

Yield stability for cereals in a changing climate

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Abstract. The United Nations Food and Agriculture Organisation (FAO) forecasts a 34% increase in the world population by 2050. As a consequence, the productivity of important staple crops such as cereals needs to be boosted by an estimated 43%. This growth in cereal productivity will need to occur in a world with a changing climate, where more frequent weather extremes will impact on grain productivity. Improving cereal productivity will, therefore, not only be a matter of increasing yield potential of current germplasm, but also of improving yield stability through enhanced tolerance to abiotic stresses. Successful reproductive development in cereals is essential for grain productivity and environmental constraints (drought, cold, frost, heat and waterlogging) that are associated with climate change are likely to have severe effects on yield stability of cereal crops. Currently, genetic gains conferring improved abiotic stress tolerance in cereals is hampered by the lack of reliable screening methods, availability of suitable germplasm and poor knowledge about the physiological and molecular underpinnings of abiotic stress tolerance traits.

Additional keywords: abiotic stress, cereals, grain number, grain size, reproductive stage, sterility.

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Introduction

By the year 2050 the world population is expected to have grown by 34%, with an additional 2.3 billion people to feed (FAO 2009). This increase will occur mainly in developing countries where the population is expected to be more affluent and predominantly urbanised. World food production is, therefore, required to increase by 70% with the demand for staple crops like cereals to rise by 43%, an increase of almost one billion tonnes. Global rice production, which feeds approximately half the world population, has to increase by 0.6–0.9% annually until 2050 to meet demand (Carriger and Vallee 2007).

Since the introduction of ‘Green Revolution’ wheat and rice varieties, yields have reached a plateau, suggesting that increased crop yield targets will not be reached (FAO 2002; Tilman *et al.* 2002; Rosegrant and Cline 2003; Edmeades *et al.* 2010). The average annual yield increase has steadily declined from 3.2% per annum in 1960, to 1.5% in 2000 as a result of limited genetic biodiversity and environmental factors. The genetic gain that can be obtained via technologies such as heterosis, molecular breeding and transgenics is currently estimated at 50%, falling short of the 70% yield increase required by 2050 (Edmeades *et al.* 2010). In Europe, climate change, rather than lack in genetic progress, is considered to be the main reason for decreasing yield growth rate in wheat (Brisson *et al.* 2010). Agriculture will be affected by climate change through higher temperatures (estimated to increase $\pm 2^\circ\text{C}$ by 2050), changing rainfall patterns and higher carbon dioxide (CO₂) levels. A change in weeds, pests and disease pressure on crops will also be associated with these climatic changes (Jaggard *et al.* 2010).

An additional challenge is that increasing areas of farmland are being diverted to biofuel production, causing competition for food production. The rising global scarcity and insecurity regarding availability of fossil fuels has caused increased interest in converting grain into biofuel, resulting in an unprecedented insecurity in food supply (Young 2009; Banerjee 2011). The increasing diversion of food crops to biofuel production risks escalating food prices and provides an additional challenge to meet future food production targets.

Under the majority of environmental conditions crop productivity is limited by water availability, light, heat and nutrients. Although higher temperatures and CO₂ levels can improve crop yields, the gain in productivity can be counteracted by other factors. For instance, free-air CO₂ enrichment (FACE) studies have shown that rice crops become more sensitive to the damaging effect of cold temperatures, thereby neutralising the expected yield improvements obtained from CO₂ enrichment (Shimono *et al.* 2008, 2009). Application of higher nitrogen levels to boost yields may also have a negative impact under certain environmental conditions. In rice, high nitrogen supply before and during the critical stage of pollen development exacerbates the effect of cold-induced pollen sterility (Williams and Angus 1994; Gunawardena *et al.* 2003). High nitrogen fertilisation levels also have an adverse effect on grain-filling and drought tolerance (Demotes-Mainard and Jeuffroy 2001; Ruuska *et al.* 2008).

In the United States the lack of adaptation to abiotic stresses is responsible for 71% of reduction in yield potential (Boyer 1982). There are opportunities to increase crop yield by closing

the gap between actual yield and the genetic yield potential (Richards 2000; Araus *et al.* 2008). However, this strategy may be compromised by climate change. Extreme weather events have already become more frequent and have caused crop losses in many parts of the world (Vellinga and Van Verseveld 2000). Boosting future yield will not only be a case of increasing yield and yield potential *per se*, but it will also be a question of maintaining this higher productivity under adverse weather conditions. Improving abiotic stress tolerance will be crucial to achieve greater yield stability within a changing environment.

Improving abiotic stress tolerance through conventional breeding methods has so far been met with limited success. Detailed accounts of the problems generally associated with quantitative trait loci (QTL) mapping for abiotic stress tolerance in cereals have recently been published (Collins *et al.* 2008; Fleury *et al.* 2010; Dolferus *et al.* 2011). Breeding programs tend to focus on commercial factors such as high yield potential and grain quality, not on abiotic stress tolerance. This has caused a bias in the selection of breeding lines, which may so far have excluded those lines with superior abiotic stress tolerance (Forster *et al.* 2000). Reintroducing stress tolerant traits in current cereal germplasm is essential and will require a focussed effort. This paper will discuss the effect of abiotic stresses on reproductive development and grain productivity in cereals, focusing on the two temperature stresses (cold/frost and heat), and extremes of water availability (drought and waterlogging).

Vegetative versus reproductive stage abiotic stresses

Plants are sessile organisms, so they must adapt their development continuously in function of the reigning environmental conditions. Abiotic stress stimuli affect both vegetative and reproductive development. Even though grain yield in cereals depends on successful reproductive development in a given environment, unrestrained development of the plant during the vegetative growth phase is critical. In cereals, 'yield' is measured as the amount of grain produced per surface area. At the plant level, grain yield is determined by both grain weight (hereafter referred to as grain size) and grain number. The timing of the stress stimulus in relation to reproductive development determines whether grain number or size will be affected. Grain number is affected by abiotic stresses such as drought mainly during the earlier stages of reproductive development and is widely considered to be the main contributor to yield losses (Fig. 1*a–g*; Savin and Slafer 1991; Fischer 1993; Abbate *et al.* 1995; Sayre *et al.* 1997; González *et al.* 2003). In contrast, the effect of drought on grain weight occurs from anthesis onwards (Fig. 1*b*) and during the grain maturation stage (Ji *et al.* 2010).

Abiotic stresses can affect tiller development and formation of spikes, as well as the number of spikelets per spike during floral meristem differentiation. Spikelets and florets also abort when stresses occur later during floral development (Dolferus *et al.* 2011). The fixation of grain number is, therefore, a dynamic process that is determined continuously by the environment throughout reproductive development. Several traits have been identified that improve vegetative stage tolerance of cereals to

abiotic stress conditions (Blum 2005, 2011). For instance, in the case of drought stress these traits include yield potential, water use efficiency (WUE), harvest index (HI), deep root penetration (to access water and nutrients) and improved transpiration efficiency. These traits are ultimately important for reproductive development but they are not the focus of this paper.

In wheat, the ability to accumulate carbohydrates in the stem and leaf sheaths and remobilise these to the reproductive structures is important for the determination of grain number and size during reproductive development. Water-soluble carbohydrates are important for maintaining grain size, particularly under drought conditions when photosynthesis is arrested (Gebbing *et al.* 1999; Yang *et al.* 2001; Ruuska *et al.* 2006, 2008). Genetic variation in the ability to mobilise stem reserves to the developing grain has been identified and used for biochemical characterisation and QTL mapping (Yang *et al.* 2007; Ehdaie *et al.* 2008; Xue *et al.* 2008). The stay-green trait, which is characterised by delayed leaf senescence, is generally considered to improve tolerance at the vegetative stage to mid-season droughts (Thomas and Howarth 2000), but the trait may also interfere with carbohydrate mobilisation to the reproductive structures and affect grain-filling (Blum 1998; Sanchez *et al.* 2002; Collins *et al.* 2008; Blum 2011).

Drought stress

Drought stress is the most common cause of yield loss, with the affected area likely to double as a result of climate change, especially in tropical regions of the world (Isendahl and Schmidt 2006; IPCC 2007; Passioura 2007). Rice is a staple food for more than half of the global population; however, production uses 2–3 times more water than other cereal crops such as wheat or maize and uses 30% of the freshwater used for crops worldwide (Barker *et al.* 1999). Half of the world's rice production is affected by water stress (Bouman *et al.* 2005; Tao *et al.* 2006; Yang and Zhang 2006).

The effect of drought on reproductive processes in cereals has been extensively reviewed (Barnabás *et al.* 2008). Drought during the pre-anthesis stage of reproductive development has a dramatic effect on grain number (Fig. 1*a–c*; Bingham 1966; Fischer 1973; Ji *et al.* 2010). Even short, mild water stress periods at the young microspore stage of pollen development (Fig. 2*b, c*) cause sterility; the ovule appears to be more resilient (Ji *et al.* 2010). The higher sensitivity of pollen to drought stress may be due to the unique properties of the tapetum, the innermost layer of the anther wall. This specialised sporophytic secretion cell layer is dedicated to feeding the nascent microspores and the deposition of the pollen cell wall. These functions occur during meiosis and at the young microspore stage when the tapetum is most active (Clément *et al.* 1996). Drought stress in rice causes a pre-mature programmed cell death (PCD) response in the tapetum (Nguyen *et al.* 2009). PCD is a process that is also responsible for pollen abortion in cytoplasmic male sterile lines in rice (Li *et al.* 2004). The capacity of the tapetum to download sugars for pollen development is downregulated, consistent with repression in cell wall invertase gene expression in rice and wheat (Sheoran and Saini 1996; Koonjul *et al.* 2005; Ji *et al.* 2010). In drought-



Fig. 1. Effect of abiotic stresses on cereal reproductive development. (a) Effect of young microspore stage drought stress (5 days; 40% relative water content) on grain number in wheat. (b) Drought stress at anthesis causes reduction in grain size in wheat. (c) Young microspore stage drought stress in rice causes reduction in grain number and in many cases the panicle fails to exert completely from the leaf sheaths. (d) Effect of young microspore stage cold stress in wheat. In the field, empty spikes (red arrows) are clearly visible against the bright background. (e) Young microspore stage cold stress (4 days at 12°C) causes massive reduction in grain number in rice. (f) Effect of heat stress (38°C, 4 days) at the young microspore stage in wheat.

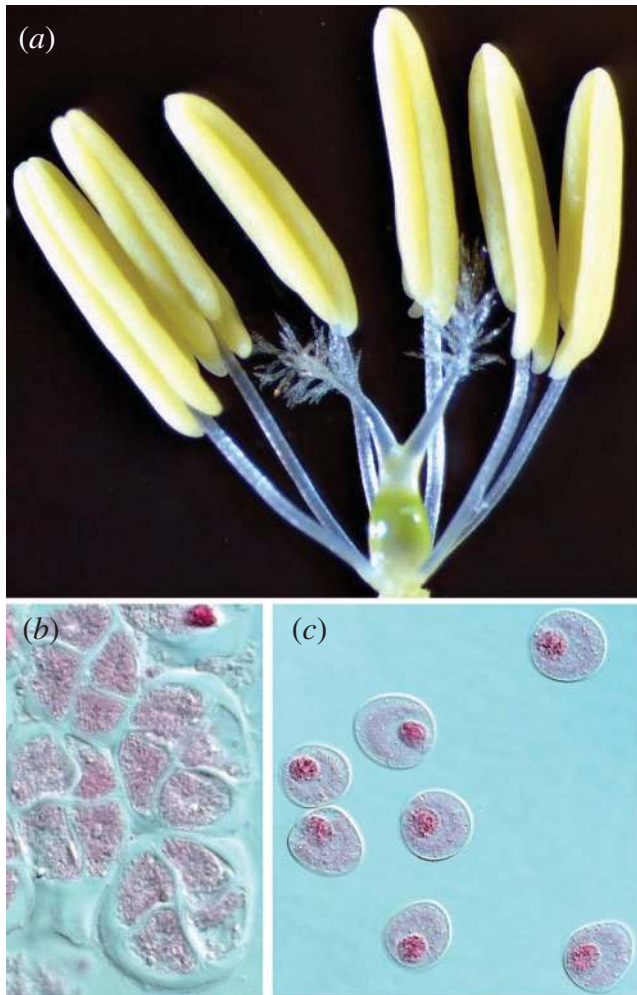


Fig. 2. The reproductive structures are very sensitive to various abiotic stresses. In rice (a) and wheat, the anthers in particular are very sensitive to stress conditions. Abiotic stresses such as cold, drought and heat stress cause abortion of male gametophyte development. Compared with pollen, the ovule is more resilient to the effect of abiotic stress. The most sensitive stage of pollen development is immediately after meiosis, when the tetrads (b) separate to form the uni-nucleate young microspores (c), the first stage of pollen development.

tolerant wheat, maintaining sugar transport to pollen and cell wall invertase expression is correlated with drought tolerance (Ji *et al.* 2010).

Drought stress at the young microspore stage causes abscisic acid (ABA) to accumulate in reproductive structures, resulting in pollen sterility. Pollen sterility can be mimicked by exogenous application of ABA (Morgan 1980; Zeng *et al.* 1985; Westgate *et al.* 1996; Ji *et al.* 2010). Application of sucrose to developing panicles reduces the detrimental effect of ABA, indicating that ABA acts via repression of sucrose metabolism (Waters *et al.* 1984). Under drought stress, the water potential in floral organs was maintained whereas it decreased in all other plant parts, suggesting that ABA is transported to the anthers from other plant parts (Morgan 1980; Saini and Aspinall 1982; Morgan and King 1984). However, ABA biosynthesis does also occur in the

anthers and ABA can repress sugar transport to pollen by downregulating cell wall invertase expression. Downregulation of anther ABA levels using transgenic approaches resulted in improved stress-tolerance (Ji *et al.* 2011).

Post-anthesis drought stress has a strong effect on grain-filling and grain size (Artlip *et al.* 1995; Jamieson *et al.* 1995; Yang and Zhang 2006; Ji *et al.* 2010). Drought stress during early seed development reduces the rate of grain filling, induces early senescence and shortens the grain-filling and ripening period by 10 days (Nicolas *et al.* 1985; Westgate 1994). The process of grain-filling is supported by carbohydrate mobilisation from the stem of the plant. Cell wall invertase is also an important component in controlling sugar transport during grain filling in rice and maize (Miller and Chourey 1992; Hirose *et al.* 2002). Under drought conditions, ABA levels increased in developing barley seeds, resulting in induction of β -amylase genes and a reduction in starch accumulation and quality (Seiler *et al.* 2011). However, the fact that wheat germplasm that maintains grain number under young-microspore-stage drought conditions but does not maintain grain size when stressed at anthesis indicates that the genetic control may be different (Ji *et al.* 2010).

In maize, drought stress reduces kernel number as a result of ovary abortion. Drought-stressed ovules show decreased vacuolar and cell wall invertase activity, starch depletion and inhibited photosynthesis (Zinselmeier *et al.* 1999). The maize nucellus is supported by the pedicel and cell wall invertase is expressed in the placento-chalaza cell layer which separates the nucellus from the pedicel (Miller and Chourey 1992). Abortion of ovary development is associated with the induction of a PCD response and sugar flow to the nucellus is restricted (McLaughlin and Boyer 2004). These events, leading to ovary abortion in maize, are analogous to loss of pollen viability in rice and wheat under drought conditions.

Genes associated with tolerance to drought stress include dehydrins, late-embryogenesis abundant-like (LEA), aquaporins, heat shock proteins and several metabolic enzymes involved in osmolyte (glycinebetaine), sugar, antioxidant, lipid and amino acid (proline) biosynthesis are likely to be expressed throughout the plant (Ergen *et al.* 2009; Matsui *et al.* 2008). Extensive studies into the signal transduction and gene regulatory events associated with drought stress have also been conducted (Seki *et al.* 2007; Qin *et al.* 2011). The transcription factors of the DREB family (dehydration responsive element binding) play a central role in regulating the expression of ABA-independent-drought-inducible genes (Lata and Prasad 2011). Elaboration of the gene networks involved in response to drought is expected to be one of the important outputs as gene expression profiling using microarrays and deep sequencing technologies continue to be applied to cereals.

Cold and frost damage

Low temperatures, chilling (0–12°C) and freezing (<0°C), are another major yield limitation to cereal productivity. Plants growing in temperate regions have evolved a cold acclimation response that is triggered under mild chilling conditions (4–6°C), which enhances tolerance to more severe, sub-zero, temperatures (Guy 1999; Thomashow 1999). In contrast to drought stress,

which establishes progressively over several weeks, yield losses due to chilling and frost conditions are often caused by short events at night ('cold spells').

Temperate climate cereals, such as wheat and barley, have the capability to sense and adapt to seasonal changes in temperatures and daylength. However, they show considerable variability in their ability to mount an acclimation response and survive freezing temperatures. Wheat and related temperate cereals that are grown under widely diverse conditions vary dramatically in their ability to withstand chilling and freezing conditions (Dubcovsky and Dvorak 2007), consistent with a broad genetic variability (Fowler and Gusta 1979; Monroy *et al.* 2007; Winfield *et al.* 2010). Throughout warm growing seasons plants have little capability to withstand freezing temperatures (below 0°C). However, as the year progresses, some are able to sense the change in environmental conditions that signal the coming winter. The gradual exposure to low non-freezing temperatures triggers an increase in freezing tolerance, known as cold acclimation (Guy 1999; Thomashow 1999). The temperature at which cold acclimation is initiated differs amongst the cereals. Acclimation in rye starts at warmer temperatures, but spring wheat and barley do not initiate acclimation until around 2°C (Fowler *et al.* 1999). There are also differences between wheat varieties in threshold temperatures at which cold acclimation is induced (Fowler 2008).

Cereals are most sensitive to freezing temperatures during the reproductive stage of development, in particular the young microspore stage (Fig. 2*b, c*). Non-freezing temperatures below 10°C are destructive at meiosis (Figs 1*d, 2*), causing male sterility (Langer and Olugbemi 1970; Downes and Marshall 1971; Qian *et al.* 1986; Demotes-Mainard *et al.* 1995, 1996; Subedi *et al.* 1998). Long-season varieties and delayed sowing can ensure that flowering is past the highest risk period for low temperatures, minimising the risk of yield loss. However, in some environments this can result in greater yield losses when flowering and grain filling is pushed to the hottest and driest periods. Some wheat varieties are quite chilling and frost hardy at the vegetative phase of development but show no tolerance at the reproductive stages, indicating that the genetic control is different (Fuller *et al.* 2007).

Winter and spring temperate cereals both exhibit a degree of chilling tolerance that is either induced by cold or constitutive (Jan *et al.* 2009). The response to cold has been extensively characterised in wheat and barley. Sugar accumulation in the vacuoles decreases the osmotic potential, causing increased ABA levels. Gene expression studies have revealed several cold-responsive genes, including signalling and transcription components, genes encoding putative protective components (cellular transport, cell membrane proteins, cryo-protectants and chaperones), as well as genes encoding metabolic, respiratory and photosynthetic components that are downregulated (Guy 1999; Thomashow 1999; Svensson *et al.* 2006; Monroy *et al.* 2007; Rapacz *et al.* 2008; Winfield *et al.* 2010). Some of these genes play an important regulatory function in the cold response (Tsuda *et al.* 2000; Iba 2002; Winfield *et al.* 2010).

Cold inducible promoters contain a C repeat/dehydration responsive element, which binds C repeat binding factors/dehydration responsive element binding proteins (CBFs/DREBs), as well as *cis*-elements binding bZIP transcription

factors (basic leucine zipper; Thomashow 2001; Zhang *et al.* 2004). It has been documented that within 15 min of exposure to low temperatures CBF transcripts accumulate within the plant (Gilmour *et al.* 1998). In barley, 20 CBF genes have been identified; half of these are located in two tight clusters on the long arm of chromosome 5H in the same region as the *Fr-H2* frost resistance locus (Francia *et al.* 2004; Skinner *et al.* 2006). A similar gene cluster at the orthologous region on chromosome 5A in diploid wheat (*Triticum monococcum*) is also located at the *Fr-A^m2* frost resistance QTL for the level of transcription of the cold-regulated gene *COR14b* at 15°C. (Snape *et al.* 2001; Vágújfalvi *et al.* 2003; Miller *et al.* 2006). The locus for frost tolerance was shown to be completely linked to the central gene cluster (*Cbf-14, -15, -12*; Sandve *et al.* 2011; Tondelli *et al.* 2011).

Flowering time in cereals is an important adaptation mechanism to protect sensitive reproductive structures against frost. Winter genotypes require a long period of cold exposure to accelerate the transition from the vegetative to the reproductive growth phase, a process called vernalisation (Trevaskis *et al.* 2007; Distelfeld *et al.* 2009). The requirement of periods of low but non-freezing temperatures is common to both vernalisation and cold-acclimation, suggesting that there is functional overlap between the two processes. The main vernalisation gene *VRN-1* co-locates with the frost resistance QTL *FR-1* on chromosome 5. When the reproductive phase has been reached in winter cereals the ability to maintain the expression of frost tolerance genes decreases and throughout the spring they de-acclimatise (Prášil *et al.* 2004). *VRN-1* is induced during vernalisation and was shown to play a role in decreasing the cold acclimation ability during reproductive development (Limin and Fowler 2006). The correlation between winter habit (*Vrn1*) and frost tolerance (*Fr1*) could be a result of pleiotropic effects of *Vrn1* loci. In spring wheat varieties the vernalisation pathway limits the expression of cold-responsive genes; expression of cold responsive genes is initially the same for spring and winter varieties but spring varieties are unable to sustain their expression (Monroy *et al.* 2007; Galiba *et al.* 2009). Further, the fact that QTL for copper tolerance were localised in the same position as the *Vrn-A1* and *Vrn-D1* alleles on chromosome 5A and 5D, respectively, suggests that the *VRN1* gene may also play a role in other abiotic stress responses (Bálint *et al.* 2008). In wheat, a QTL for ABA accumulation on chromosome 5A was also found to coincide with the *VRN1* gene (Quarrie *et al.* 1997). It is evident that response pathways to vernalisation and photoperiodism integrate a variety of other environmental cues (Distelfeld *et al.* 2009).

Some of our major cereal crops are of tropical origin (maize, rice and sorghum). Rice is increasingly grown in temperate climate zones but is not adapted to cold and does not have a cold acclimation response. In temperate climate zones rice is grown as a summer crop, but yields are compromised by cooler temperatures (Lin and Peterson 1975; Satake 1976; Board *et al.* 1980; Jacobs and Pearson 1994). The shorter temperate climate zone growing season confronts rice crops with cold conditions both at the start and end of the season. Currently, an estimated 7 million ha worldwide are prone to damage by cold at the reproductive stage (Sthapit and Witcombe 1998). In Australia, cold spells during the early booting stage cause an average yield

reduction of 5–10% annually (A\$44 million), making spikelet sterility the main yield-limiting factor.

Cold-induced sterility in rice is due to pollen abortion (Fig. 1e). Pollen development is most sensitive to cold at the young microspore stage (Fig. 2b, c). The effect of cold is irreversible and cross-fertilisation with non-cold-stressed pollen results in seed production, suggesting that the ovule is not affected (Hayase *et al.* 1969). Cold stress in rice was shown to primarily affect the endoplasmic reticulum (ER) in the tapetum layer (Gothandam *et al.* 2007). The ER plays a role in PCD of animal and plant cells (Zuppini *et al.* 2004). Physiological characterisations indicated that non-reducing sugars accumulate in cold-stressed panicles 12–24 h after cold treatment (Ito 1974); this is followed by tapetal hypertrophy (Nishiyama 1984). Cold stress induces a reduction in sink strength in anthers of sensitive rice lines; cell wall invertase activity and gene expression (*OSINV4*) are reduced and sugar transport to the pollen grains is repressed. Cold-tolerant rice maintains sink strength and pollen fertility (Oliver *et al.* 2005). ABA plays an important role in cold-induced sterility in rice. ABA accumulates in cold-sensitive but not cold-tolerant rice anthers and ABA treatments result in repression of anther cell wall invertase gene expression (Oliver *et al.* 2007). Reducing ABA accumulation in anthers by overexpressing the ABA catabolic gene ABA 8'-hydroxylase results in improved cold tolerance (Ji *et al.* 2011). Cold-induced sterility in sorghum shows the same stage-specificity; sterile pollen lacks starch and ovule development is not affected by cold stress. A high altitude sorghum line showed strong tolerance to cold at the young microspore stage (Brooking 1976, 1979). There is a striking similarity between cold and drought-induced pollen sterility. Rice germplasm that is tolerant to cold stress at the young microspore stage is also tolerant to drought stress (Fig. 3). This suggests that both stresses affect overlapping pathways and induce pollen abortion.

Heat stress

Accumulation of greenhouse gasses (carbon dioxide, methane and nitrous oxide) in the Earth's atmosphere has caused annual average temperatures to rise by 0.35–1.13°C from 1979 to 2003 (Peng *et al.* 2004). The average global surface air temperature will increase by 1.8–4°C by the end of this century (IPCC 2007). In Europe, summer precipitation is predicted to decrease and heat waves will become more common and severe, placing heat ahead of drought in terms of overall effect on crop productivity (Semenov and Shewry 2011). Higher temperatures will exacerbate the problem of heat stress on crop yields. For instance, rice yields are estimated to be reduced by 41% by the end of this century (Ceccarelli *et al.* 2010). Similarly, wheat production in Australia is estimated to decrease by 50% when average growing season temperatures increase by 2°C (Semenov and Shewry 2011). It is estimated that around 9 million ha of wheat in tropical or subtropical areas experience yield losses due to high-temperature stress (Lillemo *et al.* 2005).

The response to heat stress involves physiological adaptations that are required to protect the cellular functions (compatible osmolytes such as glycinebetaine, γ -aminobutyric acid), changes in photosynthesis and assimilate partitioning, hormonal changes (ABA and ethylene) and accumulation of secondary metabolites

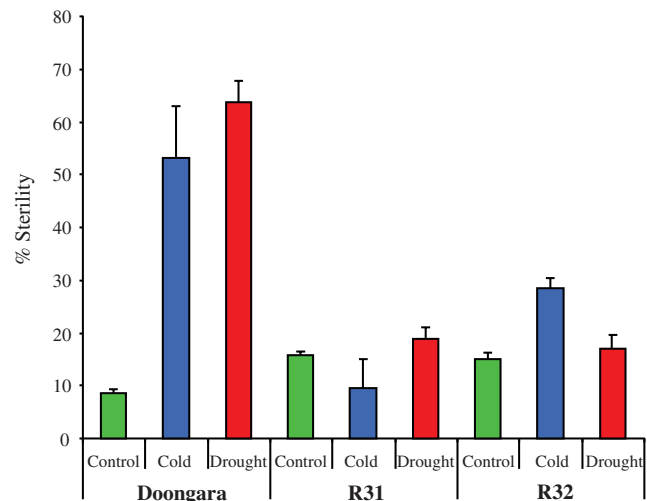


Fig. 3. Rice germplasm that is tolerant to cold stress is also tolerant to young microspore stage drought stress. The cold-sensitive Australian variety Doongara is sensitive to both cold and drought stress, whereas the cold-tolerant Chinese varieties R31 and R32 are tolerant to cold and drought stress. Apart from higher sterility levels, Doongara shows higher levels of leaf senescence compared with the tolerant lines R31 and R32.

(carotenoids, phenolics, isoprenoids; for reviews, see Kotak *et al.* 2007; Wahid *et al.* 2007; Barnabás *et al.* 2008; Krishnan *et al.* 2011). As with other abiotic stresses, heat stress induces a response to oxidative stress to protect against the damaging effect of activated oxygen species. Chaperone-like heat shock proteins are induced, as well as known drought-response proteins (late embryogenesis abundant, LEA and osmotin-like proteins). Heat stress is often combined with drought stress, with high temperatures leading to tissue dehydration. Under field conditions, selection for heat stress is often confounded by drought stress conditions and the regulatory system for both stresses may have co-evolved (Jagadish *et al.* 2011).

The effect of heat on the reproductive stage in rice ranges from pollen sterility induced at meiosis (Fig. 1f), poor anther dehiscence at anthesis, to reduced grain-filling and reduced grain quality (Stone and Nicolas 1994; Prasad *et al.* 2006; Jagadish *et al.* 2007; Shah *et al.* 2011). Research efforts on the effect of heat stress have often focussed on the effect on grain-filling and grain quality. In wheat, heat stress alters the high

molecular weight gluten protein content in the grain (Gibson and Paulsen 1999; Yang *et al.* 2002a; Don *et al.* 2005; Wahid *et al.* 2007). Heat stress during grain development reduces grain weight in wheat (Wardlaw *et al.* 1989a). During the early stages of reproductive development the effect of heat was mainly on grain number. When heat-stressed at meiosis, most pollen grains were found to lack starch, causing high levels of sterility in barley (Sakata *et al.* 2000; Abiko *et al.* 2005). In rice, exposure to heat during the fertilisation process prevents anther dehiscence and reduces pollen shedding and germination (Matsui and Omasa 2002; Prasad *et al.* 2006). High temperatures at the young microspore stage induce pollen sterility in rice as a result of premature tapetum degeneration and abnormal vacuolation and persistence of the tapetum cells in rice and wheat (Wardlaw *et al.* 1989a, 1989b; Endo *et al.* 2009). This is similar to what was observed for drought conditions (Saini *et al.* 1984; Dorion *et al.* 1996; Lalonde *et al.* 1997; Ku *et al.* 2003). The young microspore stage of pollen development is also very sensitive to heat stress in *Arabidopsis* (Kim *et al.* 2001). Similar to cold and drought stress in rice and wheat, heat stress affects carbohydrate assimilation by the tapetum and young microspores. Cell wall invertase gene expression is repressed by heat in sorghum, and starch and sugar content in anthers is downregulated (Aloni *et al.* 2001; Pressman *et al.* 2002; Jain *et al.* 2007, 2010). The hormone ABA has also been implicated in the response to heat stress (Toh *et al.* 2008). This may be due to the fact that heat and drought stress often coincide. However, ABA can induce thermo-tolerance in maize and it can activate some genes encoding heat shock proteins (Wu *et al.* 1994; Gong *et al.* 1998). In addition, heat-resistant dwarf mutants can be made sensitive to heat stress by GA treatment (Barnabás *et al.* 2008). Treatment of wheat plants with an ethylene receptor inhibitor alleviates the effect of heat stress, suggesting that ethylene plays a role in inducing kernel abortion in wheat (Hays *et al.* 2007).

Genetic variability for heat tolerance has been identified in maize, wheat and rice (Maestri *et al.* 2002; Prasad *et al.* 2006; Spiertz *et al.* 2006). In wheat, QTL for yield stability at the early grain-filling stage and grain-filling duration were mapped, and QTL for pollen heat tolerance were identified in maize (Frova and Sari-Gorla 1994; Yang *et al.* 2002b; Mason *et al.* 2010).

Waterlogging

Waterlogging affects ~10% of the global land area and an estimated 10 million hectares of land in developing countries (Samad *et al.* 2011). Periodic flooding affects many cereal crops in high rainfall environments and under irrigation conditions. About 15–20% of the world's wheat crops (10–15 million ha) are prone to periodic flooding every year (Sayre *et al.* 1994; Setter and Waters 2003). Climate change and rising sea levels are expected to affect the frequency and intensity of rainfall in some areas, thereby increasing the risk of floods. Waterlogging can cause a wide variety of symptoms that can affect yield either directly or indirectly, through affecting leaf senescence, tiller number and reduced plant height (Samad *et al.* 2011). Waterlogging causes a reduction in both grain number and size in wheat (Van Ginkel *et al.* 1992; Musgrave 1994),

but also spikelet sterility. Spikelet sterility has been blamed on the combination of reduced light intensity (due to high cloud cover) and high humidity (Fischer 1985a, 1985b). Waterlogging also causes nutrient deficiencies and it has been suggested that flooding-induced spikelet sterility in wheat is caused by reduced boron uptake (Rawson *et al.* 1996; Saifuzzaman and Meisner 1996; Saifuzzaman *et al.* 2008). Boron plays an essential role in pollen cell wall biosynthesis and pollen tube growth (Iwai *et al.* 2006).

Selecting germplasm tolerant to abiotic stress

The difficulties associated with generating tolerant cereal lines using classic breeding approaches have been abundantly illustrated in other recent review papers (Collins *et al.* 2008; Fleury *et al.* 2010; Dolferus *et al.* 2011). Many abiotic stress tolerance QTL have so far been identified in plants (for a summary, see Plant Stress, <http://www.plantstress.com>, 22 May 2012; and Gramene website, <http://www.gramene.org>, accessed 22 May 2012). Suitable germplasm is available in some cereals for cold, drought and heat tolerance, but the focus of breeding programs on commercial traits (e.g. grain quality) may have led to exclusion of germplasm that is superior in terms of abiotic stress tolerance. What has hampered the quest for tolerant germplasm so far is the lack of reliable screening methods and the lack of control in the timing, severity and even occurrence of the stress stimulus under field conditions. The use of controlled environment conditions (growth chambers) or in the field using managed environment facilities (Rebetzke *et al.* 2012; e.g. use of irrigation and rainout shelters to control water stress conditions) are valuable developments for the establishment of reliable pre-screening methods.

Manipulation of abiotic stress tolerance using transgenic approaches

Transgenic approaches using overexpression of stress-responsive genes in model plants (e.g. *Arabidopsis* and rice) have identified several genes that contribute positively to abiotic stress tolerance, including several transcription factors and metabolic genes (see the Plant Stress website, address given above). The effect of very few of these genes has been investigated at the reproductive stage. Likely candidate genes for the improvement of reproductive stage abiotic stress tolerance are CBF/DREB1 transcription factors that are affected by cold and drought stress. Overexpression of CBF/DREB1 transcription factors under control of a strong constitutive promoter improves stress tolerance, but they lead to stunted growth and there is an adverse effect on yield (Oh *et al.* 2007; Morran *et al.* 2011). The use of an inducible promoter such as the drought-inducible *rd29A* promoter was shown to overcome the negative effect of *DREB1A* overexpression (Kasuga *et al.* 2004; Pellegrineschi *et al.* 2004). CBF/DREB1 transcription factors are normally expressed in the vascular parenchyma cells (Endo *et al.* 2008) and ectopic expression of these transcription factors may also have negative effects on yield in cereals. Recently, ABA levels were reduced by expressing the ABA catabolic gene ABA 8'-hydroxylase using a strong tapetum-specific promoter in rice anthers. This resulted in reduced anther ABA levels,

maintenance of sugar supply to the pollen and improved spikelet fertility under cold conditions in rice (Ji *et al.* 2011). The choice of an anther-specific promoter was essential, because ABA plays a positive role in regulating water relationships and acclimation to abiotic stresses (Larosa *et al.* 1985; Lu *et al.* 2009). A better understanding of hormonal interactions involved in controlling pollen fertility may lead to identification of other target genes for transgenic approaches. Microarray studies have revealed that response to abiotic stresses such as cold, drought and heat shows a lot of similarity and many protective mechanisms are shared by these stresses. Genetic manipulations in rice and maize using the *Escherichia coli* cold shock proteins *CspA* and *CspB* have resulted in significant improvements in growth and grain yield under a variety of stress conditions (cold, drought and heat; Castiglioni *et al.* 2008). The *E. coli* cold shock proteins act as RNA chaperones and belong to a widespread class of proteins with homologous genes in plants. This study has illustrated that genetic manipulations *can* lead to crops with superior performance under field conditions.

Selection of germplasm with reproductive drought-tolerance has been based on grain yield-related traits, with selection often being conducted under field conditions. Several QTL with widely varying contribution to the grain yield phenotype under drought conditions were identified in wheat and rice (Kato *et al.* 2000; Lanceras *et al.* 2004; Wang *et al.* 2005; Bernier *et al.* 2007; Kirigwi *et al.* 2007; Kumar *et al.* 2007; Venuprasad *et al.* 2009). A major problem with drought tolerance selection is interference with avoidance/escape mechanisms (e.g. early flowering), especially under field conditions, where occurrence, timing, severity and length of water stress conditions cannot be controlled (Yue *et al.* 2006; Dolferus *et al.* 2011). Osmotic stress under controlled environmental conditions has been used as an alternative screening method to drought stress (Lilley *et al.* 1996; Zhang *et al.* 2001); this method has not been used at the reproductive stage to date. In maize, the anthesis-silking interval (ASI) is negatively associated with grain yield under drought conditions (Campos *et al.* 2004). By using marker assisted selection (MAS) QTL have been introduced in order to reduce the ASI (Boyer and Westgate 2004; Tuberosa and Salvi 2006). Despite the availability of tolerant germplasm, little progress has been made in breeding cereals with reproductive stage drought tolerance. Reliability of screening methods and availability of relevant and precisely defined traits remains a limitation.

Cold/frost tolerance in wheat and barley is a problem that requires a better physiological and molecular understanding. Flowering time and time of sowing can be exploited as effective avoidance mechanisms; however, then breeding will need to focus on germplasm that is better adapted to heat and drought stress. Although winter wheat and barley lines are able to survive cold and frost conditions at the vegetative stage, a lot still has to be learned about varietal differences in mounting an effective cold acclimation response that protects against cold spells and frost periods that occur during flowering in spring. Transgenic approaches using the *E. coli* cold shock proteins have shown that this technology can protect the reproductive structures (Castiglioni *et al.* 2008). In the case of cold-tolerance in rice breeding efforts have focussed on improving seedling vigour, shortening the

growth season, and improving cold-tolerance at the booting stage (Andaya and Mackill 2003a, 2003b). Genetic variability has been identified for reproductive stage cold tolerance and this material has made it possible to identify cold-tolerance QTL (Saito *et al.* 2004; Oliver *et al.* 2005; Kuroki *et al.* 2009; Suh *et al.* 2010; Zhou *et al.* 2010). Two cold tolerance loci, *Ctb-1* and *qCTB7*, have been fine-mapped (Saito *et al.* 2004; Zhou *et al.* 2010). Breeding for water-logging tolerance is complicated and needs to focus mainly on survival of the below-ground and vegetative plant parts, because the effects on reproductive development are secondary.

In conclusion, improvement of reproductive-stage abiotic stress tolerance in cereals is possible in the foreseeable future using either breeding or transgenic approaches. Critical for future achievements is defining the physiological and molecular basis of well defined abiotic stress tolerance traits at particular stages of reproductive development. This knowledge base will then provide the basis for the design of high throughput diagnostics to drive new advances in the selection of abiotic stress tolerance in our major cereal food crops.

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