

Alma Mater Studiorum Università di Bologna
Archivio istituzionale della ricerca

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

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version:

Environment-oriented selection criteria to overcome controversies in breeding for drought resistance in wheat / Poggi, Giovanni Maria; Corneti, Simona; Aloisi, Iris; Ventura, Francesca. - In: JOURNAL OF PLANT PHYSIOLOGY. - ISSN 0176-1617. - ELETTRONICO. - 280:(2023), pp. 153895-153909. [10.1016/j.jplph.2022.153895]

Availability:

This version is available at: <https://hdl.handle.net/11585/909906> since: 2022-12-19

Published:

DOI: <http://doi.org/10.1016/j.jplph.2022.153895>

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>).
When citing, please refer to the published version.

(Article begins on next page)

This is the final peer-reviewed accepted manuscript of:

Poggi, Giovanni Maria; Corneti, Simona; Aloisi, Iris; Ventura, Francesca:
Environment-oriented selection criteria to overcome controversies in breeding for drought resistance in wheat

JOURNAL OF PLANT PHYSIOLOGY VOL. 280 ISSN: 0176-1617

DOI: 10.1016/j.jplph.2022.153895

The final published version is available online at:

<https://dx.doi.org/10.1016/j.jplph.2022.153895>

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>)

When citing, please refer to the published version.

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

Giovanni Maria Poggi^{1,2}, Simona Corneti¹, Iris Aloisi^{1*}, Francesca Ventura²

¹Department of Biological, Geological and Environmental Sciences (BiGeA), Alma Mater Studiorum, University of Bologna, Bologna, Italy.

²Department of Agricultural and Food Sciences (DISTAL), Alma Mater Studiorum, University of Bologna, Bologna, Italy.

*correspondence:

Iris Aloisi; iris.aloisi2@unibo.it

Via Irnerio 42, 40126 Bologna (Italy)

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 CO₂ 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 (F₀)
- 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_s)
- 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_{E529K}*, *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 CO₂ concentration (C_i)
30 drops causing net photosynthesis (P_n) 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂
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 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, Fv/Fm, 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 ± 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 CO₂
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 CO₂ 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.

26

27

28

29

30

Acknowledgments

31 We acknowledge Giulia Feduzi for the artwork herein presented and Prof. Stefania Biondi for offering
32 help in reviewing and revising the manuscript.

33

34

35

36

37

38

39

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 FAOSTAT, <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 Hűve, 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 H₂O₂ 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
- 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

9
10
11
12

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 th 2022)	Scholar citations (April 7 th 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])

1

2

1
2

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

	STRATEGY 1	STRATEGY 2
	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].
DEVELOPMENTAL STAGE		
Pre-heading period (BBCH 1 – 4)	short	long
Heading (BBCH 5)	early	Not early
Flowering (BBCH 6)	early	Not early
Grain filling period (BBCH 7-8)	long	Short but high rate

3
4
5

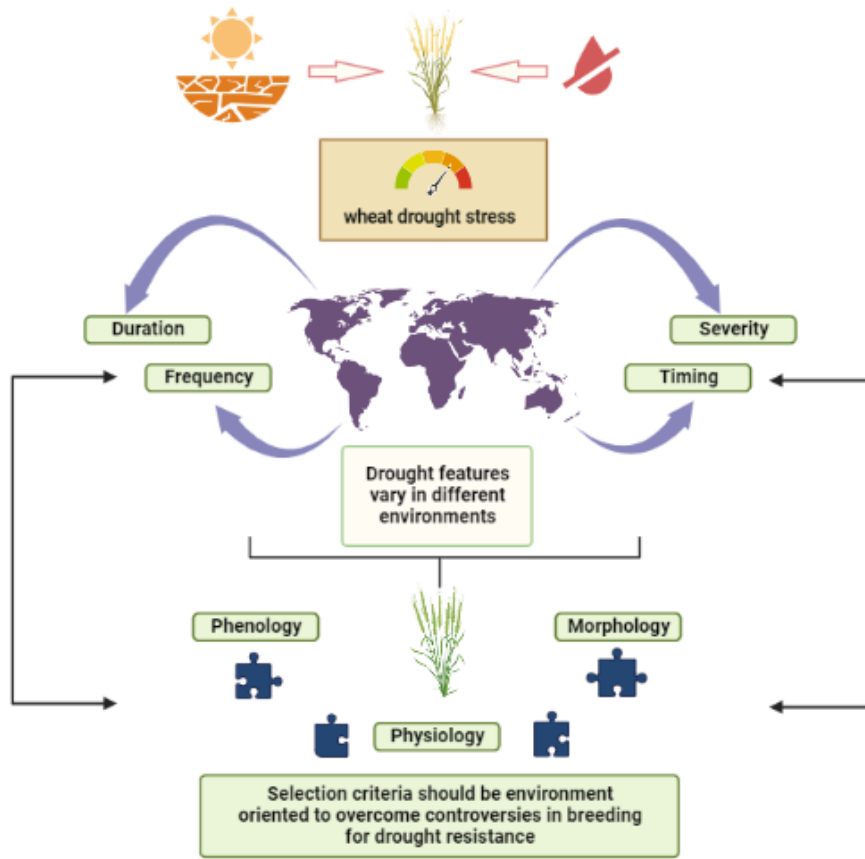
1
2

Table 3: Suitable trait combinations for different drought scenarios

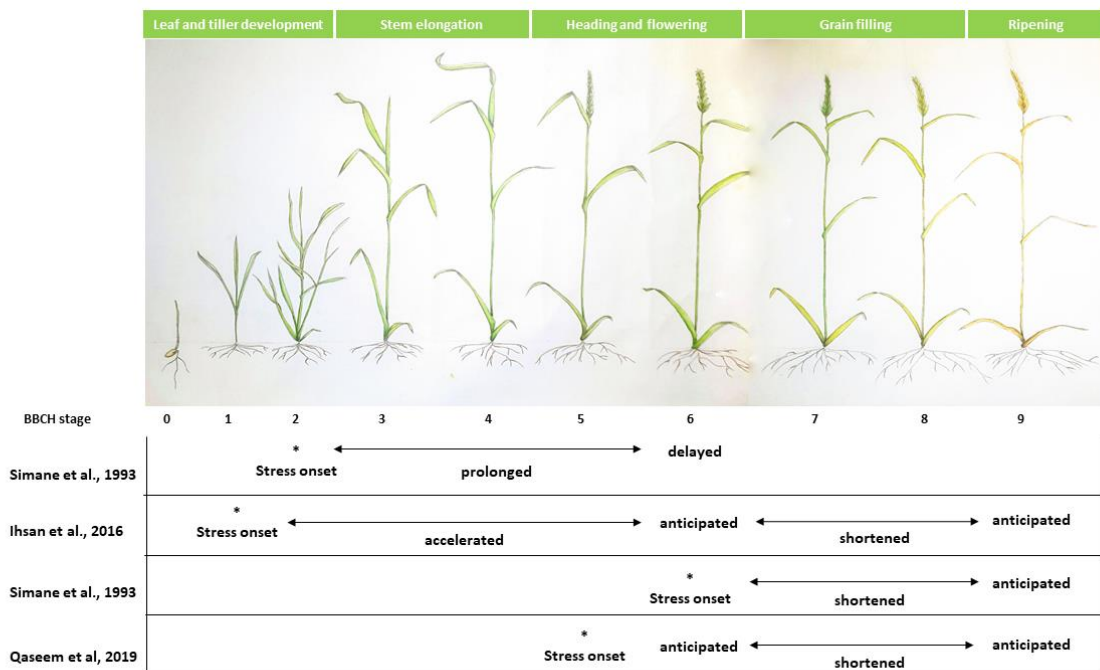
Trait	Early-season drought (pre-anthesis)	Terminal drought (post-anthesis)
Early vigor	<input checked="" type="checkbox"/>	
Peduncle Length	<input checked="" type="checkbox"/>	
RWC	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
LAI	<input checked="" type="checkbox"/>	
High number 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"/>	

3



1
2



3