Persistently smaller tassels threaten maize yield under a warming climate

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Heat waves become more serious with the warming climate, increasing the demand for developing high temperature (HT) tolerant maize germplasm. Here we compared the responses of 323 elite inbred lines released in multiple eras from both China and the United States to HT during flowering under field conditions. The newly released lines exhibit higher grain yield than the early released lines as a result of improved ear characteristics and flowering synchrony. However, the newly released lines are more susceptible to HT stress partly due to the reduced tassel size and spikelet opening angle. We identify a key threshold for spikelet/tassel (~700), over which maize can produce a stably high seed set under HT stress. According to the daily temperature during flowering, it is estimated that small-tassel (<700 spikelet/tassel) genotypes are unsuitable in 23.7% of global maize-growing regions. This work provides important information for breeding and selecting HT-tolerant maize varieties.

Main

Maize (*Zea mays* L.) as one of the most important staple crops contributes 20-30% of human calorie requirement[1]. With the warming climate, however, maize yield is expected to reduce dramatically (~7.4% for each 1°C increase in global average temperature), much larger than that in wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.)[2]. HT impacts on maize yield primarily arise from the frequent co-occurrences of HT stress and flowering stages[3, 4, 5]. It is widely believed that maize tassel is more susceptible to HT stress than ear[6, 7, 8]. Specifically, HT during flowering can advance the tasseling stage, reduce pollen shedding duration, hinder anther dehiscence, and reduce pollen viability[9, 10, 11, 12]. Evidence on rice and sorghum (*Sorghum bicolor* (L.) Moench) indicates that HT stress also reduces spikelet opening angle, which ultimately inhibits anther emergence and the subsequent process of pollen release[13, 14, 15]. To date, there have been limited studies exploring the effects of HT on spikelet opening in maize. These HT-induced changes independent and combined are capable of reducing seed set and even result in tassel sterility. Additionally, HT can slow down silk elongation and reduce silk emergence from the husk leaves[6, 7], which is often neglected in studies on HT stress. Wang et al. (2021) found that the maximum temperature threshold for silk emergence ratio was ~38°C[16], and the ratio can be reduced by more than 20% at 40°C[7]. Furthermore, even after silk emergence, HT can reduce silk receptivity, resulting in the failure of pollen germination or arrest of pollen tube growth[17]. The responses of silk growth and receptivity to HT stress however remain largely unknown.

The genetic gain in maize has been impressive in recent years, with yield increases of over 100 kg ha^{-1} $year^{-1}$ in major maize-growing regions such as Europe, Brazil, China, and the United States[18, 19, 20, 21]. This increase can be attributed to optimized morphological characteristics of maize plants, such as decreased leaf angle, leaf area, root angle, and increased root mass[18, 22, 23, 24, 25]. Likewise, maize tassel has a continuously decreasing size with breeding eras[26, 27], because each tassel can produce millions of pollen grains[28, 29]. Small tassel with fewer branches (some hybrids only have three or four branches) is widely adopted in modern hybrids, to reduce the energy cost of pollen grain production as well as minimize tassel shading on the leaves[30]. However, a small tassel is probably a factor limiting seed set under adverse conditions such as HT stress during flowering that can greatly reduce pollen shed grains[31]. The total pollen production would limit kernel number per plant at pollen shed density of less than 3000 pollen grains per silk[32]. This indicates that the widespread use of maize germplasm with a small tassel may have detrimental effects on maize yield under a warming climate.

Here, we determined the responses of different breeding-era maize germplasm to HT stress in terms of reproductive organ morphology, flowering pattern, and seed set. More importantly, we aimed to identify a key trait of tassel and/or ear that can enable maize to adapt to different environments, especially HT stress. For this, 323 maize inbred lines released in different eras from China and the United States were planted at different sowing dates at two locations in north China and southwest China to create different temperatures during flowering. We found that tassel size and flowering capacity both were decreased with the breeding era while ear silking capacity was enhanced. A key threshold of spikelet number per tassel was identified, above which maize seed set can be retained at high levels under different environments. As well, the global distribution of maize varieties with different tassel sizes was recommended. Our findings advance the conceptual understanding of seed set responses of different breeding-era maize germplasm to HT stress during flowering and identify critical HT tolerant indexes.

Results

Ear, tassel, and yield characteristics in different breeding eras

In this study, we investigated the evolutionary trends of maize tassel, ear, and yield characteristics in six various environmental conditions, especially during flowering (15 days bracketing the silking stage; Extended Data Fig. 1). A total of 323 elite maize inbred lines that were released in different eras in China (167 inbred lines) and the United States (156 inbred lines) were collected based on a previous study[24]. The Chinese inbred lines were classified into three groups based on the date of release and the use in breeding: 29 inbred lines released in the 1960s and 1970s (CN1960&70s), 88 lines released in the 1980s and 1990s (CN1980&90s), and 50 lines released after the year 2000 (CN2000&10s). The American elite inbred lines consisted of 69 public lines (Public-US) and 87 commercial lines (Ex-PVP) with expired Plant Variety Protection Act Certificates; the latter were mainly released after 2003 (Extended Data Fig. 2). Based on the genetic background, these inbred lines are divided into five groups: Stiff Stalk Synthetic (SS), Nonstiff Stalk (NSS), Iodent (IDT), Huangzaosi (specific to China), and Mix group[24]. In each of the different breeding-era germplasm, the inbred lines have at least three out of five genetic backgrounds to avoid genetic impacts (Supplementary Table 1).

We recorded four grain-related parameters, i.e., seed set, kernel number per ear (KN/ear), and thousand kernel weight (TKW), four tassel-related parameters, i.e., spikelet number per tassel (spikelet/tassel), spikelet opening angle, pollen viability, and pollen shedding duration, and six ear-related parameters, i.e., kernel row number per ear, floret number per row, floret number per ear, emerged silk number per ear, anthesis silking interval (ASI), and anthesis silking overlap (ASO) duration. The recorded values of these parameters at different environments were fit by a linear mixed model to obtain the best linear unbiased estimator (BLUE) values. The mean seed set, kernel/ear, TKW, and grain yield of CN2000&10s lines were all higher than that of CN1980&90s and CN1960&70s lines (Fig. 1). In particular, the seed set of CN2000&10s lines was 22.4% higher than that of CN1980&90s lines and 22.3% higher that of CN1960&70s lines. Likewise, the mean seed set, kernel/ear, TKW, and yield of Ex-PVP lines were all significantly higher, compared to Public-US lines (Fig. 1a).

In maize tassel, CN1960&70s, CN1980&90s, and CN2000&10s lines showed continuously declining trends in the mean spikelet/tassel, spikelet opening angle, and pollen shedding duration. Ex-PVP lines also had significantly lower values in these tassel parameters than Public-US lines. The reductions in spikelet/tassel from early to new inbred lines were larger (37.6%) than in other tassel parameters in both Chinese and US lines. Pollen viability showed no significant difference between inbred lines of different breeding eras (Fig. 1b).

In maize ear, floret row per ear, floret number per row, and especially emerged silk number per ear showed significantly increases from CN1960&70s lines to CN2000&10s lines. Floret row number per ear and floret number per row both had no significant differences between Public-US and Ex-PVP lines, but emerged silk number per ear was 36.8% higher in Ex-PVP than in Public-US lines. ASI and ASO duration were considered as ear traits due to the large effects of silking time on them (Extended Data Fig. 3). ASI significantly decreased from 3.6 days in CN1960&70s lines to 2.4 days in CN2000&10s lines and from 3.8 days in Public-US lines to 3.0 days in Ex-PVP lines. ASO duration increased with breeding eras in both Chinese and US lines (Fig. 1c).

The effects of temperature during flowering on tassel, ear, KN/ear and seed set

Growing environments especially temperature during the 15 days bracketing the silking stage had large effects on maize seed set[4, 16](Extended Data Fig. 4). Seed set values of all the lines were negatively correlated with Tmax during flowering, with newly released lines (i.e., CN2000&10s and Ex-PVP lines) having higher correlation coefficients. The decrease in seed set was 9.2% in CN1960&70s lines, 9.8% in CN1980&90s lines, and 12.8% in CN2000&10s lines for each 1°C increase in Tmax; the decrease was 7.5% in Public-US lines and 10.4% in Ex-PVP lines (Fig. 2).

To determine how Tmax affects seed set via tassel and ear, Tmax during flowering was correlated with tassel and ear flowering parameters (Extended Data Fig. 5). Spikelet opening angle, emerged silk number per ear, and ASO duration were all significantly correlated with Tmax. Spikelet opening angle and emerged silk number per ear had higher correlation coefficients. With each 1 °C increase in Tmax, spikelet opening angle on average decreased by 1.2° in CN1960&70s lines, 1.8° in CN1980&90s lines, and 2.3° in CN2000&10s lines; the decrease was 1.3° and 2.0° in Public-US and Ex-PVP lines, respectively (Fig. 3a, b). Similarly, emerged silk number per ear decreased by 16.9, 8.2, and 8.0 silks per ear in CN1960&70s, CN1980&90s, and CN2000&10s lines, respectively, with each 1 °C increase in Tmax; and the decrease was 16.1 and 13.0 silks per ear in Public-US and Ex-PVP lines, respectively (Fig. 3c, d).

Relationship between spikelet/tassel and seed set

Under a warming climate, tassel size is an important concern in maize production. Spikelet number per tassel (spikelet/tassel) as a crucial indicator for evaluating tassel size is a key factor (Extended Data Fig. 6). Hence, our emphasis is directed towards elucidating the optimal spikelet/tassel to guarantee ample pollen shed grains at HT. We found that, as spikelet/tassel increased, the seed set showed a linear increase and then retained at a stable level when spikelet/tassel was above ~700, which is close to that of CN1980&90s lines and Public-US lines (Fig. 4a). Based on this threshold, all the lines were divided into two groups, lines having more than 700 spikelet/tassel (large tassel group) and less than 700 spikelet/tassel (small tassel group). The seed set of large tassel group was lower under favorable environments but became larger under HT stress compared to the small tassel group (Extended Data Fig. 7). To test seed set responses of these two groups to HT stress during flowering, the seed set of large tassel group relative to the small tassel group under different sowing dates was calculated. The relative seed set of large tassel group was negative at Tmax below 31°C, and became positive at Tmax above 32°C; the positive value was much larger at Tmax above 35°C (Fig. 4b). To further verify the above findings, a field experiment including five sowing dates and four treatments for removal of tassel branches (tassel treatment) was carried out. Maize hybrid Zhendan958 which has a large tassel size and is widely planted in China was used. The numbers of spikelet/tassel in four tassel treatments were artificially controlled at ~1400 (control), ~700 (T1), ~550 (T2), and ~300 (T3), respectively (Fig. 4c). Treatments of Control and T1 both maintained high seed set values (~90%) in all the treatments of sowing dates, but comparatively, seed set of T2 and T3 were significantly lower once daily Tmax was above 32°C (Fig. 4d, e, f), consisting with results of relative seed set of large tassel group under different Tmax levels (Fig. 4b).

The importance of the key spikelet/tassel threshold in coping with HT stress under a warming climate

To precisely achieve this spikelet/tassel threshold, we calculated the contribution of central spike length, central spikelet density, branch number, branch length, and branch spikelet density to the seed set. Tassel branch length and central spikelet density contributed more than 60% of the seed set, which should be given more focus when improving tassel HT stress tolerance (Fig. 5a).

Each tassel spikelet contains two florets (upper and lower floret), but generally, only the upper floret can release three anthers from the glumes (Fig. 5b). Each anther on average releases ~2,000 pollen grains certainly with a large variation, and pollen viability is around 90% under natural field conditions[33] (Fig. 5e). One viable pollen has the potential to reproduce one seed, but seed set would be limited at pollen densities less than 3000 pollen grains per silk[32]. Based on the above information, 700 spikelet/tassel can produce enough viable pollen grains for 1,260 silks per ear, which is approximately equivalent to the sum of the emerged silk number of two ears in modern maize hybrids (Fig. 5c, d, e). Under HT conditions during flowering (>35°C), pollen shed number is reduced by ~38% and pollen viability is reduced to ~68% (Supplementary Table 4). In such conditions, 700 spikelet/tassel can provide viable pollen grains for ~590 silks, which is equivalent to the emerged silk number of one modern maize ear (Fig. 5c, d, f). This can be an important reference for the selection of and breeding for HT-tolerant varieties.

Besides, suitable varietal distribution at different regions can be recommended, based on the seed set responses of varieties with different tassel sizes to Tmax during flowering. We know from the results above that the seed set of small-tassel maize varieties starts to decrease at Tmax during flowering above 32°C and the decrease becomes much larger at Tmax above 35°C. Therefore, global maize-growing regions were divided into regions with Tmax during flowering below 32°C, 32-35°C, and above 35°C, respectively, based on the daily temperature in the past decade. In the regions with Tmax during flowering below 32°C, small-tassel varieties are recommended, while in other regions especially at Tmax above 35°C, large-tassel varieties are recommended (Fig. 6a). Globally, approximately 23.7% of maize-growing regions is recommended to grow large-tassel varieties, including the North China Plain, part of the central regions of the United States, almost all the regions of Paraguay, regions of north-central Africa, central region of Asia, and some regions in the Middle East. The ratio intends to increase with the warming climate based on the trends in the past 40 years (Fig. 6 b, c, d).

Discussion

Sufficient spikelet per tassel with smooth spikelet opening and high pollen viability is crucial for reproduction success in maize[7, 34]. However, modern maize breeding has resulted in a continuous decrease in tassel size[26, 27]. This reduction can decrease pollen shed number and pollen shedding duration which increase the risk of pollen deficiency, and hence reduce maize tolerance to HT stress during the flowering stage[7, 29, 35]. Pollen shed number is considered a more crucial factor limiting seed set than pollen viability when maize plants were subjected to HT stress around flowering[31]. There was no significant difference in pollen viability among CN1960&70s, CN1980&90s, CN2000&10s, Public-US, and Ex-PVP lines in our study (Fig. 1b). These results suggest that spikelet number and flowering pattern are probably more important factors affecting seed set under natural field conditions compared to pollen viability. We identified a key threshold of spikelet/tassel (~700) for successful reproduction under both normal and high-temperature conditions (Fig. 4 and 5). However, spikelet/tassel of modern maize germplasm averages ~550 spikelets in China (CN2000&10s lines) and ~480 spikelets in the United States (Ex-PVP lines), greatly below the threshold level (Fig. 1b). Furthermore, tassel capacity to flower also decreases with breeding eras. For instance, the spikelet opening angle of maize lines decreases with breeding eras and becomes more susceptible with increasing temperature (Fig. 1b and Fig. 3a, b). The reduced spikelet opening angle is consistent with changes in leaf angle with maize breeding eras[19, 24]. Likely, the small spikelet opening angle of modern maize germplasm is unintentionally achieved in the process of breeding ideotype plant architecture. It is expected that enhancing spikelet opening can potentially offset the negative effect of small tassel on seed set. These findings imply that modern maize germplasm carries a substantial risk of kernel loss, especially considering the impact of the warming climate.

Ear size, floret number, and kernel number per ear of maize continuously increase with breeding eras[36, 37] (Fig. 1a). These increased ear characteristics are estimated to improve plant adaption to HT stress during flowering[38, 49]. Additionally, modern maize germplasm performs better in flowering synchrony between tassel and ear[24, 36, 40], mainly due to the improved adaption of silking to environments (Extended Data Fig. 3). To more accurately evaluate flowering synchrony, we also focused on anthesis-silking overlap (ASO) duration, in case some inbred lines have very short pollen shedding duration. The ASO duration of the newly released lines was longer than early lines, further verifying the enhanced flowering synchrony of modern maize germplasm. The silks that emerge from the husk during pollen shedding play a crucial role in the determining seed set. The emerged silk number per ear of lines from both China and the United States increased with breeding eras (Fig. 1c), another advantage in the ear of modern maize germplasm[18]. Under HT stress, the newly inbred lines still maintained a higher and stabler number of emerged silk/ear than early lines (Fig. 3c, d), indicating ear of modern maize germplasm has an improved heat tolerance, in accordance with findings under drought stress[18, 41]. However, the seed set of new inbred lines reduces more greatly with increased temperature during flowering than early lines, reflecting these new lines have a higher susceptibility to HT stress. This also indicates that the improvement of ear characteristics of modern maize germplasm cannot completely offset the deficiency of small tassel on reproduction when coping with the warming climate.

Our results showed that the seed set of varieties with a small tassel (spikelet/tassel less than 700) started to reduce at daily maximum temperature (Tmax) above 32°C during flowering and reduced more greatly at Tmax above 35°C. Based on this, it is estimated that 23.7% of global maize-growing regions are unsuitable for growing small-tassel varieties, where the maize flowering stage frequently coincides with HT stress of Tmax above 32 or 35°C (Fig. 6). In some tropical and subtropical regions such as regions in the south and south-west of China that have more serious HT stress, however, small-tassel varieties are recommended because maize flowering stage can escape HT stress by adjusting sowing date. In double- and multi-cropping regions where maize flowering is restricted to a specific period and frequently meet with HT stress (i.e., the North China Plain), large-tassel varieties are recommended. In some rain-fed regions (i.e., Middle East, Central Asia, and Central Africa), large-tassel varieties are also recommended due to the uncertainty of rainfall timing that has the potential to result in overlap between maize flowering and HT stress occurrence[42]. The trend over the past 40 years has shown that large-tassel varieties should be planted in larger regions with the warming climate.

Methods

Field experiment design 1. The experiments were arranged in a randomized complete block design that were conducted over two years of 2021 and 2022 at Wuqiao Experimental Station (37°41′02″N, 116°37′23″E) of China Agricultural University in Hebei Province and Baishiyi Experimental Station (29°49′43″N, 106°21′13″E) of Chongqing Academy of Agricultural Sciences in Chongqing Province, China. The experiments consisted of 323 inbred lines that were sown at two sowing dates at Wuqiao Experimental Station (April 16 and June 6 in 2021; April 23 and June 6 in 2022) and one sowing date at Baishiyi Experimental Station in each year (25 May in 2021 and 16 May in 2022). Each treatment had two replicates. To adapt to the local environment, plant density, and fertilizer application at two locations were different. The plant density was 82,500 plants ha^{-1} with a row spacing of 60 cm at Wuqiao Experimental Station and 65,000 plants ha^{-1} with a row spacing of 80 cm at Baishiyi Experimental Station. There were five rows with a length of 5 m in each plot at both locations. In terms of fertilization, 60 kg N ha^{-1}, 90 kg P_2O_5 ha^{-1} and 90 kg K_2O $ha^{-1}$was applied at sowing, and additional 120 kg N ha^{-1} was applied at the 12-leaf stage at Wuqiao. At Baishiyi Experimental Station, 60 kg N ha^{-1}, 105 kg P_2O_5 ha^{-1}, and 120 kg K_2O $ha^{-1}$was applied at sowing, and additional 80 kg N ha^{-1} was applied at each of the 6-leaf and 12-leaf stages, respectively. Weeds, pests, and diseases were well controlled and water was well supplied during the entire growing season.

Field experiment design 2. The experiment was arranged in a split-plot design with the sowing date as the first factor and the removal of tassel branches as the second, which was conducted in Baishiyi Experimental Station in 2023. Maize hybrid Zhengdan 958 was widely planted in China in the past two decades was planted at five sowing dates (April 9, April 28, May 6, May 14, and May 22). In each sowing date, four treatments for removal of tassel branches were performed at the tasseling stage (tassel treatment), to realize the number of spikelet number per tassel(spikelet/tassel) at ~1400 (Control, no removal of tassel branches), ~700 (T1), ~550 (T2), and ~300 (T3), respectively. Each treatment had three replicates. Transparent plastic film was used to surround the plot to avoid cross-pollination between treatments. Plot size, planting density, fertilizer application, and field management were the same as in field experiment 1 at the Baishiyi Experimental Station.

Meteorological factors. The daily maximum temperature (Tmax, °C), mean temperature (Tmean, °C), minimum temperature (Tmin, °C), rainfall, and relative air humidity (RH) during the entire maize growing season of 323 maize inbred lines were recorded at two locations in 2021 and 2022.

Flowering dynamics. The dates of the tasseling, pollen shedding, and silking and the end of pollen shedding in each plot were recorded for all the inbred lines in two experimental years. In each plot, at least 20 representative plants were carefully selected to record flowering patterns. Tasseling dates of these individual plants were recorded when the tassel was exposed 2-3 cm, pollen shedding dates was recorded when the first anther initiated shedding pollen, silking stage was the date when the silk emerged 2-3 cm, and the end of pollen shedding was the date when no pollen grains was released from tassel. The pollen shedding duration was the days between the onset and end of pollen shedding. The anthesis-silking interval was the days between pollen shedding date and silking date. Anthesis-silking overlap duration was calculated as the days between silk emergence and end of shedding time.

Pollen viability. At the anthesis stage, fresh pollen from at least 3 plants of each inbred line was collected from the newly opening anthers between 9:00–10:00 am to evaluate pollen viability in 2022. Based on the procedures described in the Journal of Agronomy and Plant Term[43], a small quantity of fresh pollen was deposited on a microscope slide. A sufficient amount of 0.5% TTC solution was added to fully coat the pollen, followed by gentle placement of a coverslip. The slide was then incubated at ambient temperature (26-28°C) in the dark condition for 10-15 minutes. The stained pollen grains were visualized and photographed using a stereomicroscope (Olympus SZX7, Japan). Pollen grains that were stained red were considered as viable and the rest were recorded as dead. Pollen viability was expressed as the percentage of viable pollen number by the total pollen number per microscopic field.

Spikelet opening angle. At the tassel blooming stage, 5-10 representative and fully opened spikelets were selected from three plants of each inbred line at around 9:00 am and photographed in all the treatments. The spikelet opening angle was measured with Image-Pro Plus 6.0.

Tassel morphology. After the end of pollen shedding, tassels of three randomly selected plants of each inbred line were sampled to measure central spike length, spikelet number on the central spike, branch number, branch length, and spikelet number on the branches in all the treatments. Spikelet densities of the central spike and branches were calculated as spikelet numbers divided by central spike length and branch length, respectively.

Emerged silk number per ear. At the end of pollen shedding, the primary ears (the topmost ears) of three randomly selected plants of each inbred line were sampled to determine emerged silk number per ear in 2022. The fresh ears were firstly stored in the refrigerator at -20 °C until counting the silks. All the silks that emerged from the husks were counted.

Yield components and seed set. At the physiological maturity stage, the primary ears of 10 plants in two adjacent rows of each plot were harvested in all the treatments. Kernel or floret row number per ear and floret number and kernel number per row of all the harvested ears were counted to determine floret number per ear and kernel number per ear (KN/ear), respectively. KN/ear is calculated by multiplying kernel row number per ear and kernel number per row. For some ears that have very few kernels, all the kernels on the ear were counted. Floret number per ear was determined using the same method with KN/ear. Kernels of individual ears were threshed by hand and oven-dried at 80 °C to constant weight, and three samples of 200 kernels were weighed and then adjusted to 14% water content to measure 1000-kernel weight (TKW). Grain yield (g/ear) was calculated by multiplying the TKW and KN/ear. The seed set was calculated as the percentage of KN/ear by the floret number per ear.

Literature search strategy and selection criteria. To assess the ability of modern maize varieties to provide tassel pollen to ear silk, both under normal and high-temperature conditions, we conducted a literature search using the keywords "Maize", "Corn", "tassel", "spikelet", "silk", "high temperature", "heat stress", "pollen viability", "pollen shed number" and "pollen shed weight" on three databases (CNKI, WanFang DATABASE, and Web of Science) from January 1, 2010 to April 1, 2023. Our search yielded 31 records in 5 articles related to spikelet number per tassel, 105 records in 6 articles related to silk number per ear, and 261 records in 20 articles related to pollen viability and shed number (Supplementary Tables 2-4).

Global meteorological data availability. We accessed regional coordinate point data for global maize cultivation from the "Global Spatially-Disaggregated Crop Production Statistics Data for 2010 Version 2.0" available at https://mapspam.info/. These data were downscaled to a resolution of 80 km for each cluster. Additionally, we acquired daily maximum temperature (Tmax, °C) data spanning from 2012 to 2022 from the database found at https://power.larc.nasa.gov/data-access-viewer/. Utilizing local agricultural practices for each region, we computed a 15-day average of Tmax during the flowering stage.

Statistics. The values of tassel characteristics (i.e., spikelet number per tassel, spikelet opening angle, pollen viability and pollen shedding duration), ear characteristics (i.e., kernel row number per ear, floret number per ear, floret number per row, emerged silk number per ear, anthesis-silking interval, and anthesis-silking overlap duration), yield components and seed set across different environments were fit by a linear mixed model in R with the lme4 package to obtain the best linear unbiased estimator (BLUE) values as follows:

$$Y_{ij} = \mu + Line_i + Env_j + Rep_n + (\text{Line} \times \text{Env})_{ij} + (\text{Env} \times \text{Rep})_{jn} + \text{error}_{\text{ijn}}$$

where μ is the mean, Line_i is the genotype effect of the i-th inbred, Env_j is the effect of the j-th environment, Rep_n is the effect of the n-th replication, $(\text{Line} \times \text{Env})_{ij}$ is the genotype–environment interaction, $(\text{Env} \times \text{Rep})_{jn}$ is the environment–replication interaction, and error_{ijn} is the error of the j-th environment and the n-th replication. Items were set to random. The analysis of variance in meteorological factors (i.e., Tmax, Tmean, Tmin, rainfall and RH), tassel characteristics, ear characteristics, yield components and seed set were performed using SPSS Statistics 26.0. The differences between different types of inbred lines (i.e., CN1960&70s, CN1980&90s, CN2000&10s, Public-US, and Ex-PVP) were compared using the least significant difference test (LSD) at $P<0.05$. Correlations between meteorological factors, tassel characteristics, ear characteristics, yield components, and seed set were performed with Origin 2023. Variance relative importance was performed by using the R language randomForest package to calculate the relative contributions of central spike length, central spikelet density, branch number, branch length, and branch spikelet density to seed set. We specify a nonlinear fit using the Nonlinear different piecewise linear (PWL2) model:

$$y=\begin{cases} a_1 + b_1 x \\ a_2 + b_2 x \end{cases}$$

where y is the response variable (i.e., seed set), x is the dependent variable (i.e., spikelet number per tassel), a_1 and a_2 are intercepts, and b_1 and b_2 are regression coefficients.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data are freely available on Figshare at https://doi.org/10.6084/9.figshare. 24257206.

Source data are provided with this paper.

Code availability

All code used for analysis and figure creation are on Figshare at https://doi.org/10.6084/m9.figshare.24257206.

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Author contributions

S.H. and Y.Z. designed the research. Y.Z., X.D., H.W., Y.L., X.L., Q.Y., and B.L. collected data. S.H., Y.Z., X.D. and L.J. contributed to data analysis. Y.Z. and X.D. wrote the manuscript with edits from J.G., S.H. and P.W. All authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.