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ORIGINAL PAPER

Manipulating the expression of a cell wall invertase gene increases grain yield in maize

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Abstract Cell wall invertases play an important role in plant growth and development, especially in the grain filling of crop plants. However, their potential in high yield crop breeding has not been investigated. In this study, the main hybrid maize cultivar Zheng Dan 958 (ZD958) was used as a basic variety to assess whether ZmGIF1, a cell wall invertase from maize, can be used to breed new cultivars with higher grain yields. *ZmGIF1* expression, cell wall invertase activity, and sugar content in different parental inbred cultivars were compared with those in Zheng 58 and Chang 7-2, the parental inbred cultivars of ZD958. Parental cultivars which showed higher *ZmGIF1* expression and invertase activity were selected and intercrossed to improve the expression of *ZmGIF1*. Compared with the basic cultivar ZD958, higher *ZmGIF1* expression and cell wall invertase activity were observed in most hybrid F1 lines, leading to increased grain yield in them. All these results suggest that the expression of *ZmGIF1* can be manipulated using different parental cultivars to increase the grain yield of their hybrid F1 progenies.

Keywords Cell wall invertase · Grain filling · High yield · Maize · ZmGIF1

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Introduction

In higher plants, the transport of sucrose, the major form of photosynthates, between source and sink through the phloem is largely dependent on its initial cleavage in the sink tissues and organs by invertase or sucrose synthsase (Sonnewald et al. 1997). The expression of invertase has been investigated in different plants (Albaceteet al. 2014; Canam et al. 2008; Chandra et al. 2015; Chourey et al. 2006; Kim et al. 2000; Taliercio et al. 1999; Wang et al. 2008a, b; Yao et al. 2014). The biological functions of different invertases in sink strength have been studied in several plant species such as potato (Zrenner et al. 1995), rice (Wang et al. 2008a, b) and maize (Chourey and Nelson 1976). Transgenic potato plants ectopically expressing a yeast invertase produced larger tubers than did the wild type plants (Sonnewald et al. 1997). The loss of function rice mutant of *OsGIF1* exhibited decreased grain filling rate and an up to 24% reduction in seed weight. Whereas *OsGIF1* overexpressing plants showed increased grain filling rate, grain size and grain weight (Wang et al. 2008a, b). In maize, ZmGIF1, a cell wall invertase (also known as Mn1 or INCW2) encoded by *Mn1* (the ortholog of *OsGIF1*) and abundantly expressed in endosperm, works as the major determinant for sink strength in developing seeds (Chourey et al. 2012; Lowe and Nelson 1946). Similarly, the loss of function maize mutant of *mn1* showed an up to 70% reduction in seed weight (Cheng et al. 1996).

Genetic transformation has been used as a powerful technique to increase the grain yield in different crop plants, such as rice (*Oryza sativa*) (Jeong et al. 2013; Smidansky et al. 2003; Wu et al. 2008), wheat (*Triticum aestivum*) (Munns et al. 2012; Smidansky et al. 2002), potato (*Solanum tuberosum*)(Stark et al. 1992), cotton (Zhang et al. 2011), and aspen (Eriksson et al. 2000). An up to

25% grain weight increase in maize was also achieved by the ectopic expression of AGPase, a glgC-16 ADP glucose pyrophosphorylase from *E. coli* (Wang et al. 2007), or the overexpression of Sh2 (shrunken-2), the large subunit of AGPase, and Bt2, the endosperm small subunit of AGPase, from maize (Li et al. 2011). Recently, an up to 64% grain yield increase was obtained by overexpressing a modified Sh2 enzyme (Hannah et al. 2012).

Previously, we constitutively expressed the cell wall invertase encoding genes from *Arabidopsis*, rice and maize in the maize inbred line Ye478 (Li et al. 2013). Introduction of the cell wall invertase genes from different sources all significantly increased cell wall invertase activity in transgenic plants, and brought about an up to 145.3% increase in the grain yield of transgenic plants. In this study, we demonstrate for the first time that *ZmGIF1* can be engineered using different parental cultivars to breed high yield non-transgenic maize plants.

Materials and methods

Plant materials

Maize (*Zea mays* L.) cultivars used in this study were Zheng 58 and Chang 7-2 provided by Longping Hitech (Hefei, China), Ping An 24 provided by Yantai Qingyuan Hitech (Yantai, China), and different parental inbred cultivars bred at College of Agriculture, Ludong Unversity (Yantai, China). Plants were grown in green house and field as described previously (Li et al. 2013). For *ZmGIF1* expression analyses, total RNA was extracted from the leaves of different cultivars as described previously (Li et al. 2013).

Quantitative real-time PCR analyses

For *ZmGIF1* expression analyses, total RNA was extracted from the leaves of different cultivars as described previously (Li et al. 2013). Real-time PCR was performed using *ZmGIF1* forward (5′-GAACGGCAAGATATCCCT GA-3′) and reverse (5′-CATGACCG GCTTCTTCATCT -3) primers and SYBR Green Real-time PCR Master Mix (TOYOBO, Osaka, Japan), as described previously (Li et al. 2013). The expression level of *ZmActin1* in different cultivars was also determined as a quantitative control with forward (5′-ATCACCATTGGGTCAGAAAGG-3′) and reverse (5′-GTGCTGAGAG AAGCCAAAATAG AG-3′) primers. The expression of *ZmGIF1* in the fifth leaves of different parental cultivars and hybrid F1 lines at six-leaf-stage was examined.

Cell wall invertase activity and sugar content assays

Seeds of different cultivars were sown in both greenhouse and field. At six-leaf-stage, the fifth fully expanded leaves of different hybrid F1 lines were collected for invertase activity assays as described previously (Li et al. 2013). The developing grains at 20 DAP (days after pollination) of different parental cultivars grown on Nanbin Farm (Sanya, Hainan Province, China) was also collected for invertase activity and sugar content analyses as described previously (Hampp et al. 1994; Li et al. 2013).

Generation of hybrid F1 lines

To produce the hybrid F1 lines, seeds of parental cultivars which showed higher *ZmGIF1* expression and cell wall invertase activity were sown on Wuyi Farm (Urmuqi, Xinjiang Province, China) and intercrossed by hand pollination with each other in 2014.

Grain yield assays

For grain yield analyses, Zheng Dan 958 (ZD958), Ping An 24 (PA24), and different hybrid F1 lines were grown under natural condition in Dehui (Jilin Province, China) in 2015 and 2016. Seeds were sown in a population density of approximately 5500/μ. PA24 is a local main cultivar to be used as a control variety.

Results and discussion

Selection of parental inbred cultivars

To assess whether *ZmGIF1* can be used for high grain yield cultivar breeding in maize, we first performed quantitative real-time PCR and cell wall invertase activity analyses. Based on our previous studies that *ZmGIF1* was predominantly expressed in sink tissues and organs (Li et al. 2013), the transcriptional level of *ZmGIF1* in the fifth leaves of different parental inbred cultivars at six-leaf-stage were compared with that of Zheng 58 and Chang 7-2, the parental inbred cultivars of ZD958, which is being widely grown in China. A total number of 458 inbred cultivars were screened, and those which showed higher *ZmGIF1* expression and/or invertase activity were selected for further study. Initially, most cultivars, especially female parental cultivars, which produced more biomass during their vegetative growth, also showed higher *ZmGIF1* expression and invertase activity. As shown in Fig. 1, the control parental cultivars Zheng 58 and Chang 7-2 exhibited less shoot growth than did the other selected ones (Fig. 1a). Consistently, *ZmGIF1* expression in their leaves and invertase activity in their developing

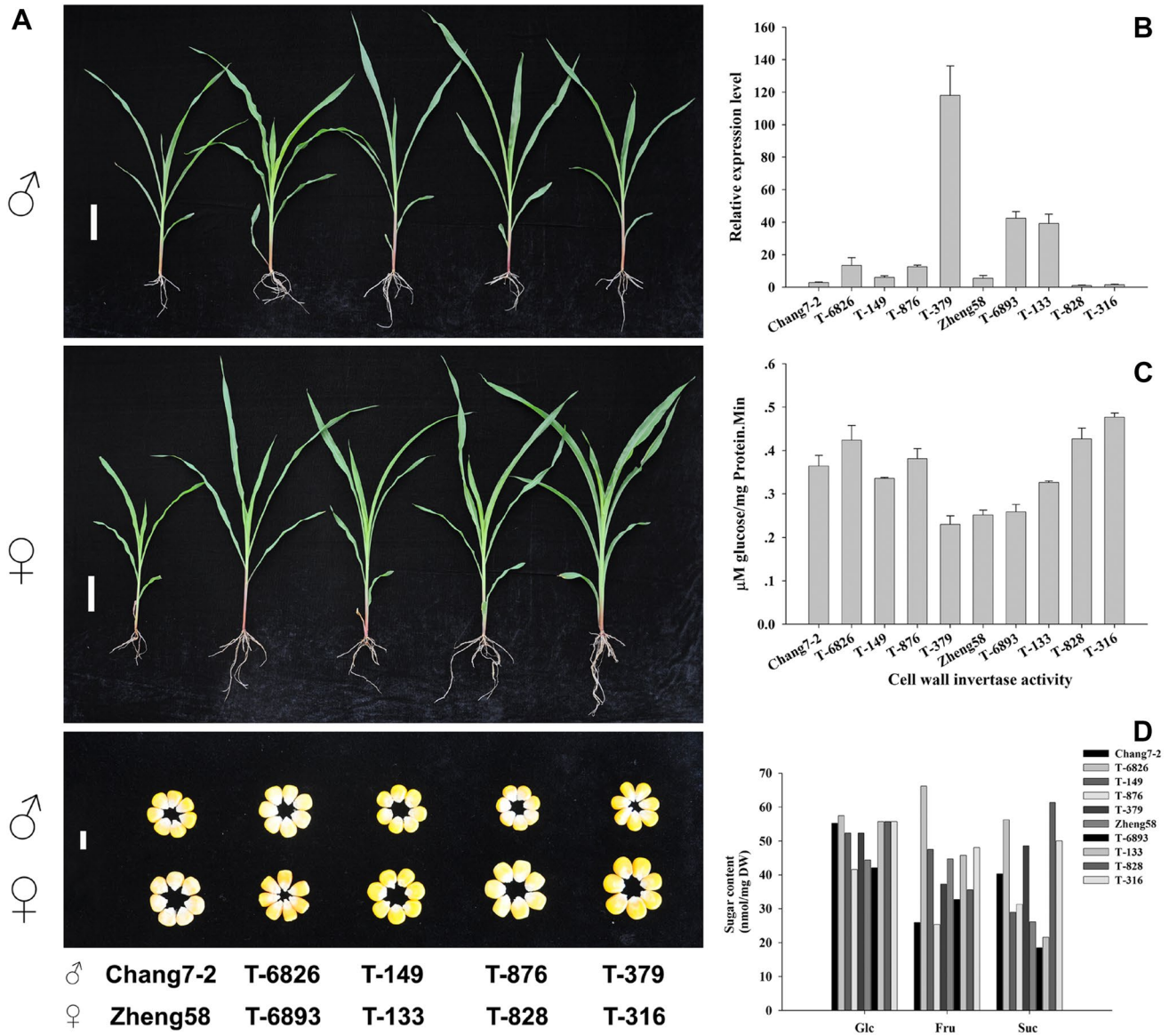

Fig. 1 Phenotype, *ZmGIF1* expression, invertase activity, and sugar content analyses. Ten representative parental inbred lines, including Chang 7-2 and Zheng 58, used in this study were shown. **a** Phenotypes of 16-day-old seedlings (scale *bar* = 10 cm) and kernels (scale *bar* = 1 cm) of the indicated parental inbred lines. **b** Relative expression of *ZmGIF1* in the fifth leaves of parental lines in (**a**) at six-leaf-stage. Real-time PCR was performed using *ZmGIF1*- or *ZmActin1*-specific primers. The house-keeping gene *ZmActin1* was used as an internal control. The expression level of *ZmGIF1* in line T-828 was assigned a value of 1.0. (**c, d**) Cell wall invertase activity and sugar content analyses in the developing seeds of parental lines in (**a**) at 20 DAP (days after pollination)

seeds were also lower (Fig. 1b, c). We also examined sugar contents in the developing seeds of different parental cultivars at 20 DAP, and no significant correlation between shoot growth and glycometabolism was observed (Fig. 1d). Possible explanation is that the difference of *ZmGIF1* expression and/or invertase activity between these cultivars is not significant enough. This is consistent with our previous study that higher glucose, fructose and sucrose contents were only observed in transgenic maize lines which showed very high expression of *AtGIF1, ZmGIF1* or *OsGIF1* (Li et al. 2013).

Manipulation of ZmGIF1 expression in hybrid F1 lines

To further explore whether *ZmGIF1* expression and invertase activity from different parental cultivars can be combined in their hybrid F1 generation, a total number of 12 parental cultivars which showed higher *ZmGIF1* expression and/or invertase activity than did Zheng 58 or Chang 7-2 were selected, grown on Wuyi farm (Urmuqi, X·injiang Province, China), and intercrossed with each other (including Zheng 58 and Chang 7-2) in July, 2014. A total number of 182

hybrid F1 lines (combinations) were generated. As expected, the expression level of *ZmGIF1*, as well as invertase activity, was successfully combined in most hybrid F1 lines. For example, the transcriptional level of *ZmGIF1* in the leaves of hybrid lines Zheng 58 × T316, Zheng 58 × T379, Zheng 58 × T6893 and Zheng 58 × T133 was higher than that in the leaves of Zheng 58 × Chang 7-2 (ZD958). Consistently, the invertase activity was also significantly higher in these hybrid lines (Fig. 2a, b). Therefore, expression of *ZmGIF1* in these parental cultivars was successfully combined in their hybrid F1 generation.

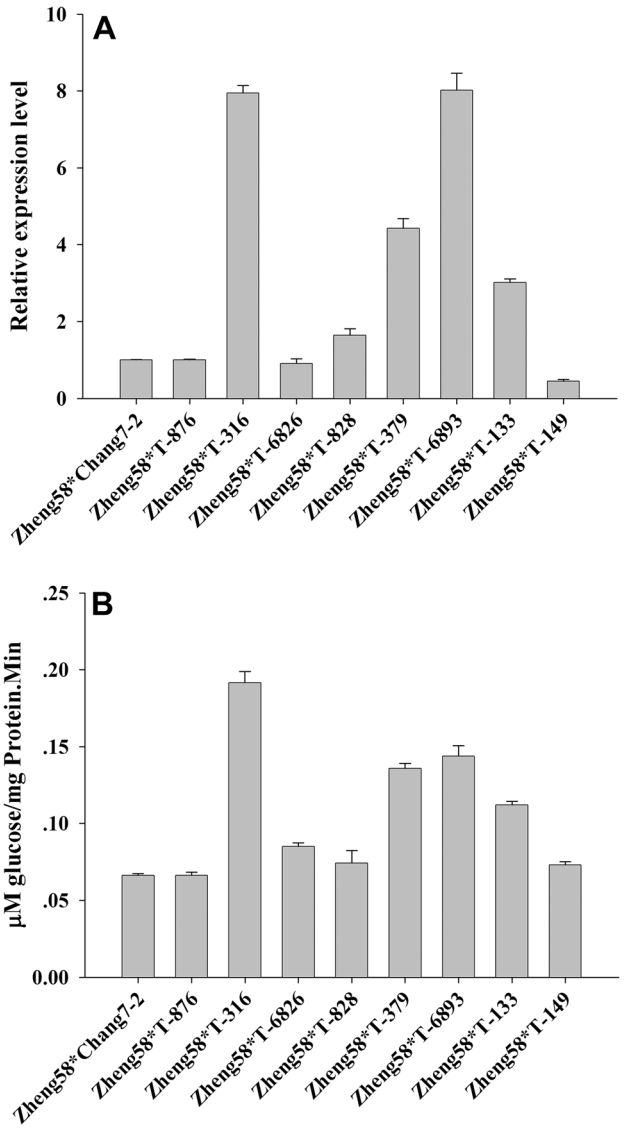

Fig. 2 *ZmGIF1* expression and cell wall invertase activity analyses in different hybrid F1 lines. Nine representative lines including Zheng Dan 958 (ZD958), the hybrid of Zheng 58 and Chang 7-2, were shown. **a** Relative expression of *ZmGIF1* in fifth leaves of six-leaf-stage seedlings. Real-time PCR was performed using *ZmGIF1*- or *ZmActin1*-specific primers. The house-keeping gene *ZmActin1* was used as an internal control. The expression level of *ZmGIF1* in hybrid line Zheng 58 and T-876 was assigned a value of 1.0. **b** Cell wall invertase activities in the fifth leaves of six-leaf-stage seedlings in (**a**)

Engineering of high grain yield maize plants

Previously, genetic expression of cell wall invertases from *Arabidopsis*, rice and maize all improved the growth rate and grain yield of transgenic maize plants. Transgenic plants grew more rapidly and produced larger cobs with increased seed size and weight than did the wild type plants (Li et al. 2013). To determine whether increased expression of *ZmGIF1* and invertase activity would also increase grain yield in the generated hybrid lines, hybrid F1 plants were grown in Dehui (Jilin Province, China) for field trials in 2015 and 2016. Again, hybrid F1 lines with higher *ZmGIF1* expression and invertase activity produced larger grain ears (Fig. 3), resulting in increased grain yield per plant (Table 1). Since all the hybrid lines were grown under natural condition (no irrigation), the grain yield increase in 2015 was lower (with an up to 13.9% increase) than that in 2016 (with an up to 28.6% increase) due to the local drought weather in 2015 (Table 2). Similar to transgenic plants expressing *AtGIF1, ZmGIF1* or *OsGIF1*, the higher grain yields in them were resulted from both increased seed number and weight per ear (Table 1). This is consistent with the observation in transgenic maize plants (Li et al. 2013).

Taken together, we reported here a new strategy for the breeding of non-transgenic high grain yield maize plants

Fig. 3 Corn cobs of selected hybrid F1 lines from the field trial of Dehui (Jilin Province, China) in 2015. Zheng Dan 958 (ZD958) and a local main cultivar Ping An 24 (PA24) were included as controls

Table 1 Mean comparisons for cob and grain yield of Zheng Dan 958 (ZD958) and different hybrid F1 lines

Year	2015				2016			
Line	Ear length (cm)	Grain row per ear	Grain number per ear	Grain weight per ear (Kg)	Ear length (cm)	Grain row per ear	Grain number per ear	Grain weight per ear (Kg)
1	17.34 ± 0.20*	18.2 ± 0.3**	37.5 ± 0.4**	0.254 ± 0.005**	18.24 ± 0.21**	16.2 ± 0.3	39.9 ± 0.5	0.305 ± 0.017**
3	18.11 ± 0.22**	17.0 ± 0.4*	40.3 ± 0.5**	0.265 ± 0.005**	18.04 ± 0.18**	15.3 ± 0.4	42.9 ± 0.6**	0.277 ± 0.004**
17	18.29 ± 0.20**	17.8 ± 0.4**	38.0 ± 0.5**	0.261 ± 0.004**	19.15 ± 0.17**	17.4 ± 0.3**	43.3 ± 0.5**	0.289 ± 0.005**
28	20.40 ± 0.22**	15.7 ± 0.3	41.3 ± 0.7**	0.256 ± 0.005**	19.47 ± 0.18**	15.1 ± 0.3	42.1 ± 0.5**	0.259 ± 0.002**
40	18.02 ± 0.24**	17.0 ± 0.3*	40.2 ± 0.5**	0.261 ± 0.005**	18.3 ± 0.18**	16.6 ± 0.4	41.8 ± 0.5**	0.298 ± 0.004**
42	20.69 ± 0.27**	16.6 ± 0.4	43.0 ± 0.5**	0.276 ± 0.006**	18.95 ± 0.21**	16.1 ± 0.3	40.6 ± 0.6*	0.264 ± 0.004**
45	18.75 ± 0.22**	17.2 ± 0.4**	42.4 ± 0.7**	0.254 ± 0.004**	19.71 ± 0.16**	17.0 ± 0.2**	46.0 ± 0.4**	0.284 ± 0.003**
48	19.24 ± 0.22**	18.1 ± 0.4**	37.3 ± 0.6**	0.255 ± 0.004**	20.78 ± 0.21**	18.1 ± 0.3**	43.7 ± 0.5**	0.292 ± 0.005**
55	19.05 ± 0.23**	18.1 ± 0.3**	42.3 ± 0.6**	0.274 ± 0.005**	19.66 ± 0.15**	17.1 ± 0.2**	43.8 ± 0.3**	0.290 ± 0.004**
60	20.66 ± 0.25**	18.1 ± 0.4**	41.9 ± 0.6**	0.281 ± 0.006**	20.04 ± 0.20**	17.1 ± 0.4**	41.0 ± 0.5**	0.266 ± 0.003**
93	18.53 ± 0.23**	15.7 ± 0.3	39.5 ± 0.7**	0.240 ± 0.005*	19.70 ± 0.19**	15.7 ± 0.4	45.3 ± 0.5**	0.270 ± 0.004**
153	21.83 ± 0.39**	16.7 ± 0.4	47.6 ± 1.0**	0.246 ± 0.007**	25.81 ± 0.88**	17.5 ± 0.3**	53.1 ± 0.6**	0.308 ± 0.006**
ZD 958	16.69 ± 0.19	15.9 ± 0.3	34.7 ± 0.5	0.223 ± 0.004	16.75 ± 0.15	15.7 ± 0.3	39.0 ± 0.4	0.237 ± 0.003

Data are from plants in randomized complete block design with three replications grown under natural condition in Dehui (Jilin Province, China) in 2015 and 2016. Seeds of ZD958 and hybrid F1 lines were sown in a population density of approximately 5500/μ. Values shown are means ± SEM. Values of hybrid F1 lines significantly different from those of ZD958 at $*0.01 < P < 0.05$ and $**P < 0.01$ were indicated using the *t* test (n = 20)

Table 2 Mean comparisons for cob and grain yield of Zheng Dan 958 (ZD958), Ping An 24 (PA24), and different hybrid F1 lines

Line	Ear length (cm)	Grain row per ear	Grain number per ear	Grain weight per ear (Kg)
1	17.34 ± 0.20*	18.2 ± 0.3**	37.5 ± 0.4**	0.254 ± 0.005**
3	18.11 ± 0.22**	17.0 ± 0.4*	40.3 ± 0.5**	0.265 ± 0.005**
15	21.00 ± 0.17**	16.3 ± 0.3	42.1 ± 0.6**	0.285 ± 0.004**
17	18.29 ± 0.20**	17.8 ± 0.4**	38.0 ± 0.5**	0.261 ± 0.004**
22	18.72 ± 0.20**	16.6 ± 0.3	35.2 ± 0.5	0.231 ± 0.002
23	19.74 ± 0.31**	17.4 ± 0.3**	38.1 ± 0.8**	0.265 ± 0.006**
24	19.89 ± 0.24**	16.9 ± 0.3*	40.8 ± 0.6**	0.252 ± 0.004**
28	20.40 ± 0.22**	15.7 ± 0.3	41.3 ± 0.7**	0.256 ± 0.005**
40	18.02 ± 0.24**	17.0 ± 0.3*	40.2 ± 0.5**	0.261 ± 0.005**
42	20.69 ± 0.27**	16.6 ± 0.4	43.0 ± 0.5**	0.276 ± 0.006**
45	18.75 ± 0.22**	17.2 ± 0.4**	42.4 ± 0.7**	0.254 ± 0.004**
48	19.24 ± 0.22**	18.1 ± 0.4**	37.3 ± 0.6**	0.255 ± 0.004**
49	19.82 ± 0.21**	17.5 ± 0.2**	40.2 ± 0.6**	0.245 ± 0.004**
53	18.69 ± 0.24**	17.6 ± 0.3**	39.0 ± 0.6**	0.254 ± 0.006**
55	19.05 ± 0.23**	18.1 ± 0.3**	42.3 ± 0.6**	0.274 ± 0.005**
60	20.66 ± 0.25**	18.1 ± 0.4**	41.9 ± 0.6**	0.281 ± 0.006**
93	18.53 ± 0.23**	15.7 ± 0.3	39.5 ± 0.7**	0.240 ± 0.005*
109	19.02 ± 0.25**	16.4 ± 0.4	35.9 ± 0.4	0.242 ± 0.0004**
118	19.13 ± 0.39**	15.9 ± 0.3	34.3 ± 0.9	0.211 ± 0.006
137	18.92 ± 0.16**	16.0 ± 0.2	37.8 ± 0.4**	0.231 ± 0.003
153	21.83 ± 0.39**	16.7 ± 0.4	47.6 ± 1.0**	0.246 ± 0.007**
ZD958	16.69 ± 0.19	15.9 ± 0.3	34.7 ± 0.5	0.223 ± 0.004
PN24	18.94 ± 0.22**	16.0	38.4 ± 0.6**	0.233 ± 0.004

Data are from plants in randomized complete block design with three replications grown under natural condition in Dehui (Jilin Province, China) in 2015. Seeds of ZD958, PA24 and different hybrid F1 lines were sown in a population density of approximately 5500/μ. Values shown are means ± SEM. Values of PA24 and hybrid F1 lines significantly different from that of ZD958 at $*0.01 < P < 0.05$ and $**P < 0.01$ were indicated using the *t* test(n = 20). PA24 is a local main cultivar to be used as an internal control

(US Patent No.9139840 authorized on November 4, 2015). The cell wall invertase gene *ZmGIF1* can be used as a selection marker, and its expression can be combined between different parental cultivars to increase the invertase activity, and as a result, increase the grain yield of their hybrid progenies.

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Compliance with ethical standards

Conflict of interest We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

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