soil.* 257(1), 219-226.  
12 <https://doi.org/10.1023/A:1026237816578>
- 13 Shangguan, Z., Shao, M., Dyckmans, J., 2000. Effects of nitrogen nutrition and water deficit on net  
14 photosynthetic rate and chlorophyll fluorescence in winter wheat. *J. Plant Physiol.* 156(1), 46-51.  
15 doi: 10.1016/S0176-1617(00)80271-0.
- 16 Sharma, D. K., Andersen, S. B., Ottosen, C. O., Rosenqvist, E., 2012. Phenotyping of wheat cultivars  
17 for heat tolerance using chlorophyll a fluorescence. *Funct. Plant Biol.* 39(11), 936-947.  
18 <https://doi.org/10.1071/FP12100>
- 19 Sharma, D. K., Andersen, S. B., Ottosen, C. O., Rosenqvist, E., 2015. Wheat cultivars selected for  
20 high Fv/Fm under heat stress maintain high photosynthesis, total chlorophyll, stomatal  
21 conductance, transpiration and dry matter. *Physiol. Plant.* 153(2), 284-298.  
22 <https://doi.org/10.1111/ppl.12245>
- 23 Sharma, A., Kumar, V., Shahzad, B., Ramakrishnan, M., Singh Sidhu, G. P., Bali, A. S., ... & Zheng,  
24 B., 2020. Photosynthetic response of plants under different abiotic stresses: a review. *J. Plant*  
25 *Growth Regul.* 39(2), 509-531. doi: 10.1007/s00344-019-10018-x
- 26 Shavrukov, Y., Kurishbayev, A., Jatayev, S., Shvidchenko, V., Zotova, L., Koekemoer, F., de Groot,  
27 S., Soole, K. and Langridge, P., 2017. Early Flowering as a Drought Escape Mechanism in Plants:  
28 How Can It Aid Wheat Production? *Front. Plant Sci.* 8, 1950. doi: 10.3389/fpls.2017.01950
- 29 Sherstneva, O., Khlopkov, A., Gromova, E., Yudina, L., Vetrova, Y., Pecherina, A., ... &  
30 Allakhverdiev, S., 2021. Analysis of chlorophyll fluorescence parameters as predictors of biomass  
31 accumulation and tolerance to heat and drought stress of wheat (*Triticum aestivum*) plants. *Funct.*  
32 *Plant Biol.* 49(2), 155-169. doi: 10.1071/FP21209
- 33 Siddique, M. R. B., Hamid, A., Islam, M. S., 1999. Drought stress effects on photosynthetic rate and  
34 leaf gas exchange of wheat. *Bot. Bull. Acad. Sin.* 40.  
35 <https://ejournal.sinica.edu.tw/bbas/content/1999/2/bot402-06.html>
- 36 Sikder, S., Foulkes, J., West, H., De Silva, J., Gaju, O., Greenland, A., Howell, P., 2015. Evaluation  
37 of photosynthetic potential of wheat genotypes under drought condition. *Photosynthetica.* 53(1),  
38 47-54. DOI: 10.1007/s11099-015-0082-9
- 39 Simane, B., Peacock, J.M., Struik, P.C. 1993. Differences in development and growth rate among  
40 drought-resistant and susceptible cultivars of durum wheat (*Triticum turgidum* L. var. durum).  
41 *Plant Soil.* 157, 155-166. <https://doi.org/10.1007/BF00011044>
- 42 Singh, V., Solanki, Y. P. S., Redhu, A. S., 2014. Phenological development, grain growth rate and  
43 yield relationships in wheat cultivars under late sown condition. *Indian J. Plant Physiol.* 19(3),  
44 222-229. <https://doi.org/10.1007/s40502-014-0105-8>



- 1 Sirault, X. R. R., Condon, A. G., Wood, J. T., Farquhar, G. D., Rebetzke, G. J., 2015. “Rolled-  
2 upness”: phenotyping leaf rolling in cereals using computer vision and functional data analysis  
3 approaches. *Plant Methods*. 11(1), 1-11. [doi:10.1186/s13007-015-0095-1](https://doi.org/10.1186/s13007-015-0095-1)
- 4 Sylvester-Bradley, R., Scott, R. K., Wright, C. E., 1990. *Physiology in the Production and*  
5 *Improvement of Cereals*. Home-grown Cereals Authority Research Review, HGCA, London, 18
- 6 Soares, G. F., Ribeiro, W. Q., Pereira, L. F., Lima, C. A. D., Soares, D. D. S., Muller, O., ... & Ramos,  
7 M. L. G., 2020. Characterization of wheat genotypes for drought tolerance and water use  
8 efficiency. *Sci. Agric*. 78 e20190304. <https://doi.org/10.1590/1678-992X-2019-0304>
- 9 Subrahmanyam, D., Subash, N., Haris, A., Sikka, A. K., 2006. Influence of water stress on leaf  
10 photosynthetic characteristics in wheat cultivars differing in their susceptibility to drought.  
11 *Photosynthetica*. 44(1), 125-129. <https://doi.org/10.1007/s11099-005-0167-y>
- 12 Sukumaran, S., Reynolds, M.P., Sansaloni, C., 2018. Genome-Wide Association Analyses Identify  
13 QTL Hotspots for Yield and Component Traits in Durum Wheat Grown under Yield Potential,  
14 Drought, and Heat Stress Environments. *Front. Plant Sci*. 9, 81. [doi: 10.3389/fpls.2018.00081](https://doi.org/10.3389/fpls.2018.00081)
- 15 Teulat, B., Zoumarou-Wallis, N., Rotter, B., Ben Salem, M., Bahri, H., This D., 2003. QTL for  
16 relative water content in field-grown barley and their stability across Mediterranean environments.  
17 *Theor. Appl. Genet*. 108, 181–188. <https://doi.org/10.1007/s00122-003-1417-7>
- 18 Tian, X., Wen, W., Xie, L., Fu, L., Xu, D., Fu, C., ... & Cao, S., 2017. Molecular mapping of reduced  
19 plant height gene *Rht24* in bread wheat. *Front. Plant Sci*. 8, 1379.  
20 <https://doi.org/10.3389/fpls.2017.01379>
- 21 Tuberosa, R., 2012. Phenotyping for drought tolerance of crops in the genomics era. *Front. Physiol*.  
22 3, 347. <https://doi.org/10.3389/fphys.2012.00347>
- 23 Ullah, A., Nadeem, F., Nawaz, A., Siddique, K. H., Farooq, M., 2022. Heat stress effects on the  
24 reproductive physiology and yield of wheat. *J. Agron. Crop Sci*. 208(1), 1-17.  
25 <https://doi.org/10.1111/jac.12572>
- 26 Urban, O., Hlaváčová, M., Klem, K., Novotná, K., Rapantová, B., Smutná, P., ... & Trnka, M., 2018.  
27 Combined effects of drought and high temperature on photosynthetic characteristics in four winter  
28 wheat genotypes. *Field Crops Res*. 223, 137-149. <https://doi.org/10.1016/j.fcr.2018.02.029>
- 29 Van Andel, J., Jager, J. C., 1981. Analysis of growth and nutrition of six plant species of woodland  
30 clearings. *J. Ecol*. 69, 871-882. <https://doi.org/10.2307/2259642>
- 31 Van den Berg, L., Zeng, Y. J., 2006. Response of South African indigenous grass species to drought  
32 stress induced by polyethylene glycol (PEG) 6000. *S. Afr. J. Bot*. 72(2), 284-286.  
33 <https://doi.org/10.1016/j.sajb.2005.07.006>
- 34 Villegas, D., Garcia del Moral, L. F., Rharrabti, Y., Martos, V., Royo, C., 2007. Morphological traits  
35 above the flag leaf node as indicators of drought susceptibility index in durum wheat. *J. Agron.*  
36 *Crop Sci*. 193(2), 103-116. <https://doi.org/10.1111/j.1439-037X.2006.00246.x>
- 37 Voltas, J., Romagosa, I., Lafarga, A., Armesto, A.P., Sombrero, A., Araus, J.L., 1999. Genotype by  
38 environment interaction for grain yield and carbon isotope discrimination of barley in  
39 Mediterranean Spain. *Aust. J. Agric. Res*. 50, 1263-1271. <https://doi.org/10.1071/AR98137>
- 40 Vosoghi Rad, M., Jami Moeini, M., Taherian, M., Armin, M., 2022. Accumulation and remobilization  
41 of assimilates in different genotypes of durum wheat under terminal drought stress. *J. Crop. Sci.*  
42 *Biotechnol*. 25,199–214 <https://doi.org/10.1007/s12892-021-00123-3>

- 1 Wang, G. P., Hui, Z., Li, F., Zhao, M. R., Zhang, J., Wang, W., 2010. Improvement of heat and  
2 drought photosynthetic tolerance in wheat by overaccumulation of glycinebetaine. *Plant*  
3 *Biotechnol. Rep.* 4, 213–222.. <https://doi.org/10.1007/s11816-010-0139-y>
- 4 Wang, Y., Chen, L., Du, Y., Yang, Z., Condon, A. G., Hu, Y. G., 2014. Genetic effect of dwarfing  
5 gene Rht13 compared with Rht-D1b on plant height and some agronomic traits in common wheat  
6 (*Triticum aestivum* L.). *Field Crops Res.* 162, 39-47. <https://doi.org/10.1016/j.fcr.2014.03.014>
- 7 Wang, Y., Du, Y., Yang, Z., Chen, L., Condon, A. G., Hu, Y. G., 2015. Comparing the effects of GA-  
8 responsive dwarfing genes Rht13 and Rht8 on plant height and some agronomic traits in common  
9 wheat. *Field Crops Research.* 179, 35–43. <https://doi.org/10.1016/j.fcr.2015.04.010>
- 10 Wang, S. G., Jia, S. S., Sun, D. Z., Wang, H. Y., Dong, F. F., Ma, H. X., ... & Ma, G., 2015b. Genetic  
11 basis of traits related to stomatal conductance in wheat cultivars in response to drought stress.  
12 *Photosynthetica.* 53(2), 299-305. DOI: 10.1007/s11099-015-0114-5
- 13 Wasaya, A., Manzoor, S., Yasir, T. A., Sarwar, N., Mubeen, K., Ismail, I. A., ... & EL Sabagh, A.,  
14 2021. Evaluation of fourteen bread wheat (*Triticum aestivum* L.) genotypes by observing gas  
15 exchange parameters, relative water and chlorophyll content, and yield attributes under drought  
16 stress. *Sustainability.* 13(9), 4799. <https://doi.org/10.3390/su13094799>
- 17 Yaghoubi Khanghahi, M., Strafella, S., Crecchio, C., 2020. Changes in photo-protective energy  
18 dissipation of photosystem II in response to beneficial bacteria consortium in durum wheat under  
19 drought and salinity stresses. *Appl. Sci.* 10(15), 5031. doi: 10.3390/app10155031
- 20 Yang, R. C., Jana, S., Clarke, J. M., 1991. Phenotypic diversity and associations of some potentially  
21 drought-responsive characters in durum wheat. *Crop Sci.* 31(6), 1484-1491.  
22 <https://doi.org/10.2135/cropsci1991.0011183X003100060018x>
- 23 Yang, J., Sears, R. G., Gill, B. S., Paulsen, G. M., 2002. Genotypic differences in utilization of  
24 assimilate sources during maturation of wheat under chronic heat and heat shock stresses.  
25 *Euphytica.* 125, 179– 188. <https://doi.org/10.1023/A:1015882825112>
- 26 Yang, J., Zang, J., 2006. Grain filling of cereals under soil drying. *New Phytol* 169, 223–236.  
27 <https://doi.org/10.1111/j.1469-8137.2005.01597.x>
- 28 Yashavanthakumar, K.J., Baviskar, V.S., Navathe, S., Patil, R.M., Bagwan, J.H., Bankar, D.N., Gite,  
29 V.D., Gopalareddy, K., Mishra, C.N., Mamrutha, H.M., Singh, S. K., Desai, S.A., Singh, G.P.,  
30 2021. Impact of heat and drought stress on phenological development and yield in bread wheat.  
31 *Plant Physiol. Rep.* 26, 357–367. <https://doi.org/10.1007/s40502-021-00586-0>
- 32 Yudina, L., Sukhova, E., Gromova, E., Nerush, V., Vodeneev, V., Sukhov, V., 2020. A light-induced  
33 decrease in the photochemical reflectance index (PRI) can be used to estimate the energy-  
34 dependent component of non-photochemical quenching under heat stress and soil drought in pea,  
35 wheat, and pumpkin. *Photosynth. Res.* 146(1), 175-187. doi: 10.1007/s11120-020-00718-x
- 36 Zampieri, M., Ceglar, A., Dentener, F., Toreti, A., 2017. Wheat yield loss attributable to heat waves,  
37 drought and water excess at the global, national and subnational scales. *Environ. Res. Lett.* 12 (6),  
38 p. 064008. <https://doi.org/10.1088/1748-9326/aa723b>
- 39 Zheng, T. C., Zhang, X. K., Yin, G. H., Wang, L. N., Han, Y. L., Chen, L., ... & He, Z. H., 2011.  
40 Genetic gains in grain yield, net photosynthesis and stomatal conductance achieved in Henan  
41 Province of China between 1981 and 2008. *Field Crops Res.* 122(3), 225-233.  
42 <https://doi.org/10.1016/j.fcr.2011.03.015>
- 43 Zhu, L., Cernusak, L. A., Song, X., 2020. Dynamic responses of gas exchange and photochemistry  
44 to heat interference during drought in wheat and sorghum. *Funct. Plant Biol.* 47(7), 611-627. doi:  
45 10.1071/FP19242

1 Živčák, M., Brestič, M., Olšovská, K., Slamka, P., 2008. Performance index as a sensitive indicator  
2 of water stress in *Triticum aestivum* L. *Plant Soil Environ.* 54(4), 133-139.  
3 <http://dx.doi.org/10.17221/392-PSE>

4 Zivcak, M., Kalaji, H. M., Shao, H. B., Olsovska, K., Brestic, M., 2014. Photosynthetic proton and  
5 electron transport in wheat leaves under prolonged moderate drought stress. *J. Photochem.*  
6 *Photobiol. B, Biol.* 137, 107-115. doi: 10.1016/j.jphotobiol.2014.01.007

7 Zlatev, Z., 2009. Drought-induced changes in chlorophyll fluorescence of young wheat plants.  
8 *Biotechnol. Biotechnol. Equip.* 23(sup1), 438-441. doi: 10.1080/13102818.2009.10818458

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Table 1. Most common stress susceptibility/tolerance indices, considering yield in both stress and non-stress conditions. Index name and corresponding equations are reported, together with environment classification and citation reports.

Index name	Equation	Reference author(s)	Most suitable selection environment	Web of Science citations (April 7 <sup>th</sup> 2022)	Scholar citations (April 7 <sup>th</sup> 2022)
Stress susceptibility index (SSI)	$[1 - (Y_s / Y_p) / 1 - (\hat{Y}_s / \hat{Y}_p)]$	Fischer and Maurer, 1978 [33]	A	1145	3332
Tolerance index (TOL)	$(Y_p - Y_s)$	Rosielle and Hamblin, 1981 [34]	A	611	1870
Yield Stability Index (YSI)	$Y_s / Y_p$	Bousslama and Schapaugh, 1984 [35]	A	345	1011
Mean productivity (MP)	$(Y_s + Y_p) / 2$	Rosielle and Hamblin, 1981 [34]	B	611	1870
Harmonic mean (HARM)	$2 (Y_p \times Y_s) / (Y_p + Y_s)$	Schneider et al., 1997 [37]	B	129	460
Geometric mean productivity (GMP)	$(Y_p \times Y_s)^{1/2}$	Fernandez, 1992 [36]	B	94	2003
Stress Tolerance index (STI)	$(Y_p \times Y_s) / (\hat{Y}_p)^2$	Fernandez, 1992 [36]	B	94	2003
Yield Index (YI)	$Y_s / \hat{Y}_s$	Gavuzzi et al., 1997 [38]	B	172	602

Note: in the above equations  $Y_p$  and  $Y_s$  are respectively the yields of a given genotype under optimum (potential) and stressed conditions;  $\hat{Y}_p$  and  $\hat{Y}_s$  are respectively the mean yields of all genotypes under study under optimum and stressed conditions

- A = to be adopted only in systematically drought stressed environment
- B = to be adopted in yearly dependent drought interested environment

(A or B classification has been implemented combining the results of Golabadi et al., 2006 [39] ; Mohammadi et al., 2010 [31] ; Mohammadi et al., 2011 [40] ; Ahmadizadeh et al., 2012 [23] ; Patel et al., 2019 [29])

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Table 2. Developmental stage trait selection to obtain early maturity for terminal drought escape based on two strategies.

	<b>STRATEGY 1</b>	<b>STRATEGY 2</b>
	Yashavanthakumar et al., 2021 [53]; Ihsan et al., 2016 [47] ; Simane et al., 1993 [46]; Shavrukov et al., 2017 [49]; Mohammadi et al, 2019 [25].	Al-Karaki 2012 [54]; Singh et al. 2014 [55].
<b>DEVELOPMENTAL STAGE</b>		
<b>Pre-heading period (BBCH 1 – 4)</b>	<b>short</b>	<b>long</b>
<b>Heading (BBCH 5)</b>	<b>early</b>	<b>Not early</b>
<b>Flowering (BBCH 6)</b>	<b>early</b>	<b>Not early</b>
<b>Grain filling period (BBCH 7-8)</b>	<b>long</b>	<b>Short but high rate</b>

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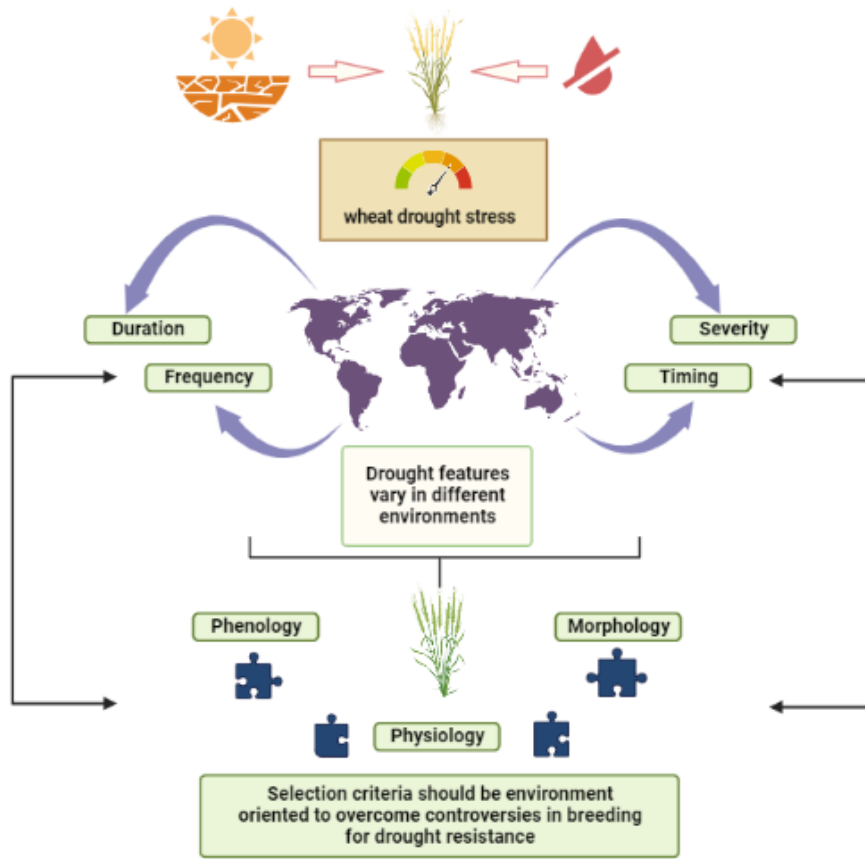
Table 3: Suitable trait combinations for different drought scenarios

Trait	Early-season drought (pre-anthesis)	Terminal drought (post-anthesis)
Early vigor	<input checked="" type="checkbox"/>	
Peduncle Length	<input checked="" type="checkbox"/>	
RWC	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
LAI	<input checked="" type="checkbox"/>	
High number of tillers	<input checked="" type="checkbox"/>	
Low number of tillers		<input checked="" type="checkbox"/>
Tall size	<input checked="" type="checkbox"/>	
Semi-dwarf		<input checked="" type="checkbox"/>
Early flowering and maturity		<input checked="" type="checkbox"/>
Prolonged - or short but high rate - grain filling		<input checked="" type="checkbox"/>
Flag leaf Pn		<input checked="" type="checkbox"/>
Fv/Fm - $T_{crit}$		<input checked="" type="checkbox"/>

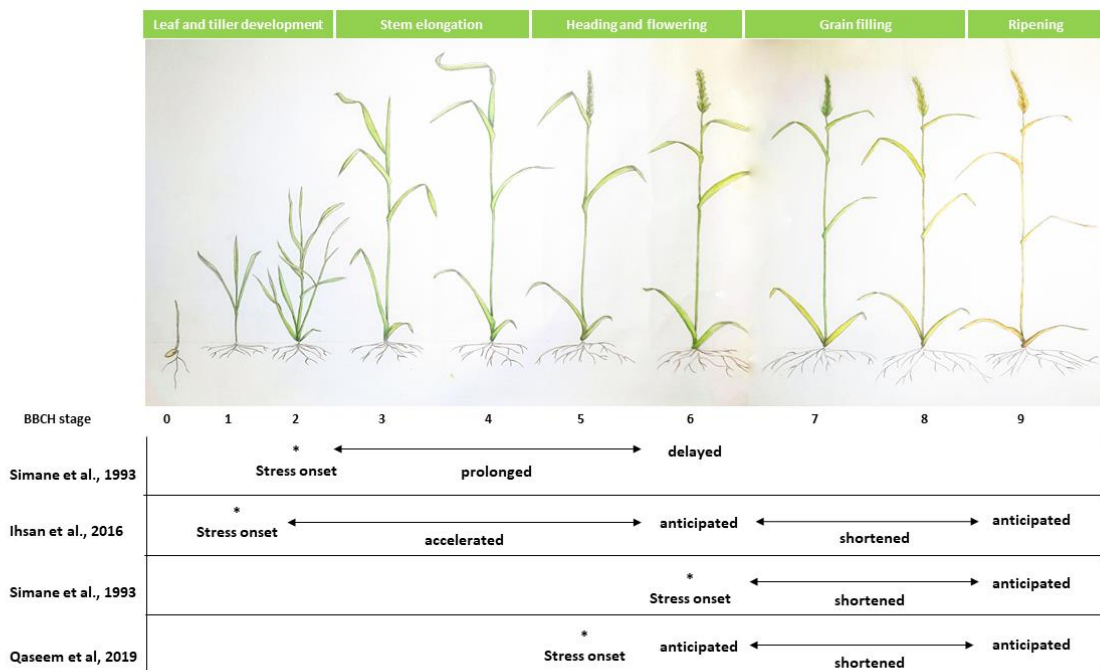
  

Trait	Mild-moderate drought	Severe drought
High $g_s$	<input checked="" type="checkbox"/>	
Reduced $g_s$		<input checked="" type="checkbox"/>
Epicuticular waxiness	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Reduced nocturnal stomatal transpiration	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
High number of tillers		<input checked="" type="checkbox"/>
Low number of tillers	<input checked="" type="checkbox"/>	
Leaf rolling		<input checked="" type="checkbox"/>
Flag leaf Pn	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Fv/Fm - $T_{crit}$		<input checked="" type="checkbox"/>
Reduced NPQ		<input checked="" type="checkbox"/>
RWC	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Tall-size		<input checked="" type="checkbox"/>
Semi-dwarf	<input checked="" type="checkbox"/>	

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