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

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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., 1997), and recently on 5B (Fr-B1; Snape et al., 2003). Vágújfalvi et al. (2003) using a diploid einkorn mapping population discovered a new QTL (designated QCut.ipk-5B) for frost tolerance on the long arm of chromosome 5A. Comparing common markers for 5A, 5B and 5D chromosomes, the results suggested that QCut.ipk-5A1, QCut.ipk-5B, and QCut.ipk-5D2 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 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 expression of several cold-regulated (cor) genes is controlled by loci located on chromosome 5A.
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 (QCut.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 (QCut.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 pleitropic 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 pleitropic 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.

References


