

The Abiotic Stress Response and Adaptation of Triticale – A Review

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After a decade of genetic manipulation and improvement, triticale stand out as a crop of high biomass and grain yield potential which generally surpass that of wheat. Its high productivity is most likely derived from high rates of carbon assimilation linked to stomatal physiology and probably low respiration rate. Being a derivative of rye, triticale has always been assumed to be relatively resistant to abiotic stress. The last review of triticale adaptation to abiotic stress as published by Jessop (1996) pointed at its general and specific fitness to harsh growing conditions. This review as based on additional data published in the last 20 years indicates that triticale retain good to excellent adaptation to conditions of limited water supply and problem soils which involve salinity, low pH, defined mineral toxicities and deficiencies and waterlogging. Despite the understandable expectations, freezing tolerance of triticale was not found to be up to the level of rye. The freezing tolerance of the rye complement in triticale is inhibited by unknown factors on the wheat parent genome. Any given triticale cultivar or selection cannot be taken a priori as being stress resistant. Research has repeatedly shown that triticale presented large genetic diversity for abiotic stress resistance and most likely this diversity has not yet been fully explored due to the very limited research and the small studied sample of the potential triticale germplasm. Triticale is a valuable stress tolerant cereal on its own accord and a potential genetic resource for breeding winter and spring cereals. Because of its high productivity and resilience it might become as important as wheat or better on a global scale if its grain technological quality will be improved to the level of wheat.

Keywords: plant breeding, wheat, rye, drought, cold, freezing, heat, salinity, mineral toxicity, mineral deficiency, waterlogging, tolerance, resistance, abiotic stress, yield, stomata

Triticale – A Historical Sketch

The very early history of triticale (\times *Triticosecale* Wittmack) constituted mainly of a botanical curiosity of no agronomic value. It took nearly a hundred years of research by botanists, geneticists and breeders to evolve triticale into a crop (Guedes-Pinto et al. 1996; Mergoum and Gómez-Macpherson 2004).

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Basically, triticale is an amphiploid species bearing the genomes of wheat (*Triticum* sp.) and rye (*Secale* sp.). The majority of today's triticales are descendants of the primaries involving either common wheat (*Triticum aestivum* L., $2n = 42 = AABBDD$) or durum wheat (*Triticum durum*, $2n = 28 = AABB$) as the seed parent and the diploid rye (*Secale cereale* L., $2n = 14 = RR$) as the pollen parent. Hexaploid wheat-derived primaries, referred to as octoploid triticales ($2n = 56 = AABBDDRR$), were the first to be produced and studied. However, the bulk of breeding and research efforts later focused on developing and improving hexaploid triticales ($2n = 42 = AABBRR$), which are the majority grown today.

While early triticale research was well underway in Europe, an important thrust to accelerate and expand triticale research on a global scale was initiated at the University of Manitoba, Canada in 1954. The program assembled a large collection of primary triticales from all over the world and by extensive intercrossing and selection developed new winter and spring octoploids and hexaploid triticales.

At about the same time triticale breeding program in Hungary and Russian Federation also succeeded in producing valuable progenies from crosses between octoploid and hexaploid primaries. Árpád Kiss and his collaborators in Hungary were the first to release two selections into commercial production grown over 40,000 hectares in 1968. The Canadian program released its first commercial triticale a year later.

Triticale research at CIMMYT Mexico started in the mid-1960 in collaboration with the University of Manitoba. The program incorporated the photoperiod insensitivity and the short stature of the new semi-dwarf Mexican wheat into the available best triticale, followed by an extensive wide testing in different environments. Work resulted in a fertile, short, day-length insensitive high yielding selection named Armadillo. Armadillo retained chromosome 2D from wheat and lost chromosome 2R from rye and was an example of the later triticales referred to as 'substituted' triticales. The wide global distribution and testing of the CIMMYT international triticale yield nurseries (ITYN) enabled further selection of superior agronomic triticale lines which presented equal or better yield than the local check wheat cultivars. These nurseries which were also grown on very diverse problem soil conditions in sites such as Australia or Brazil confirmed the better tolerance of triticale to acid soils and waterlogged conditions as compared with wheat.

Triticale breeding in Europe was highlighted by the program of Kiss and collaborators in Hungary and later by T. Wolski and collaborator in Poland. The most notable release in 1982 was triticale 'Lasco' from Poland which was widely grown in Europe.

Triticale is mainly grown as feed grain and biomass production. The largest area grown in 2008 (FAO data in thousands of hectares) was in Poland (1333), Belarus (458), Germany (399), Australia (376) and France (343). A curious growing of triticale is also for producing thatching straw in the UK and elsewhere (<http://www.ntsga.org.uk/index.htm>). A major limitation to the spread of triticale cultivation is its inferior technological grain quality for baking and other common human cereal utilization (Gustafson et al. 1991; Bona 2004; Bona et al. 2013). This obstacle must be resolved before the advantages of triticale can be exploited on a wider global scale.

Since the initiation of triticale as a commercial crop in the 1960s, breeders expected it to be more resilient than wheat, considering the relative hardiness of its rye parent. It seems that the opinions on the hardiness of rye in terms of coping with soil and atmospheric stresses were derived from ample historical experience of farmers and some research. Most work on triticale adaptation to abiotic stress attempted to obtain reliable data on the comparative stress resistance of triticale and its parents. Abiotic stress research with triticale developed from the 1970s into the early 2000s, after which it seems to dwindle. The last comprehensive review of triticale response and adaptation to abiotic stress was published by Jessop (1996).

Comparative studies to define the characteristics of a crop species are very elusive due to the extensive genetic variation within each cultivated species. Thus very often reported results might be limited to the given single cultivar chosen to represent a species. This review will try to consider this issue whenever data is weighed and conclusions are made.

Potential Yield

The potential yield of any cereal as well as triticale has an important impact on its performance under moderate stress. For drought stress the effect of yield potential on yield performance under stress takes place where cereal yield is subjected to moderate stress which does not reduce yield to below 30 to 50% of the potential (Blum 2005). Where yield is reduced below that level, specific genes for resistance are evidently expressed and become relevant and more important than potential yield. At times, yield maintenance at this severe stress level may come at the expense of the genetic yield potential.

The CIMMYT international triticale yield nurseries (ITYN) were an important instrument for studying progress in breeding and the adaptation of breeding materials. The data analysis of these nurseries by Fox et al. (1990) indicated a yield improvement from ITYN 8 to ITYN 14 as well as an expected genotype by environment interaction for adaptation on a regional and global scale. A slightly later study (Josephides 1992) over 23 environments in Cyprus indicated that triticale materials performed as well as common wheat and better than durum wheat and barley. However, the latter two species performed better than triticale when late season water shortage developed. This observation was verified by the analysis of various CIMMYT international triticale nurseries by Reynolds et al. (2002, 2004). On average triticale had the highest biomass and yield but it had lower grain yield than common and durum wheat when conditions from spike growth stage onwards were sunny and warm. Small grain variety tests in Hungary, revealed triticale yield advantage over wheat, particularly in dry years and in marginal land areas where triticale production mostly concentrated (Bona 2004). A recent study by Motzo et al. (2013) which might have tested a more recent triticale did not confirm a yield reduction in triticale due to late season water deficit, at least in comparison with durum wheat. It therefore might be suspected perhaps that for certain triticale materials a reduction in fertility can occur where conditions are not optimal during flowering.

The potential advantage of triticale over wheat in biomass and grain yield was confirmed in a later study in Spain (Estrada-Campuzano et al. 2012). The higher biomass and

yield potential of triticale in that study was explained by greater radiation-use efficiency (RUE) derived from greater radiation interception by the triticale canopy as compared with wheat. This explanation is difficult to accept as a major one unless clearly linked to a different and a unique canopy structure and morphology in triticale. However, improved RUE can also result from canopy function rather than radiation interception.

A major physiological-genetic variable accounting for biomass and yield variations among crop plant genotypes has been linked to stomatal conductance and assimilation. Productive genotypes which also sustain growth and yield under variable moisture and temperature conditions express higher stomatal conductance and gas exchange (Shimshi and Ephrat 1975; Lu and Zeiger 1994; Lu et al. 1994; Fischer et al. 1998; Horie et al. 2006; Blum 2011; Reynolds et al. 2012; Blum 2013; Wang et al. 2014). A study of triticale and durum wheat materials grown over different field environments (Motzo et al. 2013) indicated that triticale had a consistently greater stomatal conductance than durum wheat during the vegetative stage and that this was associated with a respectively greater RUE. A possible advantage of triticale in photosystem metabolism was sought by investigating its leaf ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) content and carboxylase activity in rye, wheat and triticale (Singh and Singh 2001) but this could not be established. Yield advantage due to photosynthesis can also be achieved through the temperature homeostasis of photosynthesis as seen in sorghum hybrids (Blum 2013). Winzeler et al. (1989) compared triticale rye and common wheat for single leaf photosynthesis and respiration at normal and cool temperatures in the growth chamber in order to explain species differences in growth. Growth rate of rye and triticale was greater than that of wheat at both 10/7°C and 20/15°C day/night temperatures. Photosynthesis rate of the species at both temperature regimes did not correspond to their growth rates. However, leaf respiration was substantially lower for triticale and rye than for wheat under the two temperature regimes and the difference was more pronounced at the cooler temperatures with a negative correlation to growth rate.

Therefore, greater stomatal and canopy conductance and moderate respiration can explain, at least partly the productivity advantage of triticale over wheat as well as their respective RUE.

Drought

The physiology of drought stress and the characterization and phenotyping of drought resistance have greatly advanced in recent years (e.g. Araus et al. 2002; Blum 2011; Reynolds et al. 2012). The primary reasons for yield reduction under various profiles of drought stress are now reasonably understood. The genetic and physiological background of plant drought stress and adaptation has been well studied to the extent that cereal breeding can effectively improve plant production in water-limited environments by addressing its stress physiology. The essence of this knowledge must be presented here in order to discuss well the case of triticale.

Very briefly, productivity-related drought resistance in cereal crops is quantitatively associated with sustained turgor, sustained stomatal conductance and sustained assimila-

tion as soil moisture is depleted. Turgor is sustained by effective soil moisture capture and/or by leaf osmotic adjustment. Complete stomatal regulation of transpiration can be enhanced by the total reduction of cuticular transpiration mainly through sufficient deposition of epicuticular wax which also increases canopy albedo. The combined result of any or all of the above is defined as effective use of water (EUW) (Blum 2009). Resistance of the reproductive functions under low plant water status is crucial when stress occurs at flowering. Such resistance can be controlled by turgor maintenance, carbon supply, hormonal regulation or certain constitutive traits of the gametophyte (Dolferus et al. 2011; Firon et al. 2012). Delayed senescence of the canopy after flowering can be important in supporting grain filling (Thomas and Howarth 2000). Finally, a superior capacity for stem reserve utilization for grain filling under drought or heat stress is a major tolerance mechanism under terminal stress (Yang and Zhang 2006). Any of the above resistance mechanisms might involve constitutive or adaptive plant traits and processes. These traits and functions are crucial for evaluating the relative drought resistance of crops and genotypes in experimental work. Beyond all of the above there are also issues of adapting plant phenology to the water regime and the questionable value of plant survival under extreme desiccation which might be important in certain agro-ecological or even social situations.

Twenty-four early hexaploid triticale lines from the CIMMYT ITYN-nurseries were tested in 1988/89 under drought stress (mean yield of 1720 kg ha^{-1}) and non-stress (mean yield of 7180 kg ha^{-1}) conditions as compared with the best standard wheat cultivar available (Blum unpublished data) (Fig. 1). Triticale yield advantage over wheat (expressed as percent of the standard adapted wheat cultivar) was correlated between stress and non-stress conditions. The most prominent result was the large variations in relative yield

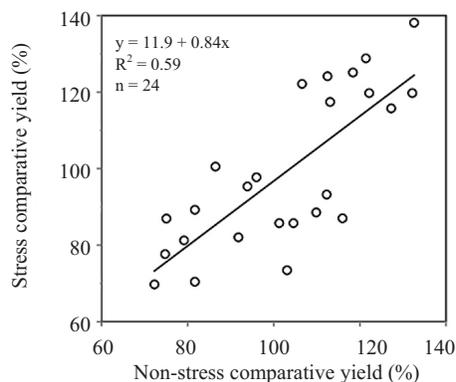


Figure 1. The linear relationship between yield under drought stress and under non-stress conditions of 24 triticale genotypes expressed as percent of a standard adapted wheat cultivar ('relative yield'). Stress yield was tested at the Gilat experiment station Israel in 1988/89 under 205 mm total rainfall. Mean yield was 1720 kg ha^{-1} . Non-stress yield was determined at Bet Dagan Station Israel on that year under full irrigation where mean yield was 7180 kg ha^{-1} . Soils at the two sites were favorable. The standard wheat cultivar in each test was different being well adapted to drought stress (cv. Bethlehem) or irrigated (cv. Lachish) conditions. Both experiments were managed under best agronomic practices and maintained free of disease. The water regime was the main differential between sites (Blum, unpublished data)

among triticale lines, under both conditions. Still a number of high yielding (non-stress) triticale lines yielded very well also under stress relative to the standard adapted wheat cultivar. This result is impressive in view of the fact that in those years CIMMYT program did not specifically select for yield under drought stress conditions.

Similarly, large diversity was found among 11 triticale genotypes in their drought susceptibility index for yield (DSI) when tested in Poland under drought stress and non-stress conditions. DSI was found to be correlated with several physiological tests (Grzesiak et al. 2003). In another study of complete and substituted triticale in Mexico drought resistance of triticale in terms of DSI for yield was better than that of durum wheat (Abdalla and Trethowan 1990). When studied under typical Mediterranean climate (Giunta et al. 1993) the yield of durum wheat was significantly reduced (by 25%, 54% and 87%) under the different tested moisture stress regimes, while triticale showed only a slight and non-significant decrease (8%) in comparison to the irrigated control. The greater drought resistance of triticale could be attributed to early heading and possibly to a greater capacity for soil moisture extraction.

Osmotic adjustment can sustain turgor and stomatal conductance at low leaf water potential. Triticale expressed a capacity for osmotic adjustment and a significant genetic variation in this respect (Barary et al. 2003). It was also shown that osmotic adjustment in triticale was associated with sustain fertility of tillers under stress.

Various triticales differ in their leaf glaucousness which might indicate variable epicuticular wax deposition in terms of content and structure. Epicuticular wax variability in triticale and its impact on cuticular transpiration has not been sufficiently investigated. Difference in epicuticular wax between two triticale varieties was associated with UV-B radiation tolerance, where the high wax cultivar was relatively more resistant (Skórska and Szwarz 2007). Saulescu et al. (2011) concluded that rye and triticale had higher albedo than most wheat cultivars and they considered these species as genetic resources for improving this trait in wheat. High albedo reduces the radiative energy load on the plant, including UV-B.

Stem reserve utilization for grain filling under stress was important in triticale (Royo et al. 1999). The contribution of pre-anthesis assimilates to grain yield was 46% in spring triticale genotypes and 65% in the later flowering winter genotypes. Various hexaploid triticale genotypes out of the CIMMYT ITYN-nurseries were tested for their capacity to fill the grain from stem reserve (Blum 1989 unpublished data) using the chemical desiccation method (Blum et al. 1983; Blum 2011). For 22 genotypes the rate of reduction in kernel weight by desiccation of the foliage at the onset of grain filling ranged from 17% to 34% as compared with 0 to 52% in different advanced wheat breeding materials. It therefore remains that while triticale genotypes present some variation in the capacity for sustaining stem reserve utilization for grain filling, selected improved wheat materials performed better in this respect.

There is no information available on non-senescence (stay-green) in triticale.

In conclusion, there are good indications that triticale genotypes of high yield potential retain certain important traits for sustained yield under drought stress and that there is genetic variation in this respect. On the other hand it is speculated that floret fertility in cer-

tain triticale materials might be more sensitive to drought or heat stress than wheat. However, the capacity of triticale for osmotic adjustment should provide some protection in this respect besides the role of osmotic adjustment in sustaining leaf turgor and stomatal conductance under stress. The main conclusion is that triticale offers ample genetic variation for the improvement of its productivity under limited water regimes. This confirms the earlier impression of Jessop (1996) that drought resistance of triticale seems to be improved with the progress of its breeding under water limited environments.

Cold

Rye is more cold tolerant than wheat. The rye genome component of triticale naturally allows expecting greater cold tolerance of triticale over that of wheat.

Seven octoploid (ABDR) triticales and their parental winter wheat and rye cultivars were assessed for cold hardiness in artificial freezing tests (Dvorak and Fowler 1978). In all instances the triticales achieved only the cold hardiness level of their parental wheat cultivars, indicating suppression of the rye cold hardiness by the wheat parent. To assess whether polyploidy *per se* caused the reduction in cold hardiness seven autotetraploid rye populations was compared with the cold hardiness of their parental diploid populations. All autotetraploid populations were not as cold hardy as the corresponding diploid populations, indicating that polyploidy has an adverse effect on the expression of genetic systems controlling cold hardiness in rye. When reciprocal wheat-rye amphiploids were studied (Limin and Fowler 1984) it was concluded that the suppression of cold hardiness in triticale by the wheat parent was not due to cytoplasmic effect. This was confirmed by the fact that the cold hardiness of alloplasmic rye with *Triticum tauschii* cytoplasm was similar to that of the rye parent. When hexaploid (ABR) triticale were compared with their rye and durum wheat parents for winter hardiness (Limin et al. 1985) it was found again that winter hardiness was similar to that of the wheat parent. This similarity in expression of cold hardiness in both octoploid and hexaploid triticales indicated that the D genome of wheat is not solely, if at all, responsible for the suppression of rye cold hardiness genes in triticale.

In a study of 10 wheat and 18 triticale lines it was confirmed that wheat was hardier than triticale in terms of field survival (McIntyre et al. 1988). Few studies which sought suitable cold tolerance phenotyping methods with triticale concluded that appreciable variation exists in triticale for this trait (e.g. Hömmö 1994; Rapacz et al. 2011). It is therefore clear that cold hardy triticale must be produced with cold hardy wheat parents and that the rye genome component *per se* is no assurance for triticale cold tolerance.

Frost damage at heading and flowering is a serious problem in certain agro-ecological zones of wheat, where one night of freezing temperatures can reduce yield appreciably. In a study with 8 triticale and 3 wheat genotypes it was found again that wheat was superior to triticale in this respect (Tshewang et al. 2010).

Salinity

According to data collected by the USDA Salinity lab (Table 1), the salinity tolerance of triticale is basically better than that of wheat and might even approach that of barley.

Table 1. The comparative rating of salinity tolerance in terms of yield reduction threshold and yield reduction rate with salinity, in triticale, wheat and barley. Data from the US Salinity lab database (<http://www.ars.usda.gov/Services/docs.htm?docid=8908>)

Common name	Botanical name	Threshold dS m ⁻¹	Yield reduction rate % per dS m ⁻¹	Rating
Barley	<i>Hordeum vulgare</i>	8.0	5.0	Tolerant
Triticale	× <i>Triticosecale</i>	6.1	2.5	Tolerant
Wheat	<i>Triticum aestivum</i>	6.0	7.1	Medium-tolerant
Wheat (common)	<i>T. aestivum</i>	8.6	3.0	Tolerant
Wheat, durum	<i>T. turgidum</i>	5.9	3.8	Tolerant

In a field study with two triticale cultivars over a range of soil salinities Francois et al. (1988) found that the threshold for yield reduction under salinity stress was 7.3 dS m⁻¹, a value higher than that cited for triticale in Table 1. Seedling growth at salinity level of 27.6 dS m⁻¹ in a nutrient solution was better in triticale than in seven wheat cultivars (Shalaby et al. 1993). Koebner et al. (1996) concluded that triticale was more salinity tolerant than wheat. They underscored the tolerance of some of the Polish materials in their test. These results were most encouraging since these triticale materials were not directly improved for salinity tolerance.

Few studies probed the basis of salinity tolerance in triticale. The high K⁺/Na⁺ discrimination ratio which is a common physiological salinity tolerance marker in crop plants was in triticale at least as high as in wheat and close to barley under saline hydroponics culture (Karray-Bouraoui et al. 2001). High K⁺/Na⁺ discrimination in triticale was fully ascribed to the wheat genome whereas the rye genome did not have any effect in this respect (Gorham 1990). Indeed, the relative susceptibility of rye as compared with wheat was linked to its lower capacity for K⁺/Na⁺ discrimination (Morant-Manceau et al. 2004).

While molecular mapping of salinity tolerance is being pursued in wheat (e.g. Genc et al. 2010; Díaz de León et al. 2011), no such work has yet been seen to-date for triticale.

Mineral Toxicity

Acid soil associated with aluminum toxicity is a widespread problem in cereals. An extensive field study of complete and substituted triticales over diverse soils in Spain (Royo et al. 1993) found that the main factor for yield variation was soil pH. Complete triticales outyielded substituted triticales in the majority of sites.

Rye has long been known for its tolerance to acid soil and the associated toxic minerals such as Al. Because of the widespread problem in Brazilian soils, triticale was expected to

sustain this tolerance in their triticale breeding programs. It was later found (Kim et al. 2002) that while Rye was indeed more Al resistant than wheat, early triticale containing a 2D(2R) substitution developed in the mid-1970s in Brazil had poor tolerance. Later improved hexaploid triticale selected for tolerance approached the tolerance level of rye. It was also seen that rye expressed large genetic variation for Al tolerance and that developing new triticale for acid soil must first perform pre-breeding testing for suitable wheat and rye parents. The large genetic variation in Al tolerance of triticale was confirmed also for materials bred in Poland (Aniol 1996, 2006).

Reports from several sources indicated that genetic variation for and heritability of Al tolerance in triticale was sufficiently high to allow good progress in selection (e.g. Zhang et al. 1989; Oettler et al. 2000; Zhang et al. 2002). The inheritance of triticale root growth under Al stress is polygenic with an important additive component (Zhang et al. 1999a).

Most initial selection work has been done by phenotyping root growth in toxified hydroponics followed by evaluation on toxic soil in pots and in the field. The common concentration of Al in such hydroponic solutions was around 5–10 $\mu\text{g g}^{-1}$ or 20 to 100 μM (depending on the specific case) where often root growth inhibition is evaluated after several days in the solution. Sometimes re-growth upon return of plants to non-toxic solution or root staining for Al was taken as an estimate of tolerance. Methods for Al toxicity screening were detailed for alfalfa (Khu et al. 2012), barley (Echart et al. 2002) and for various cereal species (Bona et al. 1991; Bona and Carver 1998; Abate et al. 2012). Studies found rye to be a most tolerant cereal and emphasized the importance of major genes for Al tolerance in rye towards the improvement of other susceptible species (durum wheat, barley) where genetic variability is low for this trait (Bona et al. 1991; Aniol 2006).

There is an agreement that Al tolerance of rye, wheat and triticale is associated mainly with inorganic acid anion secretion from roots (e.g. Abate et al. 2012). Al-stressed triticale root tips released malate and citrate but they were not well associated with tolerance as the case was with wheat (Zhang et al. 2003). In another study (Liu et al. 2007) roots of 10 triticale cultivars secreted both malate and citrate in response to Al stress. The amount of organic acid anions secreted was correlated positively with relative root elongation and negatively with Al content in root apices under Al stress, suggesting that the secretion of malate and citrate seems to be involved with the exclusion of Al from root tips. Eight primary octoploid triticale genotypes derived from four common wheat cultivars and two rye lines differing in Al tolerance were tested for Al tolerance (Stass et al. 2008). It was concluded that the degree of Al tolerance of the triticale genotypes was closely related to the Al-induced citrate exudation, which was mainly controlled by the tolerance of the wheat parent. However, in another study it was found that organic acids exudation from triticale roots under Al stress was associated with genes on the short arm 3R chromosome of triticale (Ma et al. 2000). Earlier work cited by Jessop (1996) suggested that aluminum tolerance factors were located on chromosomes 3R, 4R, 5R and 4D. The physiological source of malate and citrate exudation from root tips of Al resistant triticale is not clear, whereas it was not associated with the metabolic enzymes of these organic acids in the root (Hayes and Ma 2003).

An additional mechanism of Al tolerance in triticale was linked to plasma membrane lipid permeability to Al. When resistant and susceptible triticale lines expressed similar organic acid exudation under Al stress, the susceptible line expressed relatively greater root cell plasma membrane lipid permeability (Wagatsuma et al. 2005).

Unlike wheat, molecular mapping of Al tolerance in triticale is yet unresolved. Al tolerance in wheat was associated with 1 to 3 QTLs (Riede et al. 1996; Ma et al. 2006; Cai et al. 2008; Navakode et al. 2009). A study with triticale (Niedziela et al. 2012) concluded that putative markers were associated with 3R, 4R, 6R and 7R chromosomes, which essentially confirm previous cytogenetic studies. Transporter genes are now widely recognized to regulate of malate and citrate excretion from root of wheat (and other plants), as the case is for the malate transporter ALMT1 gene (e.g. Pereira et al. 2010).

Manganese is also released in acid soils. Eight triticale genotypes which differed in Al tolerance were tested in nutrient solution for manganese tolerance (Zhang et al. 1999b). A wide range of Mn tolerance was found but it did not correlate across genotypes with Al tolerance. Selection for acid soil tolerance should therefore consider both metals.

Mineral Deficiency

Zinc deficiency is a common problem in cereals grown on infertile and calcareous soils. Triticale has been repeatedly shown to be relatively resistant to Zn deficiency.

Cakmak and colleagues did extensive work on mineral efficiency in cereals. Working with calcareous soils they first observed the minor expression of Zn deficiency in rye and triticale as compared with pronounced expression in wheat, especially in durum (Cakmak et al. 1997b). These results were repeated in terms of plant productivity in the field. Zn efficiency declined in the order rye > triticale > bread wheat > durum wheat. In a second study (Cakmak et al. 1999) several cereal species were compared for Zn efficiency grown in soil and in nutrient solution. Deficiency symptoms in leaves and labeled Zn uptake corresponded with the relative Zn efficiency in terms of plant production. Zn efficiency declined in the order of rye > triticale > barley > bread wheat > oats > durum wheat, and it was related to uptake capacity.

In a study with disomic wheat-rye addition lines (*Triticum aestivum* L., cv. Holdfast-*Secale cereale* L., cv. King-II) and an octoploid triticale line Zn deficiency was prominent in wheat and slight in rye (Cakmak et al. 1997a). The addition of rye chromosomes, particularly 1R, 2R and 7R, into wheat reduced the severity of deficiency symptoms. The 1R and 7R chromosomes carried the genes for Zn efficiency as measured by the ratio of dry weight produced under Zn deficiency to the dry weight produced under Zn fertilization. Schlegel et al. (1999) confirmed that triticale was similar to rye rather than wheat regarding Zn concentration and Zn accumulation per shoot under both Zn-deficient and Zn-sufficient conditions.

Manganese efficiency was found to be higher in barley than in wheat and triticale when grown on Mn deficient soil (Marcar and Graham 1987). Still, chromosome 6R of rye was indicated to carry genes for Mn efficiency (Schlegel et al. 1999).

Copper efficiency of rye was transferred to wheat (Graham et al. 1987). The presence of the rye 5RL chromosome segment in four different wheat cultivars increased grain yield on copper-deficient soils by more than 100% on average. Two triticale lines and their respective parents were evaluated in pots with copper deficient soil (Graham and Pearce 1979). While wheat was extremely sensitive to copper deficiency resulting in complete sterility, rye performed completely normally. The hexaploid triticale was completely tolerant while the octoploid triticale yielded about 60% of rye. Pollen sterility was the most pronounced phenotypic expression of copper stress. A study with copper deficient soil at different pH levels (Harry and Graham 1981) confirmed that rye was extremely efficient in acquiring copper from soil while wheat was very susceptible. The specific triticale was generally intermediate in efficiency between its two parents. However, triticale was as efficient as rye at pH 5.0, but sensitive as wheat at pH 8.4. It appeared that the effect of pH in this respect was linked to copper availability. Therefore, triticale can be as copper efficient as rye, depending on its specific genotype and soil pH.

Information on major nutrient efficiency in triticale is limited. Phosphorus efficiency at different rates of P supply was evaluated in several wheat, rye and triticale cultivars (Osborne and Rengel 2002). P utilization efficiency was calculated as the amount of dry matter produced per unit of P accumulated in shoots, corrected for seed P content. Rye and triticale cultivars were generally more efficient in taking up and utilizing P than wheat.

Whereas arbuscular-mycorrhizal (AM) root colonization enhances plant acquisition of P, the degree of AM infection in a triticale genotype and its two parents was assessed in soil culture in pots (Pandey et al. 2005). AM colonization was greater in rye than both the lower rates in wheat and triticale. Plant dry matter and P content corresponded to these differences. Rye also expressed higher P efficiency without colonization with AM and triticale was better than wheat in this respect. It seems that high symbiosis efficiency exist in rye while triticale seems to inherit the low symbiosis from wheat. The medium level of P acquisition in triticale without AM infection seems to be specific to this cross when data for a large number of triticale as cited above indicate that P efficiency might be generally closer to the high level seen in rye.

Research with disomic substitution lines, derived from the triticale cultivars 'Presto' and 'Rhino' allowed to conclude that both rye and the D chromosomes of wheat were involved in the P and N efficiency under conditions of nutrient solution (Oracka and Łapiński 2006).

Information on nitrogen efficiency in triticale is even more limited than that for phosphorus. In a study with twelve triticale genotypes grown in soil in pots significant genetic variation was found in N efficiency calculated by the ratio of grain yield to N absorbed by the above-ground plant parts at maturity (Isfan et al. 1991).

Taking all of the above together, triticale can be expected to be generally more efficient than wheat in mineral efficiency, and genetic variation in this respect should allow further improvement.

Waterlogging

Setter and Waters (2003) reviewed the possibility of improving waterlogging resistance in certain cereals and provided some views on the subject in triticale. They felt that there was a perception among farmers that oats and triticale were more waterlogging resistant than wheat and barley. A study of germination survival under 4 days of waterlogging indicated that mean germination survival was greater in oats and triticale than in wheat and barley. However, the data show that the range of resistance in 3 triticale varieties was similar to the range across 11 Australian wheat cultivars studied. In another study under waterlogged field conditions oats and triticale expressed somewhat greater root aerenchyma formation than wheat and barley.

When one triticale was compared with two wheat cultivars under hypoxia stress in nutrient solution triticale performed better than wheat in root growth and better than one of the wheats in shoot dry matter (Johnson and Huang 1996). One triticale was compared with two wheat cultivars under stagnant nutrient culture and waterlogged soil (Thomson et al. 1992). Triticale performed better than wheat under these conditions with respect to shoot weight, root weight and aerenchyma development in roots. It can therefore be concluded that triticale is generally more waterlogging and hypoxia resistant than wheat, most likely due to better root growth and function.

Conclusion

Interest in the abiotic stress response and adaptation of triticale understandably developed with the expansion of triticale breeding and acceptance during the last quarter of the 20th century. While important issues still remain unresolved, research on stress response of triticale tended to decline in the 21st century. The development of crop genomics research in recent years touched triticale also (e.g. Tyrka et al. 2011) and in the future it will hopefully impact triticale breeding for abiotic stress resistance as well as its grain and baking quality.

Presently, triticale stands as a crop of high biomass and yield potential which generally surpass that of wheat. Its high potential might stem from high rates of carbon assimilation linked to stomatal physiology and probably low respiration rate. The work cited in this review indicates that triticale retain good to excellent adaptation to limited water supply and problem soils which involve salinity, low pH, and defined mineral toxicities and deficiencies. This resilience of triticale was expressed even when just one triticale cultivar was compared with numerous representatives of wheat or other cereals. In most (but not all) cases this resilience could be traced to its rye parent.

Despite the understandable expectations, freezing tolerance of triticale was not found to be up to the level of the best winter wheat. The expected effect of the rye genome towards the freezing tolerance of triticale seems to be inhibited by unknown factors on the wheat parent genome.

Any given triticale cultivar or selection cannot be taken a priori as being stress resistant. Research has repeatedly shown that triticale presented large genetic diversity for abiotic

stress resistance and most likely this diversity has not yet been fully explored due to the very limited research and the small studied sample of the potential triticale germplasm as compared with other cereals. The observed genetic variation for abiotic stress resistance is derived at least partly from the variation within the parent materials. It is therefore important that breeding superior triticale for abiotic stress resistance will begin by selecting the appropriate wheat and rye parents through pre-breeding research.

Taking account of all the pros and cons for this cereal, the emerging climate change and the spread of agriculture into marginal lands, triticale has yet to become a much more important cereal on a global scale as compared with its present standing mainly as a feed and biomass crop. A major limitation to taking full advantage of the yield potential and the general adaptation of triticale to abiotic stress is its poor grain technological quality for human consumption. If a significant genetic improvement in this respect would bring triticale on par with wheat it has a potential to become a major global solution for food production under harsh conditions. This is an important challenge for genomics and breeding research.

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