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# Characterization of the rate and duration of grain filling in wheat in southwestern China

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## ABSTRACT

Field trials were carried out during 2011–2013 in three locations on 10 wheat genotypes. Traits that were investigated included grain weight, grain-filling duration, grain-filling rates and the lag phase from flowering to the commencement of effective grain filling. The grain-filling duration and rate were fitted by Richard's equation in thermal time (growing degree-days (GDD), base temperature 9°C). A combined ANOVA across environments showed that the grain weight was mainly affected by genotype, while most of the other grain-filling characters were influenced by the environment and  $G \times E$  interactions. Grain filling lasted between 362 to 400 GDD and included a lag phase that ranged from 67 to 86 GDD. Both the effective and maximum rates of grain filling ranged from 0.12 to 0.15 mg GDD<sup>-1</sup> and 0.18–0.22 to GDD<sup>-1</sup>, respectively. The lag phase was positively correlated with grain weight and rates of grain filling, whereas days to anthesis were significantly negatively correlated with the lag phase and both rates of grain filling. Temperature during grain filling was negatively correlated with the lag phase. The variation in grain weight was positively associated with the rate of grain filling, which, in turn, was related to the grain number per unit area. A compensating variability existed among the genotypes in both the grain number and grain-filling rate. The study of genotypic stability demonstrated that Chuanmai42 and Chuanmai104 had high grain weight and stability among most of the grain-filling parameters, and also had high grain yield. Chuanmai42 and Chuanmai104 were the best genotypes for improving the yield potential and grain weight stability.

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## KEYWORDS

$G \times E$  interaction; stability; grain filling; wheat

## 1. Introduction

China is the largest wheat (*Triticum aestivum* L.) producer and consumer in the world, and wheat ranks as the third leading crop in China after rice and maize. In 2009, the Chinese wheat area, average yield and production were 24.2 million ha, 4747 kg ha<sup>-1</sup> and 115 million tons, respectively (Zheng et al., 2011). The Sichuan Basin, located in southwest China, is an important wheat-producing area with a production of 5.58 million tons harvested from an area of 1.35 million ha in 2010. Wheat in the Sichuan Basin is autumn sown and often experiences good initial rainfall with generally drier conditions through winter and early spring. However, growth can be negatively affected by low photosynthetic active radiation, along with high humidity and temperature, particularly during grain filling. This can lead to serious pest, disease and weed problems, affecting grain weight (GW) and yield losses of 20–30% (Zhu et al., 2010).

Environmental stresses during grain filling can lead to a reduction in mean GW, and although this trait is often negatively correlated with grains per m<sup>2</sup>, it can

also vary independently from this latter trait (Borrás, Slafer, & Otegui, 2004; Serrago et al., 2013; Whan, Carlton, & Anderson, 1996). As potential grain number is determined prior to anthesis, any decrease in post-anthesis photosynthesis mainly affects GW. Genetic factors can also contribute to GW, influencing the rate and duration of grain filling and their interaction (Motzo, Giunta, & Pruneddu, 2010; Sadras & Egli, 2008). Stable GWs can therefore be achieved through compensatory effects between these grain-filling components and a lack of variation in either could lead to unstable grain sizes. In recent years, significant environment fluctuations such as temperature, water availability, light intensity and nutrition between years and locations have seen significant variation in GW and yield stability. This is likely related to high environmental variations during the relatively long grain-filling period (Wu et al., 2014). Therefore, understanding the causes of GW determination across environments is critical for plant breeders and agronomists aiming to increase the yield or yield stability in this region.

It was commonly believed that the variation in the GW was mainly effected by the rate of grain filling

(Calderini & Reynolds, 2000; Motzo et al., 2010), especially under adverse conditions (Dias & Lidon, 2009). However, in some cases, the GW was more related to the grain-filling duration (GFD), while in others it was more related to the maximum grain-filling rate (Cossani, Slafe, & Savin, 2011; Rharrabti et al., 2003; Yang et al., 2008). In the case of durum wheats, there is good evidence that genetic advancement of anthesis has driven grain yield (Giunta, Motzo, & Pruneddu, 2008; Motzo, Fois, & Giunta, 2004; Motzo & Giunta, 2007; Motzo et al., 2010). The altered flowering time and senescence period may well have changed both the rate and duration of grain filling. Breeding for higher yield in bread wheat has succeeded in lengthening the grain-filling period (Loss & Siddique, 1994; Penrose, Walsh, & Clark, 1998).

Temperature is considered as the most important environmental factor affecting grain-filling parameters and GW (Calderini et al., 1999). Studies found that 20°C was the optimal temperature for grain filling in wheat (Dias & Lidon, 2009; Dupont & Altenbach, 2003) with the average temperature during the grain-filling period being positively associated with GW (Savin et al., 1999). However, higher temperatures significantly decrease GW, shortening the grain-filling period and affecting the grain filling rate. Milka et al. (2008) found that each 1°C increase in the main daily temperature above the optimum for grain filling resulted in the decrease of approximately 2.8 mg in GW and 3.1 days in GFD. He and Rajaram (1993) reported that the grain-filling rate was more temperature sensitive than GFD.

Generally, stability is defined as one genotype/trait having an unchanged performance regardless of any variation in the environmental conditions. GW has been shown to be a relatively unstable trait, likely due to complex interactions between wheat genotypes and the environment, with both the rate and GFD varying significantly (Cossani et al., 2011; Darroch & Baker, 1995; Dias & Lidon, 2009; Wu et al., 2014). Changes in the relative performances of genotypes grown in different environments indicate that  $G \times E$  interactions can be major challenges for crop-breeding programs (Mohammadi et al., 2007; Mohammadi & Amri, 2011; Mohammadi & Mahmoodi, 2008; Zobel & Talbert, 1984). To overcome this, results from multiple years and locations are necessary to produce broadly adapted varieties. Low-input farmers in developing countries grow cereals under harsh and unpredictable environments, and their need for yield stability is paramount (Ali et al., 2008; De Vita et al., 2010; Majid, Aaghar, & Murtaza, 2007; Mohammadi & Amri, 2011).

Sound statistical methods are required for the analysis of adaptation and stability. These methods allow

for subdividing the information that is contained in a complex  $G \times E$  interaction data matrix into simpler and more meaningful components (Rharrabti et al., 2003; De Vita et al., 2010). These statistical methods range from univariate parametric models, such as regression slope (Finlay & Wilkinson, 1963), deviation from regression (Eberhar & Russel, 1966), environmental variance and multivariate methods (e.g., Additive Main effect and the Multiplicative Interaction (AMMI) analysis) (Grausgruber et al., 2000; Zobel, Wright, & Gauch, 1988). Any of these measures may be of interest for breeding programs as an alternative to the regression statistic for evaluating the stability of a parameter.

This study aims (i) to characterize genotypic and environmental factors and their interactions, in the rate and duration of GFD in a weak-light ecological region environment; (ii) to evaluate the relative importance of the rate and duration of grain filling in determining the GW and to analyze associations among them; (iii) to assess the stability of GW, GFD and rate of 10 wheat cultivars across locations and years, and to analyze their relationships.

## 2. Materials and methods

### 2.1. General conditions, treatments and experimental design

The field experiments were carried out in three different locations across the Sichuan province of China, namely Guanghan (104° 25'N 30° 99'E), Jiangyou (104° 76'N 31° 78'E) and Jianyang (104° 32'N 30° 24'E). Trials were conducted in the first two sites over three growing seasons (harvested in May 2011, 2012 and 2013), whilst the last site had trials in 2012 and 2013. Guanghan and Jiangyou trials were grown in rotation with a summer rice crop, whereas Jianyang was grown in rotation with summer maize. These sites represent three main wheat-growing regions and have significant differences in tillage practice and soil fertility. The experiment was designed to provide a reliable assessment of adaptability and stability of the traits measured. All sites consisted of clay-loam soils. Guanghan, Jiangyou and Jianyang respectively contained 4.61%, 2.21% and 1.36% organic matter, 262.0 mg kg<sup>-1</sup>, 128.0 mg kg<sup>-1</sup> and 89.0 mg kg<sup>-1</sup> available N, 7.7 mg kg<sup>-1</sup>, 19.3 mg kg<sup>-1</sup> and 7.3 mg kg<sup>-1</sup> available P and 109.0 mg kg<sup>-1</sup>, 89.0 mg kg<sup>-1</sup> and 171.0 mg kg<sup>-1</sup> available K. Ten winter wheat cultivars were used for the experiments; Chuanmai42, Chuanmai51, Chuanmai55, Chuanmai56, Neimai836, Mianmai37, Chuanyu23, Xikemai5, Mianmai367 and Chuanmai104. Chuanmai42 and its derivatives, Mianmai367 and Chuanmai104 have synthetic wheat in their pedigree.

The field trials were arranged in a randomized complete-block design with three replicates. The wheat was sown by hand with no-till conditions between 29 October and 2 November each year. The seedling density was thinned to approximately 240 seedlings m<sup>-2</sup>. Plots at Guanghan were 4 m (20 rows, 20 cm apart) × 5 m. Jiangyou and Jinyang had plot sizes of 2.4 m (10 rows, 24 cm apart) × 5 m. The plots were fertilized with urea to give applied N amounts of 150–180 kg ha<sup>-1</sup>. A base fertilizer was applied to give concentrations of P<sub>2</sub>O<sub>5</sub> at 75.0 kg ha<sup>-1</sup>, K<sub>2</sub>O at 75.0 kg ha<sup>-1</sup> and Zn at 25 kg ha<sup>-1</sup>. Irrigation was used twice during the seedling stage and jointing stage in Guanghan, whilst Jiangyou and Jianyang were only irrigated during the jointing stage. Rust and powdery mildew were controlled by applying triadimefon (Chemical Industry Research and Design Institute of Sichuan Province Chengdu, China) at the seedling stage (150 mL ha<sup>-1</sup>) and with triadimefon (375 g ha<sup>-1</sup>) and propiconazole (Jiangsu Fengdeng Pesticide Co. Ltd. Chengdu, China; 75 mL ha<sup>-1</sup>) at the jointing stage. Fusarium head blight and aphids were controlled with β-cypermethrin (45 g ha<sup>-1</sup>) and acetamiprid (15 g ha<sup>-1</sup>) (both produced by Sichuan Saiwei Biological Engineering Co. Ltd., Chengdu, China) during grain filling.

## 2.2. Observation and sampling methodology

The temperature data were recorded using a standard weather station (ZENO-3200) and pluviometer located at the experimental site (Figure 1).

The number of days to anthesis was defined as the number of days from sowing to when half of the ears were flowering by observation of the whole canopy. Following anthesis, 120 spikes with spikelet range from 18 to 22, almost same size, and no pests or diseases were labeled (except those in border rows and 3 middle rows for grain yield harvested). Samples of 10 ears were harvested from each plot from 7 days after anthesis at 5-day intervals until full maturity. The ears were oven-dried at 75°C to constant weight, hand threshed and grain counted and weighed. The GW of these samples at each stage was used for non-linear regression analyses.

At maturity, three intact plant rows in middle of each plot were sampled for grain yield and 1000-GW, which was adjusted to 13% moisture.

## 2.3. Statistical analysis

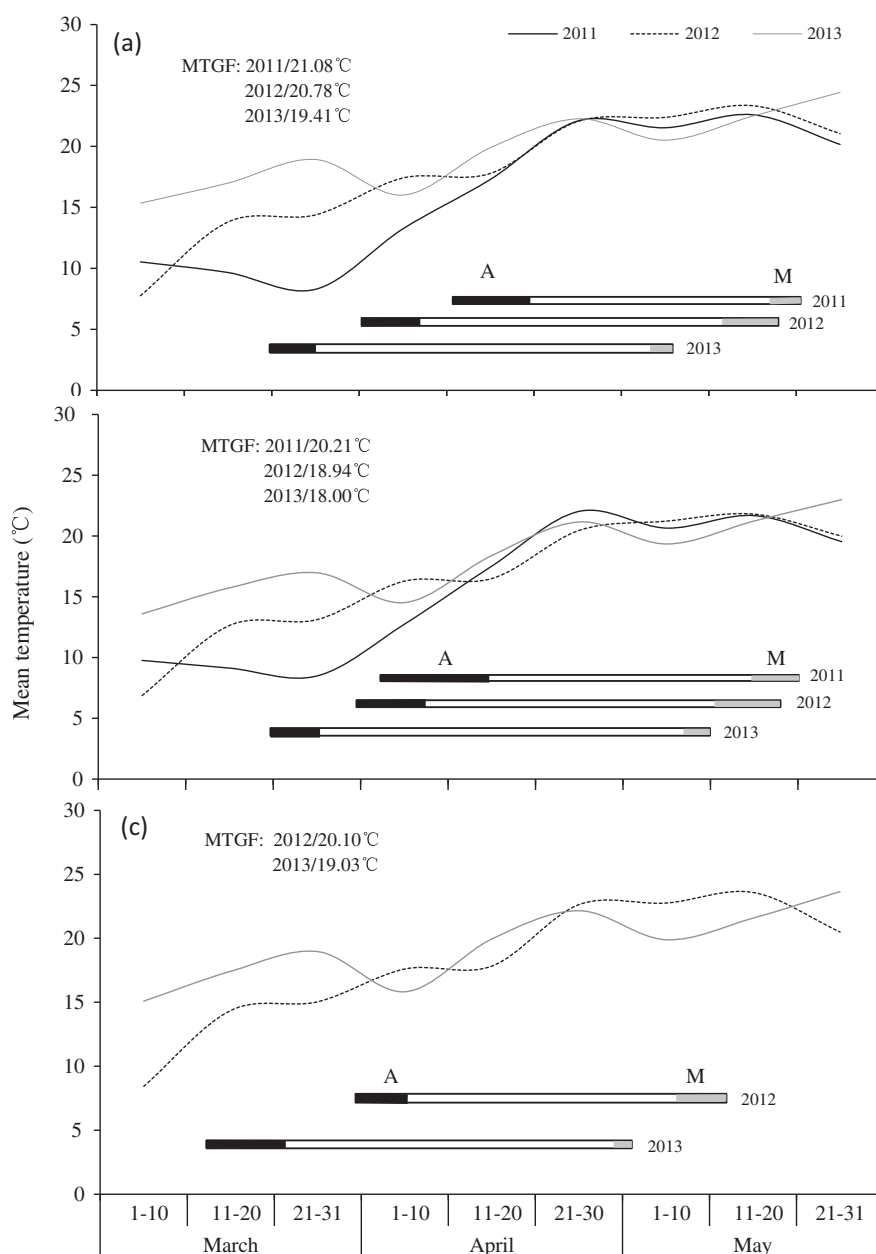
The grain-filling process was fitted to a growth equation (Richards, 1959) as described by Yang, et al. (2001). The grain-filling parameters were calculated as a function of the degree-days after flower with SAS statistical software as follows:

$$W = A / (1 + Be^{-kt})^{1/N} \quad (1)$$

where  $W$  was the GW (mg);  $t$  was the accumulated growing degree-days (GDD) from anthesis;  $A$  was the maximum GW (mg); and  $B$ ,  $k$  and  $N$  were coefficients that were determined by regression. The lag phase was calculated as the time for the grain to reach 10% of the maximal GW, as calculated from Richards equation (Loss et al., 1989; Motzo et al., 2010). Physiological maturity was assumed to occur at 95% maximal GW, GFD<sub>eff</sub> was calculated as the time for the grain from 10% to 95% of the maximal GW. GFD was calculated as the time from anthesis to physiological maturity. The maximum rate of grain filling (GFR<sub>max</sub>) was obtained from the first derivative of the above equation. The effective rate of grain filling (GFR<sub>eff</sub>) was the GW gain post-lag phase until physiological maturity divided by the time taken to achieve this weight gain, following Egli (2004). Thermal time was calculated from the local daily minimum and maximum temperatures, following Weir et al. (1984). A base temperature of 0°C was used for the period from sowing to anthesis, and 9°C was used during grain filling.

For the original data sets, the effects of the genotype (G), environment (E) and G × E interactions (GE) were calculated via a combined analysis of variance (ANOVA) using the Statistical Analysis System (SAS version 8.0 for Windows, SAS Inc., IL, USA) software package. Statistical comparisons were significant when  $p < 0.05$ (\*),  $p < 0.01$ (\*\*), or  $p < 0.001$ (\*\*\*). For the combined analysis, the variation was partitioned into relevant sources of variation to test for differences among the genotypes and for the presence of G × E. Mean comparisons between the trials for each grain-filling characteristic were performed, and least significant difference (LSD<sub>0.05</sub>) values were calculated at the 5% probability level. The correlation between the grain-filling parameters and GW and time to anthesis for 10 cultivars was calculated using Pearson's correlation analysis with SAS statistical software.

Five stability parameters were applied to assess the stability performance of the genotypes and to identify superior genotypes:  $bi$ , the linear regression of the phenotypic values on the environmental index (Finlay & Wilkinson, 1963);  $S^2_{di}$ , the deviation mean square from regression (Eberhar & Russel, 1966); and  $S^2_{xi}$ , the environmental variance. The AMMI stability value (ASV) based on the AMM model was also performed as described in Zobel et al. (1988) and Grausgruber et al. (2000), ASV is calculated by the distance of the first AMMI axis. To define genotypic stability, a genotype was considered stable for a given grain filling parameter if this genotype appeared stable in more than three (out of five) stability analyses. The genotypes that



**Figure 1.** Description of the daily mean temperature and grain-filling periods across 3 years at three sites ((a): Guanghan; (b): Jiangyou; (c): Jianyang). MTGF: mean temperature during grain filling; A: anthesis; M: maturity. Solid and dashed lines indicated anthesis and maturity duration among 10 genotypes, respectively.

proved stable for most of the stability analyses were then selected as the best.

### 3. Results

#### 3.1. Weather conditions

The three sites over 3 years differed in temperature (Figure 1). The mean temperature during grain filling in 2011, 2012 and 2013 were 20.7°C, 20.0°C and 18.8°C, respectively. There were continuous low temperatures

from mid December 2010 until early April 2011. This resulted in 10–18 days later anthesis than normal year with maturity also being delayed. The season ending in 2013 had a milder winter than normal with no exceptional late spring coldness, which resulted in early anthesis (10–20 days earlier than 2011) and maturity. The temperature of 2012 showed the normal year, the anthesis was 1–7 April; the maturity was 8–14 May. Genotypes at the three sites showed similar trends with Chuanmai56 and Chuanyu23 having the earliest

anthesis, followed by Chuanmai104 and Chuanmai42. Chuanmai55 had the latest anthesis. The difference of mean temperature during grain filling among genotypes was within 2°C, Chuanmai104 and Chuanmai51 showed above 20°C and Mianmai 367 showed below 19°C (Table 2).

### 3.2. Combined ANOVA

The ANOVAs showed highly significant effects (at least  $p < 0.01$ ) of genotypes (G), environments (E) and  $G \times E$  factors on the GW and grain-filling parameters (Table 1). In terms of the sums of squares, most of the variations in the GW were explained by the genotypes, followed by the environments and by the  $G \times E$  component. In contrast, the variation in grain-filling parameters was mainly explained by the environmental factor or  $G \times E$  interaction, followed by the genotypic component. Environment partitioning for the variation in GW were explained by year (Y), followed by location (L), while

grain-filling parameters were explained by location or  $L \times Y$ .

The total  $G \times E$  sum of squares partitioning into  $G \times L$ ,  $G \times Y$  and  $G \times Y \times L$  are shown in Table 1.  $G \times Y$  accounted for the highest percentage of the total  $G \times E$  on GW and  $GFR_{max}$ , while  $G \times Y \times L$  accounted for the highest percentage of the total  $G \times E$  in other grain-filling parameters.

### 3.3. GW and yield performance across the environments

The GW at the three locations during the three cropping seasons for all of the genotypes is shown in Table 2. The grand mean GW was 46.9 g. Significant genotypic variation was found ranging from 43.3 g for Chuanmai55 to 51.5 g for Chuanmai56. The environmental means ranged from 44.0 g in Jiayang 2012 to 50.0 g at Jiangyou 2011 (data not shown). There were significant differences in GW between genotypes in

**Table 1.** Sum of squares for the combined analysis of variance and the E and  $G \times E$  general decomposition; and tests of significance for grain weight and grain-filling parameters in wheat.

| Source                | d.f. | GW (mg) | GFD ( $\times 10^3$ )<br>GDD | Lag phase ( $\times 10^3$ )<br>GDD | GFD <sub>eff</sub> ( $\times 10^3$ )<br>GDD | GFR <sub>max</sub> ( $\times 10^3$ )<br>mg GDD <sup>-1</sup> | GFR <sub>eff</sub> ( $\times 10^3$ )<br>mg GDD <sup>-1</sup> |
|-----------------------|------|---------|------------------------------|------------------------------------|---|--|--|
| Block(Environment)    | 16   | 46*     | 14 <sup>ns</sup>             | 1.3 <sup>ns</sup>                  | 10 <sup>ns</sup>                            | 2.3 <sup>ns</sup>  | 9.1***   |
| Genotype(G)           | 9    | 1943*** | 31***                        | 6.4***                             | 21**  | 36.3***  | 16.1***  |
| Environment(E)        | 7    | 1112*** | 300***                       | 24.5***                            | 209***                                      | 97.7***  | 29.2***  |
| Location(L)           | 2    | 308***  | 110***                       | 17.8***                            | 75***                                       | 43.5***  | 15.1***  |
| Year(Y)               | 2    | 701***  | 17***                        | 5.5***                             | 17***                                       | 12.2***  | 3.1**  |
| $L \times Y$          | 3    | 104***  | 173***                       | 1.2 <sup>ns</sup>                  | 117***                                      | 42.1***  | 10.9***  |
| $G \times E$          | 63   | 794**   | 209***                       | 38.7***                            | 183***                                      | 60.6***  | 19.8***  |
| $G \times L$          | 18   | 182***  | 58***                        | 12.3***                            | 60***                                       | 12.5***  | 5.3 <sup>ns</sup>  |
| $G \times Y$          | 18   | 425***  | 74***                        | 8.9***                             | 52***                                       | 26.9***  | 6.1 <sup>ns</sup>  |
| $G \times Y \times L$ | 27   | 187*    | 77***                        | 17.5***                            | 71***                                       | 21.2***  | 8.6 <sup>ns</sup>  |
| Error                 | 144  | 15      | 3.3                          | 1.0                                | 1.7   | 0.4  | 1.0  |

GW: grain weight; GFD: Grain filling duration; Lag phase: the time to 10% of maximum grain weight; GFD<sub>eff</sub>: 10–95% of maximum grain weight; GFR<sub>eff</sub>: effective rate of grain filling; GFR<sub>max</sub>: maximum rate of grain filling. The same below on the grain filling parameter abbreviation. ns: no significant; \*Significant at  $p < 0.05$ ; \*\*Significant at  $p < 0.01$ ; \*\*\*Significant at  $p < 0.001$ .

**Table 2.** Grain yield, grain weight, duration and rate of grain filling. Means across three locations and 3 years.

| Genotype/Year       | Grain yield (t ha <sup>-1</sup> ) | GW (mg) | GFD  | GFD <sub>eff</sub> | Lag -phase | GFR <sub>eff</sub> (mg GDD <sup>-1</sup> ) | GFR <sub>max</sub> (mg GDD <sup>-1</sup> ) | MTGF (°C) |
|---------------------|-----------------------------------|---------|------|--------------------|------------|--|--|-----------|
| Genotype            |                                   |         |      |                    |            |  |  |           |
| Chuanmai56          | 7.58                              | 51.5    | 379  | 293                | 86         | 0.15                                       | 0.22                                       | 19.87     |
| Chuanyu23           | 7.85                              | 50.9    | 400  | 315                | 86         | 0.14                                       | 0.21                                       | 19.74     |
| Chuanmai42          | 9.38                              | 49.4    | 388  | 307                | 81         | 0.14                                       | 0.21                                       | 19.53     |
| Chuanmai104         | 9.96                              | 47.7    | 392  | 318                | 74         | 0.12                                       | 0.19                                       | 20.49     |
| Mianmai37           | 9.39                              | 47.1    | 391  | 321                | 70         | 0.13                                       | 0.19                                       | 19.81     |
| Mianmai367          | 10.03                             | 45.1    | 393  | 321                | 73         | 0.12                                       | 0.18                                       | 18.36     |
| Neimai836           | 8.32                              | 45.7    | 362  | 296                | 67         | 0.13                                       | 0.20                                       | 19.75     |
| Xikemai5            | 8.66                              | 44.6    | 371  | 297                | 74         | 0.13                                       | 0.20                                       | 19.94     |
| Chuanmai51          | 8.91                              | 43.5    | 378  | 299                | 78         | 0.12                                       | 0.19                                       | 20.02     |
| Chuanmai55          | 9.38                              | 43.3    | 372  | 300                | 72         | 0.12                                       | 0.19                                       | 19.85     |
| CV%                 | 9.3                               | 1.8     | 1.0  | 1.1                | 2.7        | 2.11                                       | 2.17                                       | —         |
| LSD <sub>0.05</sub> | 1.1                               | 2.0     | 31.2 | 25.4               | 9.2        | 0.01                                       | 0.01                                       | —         |
| Year                |                                   |         |      |                    |            |  |  |           |
| 2011                | 8.49                              | 49.3    | 383  | 316                | 67         | 0.13                                       | 0.20                                       | 15.94     |
| 2012                | 9.59                              | 45.2    | 376  | 306                | 70         | 0.13                                       | 0.20                                       | 17.47     |
| 2013                | 9.08                              | 46.9    | 393  | 312                | 81         | 0.12                                       | 0.19                                       | 19.09     |
| LSD <sub>0.05</sub> | 1.15                              | 2.5     | 20.0 | 10.4               | 8.8        | 0.01                                       | 0.01                                       | —         |

MTGF: mean temperature during grain filling.

The difference among cultivars or years was significant at the 5% level, when the difference of them exceeded the LSD<sub>0.05</sub>.

each environment and the rank order varied little. The mean data for GW showed that Chuanmai56, Chuanyu23 and Chuanmai42 ranked as the top three lines, while Xikemai5, Chuanmai51 and Chuanmai55 ranked as the last three lines and this status generally held across most of individual environments.

The grain yield ranged from 7.58 to 10.03 t ha<sup>-1</sup>, Chuanmai104 and Mianmai367 showed the highest grain yield, followed by Mianmai37, Chuanmai42 and Chuanmai55. The year means across sites and genotypes showed the highest yield was observed in 2012, followed by the 2013 and 2011.

### 3.4. Duration and rate of grain filling

Both the duration and rate of grain filling were obtained from the means of the Richards curves and these modeled the accumulation of GW very closely ( $R^2$  values of at least 0.95, always significant at least at  $p < 0.05$  with the estimated maximum GWs being strongly correlated with the observed maximum GWs ( $R^2 > 0.97$ ).

All of the grain-filling parameters were expressed in thermal time. The base temperature of 9°C was used to calculate the thermal time and was derived from the relationship between the developmental rate during grain filling, which was obtained from Richards equation (1 day from anthesis to physiological maturity), and the mean temperature during this period.

There was significant genotypic variation in total GFD and in GFD<sub>eff</sub>. Total GFD lasted 362–400 GDD with Chuanyu23, Chuanmai104 and Mianmai367 had higher GFD and GFD<sub>eff</sub> lasted 293–321 GDD. A significant genotypic variation was also found in the lag phase with Mianmai367, Chuanmai55, Neimai836 and Mianmai37 having values of 73, 72, 67 and 70 GDD, respectively, while Chuanmai56 and Chuanyu23 had a lag phase of both 86 GDD (Table 2). The lag phase ranged from 22% to 32% of GFD across the cultivars, Chuanmai56 and Chuanyu23 had a higher ratio of GFD in the lag phase than did the other genotypes, followed by Chuanmai42 and Chuanmai104.

Both the effective and maximum rates of grain filling differed significantly among the genotypes, ranging 0.12–0.15 mg GDD<sup>-1</sup> and 0.18–0.22 mg GDD<sup>-1</sup>,

respectively (Table 2). Chuanmai56, Chuanyu23 and Chuanmai42 showed higher relative rates of grain filling than did the other genotypes. The two rates were almost perfectly correlated with one another ( $R^2 = 0.81^{**}$  in day and  $R^2 = 0.99^{***}$  in GDD (data not shown).

### 3.5. Correlation analysis between GW, grain-filling parameters, anthesis and temperature

#### 3.5.1. GW and grain-filling parameters

Table 3 describes the relationship between the GW and the grain-filling parameters. GW was significantly positively correlated with rate of grain filling (GFR<sub>eff</sub> and GFR<sub>max</sub>) and lag phase. The lag phase also significantly positively correlated with both GFR<sub>eff</sub> and GFR<sub>max</sub>. The total GFD and GFD<sub>eff</sub> were not correlated with any grain-filling parameters.

#### 3.5.2. GW, anthesis, temperature and grain-filling parameters

Correlation analysis showed that anthesis was negatively correlated with the GW (Table 4), the correlation coefficient was 0.78. Chuanmai56, Chuanyu23, Chuanmai42 and Chuanmai104 exhibited earlier anthesis with higher GW, while Chuanmai51, Chuanmai55 and Xikemai5 showed later anthesis and the lower GW.

Table 4 shows that the anthesis was significantly negatively correlated with lag phase and both the effective and maximum GFR. In addition, MTGF also showed negatively correlated with lag phase, while in the lack of relationship between MTGF and other grain-filling parameters.

### 3.6. Stability analysis

Results from the five statistical parameters used to define genotypic stability are summarized as either positive (stable) or negative (unstable) in Tables 5 and 6. The two most stable genotypes across the grain-filling parameters were Chuanmai42 and Chuanmai104, followed by Mianmai367 and Mianmai37, and Chuanyu23, Neimai836 and Chuanmai55 were stable for half GW and grain-filling parameters. Chuanmai42 and Chuanmai104 showed positive stability in all aspects. Mianmai367 was

**Table 3.** Correlation analysis between grain weight and grain-filling duration parameters and the effective (GFR<sub>eff</sub>) and maximum (GFR<sub>max</sub>) rates of grain filling ( $n = 10$ ).

| Parameter                                  | GW (mg) | GFD                | Lag phase | GFD <sub>eff</sub> (mg GDD <sup>-1</sup> ) |
|--|---------|--------------------|-----------|--|
| Grain weight (mg)                          | –       | 0.51 <sup>ns</sup> | 0.78*     | 0.14 <sup>ns</sup>                         |
| GFR <sub>eff</sub> (mg GDD <sup>-1</sup> ) | 0.88**  | 0.02 <sup>ns</sup> | 0.79*     | –0.39 <sup>ns</sup>                        |
| GFR <sub>max</sub> (mg GDD <sup>-1</sup> ) | 0.83**  | 0.00 <sup>ns</sup> | 0.79*     | –0.42 <sup>ns</sup>                        |

ns: no significant; \*Significant at  $p < 0.05$ ; \*\*Significant at  $p < 0.01$ ; \*\*\*Significant at  $p < 0.001$ .

**Table 4.** Correlation analysis between anthesis, temperature during grain filling and grain-filling parameters.

| Parameter     | GW (mg)            | GFD                 | Lag phase | GFD <sub>eff</sub>  | GFR <sub>eff</sub> (mg GDD <sup>-1</sup> ) | GFR <sub>max</sub> (mg GDD <sup>-1</sup> ) |
|---------------|--------------------|---------------------|-----------|---------------------|--|--|
| Anthesis(GDD) | -0.78**            | -0.06 <sup>ns</sup> | -0.71*    | 0.35 <sup>ns</sup>  | -0.76*                                     | -0.73*                                     |
| MTGF          | 0.01 <sup>ns</sup> | -0.18 <sup>ns</sup> | -0.67*    | -0.02 <sup>ns</sup> | -0.12 <sup>ns</sup>                        | -0.12 <sup>ns</sup>                        |

ns: no significant; \*Significant at  $p < 0.05$ ; \*\*Significant at  $p < 0.01$ .

MTGF: mean temperature during grain filling.

Anthesis: degree-days from sow to anthesis.

**Table 6.** Summary of the stability analyses of 10 wheat genotypes grown across different environments.

| Genotype    | GW             | GFD | GFD <sub>eff</sub> | Lag phase | GFR <sub>eff</sub> | GFR <sub>max</sub> | Rank |
|-------------|----------------|-----|--------------------|-----------|--------------------|--------------------|------|
| Chuanmai56  | - <sup>b</sup> | -   | -                  | -         | -                  | -                  | 0    |
| Chuanyu23   | -              | +   | -                  | +         | +                  | +                  | 3    |
| Chuanmai42  | + <sup>a</sup> | -   | -                  | -         | -                  | -                  | 1    |
| Chuanmai104 | -              | +   | +                  | +         | +                  | +                  | 5    |
| Mianmai37   | -              | +   | -                  | +         | +                  | +                  | 4    |
| Mianmai367  | -              | -   | +                  | -         | +                  | +                  | 4    |
| Neimai836   | +              | +   | -                  | +         | +                  | +                  | 5    |
| Xikemai5    | -              | -   | -                  | -         | -                  | -                  | 0    |
| Chuanmai51  | +              | -   | -                  | +         | -                  | -                  | 2    |
| Chuanmai55  | +              | -   | +                  | -         | +                  | +                  | 4    |

<sup>a</sup>Stable.

<sup>b</sup>Unstable.

**Table 5.** Stability parameters for the considered quality traits<sup>a</sup>.

|                          | $b_i^b$ | $S_{di}^2$ <sup>c</sup> | $S_{xi}^2$ <sup>d</sup> | ASV <sup>e</sup>         | $b_i^b$ | $S_{di}^2$ <sup>c</sup> | $S_{xi}^2$ <sup>d</sup> | ASV <sup>e</sup> |
|--------------------------|---------|-------------------------|-------------------------|--------------------------|---------|-------------------------|-------------------------|------------------|
| <b>GW</b>                |         |                         |                         | <b>Lag phase</b>         |         |                         |                         |                  |
| Chuanmai56               | 0.66    | 1.43                    | 9.78                    | 8.87                     | 1.13    | 0.75                    | 1.28                    | 1.85             |
| Chuanyu23                | 1.73    | 1.41                    | 8.10                    | 6.23                     | 0.56    | 0.12                    | 0.14                    | 1.54             |
| Chuanmai42               | 0.68    | 1.43                    | 3.45                    | 1.80                     | 1.11    | 0.64                    | 0.21                    | 1.58             |
| Chuanmai104              | 0.94    | 2.05                    | 6.08                    | 3.23                     | 0.57    | 0.22                    | 0.24                    | 0.83             |
| Mianmai37                | 1.80    | 1.48                    | 17.08                   | 0.73                     | 0.62    | 0.07                    | 0.11                    | 0.97             |
| Mianmai367               | 1.38    | 0.34                    | 10.10                   | 3.63                     | 1.38    | 0.06                    | 0.22                    | 1.23             |
| Neimai836                | 0.94    | 1.50                    | 5.65                    | 1.66                     | 0.94    | 0.29                    | 0.48                    | 1.21             |
| Xikemai5                 | 1.30    | 1.46                    | 9.61                    | 1.18                     | 1.55    | 0.55                    | 0.52                    | 2.31             |
| Chuanmai51               | 0.20    | 1.47                    | 2.72                    | 1.51                     | 0.35    | 0.26                    | 0.16                    | 1.88             |
| Chuanmai55               | 0.37    | 1.47                    | 1.51                    | 1.28                     | 1.79    | 0.07                    | 0.53                    | 1.03             |
| <b>GFD</b>               |         |                         |                         | <b>GFR<sub>eff</sub></b> |         |                         |                         |                  |
| Chuanmai56               | 0.97    | 1.00                    | 4.28                    | 1.33                     | 1.30    | 0.26                    | 0.80                    | 4.92             |
| Chuanyu23                | 0.89    | 1.60                    | 2.41                    | 0.96                     | 0.82    | 0.13                    | 0.27                    | 2.50             |
| Chuanmai42               | 1.22    | 0.32                    | 3.15                    | 1.25                     | 1.27    | 0.03                    | 0.42                    | 1.37             |
| Chuanmai104              | 0.80    | 0.45                    | 1.73                    | 1.27                     | 0.65    | 0.06                    | 0.16                    | 1.73             |
| Mianmai37                | 0.82    | 0.86                    | 1.91                    | 1.33                     | 0.82    | 0.04                    | 0.20                    | 3.37             |
| Mianmai367               | 0.67    | 0.92                    | 1.54                    | 1.46                     | 0.84    | 0.04                    | 0.22                    | 1.07             |
| Neimai836                | 0.98    | 0.51                    | 2.20                    | 0.67                     | 0.92    | 0.10                    | 0.29                    | 2.57             |
| Xikemai5                 | 1.24    | 0.37                    | 3.23                    | 0.94                     | 1.30    | 0.52                    | 0.49                    | 1.76             |
| Chuanmai51               | 1.32    | 1.33                    | 3.81                    | 3.76                     | 1.30    | 0.11                    | 0.54                    | 3.49             |
| Chuanmai55               | 1.09    | 1.36                    | 3.36                    | 0.61                     | 0.78    | 0.14                    | 0.39                    | 0.76             |
| <b>GFD<sub>eff</sub></b> |         |                         |                         | <b>GFR<sub>max</sub></b> |         |                         |                         |                  |
| Chuanmai56               | 1.53    | 3.01                    | 5.19                    | 1.00                     | 0.49    | 1.18                    | 2.51                    | 0.65             |
| Chuanyu23                | 0.70    | 1.10                    | 1.55                    | 0.97                     | 0.95    | 0.23                    | 0.65                    | 0.61             |
| Chuanmai42               | 1.20    | 0.31                    | 2.04                    | 1.46                     | 1.46    | 0.07                    | 0.97                    | 1.01             |
| Chuanmai104              | 0.93    | 0.16                    | 1.22                    | 0.38                     | 0.81    | 0.10                    | 0.38                    | 0.94             |
| Mianmai37                | 0.83    | 1.25                    | 2.30                    | 0.75                     | 0.81    | 0.10                    | 0.46                    | 2.13             |
| Mianmai367               | 0.54    | 0.40                    | 0.69                    | 0.61                     | 0.84    | 0.08                    | 0.48                    | 1.67             |
| Neimai836                | 0.83    | 0.98                    | 2.10                    | 0.76                     | 0.88    | 0.34                    | 0.65                    | 1.10             |
| Xikemai5                 | 1.02    | 0.67                    | 1.81                    | 1.13                     | 1.34    | 0.21                    | 1.21                    | 1.05             |
| Chuanmai51               | 1.61    | 1.16                    | 2.24                    | 1.55                     | 1.47    | 0.15                    | 1.22                    | 3.55             |
| Chuanmai55               | 0.81    | 0.68                    | 1.46                    | 0.56                     | 0.95    | 0.09                    | 0.45                    | 1.03             |

<sup>a</sup> $b_i$ : regression slope (Finlay & Wilkinson, 1963).  $S_{di}^2$ : deviation from regression (Eberhar & Russel, 1966).  $S_{xi}^2$ : environmental variance. ASV: AMMI stability value (Grausgruber et al., 2000). Genotypes with values in underline are considered stables.

<sup>b</sup>When  $b_i$  is close to 0, or lower than 1, genotypes is considered stables.

<sup>c</sup> $S_{di}^2$  was utilized as a stability parameter only when  $b_i < 1$ , genotypes with lower values than the mean are regarded as stables.

<sup>d</sup>Genotypes with minimum variance under different environments was considered to be stables.

<sup>e</sup>Values in underline are lower than the mean. Genotypes with lower values than the mean are regarded as stables.

unstable only for GW and GFD, and Mianmai37 was unstable for GW and GFR<sub>eff</sub>. Chuanmai56 was unstable in all of the parameters tested (Table 6), Chuanmai51 was unstable in all parameters but stable in GW, Xikemai5 was unstable in all parameters but stable in GFD and GFR<sub>eff</sub>. Additionally, both Chuanmai42 and Chuanmai104 had a higher GW than that of the other genotypes except for Chuanmai56 and Chuanyu23 (Table 2), but the latter two were unstable for GW and most of the grain-filling parameters (Tables 2 and 6).

#### 4. Discussion

This study investigated the main drivers of GW in 10 elite cultivars commonly grown in the highly productive wheat growing region of the Sichuan basin. The GW amongst these cultivars was strongly correlated with early flowering. However, early flowering did not result in a longer GFD, but rather a higher GFR. Both the GW and the GFR were correlated with a longer lag phase, the time taken for grains to reach 10% maximum weight post-anthesis. This suggests that early flowering lines were devoting time soon after anthesis to accumulate more photosynthates prior to commencement of effective grain filling. The increased amount of photosynthates were then translocated to the grain in a similar time frame to those later flowering lines, resulting in an increased rate of effective grain filling and ultimately larger grains.

GFD and rate have major effects on final GW and can have significant effects on final yield (Motzo et al., 2010; Sadras & Egli, 2008; Whan et al., 1996). Wheat grown in the Sichuan basin is considered to have a heavier GW and this has presumed to be due to a longer GFD and higher grain-filling rate, although environmental variations in this region can significantly impact grain size (Feng et al., 2009; Wu et al., 2014; Zhang et al., 2010). Therefore, differential responses may easily emerge when the genotypes are exposed to a sufficiently wide range of growing conditions. In this study, we demonstrated that the determination of the GW compared to grain-filling parameters was more influenced by the genotype than by the environment or by G × E interactions (Table 1), indicating that GW has been significantly improved through breeding (Wu et al., 2014).



In addition, several studies have demonstrated that the genotype determines the grain-filling rate, whereas environmental factors, such as temperature, affect the duration of the grain-filling period (Royo et al., 2000; Wiegand & Cuellar, 1981). Our results showed that genotype had the largest overall effect on GW and although it was a significant factor in all grain-filling parameters, environmental interactions were stronger drivers of these parameters (Table 1). In particular, the year factor had a more significant effect on the GW than the location factor, agreeing with several previous studies that also demonstrated that differences among consecutive years are larger than differences among test sites within a year (Mohammadi & Amri, 2011; Sudaric, Simic, & Vratarić, 2006). Despite the Sichuan basin being a relatively uniform environment, year-to-year variability requires genotypes with high levels of stability in relation to yield and its components.

#### 4.1. Contribution of GFD and rate to grain yield

Association of GFD and rate with grain yield shows different patterns depending on crop species (Motzo et al., 2010; Rharrabti et al., 2003; Yang et al., 2008). In this study, it was observed that the rate of grain filling was strongly correlated to GW ( $p < 0.01$ ) with the lag phase having a less, but still significant effect ( $p < 0.05$ ) (Table 3). This indicates that the genotypes with a high potential grain-filling rate may reach a superior GW. These results agree with the reports of many previous studies (Calderini & Reynolds, 2000; Dias & Lidon, 2009; Giunta & Motzo, 2005; Motzo et al., 2010). In addition, other research has shown that longer grain-filling periods were associated with lower grain-filling rates (Calderini et al., 1999; Motzo, Giunta, & Deidda, 1996; Voltas et al., 1999). However, our study found that the

GFR did not correlate with the GFD; however, the lag phase was positively correlated with the  $GFR_{eff}$  and  $GFR_{max}$ . The capacity of grain to accumulate dry matter is established shortly after anthesis. This is mainly dependent on the formation of endosperm cells (Brocklehurst, 1977) and, in turn, on the supply of assimilates to the growing grains (i.e., source activity) (Jenner, Ugalde, & Aspinall, 1991). A longer lag phase with a higher rate of grain filling is thought to favor greater carbohydrate accumulation, and genotypic differences in this regard have been previously reported. In our study, Xikemai5 which had the longest GFD but a shorter lag phase was clearly source-limited during grain filling, further indicating that the lag phase, as opposed to  $GFD_{eff}$ , was a dominating effect on GW development.

The variation in GW was also associated with the rate of grain filling, which is in turn related to the grain number per unit area. This study calculated a negative correlation ( $R^2 = -0.584^*$ ) between the grain-filling rate and the grain number per unit area (Figure 2), indicating that a compensating variability exists among these genotypes in both the grain number and grain-filling rate. This relationship has been noted for several crops including wheat (Egli, 2006; Motzo et al., 2010; Slafer, Satorre, & Andrade, 1993). When this relationship derives from genetic differences in the grain-filling rate, the yield is usually neutral because the grain number per unit area adjusts to the change in the grain-filling rate to maintain a constant yield (Egli, 2006). The genotypes Chuanyu23 and Chuanyu56 had the largest GW (and consequently high rates of grain filling) with relatively low numbers of grains per unit area, whereas larger numbers of smaller grains were found in Chuanmai51 and Chuanmai55. These genotypes showed yield neutrality (Table 2).

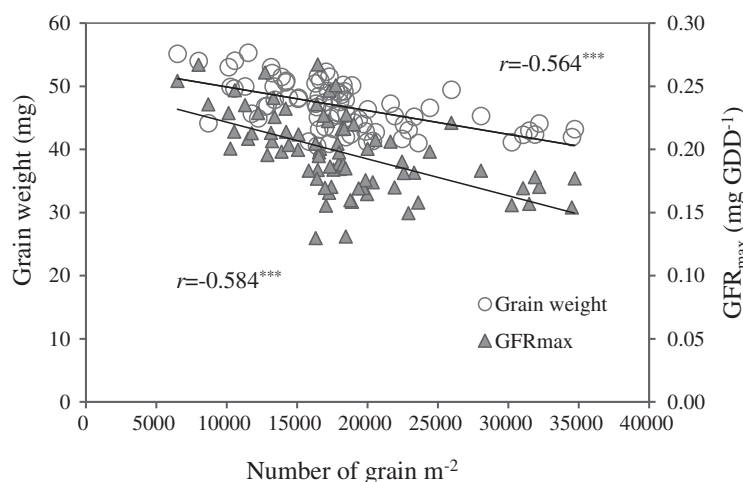


Figure 2. Relationships between grain weights, the maximum-filling rate ( $GFR_{max}$ ) and number of grains  $m^{-2}$ . \*\*\*Significant at  $p < 0.001$ .

#### 4.2. Lag phase, time to anthesis and temperature during grain filling

The duration of the lag phase was estimated due to its importance in determining the potential size of the grain via its effects on the number of endosperm cells and on the capacity of dry matter accumulation shortly after anthesis (Brocklehurst, 1977; Jenner et al., 1991; Motzo et al., 2010; Nicolas, Roslyn, & Dalling, 1984). Although the present study showed relatively little genotype effect on  $GFD_{eff}$ , genotypes with longer total GFD were associated with a longer lag phase, earlier flowering and higher GWs (Table 2). Previous studies indicated that a longer GFD has often been linked to early flowering cultivars (Metzger, Czaplewski, & Rasmusson, 1984; Van Sanford, 1985) and the progressive advance in anthesis in both bread and durum wheat and its positive effects on wheat yield are well documented (Loss & Siddique, 1994). However, this study showed that the time to anthesis was not significantly correlated with GFD and  $GFD_{eff}$  but was negatively associated with the lag phase (Table 4). This may indicate that it is possible to lengthen lag phase by advancing anthesis. Chuanmai56 and Chuanyu23, for example, had the longest lag phase, were the earliest flowering and produced the heaviest grains (Table 2, Figure 1). Earlier flowering cultivars are likely to suffer to a lesser extent from higher temperature during grain filling at the end of the crop cycle, thus facilitating the growth of larger kernels. This result was consistent with several previous reports (Motzo et al., 1996, 2010; Wu et al., 2014).

Cui et al. (2000) found that environmental factors such as soil, climate characteristics and particularly temperature mostly influenced GW and grain-filling characters on a common set of genotypes, sites and cultivation management. Generally, the mean environmental GFD values and average mean temperature during grain filling tend to be negatively related, and the differential genotypic responses during the GFD were not associated (Rharrabti et al., 2003). High temperature (31/20°C day/night) during grain filling has been shown to be a major cause for increases in the rate of grain filling (Dias & Lidon, 2009). In this study, the mean temperatures during grain filling of around 18–20°C, with anthesis commencing in mid-March to early April and grain filling lasting 6–7 weeks. The MTGF varied little and did not have any effect on the GFR or GFD. The main temperature differences between the seasons were pre-anthesis and this had significant effects on flowering time. For example, Figure 1 shows a prolonged cool period coming out of winter in 2011, whereas 2012 and 2013 experienced significant

temperature increases by mid-March. The effect of this was to delay flowering by 10–15 days in 2011. This resulted in shortening of GFD of between 7–10 days in this year (Figure 1), reducing grain numbers and increased GW. Higher pre-anthesis temperature was observed in 2013 with earlier flowering time, longer lag phase and normal GW showed in 2013. In addition, we showed MTGF had the negative correlated with lag phase, this result also indicated that the lag phase was more temperature-sensitive than GFD and rate of grain filling.

#### 4.3. Stability of GW and grain-filling parameters

Environmental variations are important in determining the performance and multi-environment trials conducted across locations and years are essential in determining yield stability (Rharrabti et al., 2003; Mohammadi & Amri, 2011; De Vita et al., 2010). In this study, four stable genotypes were detected using five stability parameters. Chuanmai42 and Chuanmai104 showed high and stable GWs (Tables 5 and 6). Chuanmai42 was released in 2003 and was the first international release of synthetic derived wheat (Yang et al., 2009). This cultivar not only has a specific adaptation to this region but can also be grown successfully in other zones of China, such as some provinces of the upper reaches of the Yangtze River. This cultivar has been recommended for farmers in high-yielding regions and has the highest farmer production record in Sichuan where it yielded 10.67 t.ha<sup>-1</sup> (Tang et al., 2013). Chuanmai104 is also synthetic derivative and it has Chuanmai42 in its pedigree, and was released in 2013, respectively. It also show highly stable grain-filling parameters and will be of interest for growers in southwest China. Previous preliminary studies also showed that it had outstanding advantages in grain number.m<sup>-2</sup> and GW (Tang et al., 2013). Mianmai367 showed stable GW and highest grain yield, which is also synthetic derivative and was released in 2013, belongs to big-spike variety, and this genotype had outstanding advantages in grain number.m<sup>-2</sup> and grains per spike. Mianmai37 was the non-synthetic derived cultivar, which showed stable GW and high grain yield. Mianmai 37 was the control cultivars in the Sichuan provincial wheat performance assessments during 2009–2014.

Higher but unstable GWs and grain-filling parameters were found in the synthetic derived cultivar of Chuanmai 56 and non-synthetic derived cultivar of Chuanyu23, These genotypes were easily affected by environments. Chuanmai56 had the highest average GW across all environments; however, it was unstable

for GW and all grain-filling parameters. This line was by far the earliest flowering variety in this study and this anomaly may have impacted on the aforementioned instability. Neimai836 and Xikemai5 had lower GW and grain yield with unstable for about half grain-filling parameters. Chuanmai51 and Chuanmai55 showed lowest GW and were unstable for most of the grain-filling parameters. These two genotypes had the latest anthesis, shorter lag phase and slower grain-filling rates.

Some variability was observed between the measurements of stability within each genotype. Thus, some of the genotypes were stable for one trait and unstable for another (Table 6), further suggesting that the genetic factors that are involved in the genotype  $\times$  environment interaction differed between the traits (Grausgruber et al., 2000; Rharrabti et al., 2003; Mohammadi & Amri, 2011). In addition, no significant correlation was found among these statistical techniques (data not shown), indicating that the GW formation and grain-filling process were complicated and that integrating statistics could be used to evaluate the stability of the GW in this area.

## 5. Conclusion

Analyzing the variation of GW through rate and duration of grain filling allows us to explain the characterization and stability between cultivar and environment. Genetic improvement has positively impacted on GW, but grain-filling parameters were more significantly affected by the environment or  $G \times E$  than by the genotype. Longer GFD cultivars have benefited from early flowering time and a longer lag phase, but temperature during grain filling was not a limiting factor on grain-filling processes. The lag phase showed a significant positive correlation with the rate of grain filling and GW, but the correlation between the time to anthesis and the lag phase, the rate of grain filling and the GW were negatively correlated. The variation in GW was more strongly associated with the rate of grain filling than with the lag phase, which, in turn, was related to the grain number per unit area. A compensating variability existed among the genotypes in both the grain number and grain-filling rate. According to stability analysis, two synthetic-derived wheat Chuanmai42 and Chuanmai104 had highest GW and stability with wide adaptation.

## Disclosure statement

No potential conflict of interest was reported by the authors.

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