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QTLs and genes for abiotic stress tolerance in cereals: Their general role in the environmental adaptation and their developmental-stage specificity¹

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SUMMARY – Plants are exposed to many types of abiotic stresses during their life cycles, i.e. cold, drought or high heavy metal concentrations in the soils. To minimize the yield loss of cultivated plants caused by unfavourable environment, better understanding of the tolerance mechanisms is needed. The current state of the studies on abiotic stress tolerance suggests the general role of some regulatory factors in the environmental adaptation mechanisms; therefore, it is also possible to find some common QTLs/genes influencing more than one adaptation process. In wheat QTLs for frost tolerance (*Fr-A1*, *Fr-A2*) and for vernalization requirement (*Vrn-A1*) were determined on chromosome 5A. Interestingly, QTLs for copper tolerance were localised in the same position as the *Vrn-A1* gene, and also in the same position as the *Vrn-D1* on the chromosome 5D. The developmental-stage specificity of QTLs for abiotic stress tolerance was shown by testing drought tolerance in barley. The results revealed that the most effective QTLs for drought tolerance in seedling-, young plant- and mature-stage are different; however, a common QTL with lower effect was also determined in each developmental phase.

Introduction

Growth and development of plants is greatly affected by abiotic stresses, such as cold (frost), drought, high temperature, soil salinity and heavy metal pollution, resulting in yield loss in cultivated plants. Plants respond to these environmental challenges through a number of defence mechanisms to maintain the optimal conditions for growth and development (Bray *et al.*, 2000). These mechanisms include several regulatory processes that activate the differential expression of genes responsible for tolerance (Shinozaki *et al.*, 2003). In the model plant *Arabidopsis thaliana* numerous transcriptional factors (i.e. *Cbf*-s: C-repeat binding factor) playing a role in the cold-, drought- and salinity-tolerance were identified in the last decade and their homologues were found in cereals also (Skinner *et al.*, 2005; Miller *et al.*, 2006), suggesting the existence of some common and conserved regulatory pathways. In the species belonging to the tribe *Triticeae* the role of group 5 chromosomes seem to be central in the defence against abiotic stresses: some regions in the group 5 chromosomes play a general role in the adaptations to the changing environment, suggesting that they share – at least particularly – the same regulatory processes (Cattivelli *et al.*, 2002). The expression of the genes responsible for abiotic stress tolerance may depend not only on stress factors: it is possible that in different developmental-stages (germination-, young plant- and mature-stage) different genes can play a role in the avoidance of the damages caused by stresses. Possibly, it is the reason that the application of molecular markers linked to the identified QTLs (Quantitative Trait Loci) for marker assisted selection of drought- and cold-tolerant genotypes was not successful up to now. Therefore, it is very important to identify the genes/QTLs affecting the tolerance in more than one developmental-phases. In this case, the common and stage-specific QTLs can be separated, and QTLs with reliable effect could be selected. Here we summarize the recent findings on the role of group 5 chromosomes in the abiotic stress tolerance (cold, drought and heavy metal) concentrating on the role of the *Vrn* (vernalization requirements) genes, and the developmental stage specificity of drought stress specific QTLs in barley.

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The role of group 5 chromosomes in abiotic stress tolerance

Frost tolerance

Frost (cold) is one of the most important factors limiting the yield of the cereals under temperate climatic conditions. Early studies in wheat using 'Chinese Spring' (recipient, frost sensitive) 'Cheyenne' (donor, frost tolerant) substitution lines revealed that genes responsible for frost tolerance are localized on chromosomes 5A, 5B, 5D, 2B, 4B, 4D and 7A (Sutka, 1981), and most effective alleles were localized on the chromosome 5A and 5D (Galiba and Sutka, 1988). Major QTLs, affecting frost tolerance, have been mapped on chromosome 5A (*Fr-A1*; Galiba *et al.*, 1995), 5D (*Fr-D2*; Snape *et al.*, 1997), and recently on 5B (*Fr-B1*; Tóth *et al.*, 2003). Vágújfalvi *et al.* (2003) using a diploid einkorn mapping population discovered a new QTL (designated *Fr-A2*) for frost tolerance on the long arm of chromosome 5A. Comparing common markers for 5A, 5B and 5D chromosomes, the results suggested that *Fr-A1*, *Fr-D1* and *Fr-B1* genes could be orthologous (Snape *et al.*, 2001; Tóth *et al.*, 2003). In barley, Francia *et al.* (2004) found two QTLs for frost tolerance on the long arm of chromosome 5H. Comparative mapping data proved that these two loci are collinear to *Fr-A1* and *Fr-A2*. For this reason these new QTLs can be referred as *Fr-H1* and *Fr-H2*.

Vernalization requirements

Vernalization (*Vrn*) genes determine the need for low temperature to induce flower development. Winter type cereals require vernalization for flower initiation, while spring types do not. Vernalization requirement and frost tolerance have always been considered as two highly associated traits. Using the mapping population developed from the cross between the chromosome substitution lines 'Chinese Spring'/'*Triticum spelta* 5A (frost-sensitive, vernalization-insensitive) and the chromosome substitution line 'Chinese Spring'/'Cheyenne' 5A (frost-tolerant, vernalization-sensitive) a more precise mapping of *Vrn* and *Fr* was achieved. Genes for vernalization requirements (*Vrn*) were mapped in a colinear region of chromosomes 5A (*Vrn-A1*; Galiba *et al.*, 1995), 5B (*Vrn-B1*; Tóth *et al.*, 2003) and 5D (*Vrn-D1*; Snape *et al.*, 1997). In barley the genes for vernalization requirements were mapped on the long arms of the chromosome 1H (*Vrn-H3*), 4H (*Vrn-H2*) and 5H (*Vrn-H1*), the last with the highest effect (Laurie *et al.*, 1995; 1997; Karsai *et al.*, 1997). The *Vrn-H1* locus was linked to the same marker as the *Fr-H1* gene (Skinner *et al.*, 2006).

Copper tolerance

Copper (Cu) is an essential plant micronutrient, however, it can be phytotoxic if present in the soil in high levels. Cereals are sensitive to high soil concentration: the toxic effect may result in reduced fertility and in yield loss of field-cultivated wheat (Moustakas *et al.*, 1997). Testing the Cu-tolerance of the 'Chinese Spring' (recipient) / 'Cappelle Desprez' (donor) wheat substitution series indicated that chromosomes 5A, 5B, 5D, 3D, 7D and 6B have an effect on copper tolerance in wheat (Bálint *et al.*, 2003). The role of homoeologous group 5 was confirmed by testing wheat/rye substitution lines (Bálint *et al.*, 2003). In the course of QTL and deletion analysis, major QTLs for Cu tolerance were identified on the long arm of chromosome 5A (*QC*ut*.ipk-5A1*), 5B (*QC*ut*.ipk-5B*) and 5D (*QC*ut*.ipk-5D1*, *QC*ut*.ipk-5D2*; Bálint *et al.*, 2007, Bálint *et al.*, unpublished).

The expression of several cold-regulated (*cor*) genes is controlled by loci located on chromosome 5A

Among the large number of wheat *cor* genes described, *cor14b* is one of the most studied. Messenger RNAs corresponding to the *cor14b* gene are accumulated in barley leaves when plants are exposed to low temperature (Cattivelli and Bartels, 1990). In wheat, two regulatory loci on chromosome 5A controlling the expression of the *cor14b* gene were mapped: one of the two loci was associated with a frost tolerance locus *Fr-A1* (Vágújfalvi *et al.*, 2000), while the other one was co-mapped with a novel QTL for frost tolerance (*Fr-A2*; Vágújfalvi *et al.*, 2003). The *Fr-A2* locus is linked to the cold-regulated transcriptional activator *Cbf3*, (Vágújfalvi *et al.*, 2003). Moreover, recently it was shown that the expressions of three other *Cbf* genes (*Cbf1A*, *Cbf1C* and *Cbf7*) are also linked to the

Fr-A2 locus (Vágújfalvi *et al.*, 2005). When the *cor14b* gene product accumulation was studied, Francia *et al.* (2004) found that only the *Fr-H2* locus was responsible for the regulation of the *cor* gene, while the *Fr-H1* locus has no effect on it.

The developmental-stage specificity of QTLs for osmotic stress and drought tolerance in barley

Drought (water deficit) is one of the most important environmental stresses affecting the growth and development of plants through alterations in cell metabolism and gene expression (Leopold, 1990). It is a permanent constraint to agricultural production in the developing countries and an occasional cause of yield loss in the developed world (Ceccarelli and Grando, 1996). Water deficit can occur during the whole lifecycle of the plants; therefore the tolerance must be screened at several developmental stages. In order to determine the QTLs involved in PEG-induced osmotic stress tolerance in barley, the Oregon Wolfe Barley (OWB) mapping population was examined at the germination and seedling stage (Szira *et al.*, 2006). To find QTLs influencing post anthesis drought tolerance (PADT) the same population was screened for drought tolerance in the greenhouse. The results revealed that the most effective QTLs for drought tolerance in seedling-, young plant- and mature-stage are different; however, a common QTL on the short arm of the barley chromosome 1(7H) with a smaller effect was also determined in each developmental phase (Szira *et al.*, 2006; Szira *et al.*, unpublished data). The QTL for drought tolerance identified on chromosome 7(5H) at the germination stage may be not specific for drought, because the same QTL was determined for salt tolerance at the germination stage (Weidner *et al.*, 2005) and for pre-harvest sprouting and dormancy (Lohwasser, pers. comm.). Therefore, this QTL seems not to be specific for drought, but rather for general abiotic stress tolerance. In barley the *Vrn-H1* gene was also mapped in this region (von Zitzewitz *et al.*, 2005).

Conclusion – can the *Vrn* genes play a general role in the defence mechanism against abiotic stresses?

Understanding the molecular processes of plant responses to abiotic stresses has a crucial role for the breeding of crop plants with better productivity under stress conditions. Recent investigations in the model plant *Arabidopsis thaliana* indicate that responses to cold-, drought- and salt-stress are controlled by common and conserved regulatory pathways. Genes, similar to the transcriptional factors determined in *Arabidopsis*, were identified in the EST (Expressed Sequence Tags) databases of many crop species, including barley and wheat. Some of the genes, encoding transcriptional factors, affecting abiotic stress tolerance in cereals are likely to be located on group 5 chromosomes, because these chromosomes play an important role in adaptation to the changing environment. Using wheat deletion stocks, the genes, affecting vernalization requirements (*Vrn-A1*; Galiba *et al.*, 1995), copper tolerance (*QC*ut*.ipk-5A1*; Bálint *et al.*, 2007), cold- and PEG-induced carbohydrate accumulation (Galiba *et al.*, 2005) were physically mapped in the same position on the long arm of chromosome 5A. Moreover, using deletion stocks for wheat chromosome 5D, genes for vernalization requirements (*Vrn-D1*, Snape *et al.*, 1997), for copper tolerance (*QC*ut*.ipk-5D2*; Bálint *et al.*, unpublished) and for stress-induced carbohydrate accumulation were also mapped into the same position. Some authors have postulated that "winter" alleles at the *Vrn-H1* and *Vrn-A1* genes would have a pleiotropic effect on frost tolerance (Brule-Babel and Fowler, 1988; Roberts, 1990) and on salt tolerance (Forster, 1992) in cereals. This hypothesis is supported by our results, suggesting that the *Vrn* genes might have pleiotropic effect on other traits. They might share the same regulatory pathways: it is most likely that transcriptional factors located in the position of the *Vrn* genes can control stress-inducible gene expression, affecting not only the flower initiation, but osmotic (PEG-induced) and heavy metal (such as copper) stress. However, the different expressions of the tolerance genes at different developmental stages make it difficult to find common regulatory pathways. Therefore, to determine the most reliable and effective QTLs, the tolerance must be screened at more developmental phases.

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