Combining ability and genetic diversity under low-temperature conditions at germination stage of maize (Zea mays L.)

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Abstract Low temperatures are important for the production of spring maize in northern China. While the low-temperature tolerance of maize seeds can be improved by coating them, this can result in environmental pollution, high costs, and instability. Therefore, identifying new varieties of maize is the most effective method of improving the ability of maize crops to withstand low temperatures. In this experiment, four low-temperature tolerant maize inbred lines (DNF266, Zhong 451, B73, Dan 340) and four low-temperature sensitive maize inbred lines (Luyuan 92, Ji 853, Huangzaosi, Si 144) were selected from the northern spring maize area. The griffing double-row hybridization design method was used to prepare 28 hybrid combinations. After analysing the general combining ability and the special combining ability of each combination, we found that the indoor low-temperature index and low-temperature seedings were extremely similar for all combinations. The hybridization and parental inbred lines were subjected to low-temperature treatments under both laboratory conditions and in the field. Several low-temperature indexes were assessed to identify what results could be produced from combining them. Under both treatments, the inbred line DNF266 had a higher general combining ability and the Zhong 451 × Dan 340 hybrid combination had a higher special combining ability. These results provide technical support for breeding new low-temperature varieties of maize.

Keywords Maize · Low-temperature tolerance · Double-column hybridization · Combining ability

Introduction

Maize (Zea mays L.) is one of the most widely grown crops in the world, comprising 40% of global cereal production (Bouis and Ross 2010). It is the most commonly planted crop in China, however, low temperatures limit maize production in temperate regions. Low temperatures reduce the emergence rate, seedling vigour, and early vigour, and produce chlorotic leaves (Miedema 1982). Therefore, improving the low-temperature tolerance of maize is a primary goal of maize breeding programs. Considering the complex genetic makeup of these target traits,
recurrent selection is the most common method of producing low-temperature tolerant maize varieties.

The key to identifying low-temperature tolerance is using reasonable indicators. Identifying the time required to produce 50% of a 1-cm coleoptile is an effective method of identifying corn hybrids that can tolerate low temperatures during the germination period and early growth stage (Hope et al. 1992). Important metrics for identifying lines susceptible to low temperatures include the percent germination, percent viability, and average time to germination (Hodges et al. 1994). The low-temperature tolerance of Andean maize accessions was analysed during the heterotrophic growth stage and in the early autotrophic growth stages by identifying the germination percentage, the germination index, and the plant growth rate (Brandolini et al. 2000). Additional metrics for assessing inbred maize varieties included measuring the emergence percentage 30 days after they were planted, assessing the emergence index (which approximates emergence rate), and measuring the seedling dry weight, which was obtained 42 days after the maize was planted (Mock and Mcneill 1979).

Few inbred maize populations can serve as base germplasm for breeding low-temperature tolerant varieties at the early stages of development. The inbred line EP80 demonstrated a high emergence percentage and quick seedling growth, while the F7 line demonstrated high emergence under low temperatures (Revilla et al. 2006). BOZM 855, PMS 636, Poblacion D, Poblacion E, and BOZM 696 were accessions that could be used to develop low-temperature tolerance in adapted maize genotypes (Brandolini et al. 2000). One study reported that B73, (V3 × B14)-2-1, and Mo17 were the best low-temperature-tolerant inbred lines (McConnell and Gardner 1979). Arangal was the best option to improve adaptation during the early sowing stage, while the Tuy × Lazcano hybrid was the optimal choice for breeding lines to adapt to low temperatures in the field (Revilla et al. 2006).

The genetic characteristics dictating maize’s tolerance to low temperatures is complicated: the growth and vigour of seedlings under field conditions are primarily due to the effects of additive and dominant genes (McConnell and Gardner 1979). Additional research found that the genetic regulation of low-temperature tolerance traits conformed to an additive-dominance model (Revilla et al. 2000). Genetic traits associated with low-temperature tolerance at both the germination stage and the seedling stage were mapped via QTL, with different populations assessed at various temperatures. For instance, five meta-QTLs (mQTLs) were detected in 26 QTLs associated with seed vigour at 18 °C. Six QTLs were identified for LTGA at 18/12 °C (day/night) (Shi et al. 2016). Forty-three QTLs were linked to the low-temperature tolerance of emergence rate, germination index, seedling root length, shoot length, and total length at 10 °C (Li et al. 2018). Based on the QTLs identified, maize low-temperature tolerance is primarily driven by genetic predisposition and current environmental factors.

In this study, the relative low-temperature sensitivity of 28 maize hybrids derived from the diallel crosses of eight inbred lines was evaluated under both laboratory and field conditions to analyse differences in low-temperature sensitivity. Similarly, estimates of general combining ability (GCA) and specific combining ability (SCA) were examined to evaluate the low-temperature performance of inbred hybrid combinations (GCA) and derived hybrids, based on parent performance (SCA) of hybrid combinations. This study identified the low-temperature tolerance of maize inbred lines and their hybrid combinations under both laboratory and field conditions during the germination period. The results of this study include results obtained under controlled laboratory conditions, as well as results obtained under field conditions. Results obtained under field conditions were more instructive for researching low-temperature tolerance during the germination period and for selecting breeding materials.

### Materials and methods

**Maize germplasm**

We placed eight parental inbred lines in an 8 × 8 diallel, which generated 28 hybrids. The eight parent lines were P1 (DNF266), P2 (Zhong 451), P3 (Luyuan 92), P4 (B73), P5 (Ji 853), P6 (Huangzaosi), P7 (Si 144), and P8 (Dan 340). Lines P1, P2, P4, and P8 were classified as low-temperature resistant, while lines P3, P5, P6, and P7 were classified as low-temperature sensitive (Fig. 1). All of the lines are germplasm from the north spring maize area and were chosen because...
they represent the various heterotic groups recently bred in Chinese programs. The origin and other characteristics of the lines used are shown in Supplementary Table 1.

These 28 maize hybrids were generated from a complete diallel table of eight parental varieties chosen for their different sensitivities to low temperatures. The parent lines were sown in the field, with 20 cm between plants and 65 cm between rows. These tests were performed in 2017 in Heilongjiang Province, China. The healthy seeds of parents and crosses were stored at 4°C after harvest. Using a standard germination test (at 25°C), we found that 28 crosses had initial germination percentages higher than 90%.

Identification of low-temperature tolerance during germination

In laboratory settings, two series of germination experiments were performed in the growth cabinet. The seed surface was first disinfected with 1% NaClO (sodium hypochlorite) for five minutes and sterile water was used to wash the seeds three times each in preparation for the experiment. The sterilized seeds were then sown on wet germination paper and on another sheet of humid paper (Li et al. 2018). In one series, the seeds were subjected to a constant temperature of 25°C. In the other series, we applied a temperature range of 6°C for five days to a constant temperature of 10°C. The seeds were observed once a day. Once seedling coleoptile length reached 1 cm, they were considered to have germinated. After incubation at 10°C for 25 days and at 25°C for six days, radicle traits were measured by the Epson PerfectionV800. Three independent experiments were performed for both the control and the treatment conditions.

Field experiments were conducted at Harbin, Heilongjiang Province, China (45.8N126.9E, 135 MASL elevation). The F1 hybrids and their parental inbreds were evaluated separately under low-temperature and normal-temperature conditions. We calculated the five-day averages of the soil temperatures in the fields. The low-temperature treatment group was sown when the ground temperature stabilized at 6°C. The normal sowing time was used as a control. A randomized block design was used to plant all of the hybrids and parental lines (including their controls), with three replications each. Each replications plant

Fig. 1 Germination rate of hybrid line at low temperature. A Germination rate of P3 line at 6°C. B Germination rate of P1 line at 6°C. C Radicle length and seedling length of P3 line at 6°C and 25°C. D Radicle length and seedling length of the line P1 at 6°C and 25°C.
three rows. Each row was 5.0 m long, with 0.25 m between plants and 0.65 m between rows. In order to compensate for the border effect, the borders of both the low-temperature and normal-temperature experiments were bounded by two hybrid rows.

Collection of phenotypic data

In laboratory settings, the germination rate (GR) was expressed as the percentage of germinating plants of the total number of seeds used. The radicle length (RL) and seedling length (SL) were measured using an Epson Perfection V800 scanner.

The field experiment statistics involving the germination rate were calculated on the last day. Plant height (PH) and ear height (EH) were recorded on ten plants per block following silking. After harvest, the hundred-grain weight (HW) and plot yield (PY) were recorded, trait by trait, for 10 plants from each block.

We identified significant differences in all traits for the half-diallel cross hybrids (Table 1). The hybrids were comprised of six tolerant × tolerant (T × T) crosses (Group I), 12 tolerant × susceptible (T × S) hybrids (Group II), four susceptible × tolerant (S × T) hybrids (Group III), and six susceptible × susceptible (S × S) hybrids (Group IV). Their mean low-temperature traits are displayed in Table 1. No significant differences were observed between each group of crosses for the two environments, except for Group IV (S × S) under low-temperature conditions.

Results

The effect of low temperatures on related hybrid traits

Under low-temperature conditions, the relative germination rate ranged from 33.00 to 84.42%, the relative radicle length ranged from 31.99 to 79.03%, the relative seedling length ranged from 48.75 to 87.56%, the relative plot yield ranged from 63.48 to 103.46%, the relative hundred-grain weight ranged from 71.42 to 105.85%, the relative ear height ranged from 59.11 to 109.34%, the relative seedling length ranged from 48.75 to 87.56%, the relative plant height ranged from 78.58 to 105.50%, the relative emergence rate ranged from 90.53% to 90.50%, and 86.35% respectively. The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively). The hybrids P2 and P3 had the highest relative radicle length (79.03%, 74.68%, and 69.95% respectively).
respectively). The hybrids with the highest relative plant height were P4 × P6, P2 × P4, and P2 × P6 (105.50%, 101.13%, and 98.11% respectively), followed by the hybrids P2 × P8, P2 × P5, and P1 × P7 (97.77%, 97.65%, and 97.41% respectively). The hybrids P2 × P4, P2 × P6, and P2 × P8 had the highest relative ear height (109.34%, 109.25%, and 105.26% respectively). Under low-temperature

| Cross       | RGR (%) | RRL (%) | RSL (%) | RER (%) | RPH (%) | REH (%) | RHW (%) | RPY (%) |
|-------------|---------|---------|---------|---------|---------|---------|---------|---------|
| Group I: Tolerant × Tolerant crosses |
| P1 × P2     | 54.93   | 36.52   | 64.61   | 63.41   | 93.04   | 95.98   | 76.01   | 98.89   |
| P1 × P4     | 67.80   | 42.10   | 90.53   | 87.56   | 90.27   | 87.99   | 101.54  | 90.56   |
| P1 × P8     | 64.63   | 41.76   | 63.53   | 80.95   | 91.32   | 90.76   | 99.49   | 78.37   |
| P2 × P4     | 64.45   | 49.69   | 57.54   | 81.27   | 101.13  | 109.34  | 81.45   | 78.11   |
| P2 × P8     | 68.41   | 79.03   | 51.88   | 67.13   | 97.77   | 105.26  | 105.85  | 84.46   |
| P4 × P8     | 49.66   | 53.88   | 54.36   | 75.86   | 95.52   | 103.05  | 91.20   | 79.11   |
| Mean        | 54.93   | 50.50   | 63.74   | 76.03   | 94.84   | 98.73   | 92.59   | 84.92   |
| Group II: Tolerant × Susceptible crosses |
| P1 × P3     | 75.33   | 44.39   | 84.87   | 75.00   | 91.07   | 87.19   | 89.53   | 91.43   |
| P1 × P5     | 65.00   | 49.43   | 82.01   | 37.33   | 88.36   | 82.64   | 96.18   | 88.00   |
| P1 × P6     | 75.34   | 37.46   | 57.33   | 79.40   | 93.38   | 95.96   | 92.38   | 90.67   |
| P1 × P7     | 83.55   | 51.50   | 75.08   | 77.94   | 97.41   | 85.03   | 98.58   | 94.88   |
| P2 × P3     | 47.94   | 55.97   | 83.22   | 58.65   | 86.20   | 85.39   | 71.42   | 71.58   |
| P2 × P5     | 81.00   | 74.68   | 90.50   | 73.58   | 97.65   | 86.59   | 84.56   | 95.70   |
| P2 × P6     | 72.67   | 48.57   | 56.22   | 73.33   | 98.11   | 109.25  | 96.59   | 82.16   |
| P2 × P7     | 79.67   | 54.31   | 78.75   | 43.00   | 95.62   | 94.03   | 95.72   | 98.33   |
| P3 × P4     | 75.67   | 39.44   | 62.04   | 77.00   | 92.86   | 89.23   | 104.34  | 86.22   |
| P4 × P5     | 58.99   | 31.99   | 52.27   | 61.87   | 78.58   | 59.11   | 99.61   | 92.43   |
| P4 × P6     | 78.23   | 47.60   | 53.61   | 41.19   | 105.50  | 82.83   | 83.15   | 103.46  |
| P4 × P7     | 69.61   | 47.74   | 81.24   | 61.50   | 88.71   | 79.34   | 104.57  | 85.89   |
| Mean        | 71.92   | 48.59   | 71.34   | 63.32   | 92.79   | 86.38   | 93.05   | 90.06   |
| Group III: Susceptible × Tolerant crosses |
| P3 × P8     | 66.79   | 69.95   | 86.35   | 63.70   | 97.25   | 94.92   | 95.64   | 99.98   |
| P5 × P8     | 68.24   | 46.88   | 58.28   | 69.93   | 95.20   | 90.80   | 86.32   | 85.37   |
| P6 × P8     | 63.18   | 57.18   | 79.52   | 77.06   | 90.70   | 86.05   | 97.34   | 78.29   |
| P7 × P8     | 65.54   | 62.47   | 60.49   | 75.37   | 85.23   | 75.92   | 88.33   | 75.33   |
| Mean        | 65.94   | 59.12   | 71.16   | 71.52   | 92.10   | 86.92   | 91.91   | 84.74   |
| Group IV: Susceptible × Susceptible crosses |
| P3 × P5     | 63.49   | 50.43   | 69.63   | 55.37   | 92.46   | 88.56   | 94.21   | 95.80   |
| P3 × P6     | 69.12   | 48.82   | 56.88   | 74.54   | 88.53   | 76.55   | 100.31  | 63.48   |
| P3 × P7     | 84.42   | 39.62   | 55.22   | 74.43   | 94.95   | 102.88  | 94.85   | 93.18   |
| P5 × P6     | 70.95   | 50.81   | 73.37   | 80.05   | 88.05   | 71.16   | 78.05   | 87.03   |
| P5 × P7     | 33.00   | 33.96   | 48.75   | 74.00   | 95.74   | 96.28   | 85.51   | 100.28  |
| P6 × P7     | 58.41   | 36.16   | 56.10   | 86.06   | 87.62   | 82.71   | 81.62   | 86.12   |
| Mean        | 63.23   | 43.30   | 59.99   | 74.07   | 91.23   | 86.36   | 89.09   | 87.65   |

*RGR* relative germination rate, *RRL* relative radicle length, *RSL* relative seedling length, *RER* relative emergence rate, *RPH* relative plant height, *REH* relative ear height, *RHW* relative hundred-grain weight, *RPY* relative plot yield
conditions, the hybrids P2 × P8, P4 × P7, and P3 × P4 had the top relative hundred-grain weight (105.85%, 104.57%, and 104.34% respectively). The hybrids with the highest relative plot yield were P4 × P6, P5 × P7, and P3 × P8 (103.46%, 100.28%, and 99.98% respectively). When considering all traits, P2 × P8 performed best under low-temperature conditions.

Phenotypic correlations of low-temperature related traits

The phenotypic correlation coefficients for the three low-temperature traits under laboratory conditions were all highly significant (Fig. 2). We performed a correlation analysis to assess the relative values of each index under low-temperature conditions. The genotypic correlations for these traits ranged from −0.21 to 0.96. There were high correlations (P < 0.001) between the following traits: relative germination rate and relative emergence rate (0.72), relative germination rate and relative seedling length (0.79), relative germination rate and relative emergence rate (0.96), relative germination rate and relative plot yield (0.51), relative radicle length and relative seedling length (0.78), relative seedling length and relative emergence rate (0.85), relative seedling length and relative plot yield (0.65), relative emergence rate and relative plot yield (0.53), and relative plant height and relative ear height (0.71). Relative radicle length and relative seedling length (0.35) were significantly correlated (P < 0.05). There were large and significant correlations between relative germination and relative emergence rate with relative plot yield. Relative emergence rate and relative plot yield were selected as traits to improve low-temperature tolerance under field conditions, when possible.

Genetic variation of parental lines and their hybrids by analysis of variance

Statistical methods were used to assess different traits surrounding specific combining ability and general combining ability (Table 2). Analysis of variance for traits related to low-temperature tolerance indicated that genotypic effects were highly significant (P < 0.01). GCA and SCA variation across these lines were both highly significant for all measured traits (P < 0.01). These results indicate that genetic effects were primarily responsible for the variance in combining ability. Heritability for relative germination rate (0.60), relative radicle length (0.63), relative seedling length (0.59), relative emergence rate (0.59), relative ear height (0.57), and relative hundred-grain weight (0.57) were all relatively high (> 0.50) under low-temperature conditions. This indicates that these three traits could be better candidates than other traits for improving low-temperature tolerance in maize. The relative importance of GCA and SCA was estimated as the ratio. As this ratio approaches one, GCA becomes more important, and the predictability of the performance of a specific hybrid could be based on GCA alone. The ratio for relative seedling length was 0.45, the ratio for relative germination rate was 0.42, the ratio for relative radicle length was 0.40, the ratio for relative plant height was 0.38, and the ratio for relative hundred-grain weight was 0.35. This indicates that relative seedling length, relative germination rate, and relative radicle length are primarily determined by additive and dominance gene effects.

Effects of general combining ability on parental inbred lines under low temperatures

GCA effects were significant for all inbred parental lines. The GCA range for relative germination rate was −7.09 to 4.40, for relative radicle length was −4.00 to 5.30, for relative seedling length was −3.11 to 7.71, for relative emergence rate was −4.94 to 2.85, for relative plant height was −4.42 to 2.64, for relative ear height was −4.39 to 3.80, for relative hundred-grain weight crosses was −3.85 to 2.51, and for highest relative plot yield was −3.84 to 2.97 (Table 3). The P1 line exhibited the highest significant positive GCA effect (4.40) and the P7 line exhibited a negative significant positive GCA effect (−7.09) for relative germination rate. Highly significant (P < 0.01) positive GCA effects were observed for the P1 line (5.30) and the P8 line (−4.00), while highly significant (P < 0.01) negative GCA effects were observed for relative radicle length. The P1 line exhibited the highest significant positive GCA effect (7.71) and the P6 line exhibited a negative significant positive GCA effect (−3.11) for relative seedling length. The highest significant positive GCA effect was observed for the P1 line (2.85) and the highest significant negative GCA effect was observed for the P5 line (−4.94) at the relative emergence rate. The highest
significant positive GCA effect was observed for line P2 (2.64) and the highest significant negative GCA effect was observed for line P8 (−4.42) at relative plant height. Highly significant ($P < 0.01$) positive GCA effects were observed for line P1 (3.80) and line P5 (−4.39), while highly significant ($P < 0.01$) negative GCA effects were observed at relative ear height. The highest significant positive GCA effect was observed for line P8 (2.51) and the highest significant negative GCA effect was observed for line P2 (−3.85) at relative hundred-grain weight. The highest significant positive GCA effect was observed for line P7 (2.97) and the highest significant negative GCA effect was observed for line P6 (−3.84) at relative plot yield. As stated above, P1 had a positive GCA effect for all traits under low temperatures.
Specific combining ability effects of diallel crosses for low-temperature related traits

Highly significant SCA effects were detected for all traits (Table 4). The range of SCA for relative germination rate was −19.03 to 21.12, for relative plant height was −13.28 to 16.32, for relative seedling length was −10.71 to 20.73, for relative emergence rate was −25.59 to 13.64, for relative ear height was −10.01 to 8.14, for relative hundred-grain weight hybrids was −12.55 to 12.18, and for highest relative plot yield was −12.15 to 18.88. The highest significant positive SCA effects were observed in the P2 × P8, P3 × P7, and P2 × P7 lines (21.12, 16.19, and 12.89 respectively), and the highest significant negative SCA effects were observed for the P5 × P7, P4 × P6, and P6 × P7 lines (−19.03, −11.54, and −8.55, respectively) at the relative germination rate. Highly significant (P < 0.01) positive SCA effects were observed for the P2 × P5, P2 × P8, and P3 × P8 lines (16.32, 15.98, and 11.71, respectively) at relative radicle length, while highly significant (P < 0.01) negative SCA effects were observed for the P5 × P7, P4 × P5, and P6 × P7 lines (−13.28, −10.67, and −7.98, respectively). The highest significant positive SCA effects were observed for the P2 × P5, P6 × P8, and P4 × P7 lines (20.73, 16.59, and 16.28, respectively), and the highest significant negative SCA effects were observed for the P3 × P7, P1 × P6, and P5 × P7 lines (−10.71, −10.70, and −10.31, respectively) at relative seedling length. The P2 × P5, P2 × P4, and P5 × P6 lines exhibited the highest significant positive SCA effects (13.64, 11.64, and 11.32, respectively), and the P4 × P6, P1 × P5, and P2 × P7 lines exhibited a negative significant positive SCA effect for relative emergence rate (−25.59, −19.61, and −14.47, respectively). The

Table 2 Analysis of variance for GCA effects and SCA effects in different lines for low-temperature related traits

| Source   | RGR    | RRL    | RSL    | RER    | RPH    | REH    | RHW    | RPY    |
|----------|--------|--------|--------|--------|--------|--------|--------|--------|
| Genotype | 8.13***| 8.74***| 8.54***| 6.86***| 3.20***| 3.42***| 6.49***| 5.86***|
| GCA      | 10.93***| 11.05***| 12.54***| 6.90***| 3.75***| 2.80***| 6.79***| 4.14***|
| SCA      | 7.43***| 8.16***| 7.54***| 6.85***| 3.06***| 3.57***| 6.41***| 6.29***|
| Ratio    | 0.42   | 0.40   | 0.45   | 0.33   | 0.38   | 0.28   | 0.35   | 0.25   |
| Heritability | 0.60   | 0.63   | 0.59   | 0.59   | 0.34   | 0.39   | 0.57   | 0.57   |

RGR relative germination rate, RRL relative radicle length, RSL relative seedling length, RER relative emergence rate, RPH relative plant height, REH relative ear height, RHW relative hundred-grain weight, RPY relative plot yield

***P < 0.001

Table 3 General combining ability effects of inbred lines for low-temperature related traits

| Line | RGR    | RRL    | RSL    | RER    | RPH    | REH    | RHW    | RPY    |
|------|--------|--------|--------|--------|--------|--------|--------|--------|
| P1   | 4.40***| 5.30***| 7.71***| 2.85***| 2.46   | 3.80***| 0.69   | 1.08   |
| P2   | 1.16   | 1.86   | −1.44  | −3.23  | 2.64***| 2.94   | −3.85***| −1.86  |
| P3   | −0.49  | −0.68  | 4.75   | −3.45  | 1.27   | 0.66   | 1.42   | −1.23  |
| P4   | 4.15   | −3.16  | −2.73  | 2.83   | 0.60   | −0.86  | 0.92   | −1.07  |
| P5   | −4.34  | 1.70   | −0.51  | −4.94***| −1.20  | −4.39***| −0.63  | 1.91   |
| P6   | 0.69   | −1.95  | −3.11***| 3.95   | −1.72  | 1.20   | −2.09  | −3.84***|
| P7   | −7.09***| 0.92   | −1.72  | 0.24   | 0.37   | 0.82   | 1.03   | 2.97***|
| P8   | 1.51   | −4.00***| −2.94  | 1.75   | −4.42***| −4.18  | 2.51***| 2.05   |

RGR relative germination rate, RRL relative radicle length, RSL relative seedling length, RER relative emergence rate, RPH relative plant height, REH relative ear height, RHW relative hundred-grain weight, RPY relative plot yield

***P < 0.001

Specific combining ability effects of diallel crosses for low-temperature related traits

Highly significant SCA effects were detected for all traits (Table 4). The range of SCA for relative germination rate was −19.03 to 21.12, for relative plant height was −11.25 to 19.73, for relative radicle length was −13.28 to 16.32, for relative seedling length was −10.71 to 20.73, for relative emergence rate was −25.59 to 13.64, for relative ear height was −10.01 to 8.14, for relative hundred-grain weight hybrids was −12.55 to 12.18, and for highest relative plot yield was −12.15 to 18.88. The highest significant positive SCA effects were observed in the P2 × P8, P3 × P7, and P2 × P7 lines (21.12, 16.19, and 12.89 respectively), and the highest significant negative SCA effects were observed for the P5 × P7, P4 × P6, and P6 × P7 lines (−19.03, −11.54, and −8.55, respectively) at the relative germination rate. Highly significant (P < 0.01) positive SCA effects were observed for the P2 × P5, P2 × P8, and P3 × P8 lines (16.32, 15.98, and 11.71, respectively) at relative radicle length, while highly significant (P < 0.01) negative SCA effects were observed for the P5 × P7, P4 × P5, and P6 × P7 lines (−13.28, −10.67, and −7.98, respectively). The highest significant positive SCA effects were observed for the P2 × P5, P6 × P8, and P4 × P7 lines (20.73, 16.59, and 16.28, respectively), and the highest significant negative SCA effects were observed for the P3 × P7, P1 × P6, and P5 × P7 lines (−10.71, −10.70, and −10.31, respectively) at relative seedling length. The P2 × P5, P2 × P4, and P5 × P6 lines exhibited the highest significant positive SCA effects (13.64, 11.64, and 11.32, respectively), and the P4 × P6, P1 × P5, and P2 × P7 lines exhibited a negative significant positive SCA effect for relative emergence rate (−25.59, −19.61, and −14.47, respectively). The
Table 4 Specific combining ability effects of low-temperature related traits in hybrids

| Hybrid   | RGR  | RRL  | RSL  | RER  | RPH  | REH  | RHW  | RPY  |
|----------|------|------|------|------|------|------|------|------|
| P1 × P2  | −7.08| −6.61| −6.91| −1.77| −2.49| −1.39| −8.38| 11.33|
| P1 × P3  | 7.96 | 1.84 | 2.10 | 7.14 | 1.20 | 1.55 | −3.51| 5.10 |
| P1 × P4  | −1.03| 2.61 | 13.82| 10.29| 0.47 | 1.88 | 6.00 | 4.29 |
| P1 × P5  | 3.55 | 3.24 | 5.21 | −19.61| 0.83 | 0.47 | 3.53 | −0.61|
| P1 × P6  | 2.72 | −2.09| −10.70| 3.04 | 7.43 | −3.82| 2.14 | 7.14 |
| P1 × P7  | 10.23| 5.57 | 1.22 | 5.66 | 4.06 | 4.24 | 3.66 | 3.49 |
| P1 × P8  | −2.30| −6.11| −6.22| 6.41 | −3.72| −2.84| 2.87 | −7.98|
| P2 × P3  | −7.02| 4.66 | 10.01| 0.96 | −10.53| −2.81| −12.55| −6.85|
| P2 × P4  | 2.03 | 2.44 | −1.77| 11.64| 2.89 | 5.35 | −4.53| 2.11 |
| P2 × P5  | −1.38| 16.32| 20.73| 13.64| 4.32 | −10.01| −0.64| −0.47|
| P2 × P6  | 6.29 | 0.38 | −2.39| 4.57 | 0.87 | −6.39| 9.84 | 3.69 |
| P2 × P7  | 12.89| 1.82 | 13.13| −14.47| −9.82| −2.98| 6.06 | 9.01 |
| P2 × P8  | 21.12| 15.98| −5.81| 2.11 | 19.73| 6.39 | 12.18| 8.10 |
| P3 × P4  | 10.19| −2.71| −4.58| 8.66 | −11.25| 8.14 | 7.37 | 3.34 |
| P3 × P5  | 7.72 | 0.67 | −1.10| 0.20 | 0.31 | 4.25 | 1.32 | 7.54 |
| P3 × P6  | 3.37 | 3.11 | −8.08| 5.69 | 5.04 | 6.40 | 7.36 | −10.95|
| P3 × P7  | 16.19| −6.66| −10.71| 9.32 | −8.80| 1.57 | 0.14 | 4.52 |
| P3 × P8  | 4.64 | 11.71| 13.86| −0.24| −2.80| 3.07 | −0.75| 10.54|
| P4 × P5  | 1.02 | −10.67| −6.65| −1.20| −8.88| −1.31| 5.87 | 4.86 |
| P4 × P6  | −11.54| 4.68 | −3.05| −25.59| −2.16| −3.06| −5.91| 18.88|
| P4 × P7  | 1.75 | 1.92 | 16.28| −6.66| −8.89| 3.39 | 7.93 | −1.11|
| P4 × P8  | 6.87 | 2.14 | −2.65| 2.61 | 6.96 | −6.15| −3.58| −5.28|
| P5 × P6  | 8.09 | 2.23 | 9.55 | 11.32| 17.72| −0.26| −7.28| 3.57 |
| P5 × P7  | −19.03| −13.28| −10.31| 10.49| −7.95| −3.92| −4.82| 6.70 |
| P5 × P8  | 9.07 | −7.97| −1.93| 5.93 | −7.53| −1.95| −5.69| −3.56|
| P6 × P7  | −8.55| −7.98| −2.20| 10.64| 1.22 | −3.14| −6.27| 1.83 |
| P6 × P8  | −3.31| 3.40 | 16.59| 2.38 | −2.61| −1.07| 4.04 | −3.12|
| P7 × P8  | −0.18| 4.51 | 0.93 | 4.83 | 6.85 | 1.33 | −5.84| −12.15|

RGR relative germination rate, RRL relative radicle length, RSL relative seedling length, RER relative emergence rate, RPH relative plant height, REH relative ear height, RHW relative hundred-grain weight, RPY relative plot yield

P2 × P8, P5 × P6, and P1 × P6 lines exhibited the highest significant positive SCA effects (19.73, 17.72, and 7.43, respectively), and the P3 × P4, P2 × P3, and P2 × P7 lines had the highest significant negative SCA effects at relative plant height (−11.25, −10.53, and −9.82, respectively). Highly significant (P < 0.01) positive SCA effects were observed for the P3 × P4, P3 × P6, and P2 × P8 lines (8.14, 6.40, and 6.39, respectively) at relative ear height, while highly significant (P < 0.01) negative SCA effects were observed for the P2 × P5, P2 × P6, and P4 × P8 lines (−10.01, −6.39, and −6.15, respectively). The highest significant positive SCA effects were observed for the P2 × P8, P2 × P6, and P4 × P7 lines (12.18, 9.84, and 7.93, respectively), and the highest significant negative SCA effects were observed for the P2 × P3, P1 × P2, and P5 × P6 lines (−12.55, −8.38, and −7.28, respectively) at relative hundred-grain weight. The highest significant positive SCA effects were observed for the P4 × P6, P1 × P2, and P3 × P8 lines (18.88, 11.33, and 10.54, respectively), and the highest significant negative SCA effects were observed for the P7 × P8, P3 × P6, and P1 × P8 lines (−12.15, −10.95 and −7.98, respectively) at relative plot yield. As stated above, the
hybrid P2 × P8 had a higher positive SCA effect for all traits under low temperatures.

**Discussion**

Maize is more sensitive to low-temperature stress in the early stages of growth and development than in later stages of development. Therefore, the focus of low-temperature tolerance research has primarily concentrated on the germination stage of maize and been conducted in the field or in the laboratory. However, few experiments have been conducted in both settings. In the laboratory, the heritability for relative germination rate was 0.59, the heritability for relative radicle length was 0.63, and the heritability for relative seedling length was 0.59. A correlation analysis demonstrated that the correlation between relative germination rate and relative emergence rate was both positive and significant. A correlation analysis also demonstrated that the relationship between relative germination rate with both relative radicle length and relative seedling length was both positive and significant. This indicates that these traits could better respond to selection measures seeking to improve low-temperature tolerance in maize. The results of this study appeared consistent with the findings of other researchers (Brandolini et al. 2000; Hodges et al. 1994; Hope et al. 1992; McConnell and Gardner 1979; Mock and Mcneill 1979). In this study, four low-temperature tolerant maize inbred lines (P1, P2, P4, and P8) were obtained using the relative germination rate as a screening index during the germination period. Our results were consistent with the findings reported by other researchers who found that the best low-temperature tolerant inbred was B73 (Hu et al. 2016; Mock and Mcneill 1979). The relative germination rate ratio indicates that this trait is primarily dictated by the effects of additive and dominant genes, which confirms previous findings (Revilla et al. 2000). Under field conditions, heritability for relative emergence rate, relative ear height, and relative hundred-grain weight was relatively high (> 0.50). The correlation coefficients for relative emergence rate and relative plot yield, and relative plant height and relative ear height were both significant. These indicated that both relative emergence rate and relative ear height could respond better to selection pressure than other traits when seeking to improve low-temperature tolerance in maize.

Several studies have demonstrated that the low-temperature tolerance of hybrid combinations is related to the parent line (Hodges et al. 1997). In laboratory settings, the general combining ability of the two parental inbred lines displayed a positive effect, and the special combining ability of hybrid combinations also displayed a positive effect. These both had strong resistance to low-temperature treatments, however, when the hybrid combination displayed a negative effect, it still displayed strong low-temperature resistance. The general combining ability of the two parental inbred lines displayed both a positive effect and a negative effect, its special combining was mostly positive, and both had high resistance to low-temperature treatments. When the two parental inbred lines displayed negative effects, the special combining ability of the hybrid combination was generally negative and had weak low-temperature resistance when low temperatures were applied during germination. Results from the field study were consistent with those obtained under laboratory conditions. Under low-temperature treatment, the P1 line displayed a high positive effect on the general combining ability of various traits. The P1 × P3, P1 × P7, and P2 × P8 lines had high special combining ability for all traits. Therefore, parents with higher general combining ability must be chosen when breeding low-temperature resistant hybrids.

This study found that tolerant x susceptible (T × S) inbred hybrid lines had better resistance to low temperatures compared to tolerant x tolerant (T × T), susceptible x tolerant (S × T), and susceptible x susceptible (S × S) inbred lines. The average relative plot yield under low-temperature conditions of the T × S hybrids (90.06%) was the highest. Of the T × S hybrids, the highest relative plot yield under low-temperature conditions was the hybrid P4 × P6 (103.45%). These results conflict with the results of other studies that found higher grain yield in T × T hybrids (Badu-Apraku et al. 2013; Menkir et al. 2010). However, our results are consistent with studies that found higher yields in hybrids consisting of stress-tolerant and non-tolerant inbred lines (Betrán et al. 2003; Derera et al. 2007; Makumbi et al. 2011). According to previously unpublished analyses of inbred lines in the laboratory, the P2 and P8 lines
produced the most low-temperature tolerant hybrids. The P1 line had a higher relative germination rate, relative radicle length, relative seedling length, relative emergence, rate relative hundred-grain weight, and relative plot yield under low-temperature conditions during the germination period. It also had a high general combining ability. The results of this study indicated that the P1, P2, and P8 lines were more effective in low-temperature tolerance breeding.

Data surrounding inbred lines can be used to assess the future performance of hybrid lines, reducing the need to evaluate them. One study reported that the germination rate of hybrids at low temperatures can be predicted by their parental inbred lines (Maryam and Jones 1983). Our results suggest that low-temperature tolerant hybrid combinations had at least one inbred line with sufficient tolerance. The materials in this study are from Reid, Lancaster, BSSS, Lucia Red Cob, and Tangsipingtou. Several hybrids shared varying degrees of common ancestry. For example, P1 × P3, P1 × P5, P1 × P7, and P2 × P8 contained germplasm from Lancaster and Reid, which was consistent with findings reported by other researchers. Therefore, the two heterosis groups of Lancaster and Reid could be used to establish an improved model of germplasm that can tolerate low temperatures using a simple heterosis model.

Conclusions

Our findings demonstrate that the relative emergence rate and relative ear height could better respond to selection for improving low-temperature tolerance in maize. Analysing the effects of the general combining ability and the special combining ability during the laboratory germination period and sowing in field conditions under the low-temperature resistance index produced similar results. Under low-temperature stress conditions, the inbred line DNF266 had a higher general combining ability, while the hybrid combination Zhong 451 × Dan 340 had a higher special combining ability. Therefore, the inbred line DNF266 had the highest general combining ability under low-temperature stress conditions and should be used in the future.

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Author contributions ZW and YZ designed the research. JZ conducted the experiments, performed the data analysis, and wrote the manuscript. HD and LZ participated in generated hybrids. YL, ZZ and XW assisted in data analysis. ZW and YZ revised the manuscript. All authors reviewed and approved this manuscript.

Declarations

Conflict of interest The authors declare that there are no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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