

The Potential Resistance to Low Temperatures in Selected *Solanum* Species

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Abstract

Brief low positive temperatures in spring negatively affect early field tomato harvests. Low-temperature stress inhibits plant growth and negatively affects pollen viability, leading to a decrease in the yield of early tomato fruits. This study applied a comprehensive assessment method to evaluate cold-stress resistance in selected *Solanum* genotypes. Plant material comprised five wild accessions: *Solanum pimpinellifolium* (lines spr 1, spr 5), *S. cheesmaniae* and cultivated *S. lycopersicum* lines (sc 4, sc 3) and the varieties Sw-7 and Flora. The study aimed to evaluate wild tomato genotypes for cold tolerance using several modes of exposure to low temperatures. Since cold resistance is a polygenic trait, the identification of cold-resistant genotypes during several consecutive treatments with low temperatures and in different variants made it possible to select plants with greater cold resistance and a greater number of genes responsible for cold resistance, which is valuable for the climatic conditions of Ukraine. Authors evaluated “growth after stress” and “pollen viability” because recovery after cold exposure is critical for achieving an early harvest. Seeds and plants were exposed to multiple temperature regimes beginning at germination. Results indicated that spr 5 and sc 3 outperformed other genotypes in multiple cold-tolerance assays across developmental stages and exhibited high to moderate stability of resistance. Although average daily temperatures have risen with climate change in Ukraine, spring cold snaps still occur; therefore, studying cold resistance among tomato genotypes remains relevant for adaptation.

Keywords

Tomato; Low temperature stress; Wild genotype; Cold tolerance; Weight gain under stress; Pollen viability

Introduction

Contemporary climate change has intensified abiotic stressors (Ivanyshyn, and Kasiyanchuk, 2024, p. 200; Opalchuk *et al.*, 2024, p. 350), such as late-season frosts — that often occur in spring following seedling transplanting. Low temperatures constitute a significant abiotic stressor and a limiting factor for plant growth, causing disruptions in physiological processes (Skliar, 2015, pp. 170–171, 178) and affecting plant production and distribution (Heidari, Amerian and Barcaccia, 2021, p. 1146). Sustained temperature declines markedly influence crop yield (Skliar, 2015, pp. 171, 179), particularly due to climate change and increasingly frequent extreme weather conditions (Wang *et al.*, 2023, p. 1716). Plant species exhibit differential tolerance to low temperatures. Thermophilic crops such as tomato are susceptible to damage even under moderately positive temperatures (Skliar, 2015, p. 178; Zhuk, Syvoraksha and Fedosiy, 2014, p. 7). Brief exposure to temperatures of +1 to +3°C may cause plant mortality (Skliar, 2015, p. 178; Zhuk, Syvoraksha and Fedosiy, 2014, pp. 7–8). Growth ceases at air temperatures below +8°C (Barabash, Taranenko and Sych, 2005, p. 277; Kravchenko and Prylipka, 2007, pp. 26, 85). Temperatures below +12°C may induce necrosis, while prolonged exposure suppresses photosynthesis and compromises membrane integrity (Venema *et al.*, 2005, cited in Heidari, Amerian and Barcaccia, 2021, p. 1146). Four commercial tomato cultivars tested were sensitive to chilling and sustained injury at approximately +6°C (Easlon *et al.*, 2013, pp. 1991, 1996).

Plant cold tolerance is ontogenetically dependent (Skliar, 2015, p. 179). Tomato, being a thermophilic species, exhibits variable temperature requirements across developmental stages (Bessonova and Yakovleva-Nosar, 2014, p. 305; Kravchenko and Prylipka, 2007, p. 26; Zhuk, Syvoraksha and Fedosiy, 2014, pp. 7–8). Low-temperature conditions significantly affect early growth stages of soybean (Wang *et al.*, 2023, p. 1716) and other heat-loving crops (Bessonova & Yakovleva-Nosar, 2014, p. 305). The optimal temperature for tomato seed germination is +20 to +25°C, with a minimum of +9°C required for seedling emergence. The seedling stage demonstrates the highest cold tolerance, enduring short-term cooling down to +5°C (Kravchenko and Prylipka, 2002, p. 68; Zhuk, Syvoraksha and Fedosiy, 2014, pp. 6–12). For cultivated tomatoes, the cardinal temperatures for vegetative growth are +10°C (base), +34°C (maximum), and +22 °C (optimum) (Pivetta *et al.*, 2007, cited in Zeist *et al.*, 2018, pp. 307–308). Although many studies have investigated low-temperature resistance, few evaluate multiple cold regimes and developmental phases in a single study; the present work addresses this gap. One treatment exposed seeds to +1.0 ± 0.5 °C for 12 h followed by +16 °C for 12 h. For the control group, the seeds were germinated at a temperature of +22...+23°C. In the second experiment in the field, seed germination was evaluated after exposure to a low temperature of +1...+12 °C for 10 days. The next temperature regime was tested on seedlings in a cold room at a temperature of +1 °C for 12 hours. The 12-h cyclic regime was chosen to simulate typical field temperature fluctuations in the study region.

Cold tolerance in plants is defined by their capacity to withstand low positive temperatures, which is particularly critical for thermophilic species (Bessonova and Yakovleva-Nosar, 2014, p. 305; Skliar, 2015, pp. 170, 178). The genetic base of modern cultivars is severely narrowed and highly homogeneous (Kravchenko and Prylipka, 2002, p. 68). Breeding for high productivity, enhanced stress tolerance, and improved

nutritional value has led to the selection of genetically uniform genotypes, resulting in a substantial reduction in genetic diversity (Bauchet and Causse, 2012, pp. 133–134; Horova and Yakovenko, 2001, pp. 268–269). Enriching the genotype with novel alleles can improve the genetic variability of tomato (Horova and Yakovenko, 2001, pp. 268–269; Kravchenko and Prylipka, 2002, p. 68). Certain wild tomato species serve as reservoirs of stress resistance, including tolerance to low temperatures (Horova and Yakovenko, 2001, pp. 268–269). These wild species inhabit diverse climatic zones and confront various ecological challenges. Natural selection has led to differentiation in stress tolerance levels (Dolferus, 2014, pp. 250–251; Grandillo *et al.*, 2011, p. 129; Maduraimuthu and Vara Prasad, 2014, pp. 201–202). The extensive range of ecological conditions has promoted the diversification of wild species. “This broad variation is expressed at the morphological, physiological, reproductive, and molecular levels” (Peralta and Spooner, 2005 cited in Bauchet and Causse, 2012, p. 134). In our previous studies, we tested 55 of the most common tomato varieties for resistance to low-temperature stress and found that they were generally not very resistant to low temperatures. So, we started looking for resistant genotypes among other members of the *Solanum* genus.

Zeist *et al.* (2022) reported that interspecific hybrids between wild species and *S. lycopersicum* often resemble their wild progenitors morpho-agronomically and physiologically. Investigations into natural variation support existing diversity and offer insights into the genetic architecture of complex traits (Bauchet and Causse, 2012, pp. 133–134). “The utilization of wild species can expand the tomato gene pool and serve as valuable sources of genetic variability for breeding” (Bolger *et al.*, 2014, p. 1034; Hanson *et al.*, 2007, p. 167; Zhou *et al.*, 2018, p. 500). Cold tolerance represents a complex trait governed by polygenic control. “Numerous cold-regulated genes have been identified in plants subjected to low-temperature stress” (Chen *et al.*, 2015, p. 1), including seedling endurance, which is a polygenic trait in rice (Andaya and Tai, 2006, cited in da Cruz *et al.*, 2013, p. 99). Interspecific hybridization between wild and cultivated forms often results in the expression of undesirable alleles, including reduced reproductive capacity. Since wild genotypes may have reduced reproductive function, we included in the study only those wild genotypes that do not have problems producing fertile offspring when hybridized with cultivated varieties. In studies by other scientists who studied the cold resistance of wild tomato genotypes, attention was mainly focused on *S. habrochaites* as the most cold-resistant genotype, and no attention was paid to the cold resistance of other wild genotypes, the resistance of which has not been fully studied, which was the aim of our study.

There are 12 recognized wild tomato species and 4 related species (Bedinger *et al.*, 2011, p. 171), among which *S. habrochaites* demonstrates notable cold tolerance. Wild tomatoes such as *S. habrochaites* exhibit rapid recovery following cold stress due to physiological adaptations (Nemati *et al.*, 2021, p. 395). The endemic Galápagos tomato (*Lycopersicon cheesmanii*) holds significant potential for breeding cultivated tomatoes (*L. esculentum*). Having evolved in isolation from mainland species, *L. cheesmanii* possesses a unique combination of morphological and physiological traits. It readily hybridizes with cultivated tomatoes, producing fertile progeny and serving as a source of variation for agronomically important traits (Nuez, Prohens and Blanca, 2004, p. 87).

Understanding the mechanisms of low-temperature stress response across diverse *Solanum* germplasm resources is essential for future breeding of new cultivars (Heidari, Amerian and Barcaccia, 2021, p. 1148). To date, only a limited number of studies have investigated the effects of low temperature, and the mechanisms underlying plant responses to this type of stress remain incompletely understood (Heidari, Amerian and Barcaccia, 2021, p. 1146). Genotypes of wild tomatoes exhibit greater resilience to both cold and heat stress compared to cultivated varieties, suggesting their utility in uncovering fundamental mechanisms of temperature stress tolerance (Zhou *et al.*, 2018, p. 500). Driedonks *et al.* (2018, pp. 66–67) studied 13 wild tomato species, assessing thermotolerance effects on reproductive traits, and concluded that success depends on the integration of all reproductive trait variants. Consequently, the study excluded wild species with interspecific crossing barriers to prevent transmission of deleterious traits to progeny. Wild tomato forms capable of freely cross-pollinating with cultivated varieties were selected for the study.

Research Methodology

The plant material comprised five wild accessions: *S. pimpinellifolium* (spr 1, spr 5), *S. cheesmaniae*, and cultivated *S. lycopersicum* lines (sc 4, sc 3) plus varieties Sw-7 and Flora. Five samples of wild species were provided by the Institute of Vegetable and Melon Growing (Kharkiv, Ukraine) and two cultivated varieties of *S. esculentum*. Wild *Solanum* genotypes were used in the study as sources of various types of stress resistance, including resistance to low temperatures. These genotypes can enrich modern tomato germplasm with cold-resistance alleles if they hybridize successfully and produce fertile progeny. It was precisely these genotypes that were selected and included in the study.

Field studies followed standard procedures for assessing homogeneity and stability (Vovkodav, 2004) and experimental methodology (Bondarenko and Yakovenko, 2001). The varieties were included in the experiment to compare and study the resistance to low temperature stress at the stage of planting seedlings in the experimental field and growing from seeds without transplanting. Since cold resistance is a polygenic trait, we planned to identify all possible variants of resistance to low-temperature stress in all simulated conditions of low-temperature stress characteristic of the forest-steppe climate zone of Ukraine. This zone experiences short nighttime drops to –1 to +5 °C for 1–2 days, after which temperatures typically return to ~+10 to +12 °C at night and +16 to +18 °C during the day. During this period, plants in production may be at different stages of growth, so seeds, seedlings, and pollen were used in the experiment, and temperature regimes were applied to this experimental material. For each stage of growth, a specific range of stressful low temperatures was used, at which industrial varieties were damaged when grown in the field.

Cold-tolerance was assessed in four experiments to characterize distinct components of resistance:

1. Germination of seeds using variable temperatures.
2. Cultivation from seedlings in experimental plots in the early stages with exposure to natural cooling.

3. Growing seedlings in sowing boxes and exposure to short-term temperature drops in the freezer.
4. Germination of tomato pollen at low temperatures.

In the experiment, the low temperature tests were similar to the climatic conditions of the growing area in the Forest-Steppe zone of Ukraine, which are characterized by short-term temperature drops to $-1...0^{\circ}\text{C}$ in early spring. The conditions of exposure to low temperatures were selected based on direct exposure to low temperatures in natural climatic conditions and in the climate chamber with short-term exposure to low temperatures. The most typical climatic conditions in the Forest-Steppe zone of Ukraine are spring return frosts and cold snaps. In recent years, planted plants have been less affected by frosts, but temperature drops during the critical period of planting seedlings or growing from seeds in the field are still frequent (Primak *et al.*, 2006, pp.12, 84–85). The most critical moments in the development of tomato plants affected by low positive temperatures are the period of seed germination, the seedling phase (the phase of the first true leaves), planting seedlings, and seedling establishment (Kravchenko and Prylipka, 2007, 26–27, 85–86).

Experiment 1 – seed treatment with low temperatures in a cooling chamber.

Group 1 seeds were incubated in a growth chamber (14-h photoperiod) at $+1.0 \pm 0.5^{\circ}\text{C}$ for 12 h followed by $+16^{\circ}\text{C}$ for 12 h. In the second group, the optimum temperature was maintained at $+22...+23^{\circ}\text{C}$ as control conditions for seed germination.

Seeds were surface-disinfected, placed on Petri dishes, and incubated until germination. Germinated seeds were counted at day 7 and monitored for 20 days. The germination rate of each sample was determined by counting the percentage of hardy plants following IVMG–NAAS methods (Bondarenko and Yakovenko (ed) Methods of Experimental Work, 2001, pp. 221–222, 275).

$$P = \frac{H_1}{H} \times 100$$

where P is the percentage of hardy plants;

H_1 is the hardy plants (seeds);

H is the viability of the plants (seeds) to the temperature.

Height increase (%) was computed after the variable treatment of 12 h at $+16^{\circ}\text{C}$ followed by 12 h at $+1^{\circ}\text{C}$. The rate of growth recovery was determined 3 days after exposure to variable low temperatures. Resistance categories: 81–100% = highly resistant; 61–80% = above-average; 41–60% = medium and plants with 21–40% resistance were included in the group of below-average resistance.

Each treatment was replicated three times; each replicate comprised 50 seeds per variant. The control group of seeds was germinated at optimal temperatures of $+22...+24^{\circ}\text{C}$, the seeds of the control group of all samples germinated in 7 days, and almost did not differ significantly in germination and other parameters among themselves.

Experiment 2 – growing plants in the open field under the influence of low temperatures
 Fifty seeds per sample were sown in experimental plots to assess the effects of low temperatures. In the field, the cold resistance was assessed by the duration of the

“sowing–germination” period, and the “plant height growth” was determined at low temperatures of +1...+12 °C for 10 days.

Experiment 3 – Treatment of seedlings with low temperatures

Part of the seedlings from the first experiment that showed high cold resistance (20 plants of each sample) in the phase of the first true leaf appearance were kept in a refrigerator at a temperature of +1 °C for 12 hours, and the trait – cold resistance of plants – was determined by the degree of damage to plants compared to the control. Seedling cold damage was scored on a 1–5 scale (1 = severe damage; 5 = minimal damage).

Direct sowing of seeds in the field has a number of advantages – early harvest, obtaining plants with a taproot system, and reducing labor-intensive plant cultivation operations. The advantages of growing plants with a taproot system are better development of the root system and greater adaptation to the moisture regime and, as a result, increased plant endurance (Kravchenko and Prylipka, 2007, pp.273–275).

Experiment 4 – Determination of pollen cold resistance using the method of pollen treatment at low temperatures. Pollen from 10 plants was placed on Petri dishes with 15% sucrose and 100 mg L⁻¹ boric acid, incubated at +9–+10 °C for 24 h, and germinated pollen was scored microscopically as viable; viability (%) = (germinated grains / total grains) × 100.

Statistical Analysis

Data were initially compiled in Microsoft Excel and analyzed using IBM SPSS (v. 23.0). First, we performed an analysis of variance to determine the significance of the difference between the variants. Based on the analysis of variance, the analysis of adaptability and stability was carried out using the appropriate computer programs of the Institute of Vegetable and Melon growing, NAAS, and the OSGE program of the V.Y. Yuriev Institute of Plant Industry. Homeostasis (HOM) for key traits was calculated following Khangildin and Litvinenko (1981, pp. 8–14). Calculations of parameters of general adaptive ability of genotypes (ZAZi) of the original forms in terms of early maturity, cold resistance, and yield were performed according to the method of Kilchevsky and Khotylova (1997, pp. 263–270). Stability (bi) was estimated following Eberhart and Russell (1966).

Results

Low-temperature stress inhibited seed germination across wild tomato accessions. More resistant accessions showed germination rates >20%. *Solanum cheesmaniae* and line spr 5 had higher germination in the experiment under cold stress conditions – 20.1 and 24.7 (significant at LSD₀₅ = 4.21) (Figure 1). No plants were completely resistant to low temperature stress. Presumably, the trait of resistance to cold is controlled by several genes and manifests itself under a set of certain conditions. Plants of cultivars in this experiment under such temperature conditions had low germination – 4–6%, which is significantly less than the resistance of the studied lines of wild forms – 10.3–24.7 %.

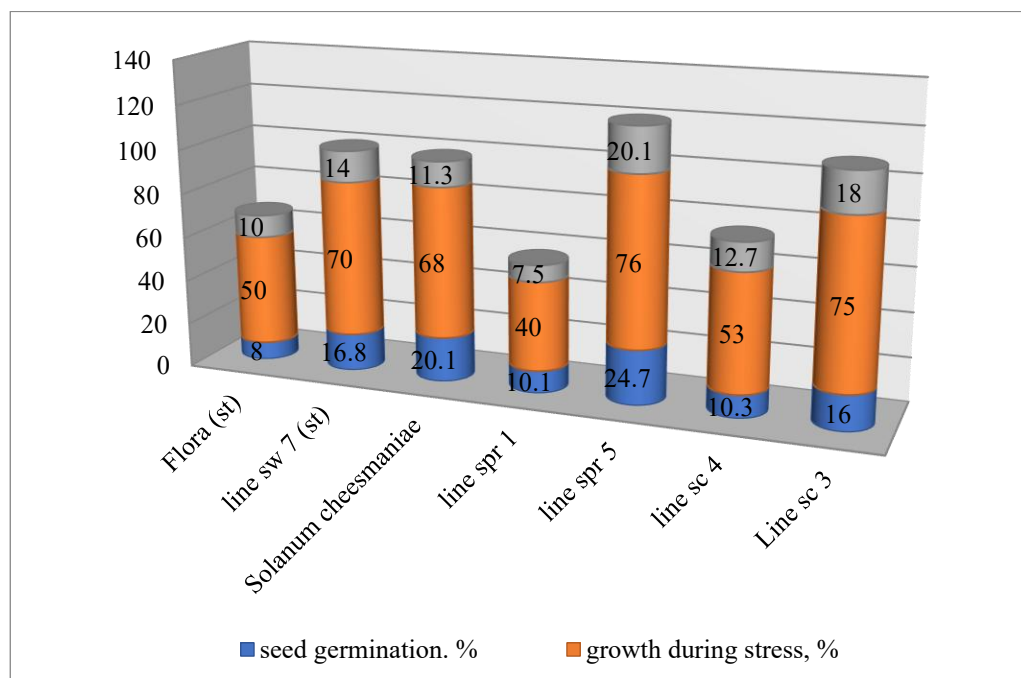


Figure 1: Seed germination cold tolerance under cyclic treatment (12 h +10 °C / 12 h +16 °C). Least significant differences: germination = 4.21%, growth during stress = 15%, growth after stress = 4%.

Table 1: Adaptability and stability of cold resistance during seed germination (laboratory conditions); Averages for 2017–2018

Wild species, no types	Trait								
	Seed germination			Growth during stress			Growth after stress		
	bi	ZAZi	HOM	bi	ZAZi	HOM	bi	ZAZi	HOM
Flora (st)	0.60	0.2	0.06	0.50	0.1	0.54	0.10	0.8	0.11
line Sw 7 (st)	1.68	6.0	0.27	1.70	-1.6	1.21	0.14	3.8	0.23
<i>Solanum cheesmaniae</i>	2.01	-3.5	0.01	1.68	1.9	0.47	1.13	-2.2	0.14
line spr 1	1.01	3.5	0.01	1.40	1.9	0.43	0.75	-6.2	0.08
line spr 5	2.47	2.5	2.8	1.76	-1.6	0.89	2.01	6.8	0.85
line sc 4	1.03	-3.5	0.10	0.53	0.9	0.82	1.27	-7.2	0.18
line sc 3	1.60	-2.0	0.13	1.75	-1.6	0.88	1.80	4.8	0.54

Legend: bi = Eberhart–Russell stability coefficient; ZAZi = general adaptive ability index; HOM = homeostasis index

Under low-temperature stress, *S. cheesmaniae*, line Sw 7 (standard), spr 5, and sc 3 exhibited high growth during stress (68–76%). Only two wild species – line spr 5 and line sc 3 – had higher growth after stress, which was significantly higher than the standard, at 20.1 and 18 %. Stability was assessed using the HOM homeostasis index; genotypes with higher HOM values were considered more stable. According to the analysis of statistical indicators, the line spr 5 (bi = 2.47, HOM = 2.8) had high stability in terms of seed germination (Table 1). At the same time, it had a moderate adaptive

capacity ($ZAZi = 2.5$). The highest adaptive capacity was in the line spr 1 ($ZAZi = 3.5$) and the standard line Sw 7 – 1 ($ZAZi = 6.0$).

In terms of growth during stress in the laboratory at variable temperatures from 0 °C to +16 °C, all samples were at the same level, on average, except for line sc 4 with low stability ($bi = 0.53$). Line spr 5 and line sc 3 had high stability but low adaptability ($HOM = 1.6$), and line Sw 7 was at the level of the standard ($bi = 1.7$, $HOM = 1.21$). High and medium indicators of stability and high indicators of adaptability based on growth after stress were also observed in line spr 5 and line sc 3 with $bi = 2.1$ and 1.8 , $HOM = 0.85$ and 0.54 , $ZAZi = 6.8$ and 4.8 . These lines also showed higher plant growth after low-temperature stress, and the high stability of germination and growth traits during and after stress in these genotypes may be associated with good adaptability to different growing conditions. Lines spr 5 and sc 3 are promising parental forms for breeding cold-resistant cultivars, showing stable resistance across the tested range (0–+16 °C) and rapid post-stress recovery.

Spring weather in the study area was variable; for example, cold snaps of –2 to 0 °C at night lasting 3–4 days with snowfall occurred in 2013, 2014, and 2015 (data not shown). Similar conditions were observed in the years of research. However, using only laboratory characteristics may not fully characterize genotypes in terms of cold resistance, so natural field conditions were used to identify the plants best adapted to cold stress. A higher level of cold tolerance of wild tomato plants was also noted in the field, where a greater number of unfavorable factors are triggered in addition to low temperatures. Thus, the period of sowing-emergence was the shortest in line spr 1 (15 days), line spr 5 (16 days) at the level of the standard – line Sw 7 (16 days) and much earlier than the standard – Flora variety (20 days) (Figure 2). The growth during stress was at a fairly high level for all wild forms. The highest growth rates were observed in sc 3 and sc 4 (90% and 86%, respectively). The complex of factors of field conditions allows us to identify the possible influence of insufficient moisture, sudden temperature changes, and other factors.

When several resistance genes are integrated into the genotype, the probability of obtaining varieties with higher resistance after unfavorable conditions increases. Stability determined by the Eberhart and Russell index (bi) and homeostaticity (HOM) in tomato genotypes during studies of seedling cold tolerance did not coincide and had different indicators of stability in the field (Table 2). Thus, according to the index of stability of *bi Solanum cheesmaniae*, line spr 5 and line sc 3 had higher values from 1.6 to 1.8 in the period of growth of sowing-seedlings, at the level of the standard. Homeostaticity during the seedling growth period was at an average level; only line spr 1 and line spr 5 had a higher level of the index, 0.64 and 0.77. In terms of adaptive capacity, no wild genotype outperformed the standard line Sw 7 – 8.3.

In their research, Georgieva and Kosev (2016, p. 109) also determined the adaptive potential of pea and vetch varieties and, based on the results obtained, selected them for adaptability and stability. The characteristics of plant weight gain under stress were also characterized by heterogeneity in levels of adaptability and stability, in contrast to the results obtained in the previous experiment at variable temperatures from 0 to +16 °C. The average level of stability by the bi index in plants was similar to the high level of

stability by the HOM index in *Solanum cheesmaniae* genotypes and the spr 5 line (Table 2). And the high level of stability in bi corresponds to the average HOM in lines sc 4 and sc 3. This confirms the assumption of similarity of bi and HOM stability indices for cold resistance in certain phases of growth and development of tomato plants.

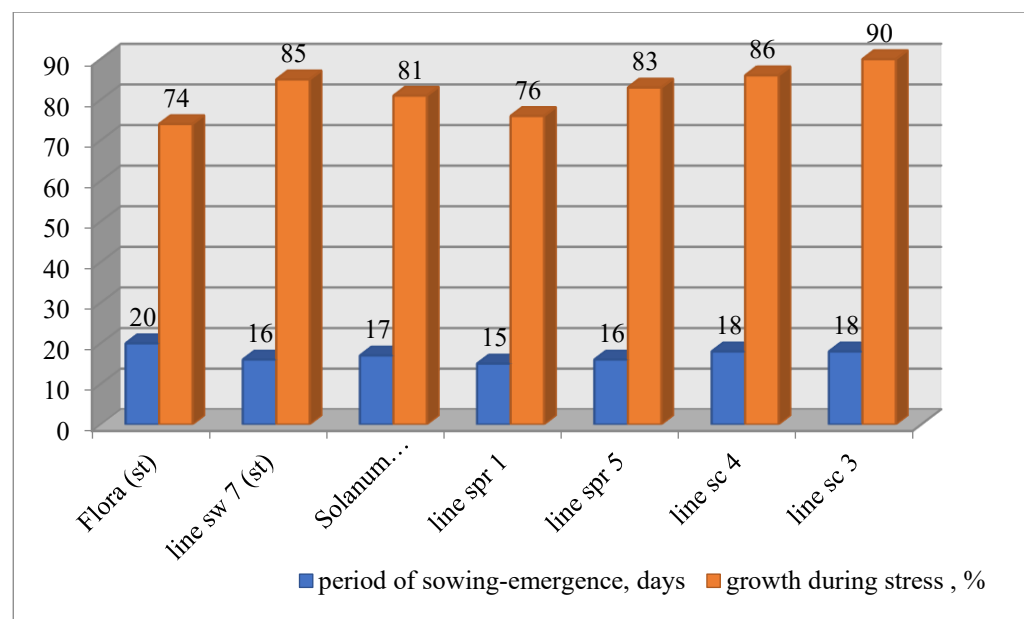


Figure 2: Cold tolerance during germination and seedling growth (first true-leaf phase) under natural temperature drops to 0–+3 °C during germination. Least significant differences: sowing–emergence = 2.8 days; growth during stress = 7.8%.

Table 2: The level of stability and adaptability indicators during exposure to cold in the field on tomato seedlings (average for 2017–2018)

Wild species, genotypes,	Period of growth, trait					
	Period of sowing-emergence			Growth during stress		
	bi	ZAZi	HOM	bi	ZAZi	HOM
Flora (st)	1.1	5.4	0.67	0.74	3.0	1.84
line Sw 7 (st)	1.6	8.3	0.35	0.85	4.1	2.01
<i>Solanum cheesmaniae</i>	1.7	0.2	0.3	1.81	-0.2	2.84
line spr 1	0.5	0.3	0.64	0.76	-0.1	1.41
line spr 5	1.6	5.3	0.77	1.83	3.2	2.84
line sc 4	0.8	-2.2	0.55	1.86	-0.7	1.67
line sc 3	1.8	0.3	0.58	1.90	0.5	2.01

Legend: bi = Eberhart–Russell stability coefficient; ZAZi = general adaptive ability index; HOM = homeostasis index

The high level of stability in all growth indicators and statistical indicators indicates that line spr 5 consistently shows resistance to low-temperature stress in the field and laboratory in different years of cultivation and will be used in further breeding work to obtain highly cold-resistant lines and F₁ hybrids. The Sw 7 and sc 3 lines showed high

but unstable levels of cold resistance in the field over the years. The value of these forms for use in practical breeding can be confirmed or refuted by the following cold resistance test. In the subsequent periods of growth and development of tomato plants, an additional study of cold tolerance was conducted to better understand the characteristics of plants for resistance to low temperatures. Some of the plants that had high cold tolerance under variable conditions of seed germination in the thermostat were subsequently kept at +1 °C for 12 hours in phase 2 of true leaves. The most resistant among the plants studied were line spr 5 and line sc 3, with resistance scores of 4.8 and 4.5, respectively, compared to the standards Flora and line Sw 7 – 2.5 and 4 points (Figure 3).

Exposure to low temperatures reduces the reproductive capacity of pollen and thus reduces the formation of tomato fruits. In terms of pollen cold resistance in the experiment (viability at low temperatures), the highest values were also observed in line spr 5 and line sc 3 – 79 % and 61 %, respectively, which is significantly higher than the standard variety and other lines in the experiment.

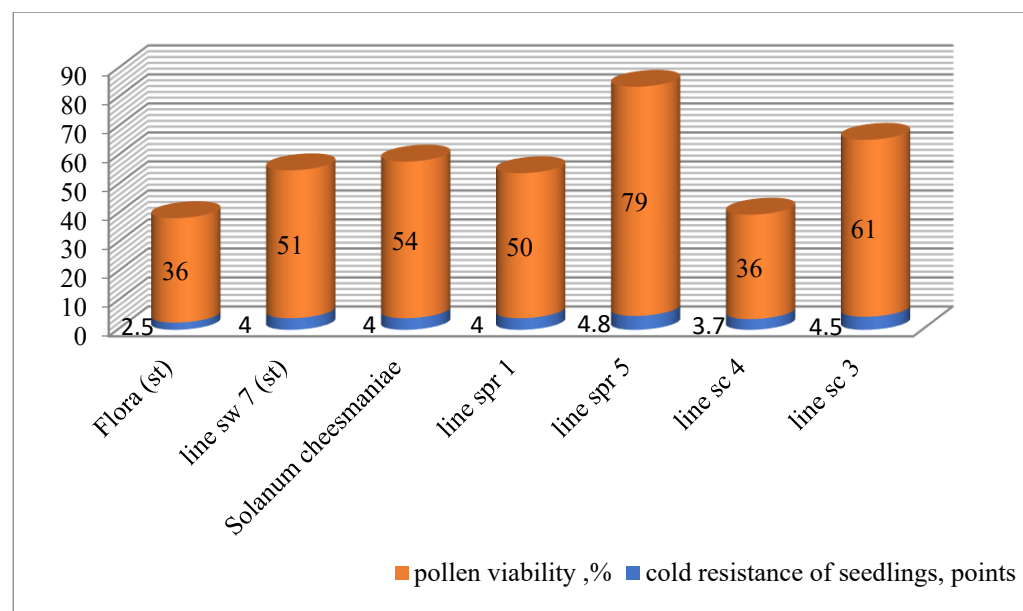


Figure 3: Percentage values and scores of pollen viability and seedling cold tolerance under treatment with low positive temperatures. The smallest significant difference in seedlings' cold resistance is 1.2 points, and in pollen viability, 10.5 %

The results of statistical processing for seedling cold tolerance and pollen viability under cold stress showed that lines based on wild species had high stability in terms of bi and medium stability in terms of HOM (Table 3). Conversely, lines with a high level of stability in HOM had an average level of stability in seedling cold tolerance in terms of bi in spr 5 and sc 3 lines (bi = 1.4 and 1.45, HOM = 0.46 and 0.53, while the standards had bi = 1.4 and 1.5, HOM = 0.23 and 0.09).

A similar trend was observed for the trait of pollen viability under cold stress in the same lines, spr 5 and sc 3, both stability indices were at a high level among other genotypes studied (HOM = 1.17 and 1.13, bi = 2.79 and 1.61). This indicates the reliability and

stability of the trait determination. In terms of general adaptive capacity, only line sc 4 had a higher index of adaptability for seedling cold hardiness ($ZAZi = 0.9$), but low pollen viability and line sc 3 had a low $ZAZi$ for seedling cold hardiness and a high level of pollen viability ($ZAZi = 14.2$).

Table 3: The level of stability and adaptability of tomato plants under the influence of cold and the possibility of fruit formation in tomato (average for 2017–2018)

Wild species, genotypes	Trait					
	Cold resistance of the seedling			Pollen viability		
	bi	ZAZi	HOM	bi	ZAZi	HOM
Flora (st)	1.5	0.8	0.09	0.36	-3.2	1.13
line Sw 7 (st)	1.4	-0.5	0.23	0.51	4.2	0.54
<i>Solanum cheesmaniae</i>	2.4	0.1	0.31	1.54	4.2	0.69
line spr 1	0.4	0.1	0.12	1.50	-31.3	1.07
line spr 5	1.48	-0.1	0.46	2.79	2.12	1.17
line sc 4	0.37	0.9	0.31	1.36	-11.8	0.34
line sc 3	1.45	-0.3	0.53	1.61	14.2	1.13

Legend: bi = Eberhart–Russell stability coefficient; $ZAZi$ = general adaptive ability index; HOM = homeostasis index.

The results of testing seedlings and pollen under cold conditions also confirmed the value of the spr 5 line for use in breeding for cold resistance and the sc 3 line, which was slightly inferior in terms of cold resistance in previous experiments, but in terms of cold resistance of seedlings and pollen, it had high cold resistance and stable manifestation of cold resistance over the years of research.

Discussion

Rising global population and climate variability increase demand for crop varieties that can maintain productivity under adverse conditions (Kononov et al., 2024, p. 22; Radha et al., 2023; Wang et al., 2023). In agricultural production, plants must exhibit comprehensive resistance to low temperatures, and young plants should be able to rapidly resume growth upon the return of favorable thermal conditions to ensure a continuous production cycle (Wang et al., 2023, p. 13). Ecogeographical studies of plant genetic resources enable the identification of species' adaptive ranges and the key environmental variables that determine their distribution (Parra-Quinajo, Iriondo and Torres, 2012, as cited in Ramires-Ojeda et al., 2021a, p. 857).

Wild tomato species related to cultivated tomatoes represent valuable genetic resources due to their ecological adaptation, which contributes to genetic diversity (Parra-Quinajo, Iriondo and Torres, 2012, as cited in Ramires-Ojeda et al., 2021a, p. 856). Therefore, it is strategically important to study climatic and soil factors that aid in understanding their current distribution patterns (Ramires-Ojeda et al., 2021b, p. 2). However, information regarding all wild and related tomato species remains insufficient, as ecological descriptors and specific climatic characteristics of their habitats are either unknown or limited (Parra-Quinajo, Iriondo and Torres, 2012, as cited in Ramires-Ojeda et al., 2021a, p. 856). Currently, plant breeders face the challenge of developing cultivars that

are not only high-yielding but also resistant to both biotic and abiotic environmental stressors. In recent years, significant fluctuations in hydrothermal conditions have been observed even within a single soil-climatic location, which substantially affects the expression of individual traits and properties, and consequently, macrotraits such as yield (Polishchuk, Konovalov and Brovdi, 2024, p. 83; Starychenko *et al.*, 2014, p. 77).

In our study, germination in the more stress-tolerant accessions exceeded 20%. The suppressive effect of low-temperature stress was manifested in reduced seed germination rates and prolonged germination periods. Under these reduced temperature conditions, the cultivars exhibited lower germination compared to the resilience observed in the tested wild lines. Only the wild species *Solanum cheesmaniae* and line spr 5 demonstrated higher germination rates under cold stress conditions – 20.1 % and 24.7 %, respectively. Researchers have found that the inheritance of seed germination ability in tomato is polygenic in nature (Timothy and Tigchelaar, 1973, pp. 314, 316) and that plants exposed to cold stress possess a wide array of cold-regulated genes (Andaya and Tai, 2006, p. 468; Chen *et al.*, 2015, p. 1).

Developing tomato cultivars tolerant to low temperatures is essential. In the experiments conducted by Sherzod *et al.* (2019, p. 350), tomato plants were grown in polyethylene-covered greenhouses under controlled night temperatures of +10 °C and +15 °C. In our study, under fluctuating temperature conditions ranging from 0 to +16 °C, *Solanum cheesmaniae*, line Sw 7 (st-standard), line spr 5, and line sc 3 exhibited high growth performance under stress, ranging from 68 % to 76 %. Following the stress period, only two wild lines (spr 5 and sc 3) demonstrated accelerated growth rates. Wild tomato species from the Galápagos Islands, *Solanum cheesmaniae* and *Solanum galapagense*, are known for their resistance to various stress factors and can be successfully crossed with cultivated tomatoes (Pailles *et al.*, 2017, p. 1). However, to effectively utilize this wild germplasm resource, it is necessary to understand the population structure and genetic variation (Lv *et al.*, 2012, as cited in Pailles *et al.*, 2017, p. 2).

The use of wild tomato species to improve the adaptability of domesticated varieties to changing environmental conditions requires knowledge of which wild species are most suitable for enhancing growth capacity (Conesa *et al.*, 2017, p. 181). For breeding purposes, it is essential to incorporate a combination of multiple resistance genes into the genotype and to identify stress-resilience mechanisms that can be utilized in further studies on stress tolerance (Wang *et al.*, 2023, p. 13; Witcombe *et al.*, 2008, pp. 710–711). Cold stress tolerance has also been investigated under field conditions to provide a comprehensive characterization of tomato genotypes for cold resistance.

A higher level of cold tolerance among wild tomato plants was also observed under field conditions, where multiple adverse factors typically interact beyond low temperatures alone. Notably, the shortest emergence periods were recorded for line spr 1 (15 days) and line spr 5 (16 days). Plant growth under stress conditions remained relatively high across all wild forms, with the fastest growth rates observed in lines sc 3 and sc 4. Tolerance to adverse conditions must be accompanied by stability, meaning that the trait should consistently manifest at a defined level. Environmental adaptability can be assessed through plasticity, expressed across various criteria (Georgieva and Kosev, 2016, p. 111). Among the studied plants exposed to a temperature of +1 °C for 12 hours

at the two true leaf stage, line spr 5 and line sc 3 exhibited the highest levels of cold tolerance, with resistance scores of 4.8 and 4.5, respectively.

The development of environmentally resilient crop varieties is a priority direction in agricultural breeding. To ensure that new cultivars possess resistance to stress factors, it is essential to have promising initial material for hybridization (Georgieva and Kosev, 2016, p. 109). Tomato is a cold-sensitive species that does not tolerate low temperatures during reproductive stages, which can lead to reduced yield (Kravchenko and Prylipka, 2007, pp. 7–8; Zhuk, Syvoraksha and Fedosiy, 2014, p. 26). In terms of pollen cold tolerance (pollen viability under low temperatures), the highest values were recorded for lines spr 5 and sc 3 –79 % and 61 %, respectively. Inter-specific crosses can lead to improvements in yield, composition, morphology, abiotic stress resistance, and heterosis (Bolger, 2014).

The use of both annual environmental conditions and cultivation settings as testing environments enables the evaluation of wheat breeding lines for adaptive capacity and stability, and facilitates the identification of the most promising genotypes (Starychenko *et al.*, 2014, pp. 79, 82). Stability, as determined by the homeostasis index (HOM), reflects the response of each genotype, with higher HOM values indicating greater stability. In our laboratory experiment assessing growth under stress conditions at fluctuating temperatures ranging from 0 °C to +16 °C, lines spr 5 and sc 3 demonstrated high stability but low adaptability (HOM = 1.6).

Statistical analysis of data on seedling cold tolerance and pollen viability under cold stress conditions revealed that lines derived from wild species exhibited high stability based on the bi coefficient and moderate stability according to the HOM index. Conversely, lines with high HOM-based stability showed only moderate cold tolerance stability in seedlings, as indicated by bi values in lines spr 5 and sc 3 (bi = 1.4 and 1.45; HOM = 0.46 and 0.53). A similar trend was observed for pollen viability under cold stress in the same lines, spr 5 and sc 3, where both stability indices were among the highest across the studied genotypes (HOM = 1.17 and 1.13; bi = 2.79 and 1.61). This indicates the reliability and consistency of trait expression. Regarding overall adaptive capacity, only line sc 4 demonstrated a higher adaptability index for seedling cold tolerance (ZAZi = 0.9), but exhibited low pollen viability, whereas line sc 3 had a low ZAZi for seedling cold tolerance and a high level of pollen viability (ZAZi = 14.2).

This study demonstrates that wild genotypes vary in their cold resistance and recovery rates after temperature normalization. However, a general pattern in trait expression was also evident, suggesting the presence of cold tolerance-related genes. According to Boyle, Li and Pritchard (2017, pp. 6–7), the previously proposed omnigenic theory suggests that nearly any gene may influence a complex trait, although their contributions vary. The theory highlights a clear relationship between almost any gene and complex trait expression, with differential gene contributions. These findings may assist breeders in selecting more diverse germplasm and avoiding less effective crosses between closely related samples (Pailles *et al.*, 2017, p. 2).

Conclusions

In this study, wild tomato genotypes were evaluated for their resistance to cold stress using several modes of exposure to low temperatures at different stages of plant development. Using sequential phases of tomato plant growth – seeds, seedlings, and pollen – under cold stress as research objects made it possible to select plants with greater cold resistance and a greater number of genes responsible for cold resistance, which is valuable for the climatic conditions of Ukraine. Many researchers have studied resistance to low-temperature stress in *Solanum* species, but often neglected to conduct a sequential study of several different phases of tomato plant growth and to combine different experiments, which was done in this study.

The study used wild *Solanum* genotypes as a source of resistance to low temperatures that cross well with other genotypes to produce fertile offspring in order to enrich the genotype of commercial tomato varieties for cold resistance. Only two wild tomato genotypes proved to be more resistant during cold stress and recovered growth better, and had better pollen viability. They also showed stable cold resistance in different years of the study. At the germination stage, spr 5 and sc 3 showed greater growth after cold stress and high stability in germination and growth traits. Across multi-year field trials, spr 5 consistently exhibited robust cold resistance and is recommended for further breeding. The subsequent study, only line spr 5 consistently showed resistance to low-temperature stress in the field in different years of cultivation and will be used in further breeding work.

The results of testing seedlings and pollen for cold resistance also confirmed the value of line spr 5 for use in breeding for resistance to cold stress. The sc 3 line was slightly inferior in terms of cold resistance in previous experiments, but in terms of cold resistance of seedlings and pollen, it had high cold resistance and stable expression of cold resistance over the years of research. These wild genotypes can be used in cold resistance studies and will be valuable for breeding programs in breeding for cold stress resistance. Recovery speed after stress is as important as absolute resistance; genotypes that recover rapidly may be more agronomically valuable than those that merely tolerate stress. Plants that recover slowly after low-temperature stress and have average resistance are less valuable than plants with average cold resistance but that recover quickly after stress. We recommend this multi-stage approach for assessing low-temperature resistance and intend to use the identified wild genotypes in future breeding to develop cold-resistant hybrids and cultivars.

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Authors' Declarations and Essential Ethical Compliances

Authors' Contributions (in accordance with ICMJE criteria for authorship)

<i>Contribution</i>	<i>Author 1</i>	<i>Author 2</i>	<i>Author 3</i>	<i>Author 4</i>	<i>Author 5</i>	<i>Author 6</i>	<i>Author 7</i>
Conceived and designed the research or analysis	Yes	Yes	Yes	Yes	No	No	No
Collected the data	No	Yes	No	No	No	No	No
Contributed to data analysis & interpretation	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Wrote the article/paper	Yes	Yes	No	No	No	No	No
Critical revision of the article/paper	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Editing of the article/paper	No	Yes	No	No	No	No	No
Supervision	Yes	No	Yes	Yes	Yes	Yes	Yes
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Research involving human bodies or organs or tissues (Helsinki Declaration)

The author(s) solemnly declare(s) that this research has not involved any human subject (body or organs) for experimentation. It was not clinical research. The contexts of human population/participation were only indirectly covered through literature review. Therefore, an Ethical Clearance (from a Committee or Authority) or ethical obligation of Helsinki Declaration does not apply in cases of this study or written work.

Research involving animals (ARRIVE Checklist)

The author(s) solemnly declare(s) that this research has not involved any animal subject (body or organs) for experimentation. The research was not based on laboratory experiment involving any kind animal. The contexts of animals were only indirectly covered through literature review. Therefore, an Ethical Clearance (from a Committee or Authority) or ethical obligation of ARRIVE does not apply in cases of this study or written work.

Research on Indigenous Peoples and/or Traditional Knowledge

The author(s) solemnly declare(s) that this research has not involved Indigenous Peoples as participants or respondents. The contexts of Indigenous Peoples or Indigenous Knowledge were only indirectly covered through literature review. Therefore, an Ethical Clearance (from a Committee or Authority) or prior informed consent (PIC) of the respondents or Self-Declaration in this regard does not apply in cases of this study or written work.

Research involving Plants

The author(s) solemnly declare(s) that this research has involved the plants for experiment and field studies. Some contexts of plants are also indirectly covered through literature review. Thus, during this research the author(s) obeyed the principles of the Convention on Biological Diversity and the Convention on the Trade in Endangered Species of Wild Fauna and Flora.

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