Cold Hardy Wheat

D. B. Fowler
Department of Plant Sciences, University of Saskatchewan,
Saskatoon, Saskatchewan

Low-temperature (LT) adaptation is determined by a complex quantitative system that is expressed by plants in anticipation of and during exposure to temperatures that approach freezing. It is controlled by a highly integrated genetic system that is regulated by environmentally responsive, complex pathways. In the last decade, a virtual flood of genetic and genomic information on LT adaptation has arisen from investigations using model plant systems and tools with an unprecedented level of sophistication for genetic analyses. This greater appreciation of the interactions that determine crop adaptation has provided us with the ability to design strategies to minimize the risk of LT damage in different stages of crop development. For example, our ability to manipulate the differences in genetic and environmental responses has allowed us to identify the genetic factors that determine LT-tolerance gene expression and to successful transfer the superior frost-tolerance genes from a hardy winter wheat variety into spring wheat. The superior LT-tolerance genes have also been tagged using molecular markers that allow plant breeders to select hardy spring and winter habit lines without having to wait for a test frost in the field. However, even with the opportunities offered by advances in technology, we have been unable to produce super hardy cultivars. As a result, while the genes within cereals have a high degree of similarity and the regulation of LT tolerance is operational across species, we have not been able to successfully exploit the superior LT tolerance of rye for cultivar improvement in related cereal species like wheat. Progress in this area will have to wait for a much clearer understanding of the plants LT-response mechanisms and the genetic and environmental interactions that control their expression.

Low temperature acclimation: To be successful in cool season and high winter stress climates, plants must be programmed to recognise and respond to temperatures that are favourable for growth and the environmental cues that signal seasonal changes typical of the regional environment for which they were selected or in which they evolved. In regions with cold winters, vernalization requirement is an important adaptive feature that delays heading by postponing the transition from the vegetative to the reproductive phase. Similarly, photoperiod requirement is an adaptation that allows the plant to flower at the optimum time. Cool season plants also have the ability to LT acclimate.

In this environmentally responsive system there is a need for plants to record the progress of seasons so they can properly anticipate the normal periods of LT stress and commit fully to growth and reproduction once the weather is favorable. The fact that both LT acclimation and vernalization have similar above freezing activation ranges suggests the likelihood of an extensive integration of LT-sensing mechanisms. These complicated time/temperature relationships and unexplained genetic interactions indicate that detailed analyses of natural genetic variation will be required to identify the critical genetic components of the highly integrated systems for LT adaptation that are regulated by environmentally-induced complex pathways.

In wheat and its relatives, LT acclimation is a cumulative process that is initiated once temperatures drop below 10 to 15ºC. There is an inverse relationship between temperature and acclimation rate and, when plants are grown at constant temperatures in the acclimation range, the most rapid changes in LT tolerance occur during the initial stages of acclimation. Exposure of hardened plants to higher temperature results in de-acclimation, but the process of LT acclimation can be re-initiated by exposing plants that are still in the vegetative stage to inducing temperatures. There is an over-winter decline in LT response due to an inability to maintain LT tolerance genes in an up-regulated state once vernalization and photoperiod requirements have been satisfied. Consequently, the ability to anticipate and respond environmental cues is dependent upon a highly integrated system of LT tolerance, vernalization and photoperiod genes.

Based on the above observations the evolution of and selection for genetic options that permit extensive modification of thermosensitive metabolic processes and critical structural components should not come as a surprise, especially in winter annual and perennial plants that must adapt to a wide range of seasonal stresses. Because LT response is determined by a highly integrated system of structural and developmental genes regulated by environmentally responsive, complex pathways that allow full expression of LT induced genes only when they are required in the plant's life cycle, it has been difficult to separate cause and effect adjustments to LT and other environmental cues that signal seasonal changes. For this reason, the long term research challenge has been to isolate the different variables involved in the expression of plant LT adaptation so that the critical responses to environment can be identified and exploited in crop management and improvement programs.

Simulation Model: A basic understanding of the LT responses found in cereals has allowed us to construct a LT tolerance simulation model for winter cereals. The model is based on a series of equations that describe acclimation, dehardening, and damage due to LT stress that are consistent with recent interpretation of LT gene regulation. LT tolerance is estimated on a daily basis relative to stage of plant development and cultivar cold hardiness potential. The model has been field validated for cereals over wintered at Saskatoon and it has application in the simulation of LT responses for a broad range of species and climates. In this model, the developmental genes (vernalization, photoperiod, etc) are assumed to be responsible for the duration of expression of LT-induced structural genes while the rate of LT tolerance acquisition is determined by cultivar differences in cold-hardiness potential. Vernalization requirements prevent the plant from going reproductive during favorable periods for growth and development in the fall and early winter and photoperiod sensitivity allows plants to maintain LT genes in an up-regulated state for a longer period of time under short day compared to long day. In both instances, the delay in the transition from the vegetative to the reproductive stage produces increased LT tolerance that is sustained for a longer period of time.

An interactive web-based version of the model has been developed for use by farmers, extension workers, and researchers interested in estimating winter survival in cereals (http://www.usask.ca/agriculture/plantsci/winter_cereals/WWModel.php; Fowler and Greer, 2003). A crop variety menu offers the choice of a wide range of winter cereal species and cultivars. The LT50 and vernalization options allow the user to expand on these choices and experiment with different values. The data files contain soil temperature records for selected years and locations that can be expanded when new data becomes available. The present files include examples from Canada and the Czech Republic. We also have weather data from Iran that will be added once the day length response variable has been satisfactorily modeled. Soil temperatures for the current year are added as the winter progresses thereby allowing interested users to monitor the predicted condition of the present crop. In addition, a Management Impact Calculator allows users to evaluate the effects of sub-optimal seeding date, seeding depth and phosphorous and nitrogen fertilization on the winter hardiness of crops grown in western Canada. A large database that can be quickly and easily supplemented combined with a flexible, interactive model which complies with the known LT responses of cereals creates a teaching tool that allows production risks, cause-and-effect processes, and genetic theories to be systematically investigated by users throughout the world.

Progress in Breeding for Low Temperature Adaptation in Cereals: The importance of reliable crop management resources and the ability to take advantage of small improvements in cultivar LT tolerance and growing season adaptation has been clearly demonstrated by winter wheat growers in the eastern prairies who have recently over-wintered crops that yielded up to 6 tonne/ha. This is a region where only 15 years ago most critics claimed that winter wheat could not be successfully grown in a normal year, let alone one with record low winter temperatures like those experienced in 2003-04. The high level of success achieved in this example is best demonstrated in Manitoba where the availability of better adapted cultivars and the adoption of improved management practices allowed farmers to increase their average grain yield of winter wheat from 1.1 in 1992 to 4.2 tonne/ha in 2004 (Figure 1). This single example demonstrates that there is still a considerable opportunity to further adapt our cropping systems to the environmental extremes experienced in western Canada. The degree of success that can be realized in this area will be dependent on our ability to develop cultivars with superior LT tolerance.

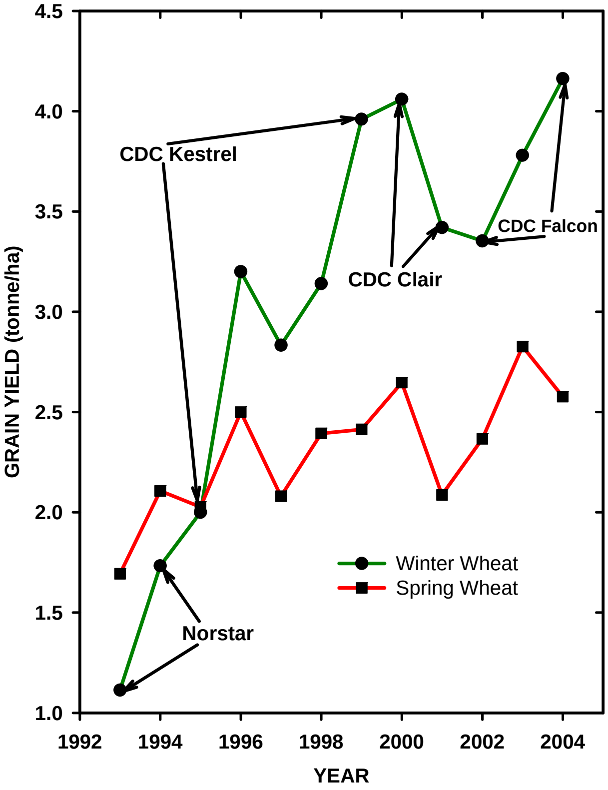

Figure 1. Average spring and winter wheat grain yield in Manitoba for the period 1992 to 2004 (source - Statistics Canada). Arrows indicate the dominant cultivar grown by farmers. CDC - Crop Development Centre University of Saskatchewan.

In a 1929 publication, Quisenberry and Clarke noted that "The possibility of developing hardier varieties through breeding has been recognized for years". However, the reality is that the maximum cold hardiness potential of most cereal crops has reached a stubborn plateau that has not been breached for decades. In fact, all the efforts of modern science have been unable to produce the super hardy cultivars needed to expand winter crop production into regions requiring a level of cultivar LT tolerance superior to that found in the land races selected by early farmers indicating that improvements in LT adaptation do not come easily. In contrast, the last 80 or more years have seen improvements in agronomic practices within most established production areas that have allowed plant breeders to reduce their selection pressure for LT tolerance. Consequently, while plant breeding efforts over the years have created cultivars with a high level of adaptation, there is still considerable potential for improvement in LT tolerance of cultivars available for most of the current winter wheat production areas around the world. Unfortunately, this is not the case for winter cereals other than rye in most of western Canada.

Our search for superior LT tolerance genes has been expanded to include attempts at interspecific and intergeneric transfers. There are considerable differences in the maximum LT tolerances found in different winter cereals and the possibility that genes can be transferred between species to increase the genetic variability available to winter cereal breeding programs has been explored. However, these attempts have done little more than demonstrate the difficulties that must be overcome before the full potential of superior species-specific LT-tolerance gene expression can be captured through interspecific gene transfers in breeding programs.

The superior LT tolerance of rye was found to be suppressed when combined with wheat to produce triticale cultivars. Artificially synthesized common wheat that was produced by combining the ancestral AB and D species also demonstrated the nonadditivity of closely related systems. Further investigation of LT gene expression in hybrids among wheat and its relatives has lead to the conclusion that chromosome dosage or ratios influence LT tolerance by shifting competitively balanced systems toward the parent with the greatest chromosome number. Molecular investigations of these hybrids have subsequently revealed that LT-induced gene families of both species are expressed in crosses combining wheat and rye to produce triticale. However, these genes were not expressed independently and the degree of LT gene expression in interspecific crosses was regulated by the higher chromosome parent (the wheat parent in the case of triticale cultivars). These observations indicate that, before we can successfully exploit the superior LT tolerance found in rye to produce super-hardy wheat cultivars, we must first acquire a greater understanding of the complex genetic mechanisms that plants have evolved for the efficient integration of LT responses into the daily processes of survival, growth, and reproduction.

The linkage of LT tolerance expression to stage of development adapts the plant to the environment for which it was selected or in which it evolved. For example, a high level of LT tolerance is no longer required after the onset of warm conditions in the spring when rapid growth and reproduction begin. Consequently, satisfaction of vernalization and photoperiod requirement results in a decline in LT tolerance of over-wintering plants. This results in complicated growth stage x LT tolerance interactions that must be optimized for each production area if cultivars are to be successful. Therefore, because individual genes are part of a complex system, a better understanding of the LT response mechanisms will greatly assist plant breeders in designing strategies to significantly improve the LT adaptation of important economic crops. For example, we have been able to successfully transfer the superior frost tolerance genes from a hardy winter wheat cultivar (Norstar) into a spring wheat line (Spring Norstar) demonstrating that the LT tolerance of spring habit wheat genotypes can be significantly improved by the inclusion of LT tolerance gene(s) from Norstar. When the superior LT determining gene(s) were combined with a rigorous photoperiod requirement, Spring Norstar was able to achieve a winter hardiness level approaching that of winter Norstar and survive the high stress winters of 2003-04 and 2004-05 in western Canada when sown in the fall at the recommended seeding date for winter wheat (Figure 2).

Figure 2. The spring habit Norstar (Spring Norstar - no vernalization requirement) in this photo was seeded September 7, 2004 and the picture was taken April 29, 2005. A photoperiod requirement and the superior cold hardiness genes that have been transferred from Norstar (winter habit with a vernalization requirement) allow Spring Norstar to achieve winter hardiness levels approaching that of Norstar when seeded in the fall.

A one or two degree improvement in LT tolerance of non-acclimated plants combined with a very rapid initial rate of acclimation once temperatures drop below 8 to 10^{o}C indicates that spring seeded Spring Norstar should suffer less damage than current spring wheat cultivars when exposed to late spring frost during the growing season. The winter wheat varieties grown in western Canada must have a very high level of cold tolerance in order to survive our winters and Norstar, which is a parent in most of our current winter wheat varieties, ranks amongst the hardiest. In contrast, spring wheat varieties grown in western Canada are damaged by exposure to even a slight frost. In the past century, plant breeding efforts that target the western Canadian prairies have created cultivars with a high level of adaptation, but we still lose millions of dollars each year in potential crop productivity and market quality due to frost damage. Consequently, the advantage offered by varieties with improved frost tolerance would be expected to produce a multi-million-dollar return when spring crops are sown on years when frost occurs during the growing season. On more average years, production of spring habit varieties with improved frost tolerance would provide additional economic opportunities by extending our growing season, allowing more flexibility in our management choices, providing opportunities to reduce herbicide costs through better crop competition, increasing crop moisture utilization, lowing energy requirements, and increasing productivity while using more environmentally friendly farming systems.

The superior frost tolerance of Spring Norstar still needs to be combined with the disease resistance, agronomic performance, and market acceptability of current spring wheat varieties. Since individual genes are part of a complex system, it will be necessary to determine the best combinations that will maximize the improvement of frost resistance in commercial spring varieties. The superior frost-tolerance genes of Norstar have been tagged using molecular markers, which will assist this process by allowing wheat breeders to select the critical genes without having to wait for a test frost in the field. This will greatly speed up the selection for cold hardiness in both spring and winter wheat breeding programs and significantly increases the chances of having the right lines in the field for evaluation when a damaging frost that permits field evaluation occurs.

While over-winter LT damage in the seedling stage is primarily a concern in temperate climates, frost damage during the reproductive stage can cause severe economic losses in most wheat producing regions of the world. Widely fluctuating late afternoon and early morning temperatures make the timing and severity of LT stress important considerations during the active growing season. Both spring and winter habit genotypes can cold acclimate after reproductive transition and before heading demonstrating that the vegetative/reproductive transition does not act as an off switch for LT-tolerance genes. However, plants have only a limited ability to cold acclimate during this period and they reach their maximum level of LT tolerance very quickly once they are exposed to temperatures in the acclimation range indicating that a short, rapid LT response mechanism is functional up to the time of heading. The lack of progress in selecting for frost resistance after head emergence suggests that LT tolerance expression is minimal at these stages. Selection for frost resistance after head emergence becomes a much more complex problem because avoidance mechanisms like supercooling play a greater role when plants are exposed to temperatures just below freezing during this period. Also, LT acclimation is a cumulative process and we do not have a clear understanding of how responsive plants are after head emergence indicating that more detailed studies are required to establish if the limited LT tolerance after heading is due to insufficient induction time or an inability to respond to temperatures in the acclimation range.

In the last decade, a virtual flood of genetic and genomic information has arisen from investigations using model plant systems and tools with an unprecedented level of sophistication for genetic analysis. However, a large gap exists between these basic scientific developments and the utilization of this knowledge in crop improvement programs that focus on breeding for complex traits like LT tolerance. Progress has been made in the mapping, isolation, and characterization of the major LT adaptation genes that will allow for the more rapid and directed incorporation of LT tolerance genes using marker assisted backcrossing and other molecular techniques. Advances in biotechnology have provided even greater opportunities for plant breeders to expand their attack on the LT tolerance barrier that has frustrated them for so long. However, exploitation of this new technology to produce adapted, super-hardy cultivars will require close co-operation between plant breeders and biotechnologists. This interdisciplinary effort will be expensive and immediate breakthroughs should not be expected, but progress to date suggests that we now have the tools to identify the pieces of the LT-tolerance puzzle.

Acknowledgements: Financial support from Genome Prairie/Genome Canada, the Natural Sciences and Engineering Research Council of Canada, and Ducks Unlimited Canada is gratefully acknowledged.