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

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Abstract

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

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

List of abbreviations

Chlorophyll-a (Chl a)
Chlorophyll-a singlet state (1Chl*)
Chlorophyll-a triplet state (3Chl*)
Critical Temperature (Tcrit)
Drought Stress (DS)
Drought Susceptibility Index (DSI)
Dry Weight (DW)
Fresh Weight (FW)
Full Turgor Weight (TW)
Genome Wide Association Study (GWAS)
Genotype x Environment (GxE)
Geometric Mean Productivity (GMP)
Gibberellic Acid (GA)
Grain Filling (GF)
Grain Yield (GY)
Harmonic Mean (HARM)
Harvest Index (HI)
Heat Stress (HS)
Internal CO_2 Concentration (Ci)
Leaf Area Index (LAI)
Leaf Rolling (LR)
Marker Assisted Selection (MAS)
Maximum quantum efficiency of photosystem II (Fv/Fm)
Minimal Chl a fluorescence (F_0)
Mean Productivity (MP)
Net Photosynthesis (Pn)
Non-Photochemical Quenching (NPQ)
Peduncle Length (PL)
PhotoSystem II (PSII)
Plant Height (PH)
Polyethylene Glycol (PEG)
Quantitative Trait Loci (QTLs)
Reactive Oxygen Species (ROS)
Relative Water Content (RWC)
Ribulose 1,5-BisPhosphate (RuBP)
Stomatal Conductance (g_s)
Stress Susceptibility Index (SSI)
Stress Tolerance Index (STI)
Thousand Kernel Weight (TKW)
Tolerance Index (TOL)
Transpiration (E)
Vapour Pressure Deficit (VPD)
Water Use Efficiency (WUE)
Yield Index (YI)
Yield Stability Index (YSI)

Wheat worldwide relevance and drought threat

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

Difficulties in breeding for drought resistance

Drought resistance can be defined as the capacity of a crop to successfully produce a satisfactory yield in water shortage conditions (Luo et al., 2010). It is a complex quantitative trait, resulting from numerous mechanisms adopted by plants to cope with water scarcity, comprising a broad spectrum of morphological, physiological, biochemical and molecular processes activated at different phenological stages (Rampino et al., 2006; Nezhadahmadi et al., 2013). All these adaptations can confer drought resistance through drought escape (ability to complete the life cycle before stressful conditions appears), avoidance (ability to maintain a good water status in a drought context) or tolerance (ability to withstand dehydration) (Ludlow, 1989 – cited by Kooyers, 2015). The highly significant Genotype x Environment (GxE) interactions consistently reduce yield heritability in drought contexts (Farooq et al., 2014), making genetic improvement very challenging for breeders. Differences in drought occurrence along the wheat life cycle, in terms of time of appearance, duration, frequency and severity, are highly significant among different environments (Reynolds et al., 2005). Moreover, in rainfed conditions, weather fluctuations in terms of temperature and precipitation distribution in the cropping season produce a consistent genotype x year interaction, further complicating the direct or indirect selection for yield in an open-field environment (Ahmadizadeh et al., 2012; Budak et al., 2013; Mohammadi et al., 2019). The concomitancy with other abiotic stresses must also be taken into consideration (see section 2.5). In this review, we report first on the direct selection for yield and highlight strengths and weaknesses of this approach. Phenological, morphological, and functional traits associated with GY in drought conditions, commonly used in the indirect selection for yield, are then dissected, highlighting the controversies that have emerged regarding their reliability as effective breeding tools. In fact, morpho-functional traits related to wheat drought resistance are well-known and documented, as reviewed by Khadka et al. (2020), but evidence is still contradictory regarding the reliability of such traits as indirect selection criteria for final GY. Disputes remain over which of these traits are most desirable (e.g., tall *vs* short genotypes), as a consequence of the high variability of drought scenarios in terms of duration, timing and severity. In an attempt to overcome these controversies, here we analyze the available literature, identify the possible causes of these disputes and, finally, offer a proposal for the most suitable selection criteria, and thus the best trait combinations, for breeders in different drought contexts.

1. Direct selection for yield

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

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

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

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

2. Indirect selection for yield

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

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

2.1 Phenology

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

The different genetic background of the cultivars examined might, at least in part, explain the apparently contradictory results. Different genotypes can in fact undertake different strategies to cope with water scarcity, either drought escape or drought avoidance (Shavrukov et al., 2017). It is quite well established that terminal drought reduces GF duration, as a consequence of accelerated leaf senescence, reduced photosynthesis, downregulation of enzyme activities, and sink limitation (Farooq et al., 2014; Ihsan et al., 2016; Pour-Aboughadareh et al., 2020a), with a negative impact on TKW. Terminal drought is typical in Mediterranean-climate regions, comprising the Mediterranean Basin (North Africa, southern Europe, and the Middle East), California, central Chile, the Cape region in South Africa, and SW Australia, where hot and dry summers follow wet and temperate winters (Acevedo et al, 1999; Shavrukov et al., 2017; Del Pozo et al., 2019). In these areas, wheat is rainfed, so DS typically emerges in spring, around anthesis, and progressively increases throughout GF (Simane et al., 1993; del Moral et al., 2003; Mohammadi et al., 2019). The semi-arid tropics, where wheat cropping relies on stored soil moisture, also experience terminal drought, thereby limiting GY during the grain development stages (Berger et al., 2016). In contexts like these, early heading and early maturity genotypes are preferable, since they avoid exposure to terminal drought by escape strategies (Simane et al., 1993; Mohammadi et al, 2019; Yashavanthakumar et al., 2021). Early heading and maturity should be accompanied in resistant genotypes by a longer GF period, in the attempt to limit stress effects on grain starch accumulation (Yashavanthakumar et al., 2021; Ihsan et al., 2016; Simane et al., 1993). Therefore, in Mediterranean-type climate areas and in semi-arid tropical zones, genotypes characterized by early maturity, i.e. short pre-heading phase and increased GF duration, should be preferred. This combination of traits minimizes exposure to terminal drought, while assuring grain starch accumulation via prolonged photosynthesis (retarded leaf senescence) and remobilization of prestored assimilates (strategy 1 in Table 2). An alternative solution to preserve high GY by avoiding terminal drought is to prefer genotypes that can reach early maturity by combining a longer pre-heading phase, and a short (but highly efficient) GF period; this maximizes earlier-forming yield components (such as tiller number or spike number per plant) and photosynthetic production, while GF influences only TKW (Al-Karaki 2012; Singh et al. 2014). This solution (strategy 2 in Table 2) derives from evidence highlighting that a reduced pre-heading phase (and therefore early flowering) could reduce yield potential; it has, however, been experimentally demonstrated that it is possible to obtain genotypes with early flowering, yet having a high yield potential (Shavrukov et al. 2017). As flowering time has a strong genetic component, this trait has been widely exploited in the last century by breeders operating in terminal drought contexts. The predominant breeding strategy is, therefore, to allow wheat to escape terminal DS by selecting for "short-cycle" genotypes, with early flowering and early maturity, while favoring GF duration (Shavrukov et al., 2017; Mohammadi et al., 2019) (strategy 1 in Table 2). In such genotypes, drought escape requires that the crop complete its short life cycle before the stress appears by a rapid and active metabolism. Therefore, the "short cycle" trait does not *per se* imply that the genotype is sensitive or tolerant to drought. Hence, phenological traits which are desirable for one environment, may be inappropriate for another (Simane et al., 1993).

2.2 Morphological traits

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

2.2.1 Plant height (PH)

Reduction in wheat PH has been an essential trait for breeding in the last century, and contributed to the huge yield increase gained during the so-called Green Revolution. Reduction in plant size led in fact to new varieties less prone to lodging, and with a boosted resource portioning directed to the spike, thus maximizing the Harvest Index (HI) (Matthews et al., 2006; De Vita et al., 2007; Rebetzke et al., 2011; Monneveux et al., 2012). The selection of semi-dwarf high performing wheats was accelerated by the identification of specific dwarfing alleles (*Rht-B1b* and *Rht-D1b*), so that already at the end of the 1990s, about 70% of the varieties on the market contained at least one dwarfing allele (Hedden, 2003; Evans, 1998). This process of intense genetic selection has however led to a notable genetic erosion in the new cultivated varieties, losing many alleles of interest, related also to tolerance to abiotic stresses. A source of allelic repertoire of drought resistance is represented by tall-size wheat landraces and wild emmer wheat, left behind by the bottleneck produced by twentieth century breeding (Budak et al., 2013; Lopes et al., 2015; Merchuk-Ovnat et al., 2016). In general, semi-dwarf modern wheats are considered to be highly performing in high-input well-managed environments, while in harsh environments, characterized by stress occurrence and low-input management, yield benefits are not so obvious, in comparison with tall-size landraces, which display better yield stability in adverse conditions (Rebetzke et al., 2011; Blum et Sullivan, 1997). There are, however, contradictory indications. If some authors indicate a positive relationship between PH and drought resistance (Acevedo et al, 2002; Gao et al., 2020), or a positive correlation between PH and yield parameters in drought contexts, such as fertile spikes and TKW (Bennani et al., 2016; El-Rawy et al., 2014), other authors find opposite relationships, and recommend the selection of small-size plants as a breeding strategy for increasing drought resistance (Mohammadi et al., 2019). Finally, some authors did not observe any correlation between PH and drought tolerance indices in rainfed conditions (Kamrani, 2015). Again, these controversies are ascribable to differences in DS intensity, duration, and moment of appearance in the different experimental conditions. Jatayev et al. (2020), summarizing many research results obtained all over the world in recent years, reports that in a context of strong and prolonged DS, such as in the very dry areas of Pakistan, China or Iran, breeders always found a positive correlation between yield and PH, favoring tall wheats with wild-haplotypes (i.e., *Rht-B1a-RhtD1a*). In the case of severe and lasting drought, stress appears already during crop establishment and vegetative growth stage, and then exacerbates during the season. In such conditions, semi-dwarf genotypes are clearly adversely affected. In fact, semi-dwarf *Rht-B1b* and *Rht-D1b* wheats have reduced coleoptile length and seedling vigor, requesting a shallow sowing, exposing young seedlings to higher risk of DS in case of low moisture of the very first centimeters of soil, resulting in poor early growth and seedling emergence (Rebetzke et al., 2001a; Rebetzke et al., 2011; Wang et al., 2015a). Moreover, early drought exacerbates the phenotype of semi-dwarf wheats, further reducing their size, resulting in smaller biomass and LAI as well as fewer tillers and spikes, ultimately causing reduced yield via shrunken and small grains (Jatayev et al., 2020). On the contrary, in these contexts, tall wheats can faster produce more biomass, LAI and tillers, passing favorably to the reproductive stage, and having more assimilates to be re-mobilized successively to the spike (Butler et al., 2005; Jatayev et al., 2020). In the case of terminal drought, typical of the Mediterranean climate, with short exposure to stress, semi-dwarf wheats have an advantage over tall genotypes, being able to express their high yield potential without being thwarted by prolonged stress, especially if dwarfing alleles are accompanied by early heading and early maturity traits, enabling drought escape (Pour-Aboughadareh et al., 2020a; Mohammadi et al., 2019; Jatayev et al., 2020).

In summary, traditional tall-size wheats show a productive advantage in case of early, severe and prolonged DS. On the contrary, semi-dwarf wheats are preferable in contexts of mild stress and / or terminal stress, which allows them to express their high yield potential. Several *Rht* genes responsive to gibberellic acid (GA) have been identified, different from *Rht-B1b* and *Rht-D1b* that are GA-insensitive; these (e.g., *Rht8* and *Rht13*) are responsible for greater coleoptile growth and seedling vigor, thus favoring crop establishment in water deficit conditions. In fact, greater coleoptile length and seedling vigor allow deeper sowing, assuring germinating seeds to reach soil moisture in deeper layers, without compromising a good emergence (Rebetzke et al., 2007). Furthermore, some *Rht* genotypes show a less pronounced reduction in stature (such as $Rht\text{-}B1b_{E529K}$, *Rht24* and *Rht 25*). These *Rht* genes could pave the way towards new wheat ideotypes for drought contexts, combining the productive advantages of semi-dwarf genotypes in mild-stress and well-watered environments, and a lower susceptibility in case of early and severe stress (Rebetzke et al., 2011; Wang et al., 2014; Wang et al., 2015a; Jatayev et al., 2020; Mo et al., 2018a; Mo et al., 2018b; Tian et al., 2017).

2.2.2 Peduncle length (PL)

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

2.2.3 Leaf rolling (LR)

Another morphological trait, commonly taken into consideration in cereals for the selection of drought resistant genotypes, is LR, phenomenon that allows wheat to reduce the leaf surface exposed to solar radiation by about 41%-48% (Clarke, 1986), consequently reducing leaf temperature and transpiration (E). Furthermore, rolling creates a microclimatic condition of greater humidity around the leaf surface, allowing the stomata to remain open, thus favoring photosynthesis (Kadioglu and Terzi, 2007), as well as enabling the interception of atmospheric water via foliar water uptake (Ali et al., 2022). While LR is recognized as an important drought avoidance mechanism (O'Toole et al. 1979; Clarke, 1986; Kadioglu and Terzi, 2007), its contribution to yield is not much investigated in wheat, and the results are not always univocal. Bogale et al. (2011) found a positive and significant correlation between LR and GY in durum wheat grown in pots under water deficit during anthesis. On the contrary, Monneveux et al. (2004) highlights no significant impact of LR on GY, when bread wheat in open-field experiments is subjected to mild long-lasting DS after anthesis. Moreover, several authors report that the degree of LR poorly correlates with leaf water potential and leaf water loss rate in both bread and durum wheat (Clarke et al., 1986; Yang et al., 1991), with LR starting only after consistent water loss, probably due to a good capacity for osmotic adjustment, which delays the phenomenon (Clarke et al., 1986; Schonfeld et al., 1988). The contradictory reliability of LR as an effective breeding tool is confirmed by genomic prediction analysis that produced an estimated breeding value of 0.16 for the trait, which is much lower, for example, compared to the estimated value obtained for PL (0.72) (Alemu et al., 2021). However, some genotypic variations in LR have been reported (Rebetzke et al., 2001b – cited by Sirault et al., 2015), and QTLs are starting to emerge (Peleg et al., 2009; Alemu et al., 2021). LR is usually phenotyped with a visual score, which assigns to each leaf a value on a scale of 1-3 or 1-5 (Bogale et al., 2011; Olivares-Villegas et al., 2007). Therefore, the operator's subjectivity can strongly influence the assigned score, making objective phenotyping difficult; the task is further complicated by the possibility of a strong intra-genotypic variability in open-field plots (Clarke et al., 1986). Recently, new objective, quantitative, and repeatable protocols to compare genotypic differences in LR have been proposed (Sirault et al., 2015), based on computer vision analysis of transverse leaf sections. Up to date, LR, which occurs only after strong dehydration when other strategies have failed (e.g., osmotic adjustment), does not appear as a solid breeding tool when stress appears suddenly, and/or is mild and long-lasting (Clarke et al. 1986). Nevertheless, LR could be an interesting selection criterion in case of severe progressive drought. Its genetic basis still remains to be investigated, but there is the possibility that the importance of this trait may grow in the future, given the opportunities supplied by new objective phenotyping approaches.

2.3 Early vigor parameters

Early drought is critical as it can jeopardize proper crop establishment, the first essential component in the expression of yield potential. Satisfactory seed germination and seedling growth, ensuring a successful crop establishment, define together the early vigor. Seed water absorption, germination percentage, seedling vigor index (calculated as the product of shoot length and germination percentage, divided by 100), root length, and coleoptile length are the main early vigor traits that can be inhibited under water deficit conditions (Acevedo et al., 2002; Almaghrabi et al., 2012; Ahmad et al., 2018). All these parameters, which are quick, easy, and cheap to phenotype, have attracted the attention of breeders as tools for improving wheat drought resistance. Since the 1960s, selection for these traits is generally carried out in germinating seeds using polyethylene glycol (PEG) (Parmar et Moore, 1966). PEG simulates drought by inducing a uniform and controlled osmotic stress, with no direct physiological damage as it is inert, non-ionic, and impermeable to cell membranes, thus influencing osmotic potential without entering the apoplast (Hohl and Schopfer, 1991). In order for PEG to mimic drought without altering plant hydraulic properties (therefore without being directly absorbed by the plant) it is essential to use a high-molecular-weight (> 6000) PEG (Kaufmann et Eckard, 1971). For these reasons, the use of PEG-6000 to simulate water deficit has been sustained by several authors (Almaghrabi et al., 2012; Van den Berg et al., 2006; Tuberosa, 2012). Significant differences among wheat genotypes for the aforementioned traits emerged in different studies, suggesting the existence of genetic variability to be exploited for obtaining breeding gains (Pour-Aboughadareh et al., 2020b; Almaghrabi et al., 2012; Moayedi et al., 2009; Dhanda et al., 2004). Despite representing an interesting tool for targeting early vigorous genotypes, the main drawback of many PEG-6000 screenings is that they stop at the seedling stage, without considering the rest of the life cycle. Consequently, promising genotypes identified as "drought resistant", and recommended as suitable for cultivation under water deficit conditions, may not show such features if drought appears later in the life cycle. Even though some evidence of an interesting correlation between seedling growth under DS and adult plant drought resistance is starting to emerge (Dodig et al., 2015), future research requires further validation of preliminary seedling screening results via pot or open-field experiments. At any rate, early vigor remains a trait of interest to ensure successful crop establishment and early drought resistance, and preserve final yield. In addition, regardless of early drought conditions, a quick canopy cover reduces water loss from the ground, thereby preserving soil water content for the future crop, i.e., improving water use efficiency in the crop cycle (Blum 2009; Rebetzke et al., 2011; Tuberosa, 2012).

2.3.1 Number of tillers

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

2.4 Physiological traits

Functional and biochemical responses to DS are well documented in wheat and mainly involve stomata closure to prevent excessive water loss. As a consequence, internal CO_2 concentration (Ci) drops causing net photosynthesis (Pn) inhibition and production of Reactive Oxygen Species (ROS) leading to oxidative damage, so that plant growth and productive performance are strongly compromised (Nezhadahmadi et al., 2013; Ahmad et al., 2018). A valuable breeding target is, therefore, to select for varieties able to maintain a good water status in drought contexts.

2.4.1 Relative Water Content (RWC)

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

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

By closely reflecting the balance between leaf water supply and E rate, it highlights significant genetic variation with high heritability, and is informative at different stages of the plant's life cycle. Moreover, it has proven to positively correlate with E and photosynthetic rate, HI, and GY in both durum and bread wheat (Merah et al., 2001; Moayedi et al., 2011; Mohammadi et al., 2019; Ahmad et al., 2018). RWC is considered a reliable tool for cereal breeding (Teulat et al., 2003; Rampino et al., 2006). In fact, as long as the crop can maintain a high leaf RWC, plant physiology is unaffected by stressful environmental conditions, allowing good productive performances (Beltrano et al., 2006). On the contrary, when leaf RWC drops, plant water balance is disrupted, affecting normal physiology and, ultimately, yield (Ahmad et al., 2018). If RWC drops, wheat implements a set of biochemical and functional responses; some of them are extensively treated in the literature, but their relative importance as breeding tools is still unclear.

2.4.2 Osmotic adjustment

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

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

Since the flag leaf is traditionally recognized as a main contributor to GY formation (Evans et al., 1970; Sylvester-Bradley et al., 1990), water deficit effects on its physiology and biochemistry have aroused great interest over time, in the attempt to find reliable breeding tools. DS is known to cause stomata closure, leading to a drop in stomatal conductance (g_s) thereby reducing both E and Pn (Subrahmanyam et al., 2006; Nezhadahmadi et al., 2013; Ahmad et al., 2018). The decline in g_s limits leaf tissue water loss, but at the same time inhibits CO_2 uptake, hence photosynthesis and eventually dry matter accumulation (Sallam et al., 2019). Thus, while reduced g_s helps to preserve leaf water status via reduced E (Farooq et al., 2009), on the other hand high g_s positively correlates with GY (Bahar et al., 2009). Therefore, drought-resistant genotypes must be able to maintain high g_s in drought conditions, while maintaining high Pn and, ultimately, yield (Saeidi et al., 2015; Wasaya et al., 2021). Once again, the solution to this dilemma relies on the environment. Stomatal closure is, in fact, a drought avoidance mechanism; as such, it is more closely linked to a plant's ability to survive, than to produce, thus limiting yield potential. Li et al. (2021), conducting a meta-analysis on wheat drought adaptation mechanisms, concluded that in severely water stressed environments, drought avoidance mechanisms (such as stomatal closure) confer an advantage in terms of GY production, while avoidance strategies are not effective in the case of moderate or mild stress. Thus, g_s inhibition may be a target trait in harsh environments to ensure plant survival and preserve GY, while genotypes able to maintain high g_s may have higher yield potential in mildly stressful contexts.

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

Further complexity derives from those plant water losses not linked to CO_2 fixation, i.e., non-stomatal E and nocturnal g_s. Non-stomatal E refers to water loss via evaporation through the leaf cuticle, which accounts for up to 30% of leaf water loss in stressful conditions (Hasanuzzaman et al., 2018). Nocturnal E is also not negligible, representing 14-55% of daytime water losses for wheat (Schoppach et al., 2014; Schoppach et al., 2020; McAusland et al., 2021). In conclusion, g_s is a trait of interest to improve wheat drought resistance. Selection should be oriented to genotypes with low g_s only in a context of severe water shortage. In moderate to mild drought scenarios, genotypes able to extract more water from the soil and thus able to maintain high g_s to sustain CO_2 fixation and GY should be preferred. In parallel, attention should be shifted from WUE to the maximization of stomatal E while minimizing water losses not related to CO_2 assimilation (non-stomatal E and nocturnal g_s). Non-stomatal water loss reduction can be achieved by increasing leaf epicuticular waxiness (Richards et al., 1996; Acevedo et al., 2002), and evidence of genotypic variation to exploit nocturnal stomatal E in wheat is starting to emerge (Schoppach et al., 2020; McAusland et al., 2021).

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

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

Schoppach et al. (2012) revealed significant phenotypic diversity across wheat genotypes for g_s and E sensitivity to VPD. The researchers concluded that genotypes with early stomata closure in response to both atmospheric or edaphic induced water stress can store more water in the soil and utilize it more sparingly during drought episodes. On the contrary, the drought tolerance of g_s insensitive genotypes to soil drying and/or increasing VPD may represent a different strategy, favoring CO_2 fixations over water conservation. Those findings are consistent with the idea that drought resistance is highly dependent on drought scenarios, with conservative and insensitive genotypes preferable in case of severe or mild-moderate stress, respectively. Therefore, as noted by Medrano et al. (2002), g_s is responsive to all factors related to leaf water status, thus representing an integrative breeding trait for the overall effects of plant water stress.

2.4.4 Flag leaf net photosynthesis (Pn)

Flag leaf Pn is considered a major contributor to GY, mostly during the GF stage, when other leaves start to senesce (Evans et al., 1970; Sylvester-Bradley et al., 1990; Loss et Siddique, 1994). As drought causes a drop in RWC and g_s, Pn is inhibited. Selection for genotypes able to maintain high Pn rates under water deficit is thus a clear target for wheat breeders, especially in post-anthesis (Inoue et al., 2004). If decreased Pn depended solely on decreased g_s, selecting and phenotyping for both traits would be redundant. However, in several cases, no significant correlation was found between g_s and Pn in drought-stressed wheat, and reduced g_s was not considered the main cause of Pn decrease for both bread and durum wheat exposed to drought (Bogale et al., 2011; Siddique et al., 1999). Other authors instead indicate a strong correlation between Pn and g_s drop in wheat under drought (Mu et al., 2021; Sikder et al., 2015; Wang et al., 2015b). This is due to the fact that in C3 plants drought can cause non-stomatal Pn limitations, related to impaired ATP synthesis and ribulose 1,5-bisphosphate (RuBP) regeneration, altered leaf photochemistry, decreased Rubisco activity, and permanent photoinhibition, as reported in Medrano et al. (2002) and Flexas et Medrano (2002). The prevalence of stomatal or non-stomatal limitations to Pn depend on stress severity and duration, as well as on the contextual presence of other stress sources. For example, in a Mediterranean climate, terminal drought is typically accompanied by HS (Li et al., 2013). Terminal HS in wheat is known to inhibit Pn due to increased photorespiration, as Rubisco kinetics is affected (Farooq et al., 2011). Some studies suggest that Pn inhibition is mainly driven by stomatal closure in mild stress - even if impairment in ATP synthesis and RuBP regeneration have been demonstrated too - while photosynthetic limitation to Pn is predominant under severe drought (Ashraf et al., 2013; Athar, 2005; Flexas et Medrano, 2002). Regardless of stomatal or non-stomatal limitation, the fact that some authors find a significant correlation between flag leaf Pn and GY under drought, or between flag leaf Pn and stress resistance (Zheng et al., 2011; Inoue et al., 2004) while others do not (Bogale et al., 2011; Guóth et al., 2009) raises some doubts about the use of Pn as a breeding target. One must consider that GY, as well as Pn and other gas exchange parameters, are highly integrative traits, strongly dependent on micro-climatic conditions during sampling. Moreover, the contribution of flag leaf Pn to GY may vary among genotypes and during the life cycle, depending on other assimilates sources (e.g., remobilization from reserves, ear photosynthesis, etc.) (Asseng et Van Herwaarden, 2003; Li et al., 2017; Ding et al., 2018). Maintaining high photosynthetic capacity in the flag leaf is clearly an interesting and desirable trait to select for. Nevertheless, it is not easy to phenotype (given the high plasticity of the trait during the day and/or over time) and should be selected in combination with other favorable traits to maximize the positive impact on GY.

2.4.5 Chlorophyll performance parameters

When Chlorophyll-a (Chl a) is excited to the singlet state (^{1}Chl*) as a result of light absorption, under CO_2-limiting conditions (e.g. stomata closure) the amount of harvested light energy and generated reducing power can easily exceed the rate of its consumption by the photosynthetic machinery. Therefore, the plant can employ several mechanisms to dissipate the excess of excitation energy, i.e. emission of fluorescence and heat. Both thermal dissipation and photochemistry mechanisms reduce the amount of emitted fluorescence, and non-photochemical processes that quench chlorophyll fluorescence are collectively called Non-Photochemical Quenching (NPQ). Otherwise, energy can be dissipated via the triplet state (^{3}Chl*), a significant valve for excess excitation that can however generate ROS, extremely damaging to the photosynthetic apparatus (Müller et al., 2001; Grieco et al., 2020). Altered leaf photochemistry and energy flow in Photosystem II (PSII), the most vulnerable part of the photosynthetic apparatus (Sherstneva et al., 2022), have received great attention, thanks to the possibility to easily assess the downregulation of photosynthesis in living plants, measuring chlorophyll fluorescence parameters by specialized equipment and easy-to-use instruments. In particular, Fv/Fm, i.e., maximum quantum efficiency PSII, is indicated by several authors as a selection criterion to improve wheat drought tolerance and/or GY in drought contexts (Flagella et al., 1995; Araus et al., 1998; Almeselmani et al., 2011; Farshadfar et al., 2014; Mohammadi et al., 2019).

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

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

Exploring more complex photosynthetic performance parameters than fluorescence alone, such as NPQ, may allow to better discriminate drought resistant wheat genotypes. However, most of the studies on NPQ variations in response to drought were carried out in controlled environments, on a small number of genotypes. According to the experimental conditions, i.e. phenological phase of stress onset and drought duration and severity, NPQ can increase (Subrahmanyam et al., 2006; Zlatev 2009; Guóth et al., 2009; Zivcak et al., 2014; Yaghoubi Khanghahi et al., 2020; Zhu et al., 2020; Grieco et al., 2020), decrease (Shangguan et al., 2000; Sherstneva et al., 2021) or not vary (Yudina et al., 2020), making it difficult at the state of the art to determine the potentiality of this trait for high-throughput screening. Moreover, NPQ might respond differently to DS and HS (Zhu et al., 2020), complicating the analysis in those environments where drought is frequently accompanied by heat waves. Recently, Grieco et al. (2020) provided a base for developing wheat phenotyping for DS tolerance based on NPQ. This study represents a breakpoint, since the majority of previous studies emphasize photodamage as the only cause of the downregulation of photosynthesis in case of harsh DS conditions, while Grieco et al. (2020) monitored NPQ kinetics in slowly increasing levels of DS in wheat, as it usually occurs in the field. Authors noted that NPQ values started to increase 13–17 days after increasing drought imposition, when soil substrate reached 30% of field capacity, with no detectable change in Fv/Fm. Subsequently, after 18-24 days of increasing DS (substrate at 20% of field capacity), both NPQ and Fv/Fm increased, indicating PSII damage. However, Grieco et al. (2020) limited their investigation on DS at early phenological stages (BBCH 23 – 33), thus at the moment not giving information on NPQ suitability as a breeding tool in case of terminal drought.

2.5 Combined heat and drought stress

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

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

Studying the effects of single and combined DS and heat-shock on wheat physiology at anthesis, Wang et al. (2010) observed that the stress combination resulted in a greater decrease in Pn, g_s and E of flag leaves than drought or heat-shock alone. Similarly, Hlaváčová et al. (2018) observed that heat-shock during anthesis and GF significantly increased the negative impact of drought on CO_2 assimilation rate. Combined terminal drought and chronic HS resulted in more severe consequences on Pn and g_s, considerably reducing growth and yield traits (Shah and Paulsen, 2003; Prasad et al., 2011).

Therefore, the aforementioned physiological parameters remain valid breeding tools for drought resistance even in case of concomitant HS. Indeed, in mild terminal drought conditions, genotypes able to extract more water from the soil, thus maintaining higher g_s to sustain Pn, should be preferred also if drought is accompanied by HS, as this strategy would ensure more CO_2 fixation, higher E (leading to tissue temperature regulation), less oxidative damage (linked to lower ROS formation), thus limiting also the negative effects of HS. Similarly, the indications about phenological breeding strategies remain valid if DS is accompanied by HS, as they both increase ovule and pollen sterility, reduce spikelet number, accelerate plant senescence, and reduce GF duration, enhancing the reduction in TKW (Barnabás et al., 2008; Ji et al., 2010; Farooq et al., 2011; Prasad et al., 2011). So, in the context of terminal drought, even when accompanied by terminal HS, early heading and early maturity genotypes can be considered preferable, avoiding exposure to terminal stressful conditions by escape strategies. As exposed in section 2.1, a short cycle could be obtained by the combination of a short pre-heading phase with an increased GF duration, or by a longer pre-heading phase, and a short (but highly efficient) GF period.

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

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

2.6 Concluding remarks

Breeding improvements for drought resistance in both bread and durum wheat can be obtained via direct or indirect selection for yield. Direct selection for yield is hampered by its low heritability, GY being a highly integrative trait, dependent on a wide range of biotic and abiotic interactions. For this reason, physiological breeding, i.e., the selection of morpho-functional traits associated with yield performance in water-stressed environments, attracts most attention. The main obstacle to physiological breeding is deciding which traits should be preferred as a reliable set of selection criteria, given the broad spectrum of drought affected environments in which timing, duration, and severity of the stress vary greatly. In fact, literature shows many conflicting results regarding the correlation between various morpho-functional traits and GY under water-limiting conditions. In this review, we offer an insight into the reasons for these controversies, while discussing the ease of use of each trait. Moreover, we provide an interpretation of how selection criteria should be combined for selection in different target environments, characterized by different drought scenarios. Table 3 summarizes our conclusions. Thus, this review does not intend to be an exhaustive treatment of all phenotypic traits associated with DS, nor of the modern high-throughput phenotyping strategies and genomic approaches available. For example, root architecture traits are extremely important for DS resistance (Manschadi et al., 2006), as well as imaging spectroscopy can be applied in remote sensing to evaluate numerous traits associated with abiotic stress tolerance (Jangra et al., 2021). New rising high-throughput phenotyping platforms, providing precise measurements of desired traits among thousands of field-grown plants, associated with genomic technologies, will accelerate breeding programs (Mwadzingeni et al., 2016b; Jangra et al., 2021). The purpose of this review is to highlight the contradictions found in the literature for different morpho-physiological and phenological traits, and to provide an environment-oriented perspective to overcome them.

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

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

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

Index name	Equation	Reference author(s)	Most suitable selection environment	Web of Science citations (April 7th 2022)	Scholar citations (April 7th 2022)
Stress susceptibility index (SSI)	$[1 - (Ys / Yp) / 1 - (\hat{Y}s / \hat{Y}p)]$	Fischer and Maurer, 1978 [33]	A	1145	3332
Tolerance index (TOL)	$(Yp - Ys)$	Rosielle and Hamblin, 1981 [34]	A	611	1870
Yield Stability Index (YSI)	Ys / Yp	Bouslama and Schapaugh, 1984 [35]	A	345	1011
Mean productivity (MP)	$(Ys + Yp) / 2$	Rosielle and Hamblin, 1981 [34]	B	611	1870
Harmonic mean (HARM)	$2 (Yp \times Ys) / (Yp+Ys)$	Schneider et al., 1997 [37]	B	129	460
Geometric mean productivity (GMP)	$(Yp \text{ x } Ys)^{½}$	Fernandez, 1992 [36]	B	94	2003
Stress Tolerance index (STI)	$(Yp \text{ x } Ys) / (\hat{Y}p)^2$	Fernandez, 1992 [36]	B	94	2003
Yield Index (YI)	$Ys / \hat{Y}s$	Gavuzzi et al., 1997 [38]	B	172	602

Note: in the above equations Yp and Ys 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 a., 2011 [40] ; Ahmadizadeh et al., 2012 [23] ; Patel et al., 2019 [29])

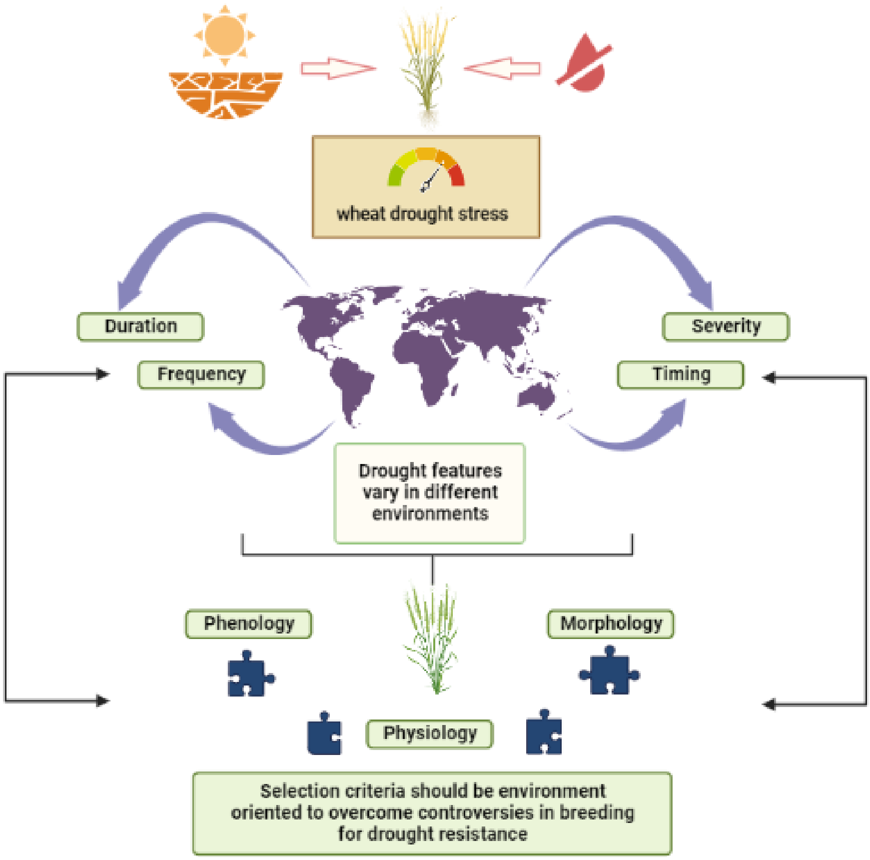
Table 2. Developmental stage trait selection to obtain early maturity for terminal drought escape based on two strategies.

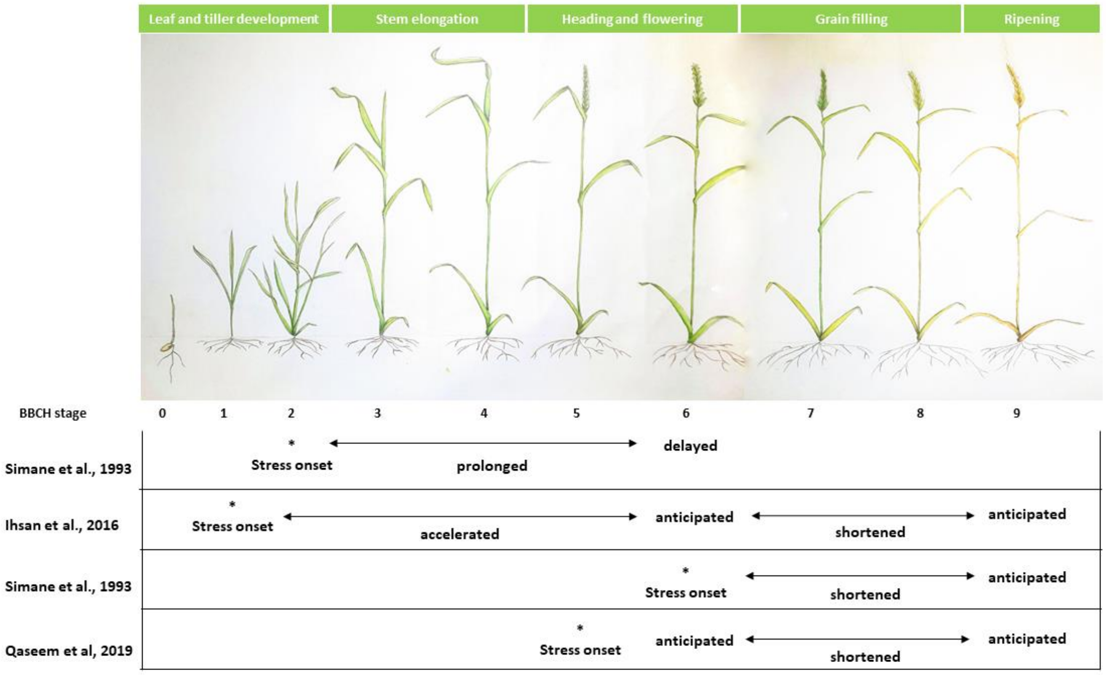
	STRATEGY 1	**STRATEGY 2**
	Yashavanthakumar et al., 2021 [53]; Ihsan et al., 2016 [47] ; Simane et al., 1993 [46]; Shavrukov et al., 2017 [49]; Mohammadi et al, 2019 [25].	Al-Karaki 2012 [54]; Singh et al. 2014 [55].
DEVELOPMENTAL STAGE		
Pre-heading period (BBCH 1 – 4)	**short**	**long**
Heading (BBCH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

Table 3: Suitable trait combinations for different drought scenarios

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

Trait	**Mild-moderate drought**	**Severe drought**
High g_s	☑	
Reduced g_s		☑
Epicuticular waxiness	☑	☑
Reduced nocturnal stomatal transpiration	☑	☑
High number of tillers		☑
Low number of tillers	☑	
Leaf rolling		☑
Flag leaf Pn	☑	☑
Fv/Fm - T_{crit}		☑
Reduced NPQ		☑
RWC	☑	☑
Tall-size		☑
Semi-dwarf	☑	


wheat drought stress
Duration
Frequency
Severity
Timing
Drought features vary in different environments
Phenology
Morphology
Physiology
Selection criteria should be environment oriented to overcome controversies in breeding for drought resistance


Leaf and tiller development
Stem elongation
Heading and flowering
Grain filling
Ripening
BBCH stage
0
1
2
3
4
5
6
7
8
9
Simane et al., 1993
*
Stress onset
prolonged
delayed
Ihsan et al., 2016
*
Stress onset
accelerated
anticipated
shortened
anticipated
Simane et al., 1993
*
Stress onset
shortened
anticipated
Qaseem et al, 2019
*
Stress onset
anticipated
shortened
anticipated