EXPRESSION OF COLD-REGULATED (cor) GENES IN BARLEY
Molecular bases and environmental interaction

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1. INTRODUCTION

Barley is grown either in the northern countries close to the polar circle or on the Himalayan mountains up to 4500 m on the sea level. Such a great diffusion, despite the differences in the climatic conditions, already suggests that the barley gene pool should contain characters for wide environmental adaptability and good stress resistance. The genetic adaptation to cold climate can be achieved either by evolving a powerful frost tolerance ability or by limiting the life cycle to the short summer season (escape strategy). It is a known fact that the winter barley varieties are less hardy than winter wheat, rye and triticale, nevertheless barley is grown till the Polar Circle because spring early maturity cultivars are able to run their life cycle in the short summer season. Plant growth habit and heading date can therefore be considered as the basic traits involved in barley adaptation to environments since they allow to synchronise the plant life cycle with seasonal changes. Nevertheless because winter barley has a higher yielding potential than spring ones, there is a great interest to improve its frost resistance capacity.

Freezing tolerance, a fundamental component of winter-hardiness, is based on an inducible process known as hardening or cold acclimation that occurs when plants are exposed to low non-freezing temperatures. Studies on frost resistance in cereal have been addressed either at genetics or at physiological-molecular levels. The genetic analysis discovered a number of loci controlling frost resistance or traits related to frost resistance.
On the other hand, physiological and molecular research identified compounds or mRNAs accumulated in response to cold. Several genes regulated by low temperatures (Cold-Regulated -cor- genes) have been isolated from the cereals genomes and their expression was found associated with the development of the frost tolerance during cold hardening. Present efforts are addressed to understand the relationship between the frost resistance loci and the physiological or molecular response associated with cold acclimation.

2. GENETIC LOCI CONTROLLING FROST RESISTANCE

Frost resistance has generally been considered as a polygenic trait, although specific loci are known to play an important role. Traditional genetics approaches were used to describe characters such as the heading-date or the growth habit and their involvement in the plant adaptation to the cold stress. More recently the application of the molecular marker technology to the analysis of quantitative traits has lead to the identification of a relative small number of quantitative trait loci (QTL) having a major effect on the ability of the plants to survive under stress conditions.

The growth habit trait, even if not involved per se in frost resistance, has been related to the plant winter survival ability. It is a known fact that winter cultivars are generally hardier than their spring counterparts. In barley, winter habit depends on the presence of the dominant allele at locus Sh and of the recessive alleles at loci sh2 and sh3. All the other allele combinations among these three genes are found in spring genotypes. The loci Sh, Sh2 and Sh3 are respectively located on chromosomes 4H, 5H and 1H. The homozygote genotype shsh is epistatic with respect to the recessive allele sh2 and sh3, and evinces a facultative behaviour towards the spring habit when sown in spring. The Sh3 allele is epistatic with respect to alleles Sh and sh2. Without vernalization and in long-day conditions, all the Sh3Sh3 cultivars are essentially spring types. Sh2, which is epistatic vis à vis alleles Sh and Sh3, has a series of multiple alleles which induce several spring-to-winter variants (Cattivelli et al., 2001). Fowler et al. (1996) have reported that the loci controlling vernalization requirement in wheat and in rye are responsible for the duration of the expression of cold-regulated genes, suggesting a relationship between growth habit, frost resistance and expression of the genes involved in cold acclimation (see below). The genetic analyses of the frost resistance in barley have found that a QTL for winter survival on barley chromosome 7 (5H) is associated with the Sh2 locus (Hayes et al., 1993) and with QTLs for heading-data and vernalization response under long day conditions (Pan et al., 1994). These results are probably due to genetic linkage rather than to pleiotropic effects, indeed recombinants between vernalization requirement and winter survival traits has been described (Doll et al., 1989).

RFLP analysis of the homeologous 5A chromosome of wheat have proved that vernalization requirement and frost resistance are controlled by two different, but tightly linked loci (Vrn-A1 and Fr1 respectively) (Galiba et al., 1995). In wheat the availability of chromosome substitution lines allowed the identification of chromosome carrying loci with relevant role in frost resistance. Thus, when the 5A chromosome of the frost-sensitive variety Chinese Spring was replaced by the corresponding chromosome of the frost resistant Cheyenne variety, the frost tolerance of Chinese Spring was greatly increased (Sutka 1981; Veisz and Sutka 1989). This phenomenon was also true in the opposite direction, namely when the 5A chromosome of Chinese Spring was substituted.