

UNDERSTANDING GENETIC CONTROL OF FREEZING RESISTANCE USING POTATO SPECIES AS A MODEL SYSTEM

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1. INTRODUCTION

Freezing stress resistance is generally regarded as a complex trait with multigenic inheritance (Marshall, 1982; Stushnoff *et al.*, 1984; Blum, 1988). However, there is no consensus on the mode of gene action. For example the gene action for freezing tolerance has been reported to vary from recessive (Puchkov and Zhironov, 1978) to partially dominant (Parodi *et al.*, 1983; Gullord *et al.*, 1975) to both additive and non-additive (Sutka, 1994) in winter wheat, largely additive (Daday and Greenham, 1960) to dominant (Perry *et al.*, 1987) in Alfalfa. The lack of consensus is, in part, due to heavy reliance on field test for assessing winter survival. Each winter is different in terms of the early fall frost episodes, lowest temperature, snow cover, mid-winter thaw periods followed by cold temperatures. Thus field selection has many inherent problems. Ideally one hopes for a "test frost episode" or a "test winter" that is severe enough to kill the most sensitive genotypes, cause various degrees of injury to intermediate genotypes, and cause no injury to most resistant genotypes. However such test frost episodes or test winters are rare. Thus when evaluating under field conditions one may not get the same results every winter or every frost episode. For example it has been shown that severity of winter or the stress level can determine whether the control of freezing tolerance was recessive or dominant (Muehlbauer *et al.*, 1970). Furthermore, rank order of wheat cultivars for hardiness has been found to depend on the hardening technique used (Roberts, 1986).

Many factors contribute to frost or winter injury in plants. For example injury to plants from a frost episode is influenced by ice nucleation temperature, freezing (cooling) rate, lowest temperature reached, duration of exposure to ice, thawing rate and post-thaw conditions (Palta and Weiss, 1993). Similarly, speed of acclimation in fall, variation in

snow cover, mid-winter thaw periods followed by very cold temperatures and speed of deacclimation in spring are major factors that contribute to winter survival. In different winters or different frost episodes specific components may be critical for survival. Our recent studies provide evidence that different components of frost or winter survival are not necessarily under same genetic control (Stone, *et al.*, 1993). Thus in order to understand the genetic control of cold hardiness one has to examine each component separately.

Potato is a cool season crop, cultivated in the temperate zone in North America, Europe and the Andean highlands of South America. In these areas frost is often a major factor limiting potato production (Estrada, 1978; Li and Palta, 1978). In the Andean region of South America, it has been estimated that potato productivity can be doubled by improving frost tolerance of cultivated potatoes (Estrada, 1978). The cultivated potato species are very frost sensitive and are often killed when tissue temperatures fall below -3°C . Several non-cultivated tuber-bearing species can survive temperatures as low as -6°C . In addition, some of these species acclimate in response to cool day/night temperatures ($5/2^{\circ}\text{C}$), while the commonly cultivated species of potato fails to cold acclimate (Masterbrock, 1956; Richardson and Estrada, 1971; Chen and Li, 1976). Based on their response to cold temperatures, potato species have been classified into five groups: (1) chilling sensitive, (2) freezing sensitive and unable to acclimate, (3) freezing sensitive but able to acclimate, (4) freezing tolerant but unable to acclimate, and (5) freezing tolerant and able to acclimate (Li *et al.*, 1981; Chen and Li, 1980). Using these potato species we have attempted to understand genetic control of various components of freezing stress resistance. A brief account of these studies is given here.

2. EVIDENCE THAT NON-ACCLIMATED FREEZING TOLERANCE AND CAPACITY TO COLD ACCLIMATE ARE UNDER SEPARATE GENETIC CONTROL

We have recently demonstrated that non-acclimated tolerance and capacity to cold acclimate have distinct genetic control (Stone *et al.*, 1993). In these studies we utilized two wild diploid potato species, *Solanum commersonii* and *Solanum cardiophyllum* as parents. These two species represent the extremes of non-acclimated freezing tolerance (NAFT) and cold acclimation capacity (increase in freezing tolerance following cold acclimation, ACC). *Solanum commersonii* is a frost tolerant species (NA -4.5°C) which is able to acclimate (acclimated freezing tolerance -9.6°C). *Solanum cardiophyllum* on the other hand is a frost sensitive species (NAFT -1.6°C) and is unable to cold acclimate. The F_1 of these parents was backcrossed to the parents to develop *Solanum* populations segregating for both the traits. Freezing tolerance of these populations were assessed, using electrolyte leakage method, before and after acclimation.

No correlation (Figure 1) was found between NAFT and ACC suggesting that the two traits have independent genetic control. In these studies we were able to recover both parental phenotypes for ACC in a limited population suggesting that cold acclimation ability is controlled by relatively few genes. For both these traits F_1 was closer to the sensitive parents (Figures 2, 3) suggesting that in this cross NAFT and ACC were somewhat recessive (or the factors from the sensitive parents suppress the expression of these traits in F_1). The generation mean analyses also showed that cold ACC can be explained by a simple additive-dominance model (Stone *et al.*, 1993). Thus our studies suggest that the cold acclimation trait is not as genetically complex as has been thought. These results from the *Solanum* populations have been confirmed in rapeseed cultivars where no relationship between NAFT and ACC was found (Teutonico *et al.*, 1993).

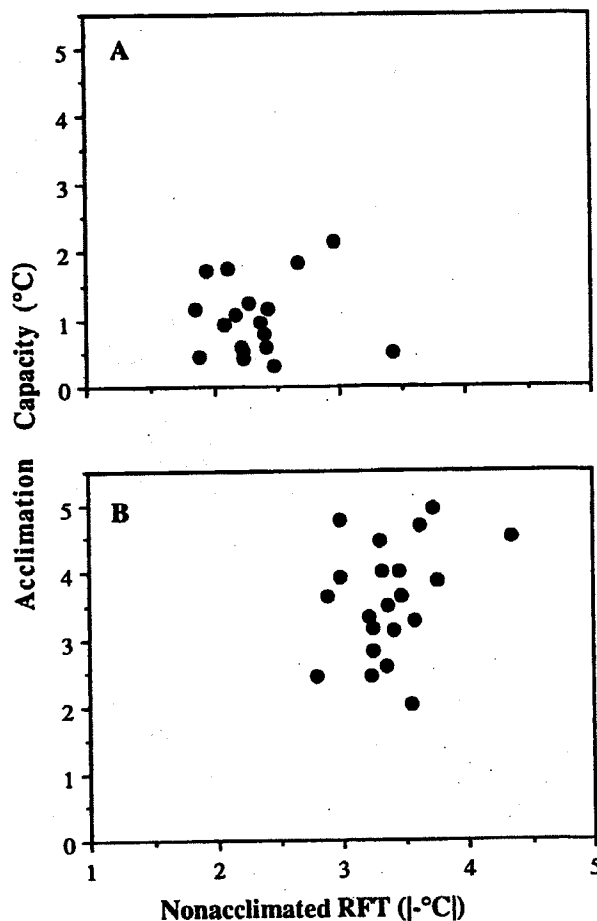


Figure 1. Correlation between nonacclimated freezing tolerance (NAFT) and acclimation capacity (ACC) (increase in NAFT following cold acclimation) of individuals in segregating backcross populations of two diploid potato species *S. commersonii* (cmm) and *S. cardiophyllum* (cph). (A) F₁ x cph backcross progeny ($r = -0.066, p > 0.5$). (B) F₁ x cmm backcross progeny ($r = -0.317, P > 0.2$). Source: Stone *et al.* (1993).

3. EVIDENCE FOR VARIABILITY IN THE SPEEDS OF COLD ACCLIMATION AND DEACCLIMATION AMONG RELATED GENOTYPES

Speeds of acclimation and deacclimation appear to be two of the several important factors responsible for frost and winter survival of plants. Ability to gain freezing stress

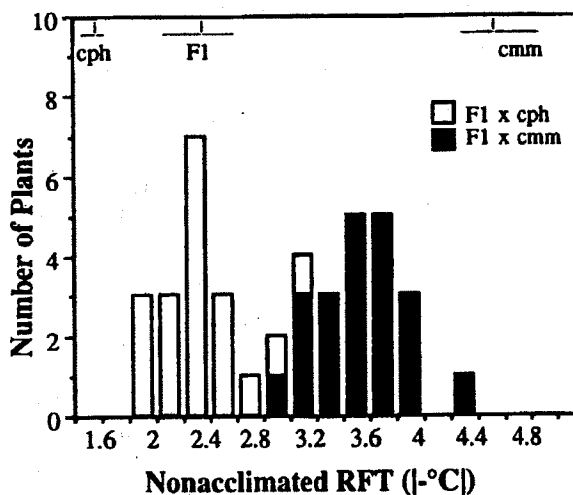


Figure 2. Distribution of NAFTs of the backcross progenies (see Figure 1 legend for details). The range and mean NAFT values for both parents (cmm and cph) and F₁ (cmm x cph) are indicated at the top of the graph. Source: Stone *et al.* (1993).

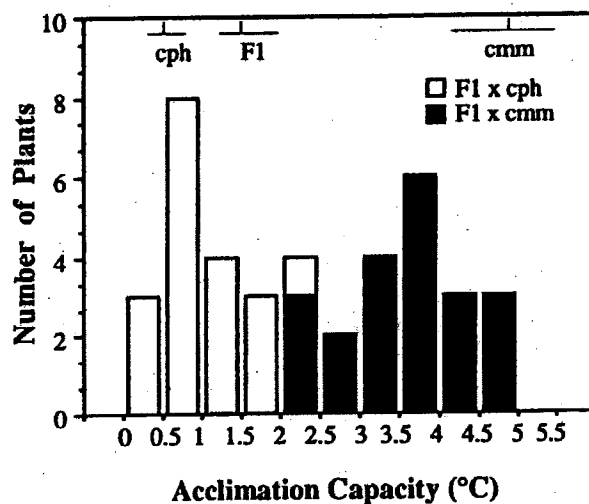


Figure 3. Distribution of ACC of backcross progenies (see Figure 1 legend for details). The range and mean ACC values for both parents (cmm and cph) and the F₁ (cmm x cph) are indicated at the top of the graph. Source: Stone *et al.* (1993).

resistance rapidly in response to decreasing air temperatures will certainly be advantageous for survival from unexpected cold spells (freezing temperatures) in fall. On the other hand, inability to deacclimate rapidly in response to mid-winter thaw will be advantageous against late winter cold spells and late spring freezes. Thus, in addition to ACC and NAFT it will be important to be able to select for rapid acclimation and slow deacclimation abilities. Our recent studies suggest that variations for these traits exist (Sutinen *et al.*, 1992; Vega *et al.*, 1995 and 1996).

We investigated seasonal changes in the freezing stress resistance of needles of red pine (*Pinus resinosa* Ait.) and Austrian pine (*Pinus resinosa* Arnold) trees (Sutinen *et al.*, 1992). Red pine needles attained much higher freezing stress resistance during the mid-winter than Austrian pine. Thus red pine needles have much higher ACC than Austrian pine even though they both have similar NAFT. Red pine needles also acclimated and deacclimated faster than Austrian pine needles. During fall there was a sharp increase in the freezing stress resistance of red pine needles whereas the freezing stress resistance of Austrian pine needles increased gradually. During the spring red pine needles deacclimated rapidly and its needles were less hardy than Austrian pine needles in late April. These results help explain why red pine is better adapted to very cold winters and shorter growing season in the northern latitudes.

We have also found variations for the speeds of acclimation and deacclimation among wild potato species (Vega *et al.*, 1995 and 1996). Freezing tolerance was measured during 12 days of cold acclimation. Among the seven potato species (*S. acaule*, *S. comersonii*, *S. megistracolobum*, *S. multidissectum*, *S. polytrichon* and *S. toralapanum*) we found four different types of acclimators (Table 1): (i) early acclimators, with a slower

Table 1. Variation in the speed of acclimation and deacclimation among wild *Solanum* species (Vega *et al.*, 1995 and 1996)

Trait	Species example
Early acclimator	<i>S. multidissectum</i>
Late acclimator	<i>S. sanctae-rosae</i>
Progressive acclimator	<i>S. megistracolobum</i>
Non acclimator	<i>S. polytrichon</i>
Fast deacclimator	<i>S. multidissectum</i>
Slow deacclimator	<i>S. toralapanum</i>

rate of cold acclimation; (ii) late acclimators, with a faster rate of cold acclimation; (iii) progressive acclimators, with a constant rate of cold acclimation; and, (iv) non acclimators. For the measurement of deacclimation speed, fully cold acclimated plants were deacclimated in warm conditions for one day. The seven species listed above were used for this study. We found significant differences in the speeds of deacclimation among these species (Table 1). While some species lost almost all of their freezing tolerance, others lost two thirds or less of their freezing tolerance. These results suggest that it may be possible to select for speeds of acclimation and deacclimation.

4. EXPRESSION OF FREEZING STRESS RESISTANCE IN F_1 HYBRIDS

We investigated the expression of freezing tolerance in F_1 hybrids produced from interspecific crosses between tolerant and sensitive species (Chen et al., 1996a). In these crosses parents with various ploidy levels were used. The freezing tolerance of these hybrids and parents were evaluated both in the field and controlled environmental conditions. For field evaluations these materials were rated for frost damage after a frost in late September 1995. Frost damage to F_1 , produced by parents with same ploidy level, was either more than or close to the parental means. Frost damage to F_1 , produced with higher ploidy level in the hardy parent, was generally less than parental means. In some cases, when hardy parent with higher ploidy level was used in the cross, the freezing tolerance of F_1 approximated the hardy parent.

Precise evaluations of nonacclimated freezing tolerance and acclimation capacity were also made for several F_1 and parent combinations (Chen et al., 1996a). Results were similar to field studies (Table 2). In general, the parent with higher ploidy level had greater influence on the expression of both the NAFT and the ACC in F_1 . Our results suggest that both the genomic ratio of hardy to non-hardy parents used to make hybrids, and the dominance of alleles in sensitive species can have a significant effect on the expression of freezing tolerance in F_1 . Similar to our results, Limin and Fowler (1988) found that the expression of hardiness in F_1 could be determined by gene dosage in Triticeae.

5. EXPRESSION OF FREEZING TOLERANCE IN THE SOMATIC HYBRIDS BETWEEN WILD AND CULTIVATED POTATO SPECIES

Many wild species are sexually incompatible with the cultivated species thus prohibiting conventional breeding approaches for moving the desired traits from the wild germplasm. With somatic hybrids (SH) one can bypass this incompatibility and create hybrids which are otherwise impossible to create. For example, *S. commersonii*, exhibiting

Table 2. Expression of frost hardiness (nonacclimated tolerance and acclimation ability) in interspecific F_1 hybrids (Chen et al., 1996a)

Case	Ploidy level	Expected frost hardiness of F_1
1	Sensitive parent = Hardy parent	At or below mid parent value
2	Sensitive parent > Hardy parent	Generally closer to the sensitive parent
3	Sensitive parent < Hardy parent	Can be higher than mid parent value

extreme cold hardiness, is sexually incompatible with the cultivated species. However, by protoplast fusion it has been possible to make SH from these two incompatible species (Cardi *et al.* 1993). In order to explore the genic interaction between hardy and non-hardy genomes we characterized the expression of NAFT and ACC in two kinds of SH: (i) hexaploid SH from *S. tuberosum* (4x) and *S. brevidens* (2x)(tbr-brd) and (ii) tetraploid SH from haploid *S. tuberosum* (2x) and *S. commersonii* (2x) (tbr-cmm) (Chen *et al.*, 1996b). We found that the freezing tolerance in *S. brevidens* was mainly from ACC. However, ACC of tbr-brd SH was similar to *S. tuberosum*, indicating that ACC of *S. brevidens* was poorly expressed in the tbr-brd SH. In tbr-cmm SH, NAFT was also as low as sensitive parent, while ACC did increase significantly and approximated to that of parental mean.

These results suggest that the suppressed expression of freezing tolerance of *S. brevidens* and *S. commersonii* in the SH was probably due to the dominance effect of alleles present in the nonhardy parent. These findings are in general agreement with the results we obtained from the evaluation of F₁ hybrids (discussed above). Recently Cardi *et al.* (1993) studied the frost tolerance of somatic hybrids between *Solanum tuberosum* and *S. commersonii*. These authors concluded that SH expressed higher NAFT and ACC than the sensitive parent. Close examination of their data show that SH only had a small increase in ACC and little or no increase in NAFT, which is in agreement with our results.

Some of the tbr-cmm SH were found to be self fertile and crossable with cultivated potatoes. We developed segregating progenies either by selfing SH or by crossing them with cultivated potatoes (Chen *et al.*, 1996c). In total, 48 selfed and 6 backcross progenies were characterized for the expression of NAFT and ACC. The NAFT derived from *S. commersonii* was still poorly recovered in both sets of progenies. However, ACC did show some variation ranging from the level of sensitive fusion parent to that of the selfed tbr-cmm SH. None of the progeny had ACC as high as the *S. commersonii* parent. Our results suggest that the expression of NAFT was suppressed by the cold sensitive genome of *Solanum tuberosum*. Thus, ACC is the form of cold tolerance from *S. commersonii*, which appears to be most easily accessed through these somatic hybrids.

6. EVIDENCE THAT IT IS POSSIBLE TO IMPROVE BOTH NON-ACCLIMATED FREEZING TOLERANCE AND ACCLIMATION CAPACITY OF CULTIVATED POTATOES

As pointed out above the cultivated potato species *S. tuberosum* is known to be quite sensitive to frost (NAFT -2.5°C) and this species is unable to cold acclimate (Palta and Li, 1979; Palta *et al.*, 1993; Vega and Bamberg, 1995). Over the last 30 years attempts have been made to incorporate frost hardiness from wild species into cultivated species (Ross and Rowe, 1965 and 1969; Richardson and Estrada, 1971; Estrada, 1978 and 1987). More recently somatic fusion has been attempted to incorporate hardiness into the cultivated species (Austin *et al.*, 1986; Preiszner *et al.*, 1991 and Cardi *et al.*, 1993). Unfortunately most of these studies have relied on field evaluation for selection purposes. Using controlled environmental conditions we have demonstrated that freezing tolerance in potatoes comprises of two independent genetic components namely nonacclimated freezing tolerance and acclimation capacity (Stone *et al.*, 1993). In field studies, although valuable information was gained, it is generally not possible to select for various components of frost hardiness.

We have utilized a systematic approach for transferring frost hardiness from hardy-wild to cultivated-sensitive species. In this study we have used *S. commersonii* (2x) and *S.*

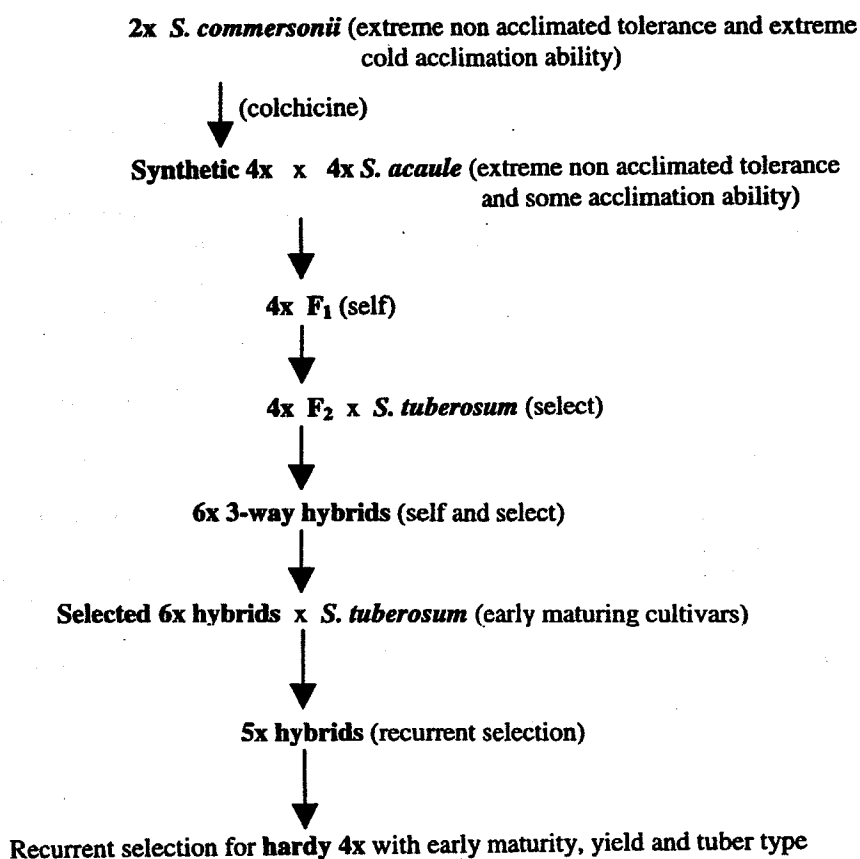


Figure 4. Scheme for transmitting cold hardiness of wild potato species (*S. commersonii*, *S. acaule*) to cultivated (*S. tuberosum*) form.

acaule (4x) which are known to have high NAFTA and ACC. Our scheme utilized synthetic 4x *S. commersonii* as a bridge species with *S. acaule* producing fertile F₁ and F₂ hybrids crossable with the cultivated *S. tuberosum* (Bamberg *et al.*, 1994). This scheme is outlined in Figure 4. The progenies (6x, 3 way hybrids) developed from the hybrids of F₁ and F₂ with the cultivated *S. andigena* and *S. tuberosum* (cv Kathadin) was screened for both NAFTA and ACC (Weiss *et al.*, 1994). We found that some of the hybrids on average had 1°C higher nonacclimated tolerance and 2°C higher acclimation capacity than the cultivated parents. Some of the 6x (3 way) hybrids produced good tubers. However, yield and earliness need much improvement.

Our results demonstrate that, by precise screening, it should be possible to move both nonacclimated tolerance and acclimation ability from hardy-wild to cultivated-sensitive species. These findings, we hope, will offer exciting opportunities to enhance potato production in frost prone areas of the world.

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REFERENCES

- Austin S, Ehlenfeldt MK, Baer MA, Helgeson JP (1986) Somatic hybrids produced by protoplast fusion between *S. tuberosum* and *S. brevidens*: phenotypic variation under field conditions. *Theor Appl Genet* 71: 682–690
- Bamberg, J.B., Hanneman, R.E. Jr, Palta, J.P., Harbage, J.F. (1994) Using disomic 4 x (2EBN) potato species' germplasm via bridge species *Solanum comersonii* Dunal. *Genome* 37: 866–870
- Blum, A. (1988) Plant breeding for stress environments. CRC Press, Boca Raton, , USA, 79–127
- Cardi, T. Ambrosio, F.D., Consoli, D., Puite, K.J., Ramulu, K.S. (1993) Production of somatic hybrids between frost-tolerant *S. commersonii* and *S. tuberosum*: characterization of hybrid plants. *Theor Appl Genet* 87: 193–200
- Chen, H.H., Li, P.H. (1980) Characteristics of cold acclimation and deacclimation in tuber bearing *Solanum* species. *Plant Physiol* 65:1146–1148
- Chen, P.M., Li, P.H. (1976) Effect of photoperiod, temperature, and certain growth regulators on frost hardiness of *Solanum* species. *Bot Gaz* 137:105–109
- Chen, Y-K., Bamberg, J.B., Palta, J.P. (1996a) Expression of freezing tolerance in interspecific F1 of Potatoes. *Amer Potato J* 73(abst):348–349
- Chen, Y-K., Bamberg, J.B., Palta, J.P. (1996c) The expression of nonacclimated freezing tolerance and acclimation capacity in progeny derived from somatic hybrids of *Solanum tuberosum* and *S. commersonii*. *HortSci* 31(abst):624
- Chen, Y-K., Palta, J.P. Bamberg, J.B., Helgeson, J.P., Haberland, G.T. (1996b) Expression of freezing tolerance in somatic hybrids between hardy wild and cultivated potato species. *Amer Potato J* 73(abst):348
- Daday, H., Greenham, C.G. (1960) Genetic hardiness on cold hardiness in *Medicago sativa* L. *J Hered* 51:249–255
- Estrada, R.N. (1978) Breeding frost-resistant potatoes for the tropical highlands. In *Plant Cold Hardiness and Freezing Stress: Mechanisms and Crop Implications*. Li, P.H., Sakai, A. eds., Academic Press, New York, 333–341
- Estrada, R.N. (1987) Utilization of wild and cultivated diploid potato species to transfer frost resistance into the tetraploid common potato, *Solanum tuberosum* L In: *Plant Cold Hardiness* Liss, A.R., Inc., 339–353
- Gullord, M., Olien, C.R., Everson, E.H. (1975) Evaluation of freezing hardiness in winter wheat. *Crop Sci* 15: 153–157
- Li, P.H., Huner, N.P.A., Toivio-Kinnucan, M.A., Chen, H.H., Palta, J.P. (1981) Potato freezing injury and survival, and their relationships to other stresses. *Amer Potato J* 58:15–29
- Li, P.H., Palta, J.P. (1978) Frost hardening and freezing stress in tuber bearing *Solanum* species. In *Plant Cold Hardiness and Freezing Stress: Mechanisms and Crop Implications*. Li, P.H., Sakai, A. eds., Academic Press, New York, 49–71
- Limin, A.E., Fowler, D.B. (1988) Cold hardiness expression in interspecific hybrids and amphidiploids of the Triticeae. *Genome* 30: 361–365
- Marshall, H.G. (1982) Breeding for tolerance to heat and cold. In: *Breeding Plants for Less Favorable Environments*. Christiansen, M.N., Lewis, C.F., John Wiley and Sons, New York, 47–69
- Masterbrock, C. (1956) Some experiences in breeding frost-tolerant potatoes. *Euphytica* 5:289–295
- Muehlbauer, F.J., Marshall, H.G., Hill, R.R. Jr. (1970) Winter hardiness in oat populations derived from reciprocal crosses. *Crop Science* 10:646–649
- Palta, J.P., Li, P.H. (1979) Frost hardiness in relation to leaf anatomy and natural distribution of several *Solanum* species. *Crop Sci* 19:665–671
- Palta, J.P., Weiss, L.S. (1993) Ice formation and freezing injury: An overview on the survival mechanisms and molecular aspects of injury and cold acclimation in herbaceous plants. In: Li, P.H., Christersson, L. eds. *Advances in plant cold hardiness*. CRC Press, Boca Raton, USA, 143–176
- Palta, J.P., Whitaker, B.D., Weiss, L.S. (1993) Plasma membrane lipids associated with genetic variability in freezing tolerance and cold acclimation of *Solanum* species. *Plant Physiol* 103:793–803
- Parodi, P.C., Nyquist, W.E., Patterson, F.L., Hodges, H.F. (1983) Traditional combining-ability and Gardner-Eberhart analyses of a diallel for cold resistance to winter wheat. *Crop Science* 23:314–318
- Perry, M.C., McIntosh, M.S., Wiebold, W.J., Welterlen, M. (1987) Genetic analysis of cold hardiness and dormancy in alfalfa. *Genome* 29:144–149
- Preisner, J., Feher, A., Veisz, O., Sutka, J., Dudits, D. (1991) Characterization of morphological variation and cold resistance in interspecific somatic hybrids between potato (*Solanum tuberosum* L) and *S. brevidens* Phil. *Euphytica* 57: 37–49

- Puchkov, Y.M., Zhiron, E.G. (1978) Breeding of common wheat varieties with a high frost resistance and genetic aspects of it. World Science News, India 15: 17-22
- Richardson, D.G., Estrada, R.N. (1971) Evaluation of frost resistant tuber-bearing *Solanum* hybrids. Amer Potato J 48:339-343
- Roberts, D.W. (1986) Chromosomes in "Cadet" and "Rescue" wheat carrying loci for cold hardiness and vernalization response. Can J Genet Cytol 28:991-997
- Ross, R.W., Rowe, P.R. (1965) Utilizing the frost resistance of diploid *Solanum* species. Amer Potato J 46:5-13
- Ross, R.W., Rowe, P.R. (1969) Frost resistance among the *Solanum* species in the IR-1 potato collection. Amer Potato J 42:177-185
- Stone, J.M., Palta, J.P., Bamberg, J.B., Weiss, L.S., Harbage, J.F. (1993) Inheritance of freezing resistance in tuber-bearing *Solanum* species: evidence for independent genetic control of nonacclimated freezing tolerance and cold acclimation capacity. Proc Natl Acad Sci USA 90:7869-7873
- Stushnoff, C., Fowler, D.B. Bruele-Babel, A. (1984) Breeding and selection for resistance to low temperature In: Plant Breeding-A Contemporary Basis. Voss, E.B., ed., Pergamon Press. Elmsford. 115-136
- Sutinen, M.L., Palta, J.P., Reich, P.B. (1992) Seasonal differences in freezing stress resistance of needles of *Pinus nigra* and *Pinus resinosa*: evaluation of the electrolyte leakage method. Tree Physiol 11:241-254
- Sutka, J. (1994) Genetic control of frost tolerance in wheat (*Triticum aestivum* L.) Euphytica 77:277-282
- Teutonico, R.A., Palta, J.P., Osborn, T.C. (1993) *In vitro* freezing stress resistance in relation to winter survival of rapeseed cultivars. Crop Science 33:103-107
- Vavilova, M.A. (1978) Use of wild-frost resistant species of the potato *S. commersonii* Dun. and *S. chomatophilum* Bitt in interspecific hybridization. In: Systematics, Breeding, and Seed Production of Potatoes. Leningrad 1978. Translated from Russian by Dhote, A.K., Kothekar, V.S., ed Published for the United States Department of Agriculture, and National Science Foundation, Washington, D.C. Amerind Publishing Co. Pvt. Ltd., New Dehli, 1985
- Vega, S.E., Bamberg, J.B. (1995) Screening the US potato collection for frost hardiness. Am Potato J 72:13-21
- Vega, S.E., Bamberg, J.B., Palta, J.P. (1995) Evidence for genetic variability in the speed of cold acclimation among tuber-bearing wild potato species. HortSci 30(abst):775-776
- Vega, S.E., Palta, J.P., Bamberg, J.B. (1996) Variability in the speed of deacclimation among tuber-bearing wild potato species. HortSci 31(abst):579-580
- Weiss, L.S., Bamberg, J.B., Palta, J.P. (1994) Freezing tolerance and acclimation capacity increased in cultivated potato crossed to wild potato species. HortSci 29 (abst):563

