J. Amer. Soc. Hort. Sci. 126(2):216–220. 2001.

Relationship Between Cold Tolerance during Seed Germination and Vegetative Growth in Tomato: Analysis of Response and Correlated Response to Selection

M.R. Foolad[1] and G.Y. Lin[2]

Department of Horticulture, 103 Tyson Bldg., The Pennsylvania State University, University Park, PA 16802

Additional index words. *Lycopersicon esculentum*, abiotic stress, chilling tolerance, heritability, seed germination, selection response, stress tolerance

Abstract. The genetic relationship between cold tolerance (CT) during seed germination and vegetative growth in tomato (*Lycopersicon esculentum* Mill.) was determined. An F_2 population of a cross between accession PI120256 (cold tolerant during both seed germination and vegetative growth) and UCT5 (cold sensitive during both stages) was evaluated for germination under cold stress and the most cold tolerant progeny (the first 5% germinated) were selected. Selected progeny were grown to maturity and self-fertilized to produce F_3 families (referred to as the selected F_3 population). The selected F_3 population was evaluated for CT separately during seed germination and vegetative growth and its performance was compared with that of a nonselected F_3 population of the same cross. Results indicated that selection for CT during seed germination significantly improved CT of the progeny during germination; a realized heritability of 0.75 was obtained for CT during seed germination. However, selection for CT during germination did not affect plant CT during vegetative growth; there was no significant difference between the selected and nonselected F_3 populations in either absolute CT [defined as shoot fresh weight (FW) under cold stress] or relative CT (defined as shoot FW under cold as a percentage of control). Results indicated that, in PI120256, CT during seed germination was genetically independent of CT during vegetative growth. Thus, to develop tomato cultivars with improved CT during different developmental stages, selection protocols that include all critical stages are necessary.

Most commercial cultivars of tomato, *Lycopersicon esculentum*, are sensitive to chilling temperatures (0 to 15 °C) during all stages of plant development, including seed germination, vegetative growth, and reproduction. During seed germination, for example, under low temperatures many seeds do not germinate or germinate so sporadically that plants grow differentially, delaying plant establishment and leading to variability in crop maturation. During later stages, plant growth and development are highly retarded and limited or no flowers and fruit are produced. Chilling sensitivity may limit the geographic distribution of tomato cultivation and the time of year for planting in temperate regions. Furthermore, spring soil temperatures, which are often below 15 °C, may restrict direct seeding of tomato (Liptay et al., 1982). Chilling sensitivity also affects greenhouse tomato production, as cold sensitive cultivars may require expensive greenhouse heating throughout the life of the plant.

Development of tomato cultivars with improved cold tolerance (CT) may offer significant advantages for tomato production under suboptimal temperatures in the field or in the greenhouse (Foolad and Lin, 2000b). For example, cold tolerant plants may grow more rapidly at early stages and thus become established faster than cold sensitive plants. This may result in improved earliness, adaptability, water use, and yield of high-quality fruit when grown under suboptimal temperatures. Furthermore, cold tolerant cultivars could be planted early and harvested early when the crop may have higher values. Also, the crop could be grown in the field for longer periods of time (i.e., extended growing season) and thus, the final yield may be higher. Production may also be improved because early plantings avoid high temperatures, which can reduce fruit set during midsummer. Finally, CT may result in water savings in areas with a Mediterranean climate, because early plant growth makes better use of early-season rains and water available in the root zone.

Considerable genetic variation exists within and between species and cultivars of tomato for CT during different stages of plant development, including seed germination, vegetative growth, and reproduction (Cannon et al., 1973; Damidaux and Martinez, 1992; Foolad and Lin, 1998, 2000a, 2000b; Lyons, 1973; Ng and Tigchelaar, 1973; Patterson, 1988; Patterson et al., 1987; Patterson and Payne, 1983; Scott and Jones, 1985b; Wolf et al., 1986). Such variation is potentially useful for development of tomato cultivars with improved CT. However, no cold tolerant tomato cultivar has yet been developed or released for commercial use. This is due in part to the complexity of the trait, insufficient genetic knowledge of tolerance components, lack of efficient selection criteria, and limited breeding efforts. Development of tomato cultivars with improved CT can be greatly accelerated by knowledge of the genetic control of tolerance at individual developmental stages and that of the relationships between tolerance at different stages. To date, considerable research has been conducted to discern the genetic and physiological basis of CT during seed germination (Cannon et al., 1973; DeVos et al., 1982; Foolad et al., 1998, 1999; Foolad and Lin, 1998, 1999a, 1999b; Leviatov et al., 1994; Ng and Tigchelaar, 1973) and vegetative growth in tomato (Foolad and Lin, 2000a; Patterson and Payne, 1983; Vallejos, 1991; Yakir et al., 1986). However, limited effort has been devoted to determine relationships between CT at different developmental stages.

Recently, we evaluated CT of 31 tomato accessions (cultivars, breeding lines, and plant introductions), representing six *Lycopersicon* Mill. species, during seed germination and vegetative growth (Foolad and Lin, 2000b). Across accessions, there was generally no phenotypic relationship between CT during seed germination and

Received for publication 25 Feb. 2000. Accepted for publication 13 Dec. 2000. Contribution 400 of the Department of Horticulture, The Pennsylvania State University. Financial support from the College of Agricultural Sciences, The Pennsylvania State University, and the Pennsylvania Vegetable Marketing and Research Program is appreciated. We thank Michael Orzolek and Charles Heuser for reviewing the manuscript before submission. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

[1]Associate professor and corresponding author; e-mail: mrf5@.psu.edu.
[2]Research assistant.

vegetative growth. However, a few accessions, including *L. hirsutum* Humb. and Bonpl. PI127826 and LA1777 and *L. esculentum* PI174263 and PI120256, were identified with CT during both seed germination and vegetative growth. The purpose of the present study was to determine the genetic relationship between CT during seed germination and vegetative growth in PI120256, by examining the response and correlated response to selection for CT in segregating progeny derived from a cross between PI120256 and a cold sensitive tomato line, UCT5.

Materials and Methods

Plant materials. Crosses were made between *L. esculentum* UCT5 (pistillate parent) and PI120256, and F_1 seeds produced. UCT5 is an advanced tomato breeding line from the University of California, Davis, that is cold sensitive during all stages of plant development, and PI120256 is a primitive tomato cultivar from Turkey that exhibits CT during seed germination and vegetative growth (Foolad and Lin, 2000a, 2000b; Scott and Jones, 1985a). Original seed of UCT5 and PI120256 were received from C.M. Rick Tomato Genetics Resource Center, University of California, Davis, and U.S. Department of Agriculture Plant Genetic Resources Unit, Geneva, N.Y., respectively. Seed of the F_2 generation was produced by controlled self-pollination of field-grown F_1 plants in Summer 1996. Nonselected F_3 seeds were produced by bulk-harvesting ripe fruit from 200 random F_2 plants grown under field conditions in Summer 1997. Selected F_3 seeds were produced as described below in Summer 1997. Large quantities of seeds of the parental lines (UCT5 and PI120256) were produced by growing and self-pollinating plants under field conditions in Summer 1997. To produce seeds of similar physiological age and quality for germination assays, fruit of the same maturity level in all cases were harvested from field-grown plants and seeds extracted.

Germination evaluation of the parental F_2 population. Sterile germination medium (0.8% agar) was prepared and poured in 15 × 1.0-cm petri plates. Seeds of the F_2 generation were surface-sterilized with 0.5% NaOCl solution for 10 min, rinsed with sterile, distilled water, and briefly blotted. Seeds were plated onto petri plates under aseptic conditions. For each treatment, 400 F_2 seeds were plated onto five petri plates (80 seeds per plate). Petri plates were arranged in completely randomized designs in incubators maintained in darkness at either 11 ± 0.5 °C (cold-stress treatment) or 20 ± 0.5 °C (control treatment) (seeds were exposed to light only during data collection). These temperature regimes were determined previously as being the most optimal for comparison of tomato seed germination (Dahal and Bradford, 1990, 1994; Scott and Jones, 1982, 1985b). Germination response was scored visually, as radicle protrusion, at 8-h intervals each day for 37 consecutive days. In each treatment, the time to 50% germination (T50) was calculated as described below.

Selection for rapid seed germination under cold stress in the parental F_2 population. The first 20 F_2 seeds (5% of the total) that germinated under cold stress were selected as the most cold-tolerant individuals. Selected seedlings were transferred to a greenhouse and subsequently to the field (Summer 1997) where they were grown to maturity. Plants were self-pollinated and F_3 family seeds were collected from individual plants. Samples of the 20 selected F_3 families (hereafter referred to as the selected F_3 population) were evaluated separately for CT during seed germination and vegetative growth as described below.

Progeny test 1: Evaluation of the selected and nonselected F_3 progeny during germination. Selected and nonselected F_3 progeny and the parental lines (UCT5 and PI120256) were evaluated for seed germination under both control and cold-stress conditions. In each treatment, 480 seeds of each of the 20 selected F_3 family, 480 seeds of the nonselected F_3 population, and 240 seeds of each parent were included. Seed plating and arrangement of petri plates were as described for the F_2 population. All progeny tests were repeated for a second time. Thus, a total of 960 seeds of each of the selected F_3 families (for a total of 19,200 F_3 seeds), 960 seeds of the nonselected F_3 population, and 480 seeds of each parent were evaluated for germination in each treatment.

When calculating the time to germination, seeds that germinated within an interval were presumed to have germinated at the midpoint of that interval. Seeds that failed to germinate in the control treatment were assumed to be nonviable. Thus, the percentage of nonviable seed was determined from the control treatment (in all cases nonviability was <5%). Above this percentage, seeds that failed to germinate in the cold-stress treatment were included in the analysis as right-censored observations (i.e., seeds that presumably were viable but failed to germinate by the last observation time; see statistical analysis below). Hence, the sample size for each replicate was the number of viable seeds, not the number of seeds that were sown or germinated.

Germination distributions of the parental lines and the selected and nonselected F_3 populations were analyzed by survival analysis (Gehan, 1969). This is a nonparametric procedure that measures time to a percentage germination and provides estimates of descriptive statistics for responses over time. These statistics include the number of seeds exposed to risk (potentially able to germinate), the number germinated, and the number withdrawn (i.e., censored observations due to lack of germination of viable seeds by the end of experiment). The median time in days to 50% germination (T50) was derived from this analysis to represent mean germination rate in the control and cold-stress treatments. Means and variances were determined for samples within each replicate (petri plate) and pooled over replicates (Foolad and Lin, 1997).

For each of the parental lines and the selected and nonselected F_2 and F_3 populations a germination tolerance index (TI_G) was calculated as the inverse of the ratio of germination time (T50) under cold-stress to germination time under control conditions. This is a measure of relative CT of a genotype (or a population) during germination: the larger the index, the higher the CT (Rawson et al., 1988).

Response to selection (genetic gain, R) during seed germination was measured as the difference between the mean T50 (or TI_G) of the selected F_3 population and that of the nonselected F_3 population (e.g., R = T50 of the selected F_3 population – T50 of the nonselected F_3 population). Statistical significance of the genetic gain (for T50) was determined by an unpaired *t* test using the formula for unpaired observations and unequal variances (Steel and Torrie, 1980).

Realized heritability (H_R) for CT during seed germination was calculated using the formula $H_R = R/S$ (Falconer, 1989), where R is the response to selection, and S is the selection differential (i.e., S = T50 of the selected F_2 individuals – T50 of the F_2 population before selection). Because F_2 parents and F_3 progeny were evaluated in different times (different years), to reduce the scaling effects of different environments, the realized heritabilities were computed based on standard-unit data (Foolad, 1996; Frey and Horner, 1957).

Progeny test 2: Evaluation of the selected and nonselected F_3 progeny during vegetative growth. Seeds of the 20 selected F_3 families, the nonselected F_3 population and parental lines were sown in greenhouse seedling trays containing a medium of 1 peat : 1 perlite : 1 vermiculite (by volume). Initially plants were grown in a

greenhouse with 12 h days/12 h nights of ≈28/18 °C and a daily average irradiance of ≈350 mmol·m^{-2}·s^{-1}. Plants were fertigated using commercial recommendations for tomato (Jones, 1999). Three-week-old seedlings were transplanted into 1-L plastic pots containing the same growing medium. Three days after transplantation, plants were transferred to two walk-in growth chambers with 12 h days/12 h nights of either 12/5 °C (cold-stress treatment) or 28/18 °C (control treatment). In both chambers, a 12 h photoperiod was provided with a photosynthetic photon flux of ≈350 µmol·m^{-2}·s^{-1} and a relative humidity of ≈50%. In each chamber, plants were arranged in a randomized complete block design with nine blocks. A block (replicate) contained one plant from each of the 20 selected F_3 families, 15 plants of the nonselected F_3 population and 5 plants of each parental line. Thus, in each treatment, 180 selected and 135 nonselected F_3 plants and 45 plants of each parent were used. Plants were fertigated using commercial recommendations for tomato. Plants were grown for 3 weeks before they were individually harvested for shoot (leaf + stem) FW determination. All experiments were repeated a second time, thus a total of 360 selected and 270 nonselected F_3 plants and 90 plants of each parent were evaluated for growth in each treatment.

Means and variances for shoot FW of the selected and nonselected F_3 populations and the parental lines were determined for samples within an experimental unit (one replicate) and pooled over replications, as described elsewhere (Foolad and Lin, 1997). For each of the parental lines and the selected and nonselected F_3 populations, a vegetative growth tolerance index (TI_{VG}) was calculated as the ratio of shoot FW under cold to shoot FW under control, and used as a measure of relative CT. Correlated response (CR) to selection was calculated as the difference between shoot FW (or TI_{VG}) of the selected F_3 population and that of the nonselected F_3 population under cold stress (e.g., CR = FW of selected F_3 population – FW of nonselected F_3 population). Statistical significance of the genetic gain (for shoot FW) was determined by an unpaired *t* test using the case formula for unpaired observations and unequal variances (Steel and Torrie, 1980).

Results

Germination of the parental lines and nonselected progeny. Seed of PI120256 germinated more rapidly than seed of UCT5 in both control and cold-stress treatments; the difference between the two, however, was greater under cold stress (Table 1). Germination tolerance index (TI_G) of PI120256 was also 10% larger than TI_G of UCT5. In both treatments, seeds of the nonselected F_2 and F_3 populations germinated intermediate between the two parents and exhibited tolerance indices similar to UCT5 (Table 1).

Vegetative growth of the parental lines and nonselected progeny. Plants of PI120256 grew more rapidly (produced more shoot FW) than plants of UCT5 in both control and cold-stress treatments (Table 2), indicating greater plant vigor for PI120256. The shoot FW of both parents was reduced in response to cold stress; however, the reduction was less in PI120256 (44%) than in UCT5 (61%) indicating a greater CT for PI120256 (Table 2). For the nonselected F_3 population, the reduction in shoot FW due to cold stress was intermediate (51%) between the two parents, indicating that CT of PI120256 was inherited in an additive fashion (Table 2).

Effect of selection for cold tolerance during germination on progeny seed germination. Selection for rapid seed germination under cold stress (in the F_2 population) significantly improved germination performance of the F_3 progeny under cold stress; there was a 19.1% improvement in the rate of seed germination (T50) of the selected F_3 population, compared to that of the nonselected F_3 population (Table 1). A realized heritability (H_R) of 0.75 was obtained for CT during seed germination. Selection for rapid seed germination under cold stress also resulted in a significant (13.9%) improvement in T50 of the progeny under nonstress conditions (Table 1), indicating that genes that contributed to rapid germination under cold-stress also facilitated rapid germination under control conditions. Furthermore, selection for rapid seed germination under cold stress improved progeny TI_G by 6.7% (Table 1).

Effect of selection for cold tolerance during germination on progeny vegetative growth. Selection for rapid seed germination under cold stress did not affect progeny CT during vegetative growth; the selected F_3 progeny families exhibited similar CT as the nonselected F_3 population, based on both absolute growth (FW under cold stress) and relative growth (FW under cold stress as a percentage of FW under control, the TI_{VG}) (Table 2). Furthermore, selection for CT during germination did not affect plant growth (FW) under control conditions (Table 2).

Discussion

Plant response to cold stress can be measured in either absolute or relative terms. For example, CT during seed germination may be defined by the germination time (e.g., T50) under cold stress (a

Table 1. Mean days to 50% germination (T50) of the parents and nonselected and selected F_2 and F_3 progeny of a cross between *L. esculentum* lines UCT5 and PI120256 in the control and cold-stress treatments and the selection responses.

Generation	Seeds evaluated (no.)[z]	Control (T50)	Cold stress (T50)	TI_G[y]
UCT5	480	3.12 a[x]	10.37 a[x]	0.30
PI120256	480	2.30 c	6.88 d	0.33
F_2 (nonselected)	400	2.78 b	9.24 b	0.30
F_3 (nonselected)	960	2.80 b	9.32 b	0.30
F_3 (selected)	19200	2.41 c	7.54 c	0.32
Selection response[w]		–0.39 (13.9%)[*]	–1.78 (19.1%)[*]	0.02 (6.7%)

[z]Total number of seeds evaluated for germination in each treatment.
[y]Germination tolerance index (TI_G), measured as the inverse of the ratio of T50 under cold-stress to T50 under control conditions.
[x]Mean separation within a column by Duncan's new multiple-range test, $P \leq 0.05$.
[w]Selection response was calculated as the difference between the T50 (or TI_G) of the selected F_3 families and T50 (or TI_G) of the unselected F_3 population. Figures in the parenthesis are the selection responses in percentage relative to the unselected F_3 population.
[*]Significant at $P \leq 0.01$ as determined by an unpaired *t* test.

Table 2. Shoot FW (g/plant) of the parents and nonselected and selected F_3 progeny of a cross between *L. esculentum* lines UCT5 and PI120256 in the control and cold-stress treatments and the selection responses.

Treatment	Plants evaluated (no.)[z]	Control	Cold stress	TI_{VG}[y]
UCT5	90	12.82 c[x]	4.95 c[x]	0.39
PI120256	90	16.63 a	9.38 a	0.56
F_3 (nonselected)	270	13.60 bc	6.69 b	0.49
F_3 (selected)	360	14.13 b	6.96 b	0.49
Selection response[w]		0.53 (3.9%)	0.27 (4.0%)	0.00 (0.0%)
S. E. of the difference		0.23	0.16	
t (df = 628)		2.30[NS]	1.69[NS]	

[z]Total number of plants evaluated for vegetative growth in each treatment.
[y]Growth tolerance index (TI_{VG}) was measured as the ratio of shoot FW under cold-stress to shoot FW under control conditions.
[x]Mean separation within a column by Duncan's new multiple-range test, $P \leq 0.05$.
[w]Selection response was calculated as the difference between shoot FW of the selected F_3 families and shoot FW of the nonselected F_3 population. Values in parentheses are the selection responses in percentage relative to the nonselected F_3 population.
[NS]Nonsignificant at $P \leq 0.01$ as determined by an unpaired *t* test.

measure of absolute CT) or by the relative increase in germination time under cold-stress compared to control conditions (a measure of relative CT, also called germination tolerance index, TI_G). Similarly, CT during vegetative growth may be measured either as plant weight under cold stress (absolute CT) or as the relative decrease in plant weight under cold stress compared to control conditions [relative CT, also called vegetative growth tolerance index (TI_{VG})]. While TI_G and TI_{VG} are good measures of relative CT, they may not be useful solely for breeding purposes. For example, a genotype that germinates rapidly under cold stress but exhibits small TI_G may be more useful than a genotype that exhibits large TI_G but germinates slowly under both control and cold-stress conditions. Ideal genotypes are those capable of rapid germination under cold stress and with high TI_G. Similarly, CT breeding during vegetative growth must be based on both absolute and relative CT criteria. Absolute growth under cold stress is a function of both plant vigor and CT. Genes controlling plant vigor may be different from genes conferring stress tolerance (Forster et al., 1990). Thus, absolute growth under cold stress may not be a good indication of CT when considered alone. Similarly, TI_{VG} alone may not be a good selection criterion for CT breeding because a genotype may exhibit large TI_{VG} but does not grow much in either control or cold-stress treatment. When breeding for efficient production under cold stress, genes for both plant vigor and CT are important.

Accession PI120256 was more CT than breeding line UCT5 during seed germination as judged based on both its T50 under cold stress (ca. 34% more rapid germination) and its TI_G (10% larger); this is consistent with previous reports on CT of this accession during seed germination (Foolad and Lin, 1998, 1999b, 2000b; Scott and Jones, 1985a). Thus, PI120256 is potentially a useful source of germplasm for breeding tomatoes for rapid seed germination under cold stress. Similarly, PI120256 was more CT than UCT5 during vegetative growth as judged based on both its absolute growth under cold stress (ca. 89% larger) and its TI_{VG} (ca. 44% larger), consistent with previous results (Foolad and Lin, 2000a, 2000b). Previously, we examined genetic bases of CT of PI120256 during both seed germination (Foolad and Lin, 1998) and vegetative growth (Foolad and Lin, 2000a) and determined that at both stages, CT of PI120256 was under additive genetic controls. The present study substantiates the previous results by the following two findings. First, during both seed germination and vegetative growth the nonselected F_2 and F_3 populations exhibited CT intermediate to the parents, indicating that CT characteristics of PI120256 were transmitted to the progeny in an additive fashion. Second, selection for CT during seed germination was effective and significantly improved CT of the progeny during germination (see below). The latter observation also demonstrated the effectiveness of the selection as practiced in this study.

In a previous study, we demonstrated that the rate of tomato seed germination under cold stress was determined by two types of genes [quantitative trait loci (QTLs)], those that affected germination vigor in general (referred to as stress-nonspecific QTLs) and those that affected CT (referred to as stress-specific QTLs) (Foolad and Lin, 1999a). Thus, selection for improved germination under cold stress may affect allele frequencies of both stress-nonspecific and stress-specific QTLs. Furthermore, in another study we demonstrated that selection for rapid germination under nonstress (control) conditions did not affect the rate of tomato seed germination under cold stress (Foolad and Lin, 1998). We conclude that, in the present study, selection for improved germination under cold stress increased CT as well as germination vigor of the progeny.

Because PI120256 is CT during both seed germination and vegetative growth, it is expected that F_2 individuals, derived from crosses between PI120256 and UCT5, would segregate for CT during both stages. Theoretically, if the same genes control CT during both germination and vegetative growth, any genetic change (e.g., by selection) in CT at one stage should affect CT at the other stage. In this study, selection for CT during seed germination (i.e., rapid germination under cold stress) did not affect CT of the progeny during vegetative growth; that is, the selected F_3 population was as cold tolerant (or cold sensitive) as the nonselected F_3 population (Table 2). The results indicate that, in these genetic materials, genes affecting rapid germination under cold stress do not influence plant growth under cold stress. Thus, CT during vegetative growth may not be improved by selecting for improved germination under cold stress. It is conceivable that different genetic and physiological mechanisms control CT during seed germination and vegetative growth. Because parents (F_2) and progeny (F_3) populations were evaluated in different times (different environments), the response and correlated response to selection were not biased by $G \times E$ interactions (Casler, 1982) and minimally inflated by environmental correlations among parents and progeny (Vogel et al., 1980). Thus, the results are genuine and should be useful to breeders

interested in developing tomato cultivars with enhanced CT during seed germination and/or vegetative growth.

To the authors' knowledge, this is the first report of the absence of a genetic relationship between CT during seed germination and vegetative growth in tomato. However, it should be validated in other tomato germplasm before an unequivocal conclusion regarding this relationship can be drawn. Previously, by examining the response and correlated response to selection (Foolad and Lin, 1997) and by the comparison of the contributing QTLs (Foolad, 1999; Foolad and Lin, 1999a) we determined that, in different intra- and interspecific populations of tomato, salt tolerance during seed germination was genetically independent of salt tolerance during vegetative growth. It is likely that this is also true for CT. Thus, when breeding for improved stress tolerance, each stage of plant development should be evaluated separately for assessment of tolerance and identification and utilization of useful genetic components. Simultaneous or sequential selections at individual developmental stages may lead to a single cultivar with improved tolerance throughout the ontogeny of the plant.

In conclusion, results herein clearly indicated that in PI120256 cold tolerance during vegetative growth was independent of CT during seed germination. Thus, when breeding for improved CT in tomato, selection protocols that include all critical developmental stages are necessary. However, a thorough understanding of the genetic relationship between CT at different stages requires identification, genetic mapping, cloning, and characterization of functional genes conferring tolerance at each stage. Such information may also be useful for development of cultivars with improved CT throughout the ontogeny of the plant including fruit set and ripening.

Literature Cited

Cannon, O.S., D.M. Gatherum, and W.G. Miles. 1973. Heritability of low temperature seed germination in tomato. HortScience 8:404–405.

Casler, M.D. 1982. Genotype × environment interaction bias to parent–offspring regression heritability estimates. Crop Sci. 22:540–542.

Dahal, P. and K.J. Bradford. 1990. Effects of priming and endosperm integrity on seed germination rates of tomato genotypes: II. Germination at reduced water potential. J. Expt. Bot. 41:1441–1453.

Dahal, P. and K.J. Bradford. 1994. Hydrothermal time analysis of tomato seed germination at suboptimal temperature and reduced water potential. Seed Sci. Res. 4:71–80.

Damidaux, R. and J. Martinez. 1992. Tomato cold resistance: Present status and future trends. Acta Hort. 301:73–86.

DeVos, D.A., J.R.R. Hill, and R.W. Helper. 1982. Response to selection for low temperature sprouting ability in tomato populations. Crop Sci. 22:876–879.

Falconer, D.S. 1989. Introduction to quantitative genetics. 3rd ed. Longman Scientific and Technical, London.

Foolad, M.R. 1996. Response to selection for salt tolerance during germination in tomato seed derived from P.I. 174263. J. Amer. Soc. Hort. Sci. 121:1006–1011.

Foolad, M.R. 1999. Genetics of salt tolerance and cold tolerance in tomato: Quantitative analysis and QTL mapping. Plant Biotechnol. 16:55–64.

Foolad, M.R., F.Q. Chen, and G.Y. Lin. 1998. RFLP mapping of QTLs conferring cold tolerance during seed germination in an interspecific cross of tomato. Mol. Breeding 4:519–529.

Foolad, M.R., J.R. Hyman, and G.Y. Lin. 1999. Relationships between cold- and salt-tolerance during seed germination in tomato: Analysis of response and correlated response to selection. Plant Breeding 118:49–52.

Foolad, M.R. and G.Y. Lin. 1997. Absence of a relationship between salt tolerance during germination and vegetative growth in tomato. Plant Breeding 116:363–367.

Foolad, M.R. and G.Y. Lin. 1998. Genetic analysis of low temperature tolerance during germination in tomato, *Lycopersicon esculentum* Mill. Plant Breeding 117:171–176.

Foolad, M.R. and G.Y. Lin. 1999a. Comparison of QTLs for seed germination under non-stress, cold stress and salt stress in tomato. Plant Breeding 118:167–173.

Foolad, M.R. and G.Y. Lin. 1999b. Relationships between cold- and salt-tolerance during seed germination in tomato: Germplasm evaluation. Plant Breeding 118:45–48.

Foolad, M.R. and G.Y. Lin. 2000a. Genetic analysis of cold tolerance during vegetative growth in tomato, *Lycopersicon esculentum* Mill. Euphytica (In press).

Foolad, M.R. and G.Y. Lin. 2000b. Relationship between cold tolerance during seed germination and vegetative growth in tomato. Germplasm evaluation. J. Amer. Soc. Hort. Sci. 125:679–683.

Forster, B.P., M.S. Phillips, T.E. Miller, E. Baird, and W. Powell. 1990. Chromosome location of genes contolling tolerance to salt (NaCl) and vigor in *Hordeum vulgare* and *H. chilense*. Heredity 65:99–107.

Frey, K.J. and T. Horner. 1957. Heritability in standard units. Agron. J. 49:59–62.

Gehan, E.A. 1969. Estimating survival functions from the life table. J. Chronic Dis. 21:629–644.

Jones, J.B.J. 1999. Tomato plant culture in the field, greenhouse, and home garden. ed. CRC Press, New York.

Leviatov, S., O. Shoseyov, and S. Wolf. 1994. Roles of different seed components in controlling tomato seed germination at low temperature. Scientia Hort. 56:197–206.

Liptay, A., E.F. Bolton, and V.A. Dirks. 1982. A comparison of field-seeded and transplanted tomatoes grown on a clay soil. Can. J. Plant. Sci. 62:483–487.

Lyons, J.M. 1973. Chilling injury in plants. Annu. Rev. Plant Physiol. 24:445–466.

Ng, T.J. and E.C. Tigchelaar. 1973. Inheritance of low temperature seed sprouting in tomato. J. Amer. Soc. Hort. Sci. 98:314–316.

Patterson, B.D. 1988. Genes for cold resistance from wild tomatoes. HortScience 23:795–795.

Patterson, B.D., L. Mutton, R.E. Paull, and V.Q. Nguyen. 1987. Tomato pollen development: Stages sensitive to chilling and a natural environment for the selection of resistant genotypes. Plant Cell Environ. 10:363–368.

Patterson, B.D. and L.A. Payne. 1983. Screening for chilling resistance in tomato seedlings. HortScience 18:340–341.

Rawson, H.M., R.A. Richards, and R. Munns. 1988. An examination of selection criteria for salt tolerance in wheat, barley and triticale genotypes. Austral. J. Agr. Res. 39:759–772.

Scott, S.J. and R.A. Jones. 1982. Low temperature seed germination of *Lycopersicon* species evaluated by survival analysis. Euphytica 31:869–883.

Scott, S.J. and R.A. Jones. 1985a. Cold tolerance in tomato. I. Seed germination and early seedling growth of *Lycoperscion esculentum*. Physiol. Plant. 65:487–492.

Scott, S.J. and R.A. Jones. 1985b. Quantifying seed germination responses to low temperatures: Variation among *Lycopersicon* spp. Environ. Expt. Bot. 25:129–137.

Steel, R.G.D. and J.H. Torrie. 1980. Principles and procedures of statistics. 2nd ed. McGraw–Hill, New York.

Vallejos, C.E. 1991. Low night temperatures have a differential effect on the diurnal of gene expression in cold-sensitive and tolerant tomatoes. Plant, Cell Environ. 14:105–112.

Vogel, K.P., F.A. Haskins, and H.J. Gorz. 1980. Parent–progeny regression in indiangrass: Inflation of heritability estimates by environmental covariances. Crop Sci. 20:580–582.

Wolf, S., D. Yakir, M.A. Stevens, and J. Rudich. 1986. Cold temperature tolerance of wild tomato species. J. Amer. Soc. Hort. Sci. 111:960–964.

Yakir, D., J. Rudich, and B.A. Bravdo. 1986. Adaptation to chilling: Photosynthetic characteristics of the cultivated tomato and a high altitude wild species. Plant, Cell Environ. 9:477–484.