REVIEW PAPER

The physiological and genetic basis of combined drought and heat tolerance in wheat

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Abstract

Drought and heat stress cause losses in wheat productivity in major growing regions worldwide, and both the occurrence and the severity of these events are likely to increase with global climate change. Water deficits and high temperatures frequently occur simultaneously at sensitive growth stages, reducing wheat yields by reducing grain number or weight. Although genetic variation and underlying quantitative trait loci for either individual stress are known, the combination of the two stresses has rarely been studied. Complex and often antagonistic physiology means that genetic loci underlying tolerance to the combined stress are likely to differ from those for drought or heat stress tolerance alone. Here, we review what is known of the physiological traits and genetic control of drought and heat tolerance in wheat and discuss potential physiological traits to study for combined tolerance. We further place this knowledge in the context of breeding for new, more tolerant varieties and discuss opportunities and constraints. We conclude that a fine control of water relations across the growing cycle will be beneficial for combined tolerance and might be achieved through fine management of spatial and temporal gas exchange.

Keywords: Cereal, climate, stress, temperature, water, yield.

Introduction

Wheat is the major food for numerous regions around the world, providing approximately 20% of daily calories and protein for 4.5 billion people (Shiferaw *et al.*, 2013). Wheat ranks first in terms of harvested area (223.67 million hectares in 2016) and is the second most produced crop with a global production of 735.3 million tons in 2016 (USDA, 2017). A recent study predicted that wheat yields will decline by 4.1% to 6.4% for each global increase of 1 °C due to climate change (Liu *et al.*, 2016) while wheat consumption is expected to increase by over 30% in the next 40 years (Weigand, 2011). Wheat production would need to reach 858 million tons by 2050 in order to match the predicted global food demand (Alexandratos and Bruinsma, 2012).

Drought and heat are two major abiotic stresses constraining wheat productivity worldwide, causing yield losses of up to 86% and 69%, respectively (Fischer and Maurer, 1978; Prasad *et al.*, 2011). Both stresses are more likely to occur simultaneously rather than separately in semi-arid and hot growing regions in North Africa, Argentina, Mexico, Australia, South Africa, and the Mediterranean countries, and in high latitude, semi-arid growing regions of central and eastern Asia, Canada, the USA, and Kazakhstan (Mooney and Di Castri, 1973; Araus *et al.*, 2002; Pradhan *et al.*, 2012; Tricker *et al.*, 2016). Yield penalty is associated with long periods of drought coinciding with heat waves above 32 °C during heading and grain filling stages (Wardlaw and Wrigley, 1994). In

Abbreviations: G×E, genotype by environment; GS, genomic selection; HI, harvest index; HSF, heat shock factor; HSP, heat shock protein; QTL, quantitative trait locus; ROS, reactive oxygen species; VPD, vapour pressure deficit; WU, water use; WUE, water use efficiency.

the Australian wheat belt, average daily maximum temperatures and numbers of days over 30 °C during the period of grain filling have been steadily increasing over the past three decades, and further rises are projected with climate change (ABS, 2012). The major decrease in wheat production across central Europe in the exceptionally hot summer of 2003 was likely to be due to short, but severe, heat waves during reproductive development (Wheeler, 2012). Stress tolerance is particularly critical in growing regions where the gap between attained yields and maximum yields is highest, and may have more consequence globally than where differences are lower (Tester and Langridge, 2010). Hence, producing wheat varieties with high and stable yield under these environmental stresses is one of the most important aims of breeding (Gavuzzi *et al.*, 1997; Tilman *et al.*, 2011).

Whereas responses to either drought or heat stress have been studied extensively in wheat, the combination of both environmental stresses has only recently become a matter for research. When irrigated, and with saturated atmospheric humidity (low vapour pressure deficit; VPD) at high temperatures, Australian modern wheat varieties did not show symptoms of heat stress: plants were lush and produced up to 6.8 t ha^{-1} (Parent *et al.*, 2017). This example and others demonstrate that wheat is heat tolerant when water is available. To improve wheat for dual tolerance, plants must be studied under the combination of stresses.

Overall, the combination of both high temperature and drought has a negative, additive impact on plant phenology and physiology, i.e. growth, chlorophyll content, leaf photosynthesis, grain number, spikelet fertility, grain filling duration, and grain yield (Altenbach *et al.*, 2003; Shah and Paulsen, 2003; Prasad *et al.*, 2011; Pradhan *et al.*, 2012; Perdomo *et al.*, 2015, 2017). Although responses to the two stresses share some common mechanisms, other physiological processes are antagonistic (Machado and Paulsen, 2001). For instance, combined drought and heat stress decreases leaf chlorophyll content by 49% while drought or heat alone reduce it by 9% or 27%, respectively (Pradhan *et al.*, 2012; Awasthi *et al.*, 2014). This early senescence of green tissues affects the total amount of carbohydrates transported to the grains and final grain weight. Delayed senescence, a stay-green phenotype, has been associated with drought tolerance (e.g. Pinto *et al.*, 2010) and with heat tolerance in experiments using irrigation (e.g. Shirdelmoghanloo *et al.*, 2016) where water reserves are available and accessible in deep soils for continued water use and transport of assimilates to grains post-anthesis (Reynolds *et al.*, 2005; Christopher *et al.*, 2008). In contrast, a stay-green phenotype is unlikely to contribute to combined drought and heat tolerance where no water reserves are available for continuous water use and might exacerbate the combined stress.

Although plants' responses to the combination of drought and heat have been described (reviewed in Zandalinas *et al.* 2018), few models or explanations are proposed for the physiological traits underlying combined tolerance (Pinto and Reynolds, 2015), and very little is known about genes and loci underlying these physiological mechanisms in wheat. Quantitative trait loci (QTLs) for drought and heat tolerance

have, to date, mostly been reported for low-yield field environments where stress is present (such as the mega-environments 1 and 4 defined by CIMMYT, http://wheatatlas.org/), but not controlled and often not measured (Table 1). Complex interactions between QTLs and environments exist that may limit the usefulness of a particular allele. For example, using multi-environment analysis, Bonneau *et al.* (2013) showed that alternative parental alleles of a major QTL for yield in dry and hot environments (*qDHY.3B*) were positive, depending on the severity of the water deficit, soil depth, and co-occurrence with high temperatures.

A greater understanding of the physiology underlying combined drought and heat tolerance should enable researchers and breeders to discriminate between traits and loci useful for improvement. With improving genomic resources and high-throughput phenotyping methods, it becomes possible to identify loci and genes for tolerance and incorporate favourable alleles into breeding programmes. In this review, we outline what is known in wheat of the physiology and genetic variation underlying drought and heat tolerance – defined here as the ability to maintain yield under stress. We propose traits to measure in genetic mapping populations that are likely to prove beneficial for combined tolerance (Fig. 1) and discuss opportunities and constraints for incorporating alleles into breeding for tolerant wheat.

Wheat growth, architecture and biomass partitioning under drought and heat

Water deficit and high temperature affect every aspect of wheat growth from germination to maturity. The impact on yield components depends on the duration and the severity of the stress as well as the stage of plant development when stress occurs (Salter and Goode, 1967; Barnabás *et al.*, 2008; Parent *et al.*, 2017). As water stress reduces plant growth through reduced tillering and leaf expansion (Acevedo *et al.*, 1971), and high temperature accelerates plant growth and shortens developmental stages (Parent and Tardieu, 2012), under combined stress plants flower earlier and produce less biomass than under single stress. Reproductive organs are especially sensitive to drought and heat stress (Stone and Nicolas, 1995; Saini and Lalonde, 1997). Episodes of drought and heat stress around anthesis severely reduce the final number of grains per spike by more than either individual stress due to an increased abortion of ovules (Asana and Williams, 1965; Hochman, 1982; Saini and Aspinall, 1982; Pradhan *et al.*, 2012; Weldearegay *et al.*, 2012). During grain filling, combined drought and high temperature, as frequently occur in major growing regions, reduce the size and weight of individual grains by reducing the division rate of endosperm cells and shortening the duration of grain filling (Jenner, 1994; Barnabás *et al.*, 2008; Prasad *et al.*, 2011; Pradhan *et al.*, 2012).

Complex source–sink interactions underlie tolerance to drought and heat stress, and remobilization of stored assimilates to grain filling following stress at sensitive periods is dependent on sink strength. In maize, grain size, determining

Table 1. *QTL identified in wheat under combined dry and hot conditions, drought or heat stress*

Trait	Chromosome	References
Combined dry and hot conditions		
Grain yield	1AL, 1B, 1D, 2A, 2BL, 3A, 3B, 4AL, 4B, 5A, 6A, 6B, 7A, 7B, 7D	Kirigwi *et al.* (2007)[a], Maccaferri *et al.* (2008)[a,b], Pinto *et al.* (2010)[a], Golabadi *et al.* (2011)[a], Bennett *et al.* (2012)[a], Merchuk-Ovnat *et al.* (2016)[a], Tahmasebi *et al.* (2017)[a]
Thousand grain weight	1D, 2B, 3A, 3B, 4A, 6A, 7A, 7B, 7D	Pinto *et al.* (2010)[a], Golabadi *et al.* (2011)[a], Bennett *et al.* (2012)[a], Tahmasebi *et al.* (2017)[a]
Kernel weight index (large grains–all grains)	1A, 2B, 6A	Pinto *et al.* (2010)[a]
Grain weight spike^{-1}	5B, 6A, 7B	Golabadi *et al.* (2011)[a]
Grain number m^{-2}	1B, 2A, 3B, 3D, 4AL, 6B, 7A	Kirigwi *et al.* (2007)[a], Pinto *et al.* (2010)[a], Bennett *et al.* (2012)[a]
Grain number spike^{-1}	2B, 7B	Golabadi *et al.* (2011)[a], Tahmasebi *et al.* (2017)[a]
Harvest index	1B, 2A, 2B, 3B, 4A, 5A, 5B, 6A, 6B, 7B	Peleg *et al.* (2009)[d], Golabadi *et al.* (2011)[a]
Spike weight	1B, 2A, 4A, 6A, 7A, 7B	Peleg *et al.* (2009)[d], Golabadi *et al.* (2011)[a]
Spike number m^{-2}	2B, 4AL, 5B	Kirigwi *et al.* (2007)[a], Golabadi *et al.* (2011)[a]
Spike harvest index	2B, 3B	Golabadi *et al.* (2011)[a]
Spikelet number spike^{-1}	5A	Tahmasebi *et al.* (2017)[a]
Biomass	2BS, 4AL, 4B, 5A, 7AS	Kirigwi *et al.* (2007)[a], Peleg *et al.* (2009)[d], Merchuk-Ovnat *et al.* (2016)[a]
Plant height	1A, 1B, 2BL, 3AL, 3BS, 4A, 4B, 5A, 7AS	Maccaferri *et al.* (2008)[ab], Pinto *et al.* (2010)[a], Tahmasebi *et al.* (2017)[a]
Shoot length	2B, 3B, 4A, 4B, 6B, 7A, 7B	Peleg *et al.* (2009)[d]
Peduncle length	3A, 3B	Bennett *et al.* (2012)[a]
Flag leaf width	2B, 3B	Bennett *et al.* (2012)[a]
Days to heading	1A, 1B, 1D, 2AS, 2BS, 2BL, 3A, 3B, 4AL, 4B, 4D, 5A, 6A, 7AS, 7BS, 7D	Kirigwi *et al.* (2007)[a], Maccaferri *et al.* (2008)[a,b], Peleg *et al.* (2009)[d], Pinto *et al.* (2010)[a], Merchuk-Ovnat *et al.* (2016)[a], Ogbonnaya *et al.* (2017)[a], Tahmasebi *et al.* (2017)[a]
Days to maturity	1A, 1D,5A, 7B, 7D	Pinto *et al.* (2010)[a], Tahmasebi *et al.* (2017)[a]
Days from heading to maturity	1B, 2B, 4A, 4B, 5A, 5B, 7A, 7B	Peleg *et al.* (2009)[d]
NDVI at the vegetative stage	1B, 3B, 4A, 7A	Pinto *et al.* (2010)[a], Bennett *et al.* (2012)[a]
NDVI at the grain filling stage	1B, 1D, 2A, 2B, 4A, 4B, 5A, 6A, 6B, 7A, 7B	Pinto *et al.* (2010)[a]
Stem WSC	1A, 1B, 3A, 3B, 4A, 6D	Pinto *et al.* (2010)[a], Bennett *et al.* (2012)[a]
Grain fill rate	4AL	Kirigwi *et al.* (2007)[a]
Grain fill duration	4AL	Kirigwi *et al.* (2007)[a]
Canopy temperature at the vegetative stage	1B, 2B, 3B, 4A, 4B, 6B, 7A	Pinto *et al.* (2010)[a], Tahmasebi *et al.* (2017)[a]
Canopy temperature at the grain filling stage	1A, 1B, 2B, 3B, 4A, 5A, 6B, 7A	Pinto *et al.* (2010)[a]
Canopy temperature depression	1A, 2A, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 7A, 7B	Diab *et al.* (2008)[a]
Flag leaf rolling	1A, 2A, 2B, 4B, 5A, 5B, 6B, 7A, 7D	Peleg *et al.* (2009)[d], Tahmasebi *et al.* (2017)[a]
Early vigour	2B, 2D, 3B, 4A	Bennett *et al.* (2012)[a]
Early ground cover	6AS	Mondal *et al.* (2017)[a]
Chlorophyll content	1A, 1B, 3A, 4A, 4B, 4D, 5A, 5B, 6A, 6B, 7A	Diab *et al.* (2008)[a], Peleg *et al.* (2009)[d], Bennett *et al.* (2012)[a]
Chlorophyll fluorescence	1A, 1B, 2A, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 7A, 7B	Diab *et al.* (2008)[a]
Carbon isotope discrimination	1B, 2A, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6B, 7A, 7B	Diab *et al.* (2008)[a], Peleg *et al.* (2009)[d]
Photosynthetically active radiation	1A, 1B, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 7A, 7B	Diab *et al.* (2008)[a]
Stomatal density	4AS, 5AS, 7AL	Shahinnia *et al.* (2016)[a]
Stomatal index	2BL, 7BL	Shahinnia *et al.* (2016)[a]
Stomatal aperture area	7AL	Shahinnia *et al.* (2016)[a]
Stomatal aperture length	2BS, 2BL, 7AL	Shahinnia *et al.* (2016)[a]
Guard cell length	1AS, 3BL, 7AL	Shahinnia *et al.* (2016)[a]
Guard cell area	1BL, 4BL, 5AL, 5DL	Shahinnia *et al.* (2016)[a]

Table 1. *Continued*

Trait	Chromosome	References
Transpiration efficiency	1A, 1B, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 7A, 7B	Diab *et al*. (2008)[a]
Leaf relative water content	1B, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B	Diab *et al*. (2008)[a]
Water index	1A, 1B, 2A, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 7A, 7B	Diab *et al*. (2008)[a]
Leaf osmotic potential	2A, 2B, 3A, 3B, 4B, 5A, 5B, 6B	Peleg *et al*. (2009)[d]
Osmotic adjustment	1A, 3A, 3B, 4A, 7A	Diab *et al*. (2008)[a]
Metabolites (mQTL)	2B, 4A, 5A, 7A, 7D	Hill *et al*. (2015)[a]
Expression of stress-related genes (eQTL)	6BL	Aprile *et al*. (2013)[c]
Drought stress		
Grain yield	2D, 3D, 3DL, 4AL, 4BS, 4DL, 5A, 5B, 5DL, 6B, 6D, 7AL, 7BL, 7D	Quarrie *et al*. (2005)[a], Czyczyło-Mysza *et al*. (2011)[d], Kadam *et al*. (2012)[c], Tahmasebi *et al*. (2017)[a]
Grain weight spike^{-1}	1B, 1D	Xu *et al*. (2017)[a]
Thousand grain weight	1B, 1D, 2A, 2B, 3A, 3D, 4A, 4D, 5A, 6A, 6D, 7A, 7B	Quarrie *et al*. (2005)[a], Dashti *et al*. (2007)[c], Yang *et al*. (2007)[a], Tahmasebi *et al*. (2017)[a], Xu *et al*. (2017)[a]
Grain number m^{-2}	1B, 5B, 7D	Tahmasebi *et al*. (2017)[a]
Grain number spike^{-1}	1A, 2A, 2B, 2D, 3A, 3B, 4A, 4B, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B	Quarrie *et al*. (2005)[a], Czyczyło-Mysza *et al*. (2011)[d], Xu *et al*. (2017)[a]
Harvest index	1B, 2D, 4BS, 5A	Kadam *et al*. (2012)[c], Xu *et al*. (2017)[a]
Spike number plant^{-1}	1A, 2A, 2B, 2D, 4B, 5A, 7B	Quarrie *et al*. (2005)[a], Xu *et al*. (2017)[a]
Spikelet compactness	6A, 7A	Xu *et al*. (2017)[a]
Spikelet number spike^{-1}	1A, 7D	Tahmasebi *et al*. (2017)[a], Xu *et al*. (2017)[a]
Sterile spikelet number spike^{-1}	7A	Xu *et al*. (2017)[a]
Fertile spikelet spike^{-1}	2A	Xu *et al*. (2017)[a]
Biomass	1B	Xu *et al*. (2017)[a]
Shoot biomass	4B	Kadam *et al*. (2012)[c]
Root biomass	2D, 4BS	Kadam *et al*. (2012)[c]
Plant height	1B, 4B, 7D	Tahmasebi *et al*. (2017)[a], Xu *et al*. (2017)[a]
Peduncle length	3B	Dashti *et al*. (2007)[c]
Coleoptile length	6AS	Spielmeyer *et al*. (2007)[c]
Spike length	2B, 7A, 7B	Xu *et al*. (2017)[a]
Root length	2D, 4B, 5D, 6B	Kadam *et al*. (2012)[c]
Growth rate	5BL	Parent *et al*. (2015)[c]
Relative growth rate	4AL	Parent *et al*. (2015)[c]
Inflexion point in growth curves	7DS	Parent *et al*. (2015)[c]
Leaf expansion rate	5BL	Parent *et al*. (2015)[c]
Inflexion point in leaf expansion curves	5BL	Parent *et al*. (2015)[c]
Days to heading	1D, 4B, 7D	Tahmasebi *et al*. (2017)[a]
Days to flowering	2D	Kadam *et al*. (2012)[c]
Stem WSC at the flowering stage	1A, 1D, 2D, 4A, 4B, 7B	Yang *et al*. (2007)[a]
Stem WSC at the grain filling stage	4A	Yang *et al*. (2007)[a]
Stem WSC at the maturity stage	6B	Yang *et al*. (2007)[a]
Accumulation efficiency of stem WSC	1A, 2A, 5A, 7B	Yang *et al*. (2007)[a]
Remobilization efficiency of stem WSC	7A	Yang *et al*. (2007)[a]
Grain filling efficiency	2A, 4B, 5A,	Yang *et al*. (2007)[a]
Flag leaf rolling	4B, 5A	Tahmasebi *et al*. (2017)[a]
Chlorophyll content	1B, 2B, 5B, 7A, 7B	Ilyas *et al*. (2014)[c], Tahmasebi *et al*. (2017)[a], Xu *et al*. (2017)[a]
Flag leaf persistence	2D, 3B, 4B, 5A, 6A	Verma *et al*. (2004)[a]
Net photosynthetic rate	6B	Xu *et al*. (2017)[a]
Chlorophyll fluorescence	1B, 2A, 2D, 3A, 3B, 3D, 4A, 4B, 4D, 5A, 5B, 6A, 6B, 7A, 7B, 7D	Czyczyło-Mysza *et al*. (2011)[d]
Stomatal conductance	5A	Xu *et al*. (2017)[a]

Table 1. *Continued*

Trait	Chromosome	References
Stomatal density	5BS	Shahinnia et al. (2016)[c]
Stomatal index	5BS, 6DL	Shahinnia et al. (2016)[c]
Stomatal aperture length	2BL, 4BS, 7AS, 7DL	Shahinnia et al. (2016)[c]
Guard cell area	1BL, 5BS	Shahinnia et al. (2016)[c]
Guard cell length	1BL, 4BS, 7AS	Shahinnia et al. (2016)[c]
Transpiration rate	3AI, 4BL, 6D	Parent et al. (2015)[c], Xu et al. (2017)[a]
Water use efficiency	2AL, 4D	Parent et al. (2015)[c], Xu et al. (2017)[a]
Heat stress		
Grain yield	1A, 1BL, 1D, 2BS, 3A, 3BS, 3BL, 3D, 4A, 4B, 4DL, 5A, 5B, 6A, 6B, 6D, 7AS, 7AL, 7BS, 7BL	Quarrie et al. (2005)[a], Maccaferri et al. (2008)[a,b], Pinto et al. (2010)[a], Golabadi et al. (2011)[a], Bennett et al. (2012)[a], Paliwal et al. (2012)[a], Merchuk-Ovnat et al. (2016)[a], Ogbonnaya et al. (2017)[a]
Grain weight spike^{-1}	3A, 3BS, 6A, 7A, 7B	Golabadi et al. (2011)[a], Shirdelmoghanloo et al. (2016)[c], Ogbonnaya et al. (2017)[a]
Thousand grain weight	1A, 2A, 2B, 2D, 3A, 3BS, 3D, 4A, 4B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7D	Quarrie et al. (2005)[a], Pinto et al. (2010)[a], Golabadi et al. (2011)[a], Bennett et al. (2012)[a], Ogbonnaya et al. (2017)[a], Tahmasebi et al. (2017)[a]
Single grain weight	2D, 3BS, 5B, 6A	Shirdelmoghanloo et al. (2016)[c]
Kernel weight index (large grains–all grains)	1A, 1D, 2B, 3B, 4B, 5A, 5B, 6A, 6B, 6D	Pinto et al. (2010)[a]
Grain number m^{-2}	1A, 1B, 1D, 3BS, 3BL, 3D, 4A, 4B, 4D, 5B, 6A, 6B, 6D, 7A	Pinto et al. (2010)[a], Bennett et al. (2012)[a]
Grain number spike^{-1}	1A, 1B, 2A, 3B, 4B, 4D, 5D, 6A, 7B, 7D	Quarrie et al. (2005)[a], Golabadi et al. (2011)[a], Ogbonnaya et al. (2017)[a], Tahmasebi et al (2017)[a]
Threshing index	1A, 1B, 5B	Ogbonnaya et al. (2017)[a]
Harvest index	1B, 2B, 3B, 4A, 5A, 5B, 6A, 6B, 7B	Peleg et al. (2009)[d]
Spike number m^{-2}	1A, 1B, 3A, 3B, 4B, 5A, 5B, 7B, 7D	Golabadi et al. (2011)[a], Ogbonnaya et al. (2017)[a]
Spike number plant^{-1}	3A	Quarrie et al. (2005)[a]
Spike weight	1B, 2B, 2D, 3D, 4A, 5D, 6A, 7B	Peleg et al. (2009)[d], Golabadi et al. (2011)[a], Ogbonnaya et al. (2017)[a]
Spike harvest index	2B, 5B, 7A, 7B	Golabadi et al. (2011)[a]
Spikelet compactness	1A	Tahmasebi et al. (2017)[a]
Spikelet number spike^{-1}	1B, 1D, 2B, 4A, 5B, 6A, 6B	Ogbonnaya et al. (2017)[a], Tahmasebi et al. (2017)[a]
Number of productive tiller	1B	Sharma et al. (2016)[a]
Biomass	1BL, 2BS, 7AS, 7BS	Merchuk-Ovnat et al. (2016)[a]
Shoot biomass	3BS, 4A, 6B	Shirdelmoghanloo et al. (2016)[c]
Plant height	1A, 1B, 2A, 2B, 2D, 3A, 3B, 3D, 4A, 4B, 5A, 5B, 6A, 6D, 7A, 7B, 7D	Maccaferri et al. (2008)[a,b], Pinto et al. (2010)[a], Ogbonnaya et al. (2017)[a], Tahmasebi et al. (2017)[a]
Shoot length	1B, 2B, 3A, 3B, 4A, 4B, 5D, 7A, 7B	Peleg et al. (2009)[d], Ogbonnaya et al. (2017)[a]
Peduncle length	1A, 1B, 2B, 3A, 3B, 5B, 7A	Ogbonnaya et al. (2017)[a]
Flag leaf length	3B, 5B	Mason et al. (2010)[c]
Flag leaf width	1D, 2B, 3BL, 7A, 3BL	Mason et al. (2010)[c], Bennett et al. (2012)[a]
Wax score	1B, 2A, 2B, 2D, 3A, 3B, 5A, 6A, 6B, 7B	Mason et al. (2010)[c], Ogbonnaya et al. (2017)[a]
Days to heading	1BL, 1D, 2A, 2BS, 3B, 3A, 4A, 4B, 4D, 5A, 6A, 7AS, 7BS, 7D	Maccaferri et al. (2008)[a,b], Peleg et al. (2009)[d], Pinto et al. (2010)[a], Merchuk-Ovnat et al. (2016)[a], Ogbonnaya et al. (2017)[a]
Days to flowering	1B, 1D, 4A, 4B, 4D, 5B	Mason et al. (2010)[c], Pinto et al. (2010)[a]
Days to maturity	1B, 1D, 2A, 2B, 3B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B, 7DS	Pinto et al. (2010)[a], Bennett et al. (2012)[a], Paliwal et al. (2012)[a], Ogbonnaya et al. (2017)[a]
NDVI at the vegetative stage	1B, 1D, 2B, 2D, 3A, 3B, 4A, 4D, 5A, 6A, 6B, 6D, 7A	Pinto et al. (2010)[a], Bennett et al. (2012)[a]
NDVI at the grain filling stage	1A, 1B, 3A, 4A, 4B, 5A, 5B, 6A, 7B	Pinto et al. (2010)[a]
Stem WSC	1A, 1B, 2D, 3A, 3BL, 5A, 5B, 6A	Pinto et al. (2010)[a], Bennett et al. (2012)[a]
Grain filling duration	1B, 1D, 2A, 2B, 2D, 3BS, 5A, 6A, 6B, 6D	Mason et al. (2010)[c], Shirdelmoghanloo et al. (2016)[c], Ogbonnaya et al. (2017)[a]
Canopy temperature at the vegetative stage	1A, 1B, 1D, 2B, 3A, 3BL, 4A, 4B, 5B, 6B, 7A	Pinto et al. (2010)[a], Bennett et al. (2012)[a]
Canopy temperature at the grain filling stage	1A, 1B, 1D, 2B, 3BS, 3BL, 4A, 4D, 5A, 5D, 7A, 7B	Pinto et al. (2010)[a], Bennett et al. (2012)[a]
Canopy temperature depression	7BL	Paliwal et al. (2012)[a]
Flag leaf rolling	1A, 2A, 2B, 2D, 3D, 4B, 5A, 5B, 6A, 6B, 7A, 7B	Peleg et al. (2009)[d], Ogbonnaya et al. (2017)[a], Tahmasebi et al. (2017)[a]
Early vigour	2B, 2D, 3BL	Bennett et al. (2012)[a]

Table 1. *Continued*

Trait	Chromosome	References
Chlorophyll content	1A, 1B, 1D, 2B, 3A, 3BS, 4A, 4D, 5A, 5B, 6A, 6D, 7A, 7B, 7D	Peleg *et al.* (2009)[d], Pinto *et al.* (2010)[a], Bennett *et al.* (2012)[a], Tahmasebi *et al.* (2017)[a]
Flag leaf persistence	1B, 1D, 2A, 3A, 3BS, 6A, 6B, 7A,	Vijayalakshmi *et al.* (2010)[c], Talukder *et al.* (2014)[c], Shirdelmoghanloo *et al.* (2016)[c]
Chlorophyll loss rate	3BS, 6BL	Shirdelmoghanloo *et al.* (2016)[c]
Chlorophyll fluorescence	7A	Vijayalakshmi *et al.* (2010)[c]
Carbon isotope discrimination	1A, 2A, 4A, 5B, 6A, 6B, 7B	Peleg *et al.* (2009)[d]
Leaf osmotic potential	2A, 3A, 3B, 5A, 5B, 6A, 6B	Peleg *et al.* (2009)
Plasma membrane damage	1D, 2B, 7A	Talukder *et al.* (2014)[c]
Thylakoid membrane damage	1D, 6A, 7A	Talukder *et al.* (2014)[c]

Dry and hot field conditions are defined using the CIMMYT mega-environments 1 and 4 (Rajaram *et al.*, 1994). NDVI, near differential vegetative index; WSC, water-soluble carbohydrates
[a] Field conditions.
[b] Trials in Italy, Tunisia and Morocco with maximum temperature at grain filling ≤26.1 °C.
[c] Controlled conditions.
[d] Semi-controlled conditions.

sink strength for grain filling, is determined by expansive plant growth, which is the increase in volume due to water entry into growing cells (Tardieu *et al.*, 2014). There is limited evidence for differences in carbon metabolism or status in ovules under stress, but many studies demonstrate reductions in organ elongation rates at sensitive periods with either drought or heat stress. In maize, silk growth and leaf elongation rate are highly correlated (Parent and Tardieu, 2012; Tardieu *et al.*, 2014). When the *PLASTOCHRON1* (Zm*PLA1*) gene was expressed in maize, increasing the length of the cell division zone, the duration of cell division, the duration of leaf elongation, kernel number, and size were increased in field experiments under mild drought (Sun *et al.*, 2017). QTLs for organ size and growth and expansion rates have been identified in wheat under drought (Table 1) but have not been studied under combined drought and heat stress, and no studies of genetic variation for the expansive growth trait have yet been carried out. Theoretically, increased expansive growth will be beneficial for combined drought and heat tolerance where loss of grain number is due to reduction in spike growth and development. Expansive growth will increase sink strength and be beneficial for remobilization of assimilates to the grain during filling.

Traits that increase overall assimilation should increase drought and heat tolerance when partitioned beneficially to the grain. Several QTLs for harvest index (HI) have been reported (Table 1). Meta-analysis of reported QTLs for drought or heat stress revealed meta-QTLs for spike weight/density and plant height were significantly (at $P<0.1$) associated with meta-QTL regions for yield under drought or heat in wheat (Acuña-Galindo *et al.* 2015). Major clusters were located at the *Rht-B1* and *Rht-D1* dwarfing loci. Plant height restriction due to the *Rht-B1* allele increases HI and is due to gibberellin insensitivity (Peng *et al.*, 1999). In barley, exogenous gibberellin application increases sensitivity to high temperature stress (Vettakkorumakankav *et al.*, 1999), so it is possible that widely used dwarfing alleles in modern, semi-dwarf wheat varieties already contribute to heat tolerance through the gibberellin pathway. Modern, semi-dwarf

phenotypes are already widely used to prevent undesirable lodging, but there are alleles that appear more or less beneficial in particular environments. For example, Wang *et al.* (2014b) suggested that the *Rht13* or combination of *Rht13* + *Rht8* alleles could be favourable in water-limited environments. Thus, there is scope to study and improve wheat drought and heat tolerance through the deployment of new combinations of dwarfing alleles, identification of genes controlling the gibberellin pathway, and optimization of expansive growth (Fig. 1).

Breeding for canopy temperature and evapotranspiration under drought and heat

The main mechanism wheat plants use to decrease their internal temperatures under heat stress is evaporative cooling, driven by transpiration. Under drought, plants close their stomata to avoid excessive water loss; this reduces transpiration and evaporative cooling and, as a result, drought-stressed plants display higher leaf and canopy temperatures than well-watered plants (Reynolds *et al.*, 2009). Cool canopies were always associated with better yield performance (Pinto and Reynolds, 2015). Several QTLs have been reported for canopy temperature depression under drought and heat in wheat grown in deep soils of northern Mexico (Pinto *et al.*, 2010; Pinto and Reynolds, 2015). The major QTLs on chromosome 2B were shown to be associated with root distribution, with cool canopy genotypes able to extract more water at depth under water stress due to a greater proportion of deeper roots (Pinto and Reynolds, 2015). The deep root trait was not recapitulated under heat stress alone (with irrigation) (Pinto and Reynolds, 2015). This suggested that the beneficial physiological trait conferred by the 2B QTL was not a different root system architecture or distribution *per se*, but the ability to optimize root distribution to capture water for continued cooling dependent on water distribution in the soil.

Transpiration efficiency is a ratio between biomass and transpiration, while water use efficiency (WUE) is the biomass
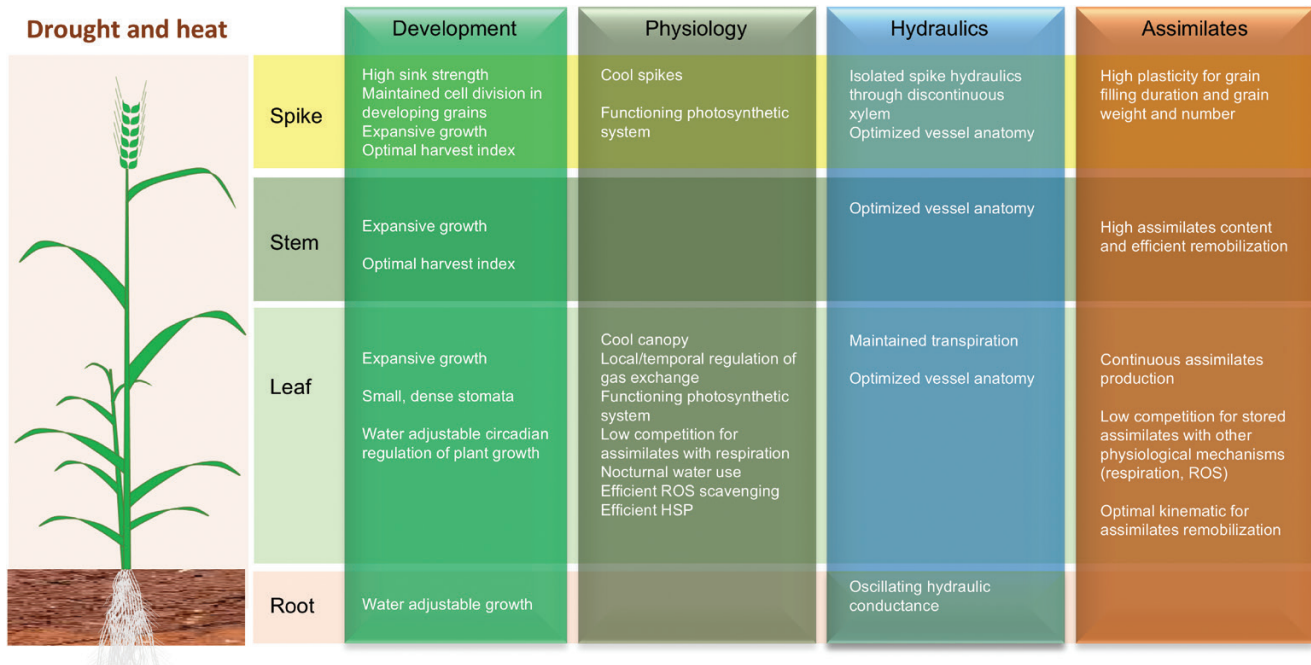
Drought and heat

	Development	Physiology	Hydraulics	Assimilates
Spike	High sink strength Maintained cell division in developing grains Expansive growth Optimal harvest index	Cool spikes Functioning photosynthetic system	Isolated spike hydraulics through discontinuous xylem Optimized vessel anatomy	High plasticity for grain filling duration and grain weight and number
Stem	Expansive growth Optimal harvest index		Optimized vessel anatomy	High assimilates content and efficient remobilization
Leaf	Expansive growth Small, dense stomata Water adjustable circadian regulation of plant growth	Cool canopy Local/temporal regulation of gas exchange Functioning photosynthetic system Low competition for assimilates with respiration Nocturnal water use Efficient ROS scavenging Efficient HSP	Maintained transpiration Optimized vessel anatomy	Continuous assimilates production Low competition for stored assimilates with other physiological mechanisms (respiration, ROS) Optimal kinematic for assimilates remobilization
Root	Water adjustable growth		Oscillating hydraulic conductance	

Fig. 1. Beneficial traits for combined drought and heat tolerance in wheat.

produced per unit of water used, at the whole plant level or whole plot in the field. Carbon isotope discrimination ($^{12}C/^{13}C$ ratio) in dry matter is negatively correlated to transpiration efficiency in wheat and a surrogate for this trait (Condon *et al.*, 1990). It has been successfully used for breeding water use efficient wheat for dry regions in Australia (Condon *et al.*, 1990, 2002). Increased transpiration efficiency alone might not improve tolerance. The equation for grain yield in water-limited environments includes harvest index (HI) and water use (WU) as well as WUE (Passioura, 1977; Passioura, 1996): GY=HI×WU×WUE. The theoretical physiology underlying this relationship has been extensively explained and reviewed (Ehrler *et al.*, 1978; Araus *et al.*, 2002; Blum, 2005; Reynolds *et al.*, 2007; Fischer, 2011; Vadez *et al.*, 2014). It has been argued that, if transpiration efficiency is increased by a reduction in the transpiration term of the equation, a low intrinsic stomatal conductance and transpiration reduces growth, biomass accumulation and light interception. Therefore, selecting plants with high transpiration efficiency might select for smaller plants (Blum, 2009). When small plants are selected, sink strength is lost and fewer assimilates are mobilized to the grain. Under the combination of drought and heat, low intrinsic transpiration could, additionally, penalize evaporative cooling. Reynolds *et al.* (2007) found that carbon isotope discrimination, together with canopy temperature linked to water uptake, was associated with improved performance in drought-stressed environments. Diab *et al.* (2008) found QTLs associated with tolerance in wheat for canopy temperature depression, transpiration efficiency, water index, and grain carbon isotope discrimination in dry and hot field conditions (Table 1).

Evaporative demand, or VPD, which depends on the amount of moisture in the air and the air temperature, also plays a critical role in transpiration and transpiration efficiency. Different sensitivities of transpiration to high VPD have been found amongst wheats and its genetic control described in the Australian wheat population RAC875/Kukri (Schoppach *et al.*, 2016). Six QTLs were identified for transpiration response to VPD, with one QTL on chromosome 5A individually explaining 25.4% of the genetic variance (Schoppach *et al.*, 2016). A study of 23 Australian wheat varieties released from 1890 to 2008 showed that whole-plant transpiration rate in response to VPD was limited at VPD above a breakpoint of about 2 kPa (Schoppach *et al.*, 2016). The breakpoint and transpiration response at VPD>2 kPa were correlated with the year of release indicating that breeders, by selecting for yield in the hot and dry climate of southern Australia, selected lines with limited whole-plant transpiration rate.

Transpiration rate might also be moderated by patchy stomatal closure and the threshold for closure might differ in sensitivity between VPD and soil moisture deficit (Vadez *et al.*, 2014). In maize, the relationship between expansive growth (leaf expansion rate; LER) and stomatal conductance was rapid and linear in contrast to the relationship between LER and transpiration rate (Caldeira *et al.*, 2014b). Tardieu *et al.* (2014) suggest that this is because increases in biomass and in expansive growth in volume are under different genetic controls and that, under water deficit, they are uncoupled over time. Because of the dependence of transpiration efficiency on both the biomass term and VPD, transpiration response traits should be evaluated in QTL studies. To keep an optimal balance between evaporative cooling and water saving, plants with fine adjustment of transpiration should have an advantage under combined drought and heat (Fig. 1).

Temporal regulation of gas exchange

Vadez *et al.* (2014) have argued that the total plant water use over the growing season and WUE for yield depend on available water and use at critical stages. Plants can increase

effective use of water by timely modifications of water uptake at critical stages. Timely modifications in stomatal conductance, transpiration, and water use might include different patterns of stomatal opening with developmental stage, time of the day, time of season, and microclimate VPD driven by differences in plant architecture.

High stomatal densities and conductance are associated with increased yield potential in both well-watered and water-limited environments (reviewed in Roche, 2015). High stomatal density could give more flexibility to the plant to adjust stomatal opening depending on the local environmental conditions and ensure continued water uptake and use under favourable conditions. For example, the Australian line RAC875, which is drought and heat tolerant, has many small stomata by contrast with the susceptible Australian variety Kukri with fewer large stomata (Shahinnia *et al.*, 2016). QTLs for stomatal size and density have been identified in dry and hot field conditions in wheat (Table 1). While no correlation was found between yield and stomatal traits in the RAC875/Kukri population, we found a locus for stomatal density and size on chromosome 7A that overlaps with QTLs for grain number per spike, normalized difference vegetation index, harvest index, and yield in the same population (Shahinnia *et al.*, 2016).

When heat stress is severe, leaf stomata will open to allow evaporative cooling despite water limitation. At very high temperatures, the photosynthetic machinery is damaged (Berry and Bjorkman, 1980) and leaf or other vegetative tissues may be sacrificed (Lohraseb *et al.*, 2017). Under combined drought and heat stress, this balance between open stomata and damaged photosynthetic machinery can become critical to allow continued assimilation and can depend on the fine spatiotemporal regulation of gas exchange. That is, continued assimilation in periods of lower stress, as temperatures rise and cool diurnally, may make a plant more tolerant (Richards *et al.*, 1986). Diurnal regulation of gas exchange will make a difference during stress exposure and circadian use of water and regulation of transpiration may both alleviate combined drought and heat stress and be a source of tolerance. A shift in transpiration to cooler times of the day could confer tolerance.

Nocturnal water use, particularly night-time transpiration, is of increasing interest for its role in sustaining sugars export at night (Marks and Lechowicz, 2007) and its potential role in drought tolerance in wheat (Schoppach *et al.*, 2014; Resco de Dios *et al.*, 2016; Sadok, 2016). Genotypic variation for night-time transpiration and its sensitivity to VPD has been documented in wheat and influences the next day's gas exchange under normal conditions and drought (Schoppach and Sadok, 2013; Schoppach *et al.*, 2014; Claverie *et al.*, 2017). Night-time transpiration rate in response to VPD varied consistently with the sensitivity of the genotypes to drought and increased under soil water deficit (Claverie *et al.*, 2017). The effect of night-time temperature was also significant, with an increase in transpiration with increasing temperature observed, as well as genotypic variation. Despite the importance of nocturnal water use for potential drought and heat stress tolerance, no genetic studies have yet been carried

out in wheat and no QTLs are known. The interplay between night-time export of assimilates and day-time gas exchange is also yet to be explored. Supply and demand ratios are likely to play a role in determining assimilation and export and, as yet, no studies of circadian regulation in wheat have been carried out in plants during grain filling when grains determine sink strength. With the development of non-destructive phenotyping methods, it will become possible to collect plant data over time and examine the kinematics of plant physiology.

Optimal hydraulic conductance for drought and heat tolerance

Hydraulic conductance is a measure of the flow induced by a pressure or water potential gradient normalized to the plant/organ geometry. Caldeira *et al.* (2014*b*) proposed that circadian oscillations of hydraulic conductance accounted for fluctuating growth (leaf elongation rates) in Arabidopsis. The degree of oscillation was highly dependent on evaporative demand and water stress. High root hydraulic conductance oscillation under water deficit likely led to the ability to control water uptake in response to available soil water when needed. Soil water status regulates the root hydraulic conductance of maize (Caldeira *et al.*, 2014*a*) adjusting growth to water availability. Maintenance of high hydraulic conductance in spikes of long-awned cultivars of wheat significantly reduces spike temperature during grain filling (Maydup *et al.*, 2014). The end of grain filling correlates with a loss of hydraulic conductance at the rachis-xylem conduit (Neghliz *et al.*, 2016). Thus, we hypothesize that by maintaining optimal hydraulic conductance in the different tissues under drought and heat stress (Fig. 1), wheat plants could extend grain filling duration, cool down grain and spike, and optimize water uptake for expansive growth.

In grapevine, soil–leaf differences in water potential among genotypes were shown to be less related to sensitivity of transpiration to soil water deficit than to change in soil–leaf hydraulic conductance, likely due to rapid changes in water transport within the plant (Scharwies and Tyerman, 2017). The ability to partition and channel water between stem, leaf, tillers, and spikes determines both expansive growth in these tissues and remobilization of assimilates following stress. Differences in hydraulic resistances in different tissues influence water transport capacity and drought and heat tolerance (Coupel-Ledru *et al.*, 2014; Bramley *et al.*, 2015). Hydraulic resistance may be determined by differences in structure and architecture of stems, peduncles, and rachis, and differences in xylem vessel diameter and leaf venation (Scharwies and Tyerman, 2017). Vessel structure has an important role in the control of water conductivity in plants in water-limited environments (Tixier *et al.*, 2013; Caringella *et al.*, 2015; Kadam *et al.*, 2015). In wheat, Barlow *et al.* (1980) demonstrated that a xylem discontinuity at the base of the peduncle permitted the isolation of spike hydraulics from the rest of the plant, and that this anatomical feature was crucial during water scarcity, resulting in the independence of water relations in the spike from the rest of the plant. The xylem in wheat is

also discontinuous between rachis and grains, isolating grains and, potentially, preventing water loss during stress (Zee and O'brien, 1970). Photoperiod response (*Ppd* loci) genes have pleiotropic effects on plant growth and development (Cockram *et al.*, 2007) that can modify plant hydraulics. The photoperiod sensitive allele *Ppd-D1* increases daytime and night-time transpiration while decreasing whole-plant leaf area in response to VPD increase in wheat (Schoppach *et al.*, 2016). This suggests that whole-plant hydraulics are developmentally controlled. Deciphering the relationship between vessel structure and plant hydraulics and the genetic control of plant development in wheat will provide a better understanding of the involvement of these physiological mechanisms in tolerance to combined drought and heat stress and their potential for breeding tolerant varieties.

Competition for assimilates under drought and heat stress

Redox balance is crucial for the normal function of many cellular processes. Its fine control is essential for a proper integration of environmental and developmental stimuli and signal transduction (Choudhury *et al.*, 2017). Recent studies demonstrated the important role of photorespiration in maintaining redox homeostasis (Scheibe and Dietz, 2012), mitigating oxidative stress and protecting the photosynthetic apparatus from photoinhibition (Rivero *et al.*, 2009; Peterhansel and Maurino, 2011; Voss *et al.*, 2013). With either drought or heat stress, net photosynthesis is reduced and photorespiration increased (Long and Ort, 2010), but the relative contributions of photorespiration and mitochondrial respiration to combined drought and heat stress tolerance in wheat are unknown and genetic variation for this ratio has not been explored.

Heat stress affects membrane stability and the quantum efficiency of photosystem II, which can be measured, respectively, as cell viability and chlorophyll fluorescence (Blum, 1988; Mohammed and Tarpley, 2009). Drought stress also affects chlorophyll fluorescence with a dramatic decrease of F_v/F_m ratio in susceptible wheat compared with tolerant lines (Izanloo *et al.*, 2008). QTLs have been reported for chlorophyll fluorescence in drought- or heat-stressed wheat (Table 1), but studies in other species suggest that responses to combined drought and heat stress are unique in comparison with either individual stress (Mittler, 2006). At the ecosystem level, drought may actually reduce heat-driven increases in plant respiration due to reduction in carbon substrates available (Schauberger *et al.*, 2017). However, if stored carbohydrates are used for respiration and less available for remobilization following heat stress, drought may exacerbate the effect of heat stress-induced increases in respiration. The rate of grain filling from stem reserves is increased with increasing temperature, reducing grain filling duration (Blum *et al.*, 1994). Tolerance to drought and heat stress will then depend on both the initial concentration of remobilizable carbohydrates and the use of these reserves for respiration. Genetic variation for stem water-soluble

carbohydrate content has been explored with known QTLs in drought or heat stress and in combined drought and heat stress (Table 1). Yang *et al.* (2007) also investigated genotype × environment (G×E) interactions for QTLs for stem water-soluble carbohydrate content and remobilization efficiency under water stress in wheat and found significant interactions for all traits. They showed that not all reserves were translocated to grain following water stress and suggested that losses due to respiration could be significant. Zhang *et al.* (2014) explicitly investigated water-soluble carbohydrate QTLs under drought, heat, and combined drought and heat stress and were able to identify additive effects and combinations of favourable alleles for both content and remobilization, suggesting that the genetic mechanisms underlying tolerance will not depend purely on accumulation of stored carbohydrates. QTLs for respiration are now being studied in wheat for the first time under the International Wheat Yield Partnership umbrella (http://iwyp.org/wp-content/; accessed 5 February 2018).

Under prolonged stress exposure, photosynthetic activity is further inhibited by excessive accumulation of reactive oxygen species (ROS), causing damage to the membranes, proteins, and chlorophyll molecules of the photosynthetic apparatus (Price and Hendry, 1991; Jiang and Huang, 2001; Allakhverdiev *et al.*, 2008; Silva *et al.*, 2010; Redondo-Gómez, 2013; Awasthi *et al.*, 2014; Das *et al.*, 2016). Plants use a complex antioxidant system to regulate ROS levels and avoid toxicity, but changes in redox status are also perceived by plants as a signature of a specific stress that will result in a corresponding acclimation response (Foyer and Noctor, 2005; Choudhury *et al.*, 2017). The balance between accumulation of ROS in response to stress and their signalling role under stress is yet to be defined. ROS scavenging is generally induced under drought and heat stress, and higher antioxidant capacity is generally correlated with tolerance to stress (Koussevitzky *et al.*, 2008; Suzuki *et al.*, 2014; Wang *et al.*, 2014*a*). In some wheat genotypes, tolerance to drought or heat stress was associated with increased antioxidant capacity and reduced oxidative damage (Sairam and Saxena, 2000; Sairam *et al.*, 2000; Lascano *et al.*, 2001; Almeselmani *et al.*, 2006; Sečenji *et al.*, 2010; Lu *et al.*, 2017; Zang *et al.*, 2017; Zhang *et al.*, 2017). The effects of combined drought and heat on the ROS system in wheat are unknown, but recent studies highlight the importance of modulation of ROS scavenging, some pathways being specifically induced by combined stress (Rizhsky *et al.*, 2002; Koussevitzky *et al.*, 2008; Demirevska *et al.*, 2010; Zandalinas *et al.*, 2017). The alleles that regulate photorespiration, membrane stability and antioxidant capacity under drought and heat are yet to be discovered in wheat.

As genomics and phenomics advance, the ability to analyse differences in physiological traits in empirical experiments has improved. Important advances in phenotyping with imaging or other equipment mean that it is possible to, for example, measure senescence or canopy temperature in real time in fields (Araus and Cairns, 2014). Further advances that allow, for example, field-scale simultaneous measurements of gas exchange, or non-destructive measurements of water-soluble carbohydrate movement can be anticipated. For researchers,

these will provide a wealth of previously unquantifiable data for physiological traits.

Breeding for stability, plasticity, and G×E interaction under drought and heat

In past breeding of tolerant varieties, efforts have been concentrated on the search for stable QTLs that show the same allelic effect across environments to produce generalist, high-yielding varieties (Eberhart and Russell, 1966). Acuña-Galindo *et al.* (2015) conducted a meta-QTL analysis of 24 genetic studies where QTLs had been mapped for drought, heat, or combined stress in wheat. Co-localization with meta-QTLs for yield was only significant (at $P<0.1$) for the maturity/date of anthesis, spike weight/density, plant height, and canopy temperature depression QTLs. This analysis underscored the pleiotropic effects of phenology and dwarfing alleles on wheat stress response. These generalist QTLs are already bred for with *Ppd* and *Vrn* alleles routinely used in marker-assisted selection. Other stress tolerance QTLs are not generalist and have strong G×E interaction.

In wheat, directional selection (Chapman *et al.*, 2012) has been used to breed varieties that respond consistently to the target environment and management practice. Whilst this approach has been successful in achieving yield gains in some tested environments, strong G×E interactions mean that it is difficult to identify genotypes responding consistently positively in a range of stressful environments, even for a single physiological trait (Reynolds *et al.*, 2009; Lopes *et al.*, 2012). When testing lines bred in high- and low-moisture and reciprocal environments at different sites, Kirigwi *et al.* (2004) found significant environment × selection regime interactions. In this study, development in alternating high-to-low or low-to-high-moisture regimes facilitated the selection of lines that performed well for yield in both, whereas lines selected in either continuous high- or continuous low-moisture regimes had lower yields in these respective environments. The authors suggested that selection under these alternating environmental conditions favoured retention of both high yield under stress and high responsiveness to water input.

In a changing environment, trait plasticity is theoretically beneficial (Bradshaw, 1965; Aspinwall *et al.*, 2015). Plasticity can be defined as the variance in genotypic response across an environmental gradient – that is the slope of its reaction to change, with a steeper slope indicating higher plasticity (Nicotra *et al.*, 2010). Plasticity can be measured as phenotype versus an environmental range for any trait and considered as a trait in itself (Sadras and Slafer, 2012), i.e. it has its own genetic variation and underlying QTLs. Phenotypic plasticity should be advantageous for fitness in variable environments and neutral in stable environments (Bradshaw, 1965; Nicotra *et al.*, 2010). It can be argued that selection for plasticity QTLs, against the background of the increased pace of climate change, will prove beneficial for maintaining or improving agricultural yields (Aspinwall *et al.*, 2015). However, plasticity is particular to the trait. For example, Sadras *et al.* (2009) found that high yield plasticity in wheat

was disadvantageous in low-yield environments when it was associated with low plasticity of post-anthesis development. Breeding for plasticity in grain yield components coupled with plasticity for the length of the grain-filling phase will be useful but is limited due to a trade-off between low plasticity in grain size and high plasticity in grain number during this stage.

Many QTLs have been found for grain production in dry and hot climates (Table 1), but very few (possibly none) are used in breeding programs. The main limiting factor to the deployment of these QTLs in breeding is the inconsistency in performances of the introgressed lines due to the strong QTL×E interaction. Although only field experiments are relevant for evaluating crop tolerance to stress as performance in an agricultural system, most studies fail to explain why a QTL is significant in one environment and not in another. Field trials are usually considered as a qualitative factor, which enables detection of G×E interactions but not its measurement (Acuña-Galindo *et al.*, 2015). Recent development in phenomics and sensors means that we can now continuously measure soil water potential and air temperature across the crop cycle in field conditions. But how can we use these data to understand G×E?

Uncoupling responsive and adaptive physiological traits is often complex and disentangling the effect of a specific environmental condition is not simple in experiments and often requires complex analysis and modelling (reviewed by Parent and Tardieu, 2014). Parent *et al.* (2017) described new models that exploit such data and measure a plant's response to quantitative variations in drought and heat stress. Applied to lines that segregated for specific yield QTLs, such models revealed, in Australian wheats, that a QTL on chromosome 1B was constitutively expressed under various combinations of soil water potential and high temperature, while a QTL on chromosome 3B was heat responsive with a positive effect of the drought-tolerant parental line RAC875 when temperature was above 23 °C around flowering stage (Parent *et al.*, 2017). This information is highly valuable as it enables us to understand a QTL's function and use it in appropriate environments. By equipping national variety trials with sensors to measure soil moisture and air temperature, such models could also predict the level of tolerance of new varieties to quantified drought and heat. Combined with whole genome genotyping, this would provide information on the effects of haplotypes on yield in response to specific environmental conditions.

Find the drought and heat tolerance genes and design the genome

Another obstacle in using yield QTLs in breeding programmes is the small effect of a single QTL and the need to introgress several QTLs to gain a significant increment in yield improvement. As breeders can only recombine as many loci as the size of their breeding programmes allows, they prioritize those with strong and stable effects, such as phenology, plant height, and disease resistance, and select for yield

under dry and hot environment empirically or, more recently, by genomic selection (GS). So, were the efforts in finding QTLs for drought and heat tolerance wasted? The answer is probably yes, unless we carry on the positional cloning of these QTLs and find the genes controlling combined drought and heat tolerance. Gene-level knowledge of the control of drought and heat tolerance will enable the identification and creation of new sequence variants.

Although many QTLs have been found for drought or heat tolerance (Table 1), little is known about the genes underlying these effects in wheat. The molecular network of drought and heat stress response in model species includes heat shock proteins (HSPs, chaperone proteins that protect the cell machinery), a number of drought stress response or heat stress transcription factors (DSF, HSF), and signal transduction proteins (Mittler *et al.*, 2012). A study in adult durum plants identified genes that respond specifically to combined drought and heat including a chaperone homologous to a putative t-complex protein 1 theta chain (Rizhsky *et al.*, 2002, 2004; Rampino *et al.*, 2012). Two classes of heat shock factors, A6 and C2, have been shown recently to enhance heat tolerance in transgenic wheat (Xue *et al.*, 2014; Hu *et al.*, 2018). Overexpression of TaHsfC2a-B in transgenics up-regulated a cascade of HSP genes in grains during grain filling under heat and also in leaves under drought stress. Combining positive alleles of HSF and DSF such as dehydration-responsive element-binding (DREB) proteins (Morran *et al.*, 2011) might be a way to enhance wheat tolerance to simultaneous stress, but the positive effects will need to be tested in the field in dry and hot climates and redundancy and interactions measured. The forward genetics approach starting with a locus with a demonstrated yield effect is attractive but, to date, none of the QTLs for drought and heat tolerance (Table 1) has been cloned in wheat.

While GS is an efficient tool to quickly identify the best haplotypes, it still requires the incorporation of new alleles into the breeding programme New alleles can also be found in wild relatives of wheat and landraces well adapted to local environments (Lopes *et al.*, 2015), including hot and arid environments. Natural diversity encompasses adaptive mechanisms that wheat plants developed to cope with harsh conditions (Huang and Han, 2014). Emmer wheat and cultivated wheat's wild relatives are sources of tolerance to high temperature or water limitation that could be used to overcome the bottleneck in genetic diversity within the cultivated wheat genepool (Feuillet *et al.*, 2008). The usefulness of a wider germplasm is illustrated by the QTLs deriving from wild emmer wheat for drought (Peleg *et al*, 2005; 2009) and QTLs for salinity tolerance from *Triticum monococcum* (Munns *et al.*, 2012). This is a rare example of successful introgression of a locus (*Nax2*) for abiotic stress tolerance in wheat, following both physiological characterization (James *et al.*, 2006) and positional cloning of the causative gene (*TmHKT1;5-A*) and demonstrates the power of this approach.

New alleles of known genes can also be created by deliberate mutagenesis or genome design (E. Buckler, Plant and Animal Genome conference XXVI, 2018). The ability to efficiently screen for mutations by sequencing (TILLING (Targeting Induced Local Lesions IN Genomes) by sequencing) is quite recent in wheat (Tsai *et al.*, 2011) and is based on both an increased understanding of genomics and advances in next generation sequencing and analysis. Using this approach, Simmonds *et al.* (2016) were able to rapidly identify the causative mutation for the locus *TaGW2-A1* and cross the mutant allele into durum and bread wheat to develop isogenic lines with increased grain weight. The advantage of a mutant collection over wild germplasm is that the new alleles are in agronomically relevant backgrounds where their effect can be readily measured. As the current sequenced collections are in English and US genetic backgrounds, namely Kronos and Cadenza (Tsai *et al.*, 2011), the sequencing of new TILLING collections in varieties that are locally relevant to hot and dry climates is urgently needed.

An alternative method is to specifically edit genes for drought and heat tolerance in a modern, relevant variety. The ability to specifically edit the wheat genome using CRISPR-cas9 ribonucleoproteins has been demonstrated in bread wheat (Liang *et al.*, 2017). This technique promises transgene-free modification of the genome to enhance traits of agronomic interest including abiotic stress tolerance. The use of this technique, however, depends on a detailed knowledge of the sequences underlying tolerance and is likely to require cassettes of sequence edits in the case of editing for combined drought and heat tolerance for wheat. With three highly similar sub-genomes, the majority of wheat gene sequences have homoeologues and the contributions of these homoeologues to copy number variation and dosage-dependent expression as well as functional redundancy are often unknown in wheat but will influence the success of gene editing approaches. In some cases, a gene/QTL effect could be increased if we were to combine the positive alleles of the three homoeologous copies. On a whole genome level, pan-genome data are now being used to understand and mark structural variation of this kind, for instance in maize (Lu *et al.*, 2015). The coming together of advances in genome editing and pan-genomics in wheat should facilitate editing for the future.

Conclusions

Because wheat is heat tolerant when water is available (Parent *et al.*, 2017), to improve wheat for dual tolerance, plants must be studied under the combination of stresses. Results from experiments with heat treatments and well-watered conditions are unlikely to be relevant when water is limiting in the field. There is a large body of evidence showing that water use is essential for either drought or heat tolerance and that, for tolerance of the combined stress, fine control of water relations across the growing cycle will be beneficial. This might be achieved through fine management of spatial and temporal gas exchange. For a wheat plant to be drought and heat tolerant, beneficial traits likely include the following: finely regulated transpiration through small, dense stomata, able to respond to the micro-environment (shade, water, VPD, radiation); maintenance of optimal hydraulic conductance in different tissues; a root system able to grow fast in response

to water availability; water-adjustable circadian regulation of plant growth; ability to retain water in essential organs to avoid tissue dehydration; efficient HSPs to protect enzymes and membranes against high temperature; efficient carbohydrate synthesis, export, and remobilization; and an efficient ROS scavenging system (Fig. 1).

The rationale for identifying and deploying alleles for combined drought and heat tolerance in wheat breeding is compelling. Improvements in phenotyping of physiological traits and genomic information are particularly encouraging as we seek to discover and incorporate, possibly, rare, novel tolerance alleles in breeding programmes. Improvement of methods capturing plant and environmental data over time will enable us to phenotype genetic populations for kinematic traits, and this will help us unravel the genetic basis of complex biological processes. Although wheat physiology under drought and heat stress is complex, this complexity and plasticity in itself provides sources of tolerance and hope.

Modifying a single trait might not have a significant effect on yield under stress as some of these traits are co-dependent and would be effective only in combination. Rather than improving a single trait at a time, we might need to combine them in order to increase yield. With underscoring genetic resources and a clear picture of valuable physiological traits, combined drought and heat tolerance in wheat can now be realized in research for use in breeding programmes.

Acknowledgements

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