

Inheritance of morphological traits of the second basal internode in bread wheat (*Triticum aestivum* L.)

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Abstract

The genetic effect of culm diameter (CD), culm wall thickness (CWT) and culm weight per cm ($Cw\text{ cm}^{-1}$) of the second basal internode was investigated in a 7×7 incomplete diallel cross of seven wheat parents (Ningmai 8, Ningmai 9, Yangmai 5, Yangmai 9, Yangmai 11, Sumai 3, and Wangshuibai) in the 2009-2010 season. Significant differences were observed among genotypes for all the traits, and the general combining ability (GCA) and specific combining ability (SCA) were highly significant. The GCA variances were greater than SCA, indicating the predominance of additive effects. The estimates of GCA showed that parents with the best GCA for CD, CWT and $Cw\text{ cm}^{-1}$ were Ningmai 8 and Yangmai 5. Adequacy tests revealed that data of all the traits were partially adequate for genetic interpretation except CWT. Greater value of D over H_1 demonstrated additive nature of gene actions for CD and $Cw\text{ cm}^{-1}$, which supports the utilization of pedigree selection for improvement of these two traits. CD and $Cw\text{ cm}^{-1}$ might be controlled by two and seven groups of genes, respectively, and exhibited lower values of narrow sense heritability.

Keywords: diallel cross, combining ability, inheritance, basal internode, *Triticum aestivum* L.

Abbreviation: AD_additive-dominance; GCA_ general combining ability; SCA_specific combining ability; CD_culm diameter; CWT_culm wall thickness; $Cw\text{ cm}^{-1}$ _culm weight per cm.

Introduction

Wheat culms are erect, cylindrical, jointed and consist of five to six internodes. The basal internode is very short, the second internode elongates somewhat more and each successive internode elongates progressively more. The basal part of the culm plays an important role in lodging resistance as it provides a lever to hold the plant upright. Lodging in wheat occurs commonly as a result of culm structural failure rather than loss of root anchorage (Neenan and Spencer-Smith, 1975). The nature and extent of lodging are closely related with culm characteristics, as lodging usually occurs when the stems bend or break at the basal internode (Pinthus, 1973). Many researchers reported associations of lodging resistance with morphological characters of the basal internodes. Lodging resistance was significantly and positively correlated with stem diameter and wall thickness of basal internodes (Xiao et al., 2002; Dong et al., 2003; Hai et al., 2005; Wei et al., 2008). Lodging resistant cultivars exhibit wider basal diameter and thicker culm wall than those susceptible to lodging (Mukherjee et al., 1967; Zuber et al., 1999). Many researches have been revealed that culm dry weight per cm ($Cw\text{ cm}^{-1}$) for the basal internodes was highly related with lodging resistance (Wang et al., 2000; Li et al., 2005; Xu et al., 2009). Yao et al. (2011b) reported that stem strength was highly and positively correlated with the $Cw\text{ cm}^{-1}$ of the second basal internode. Thicker stems and heavier stems (mg per cm) were indicative for better lodging resistance (Zuber et al., 1999). Therefore, it was suggested that selection for lodging resistant cultivars should emphasize larger stem diameter and wall thickness of basal internodes (Tripathi et al., 2003). There are few studies on the inheritance of morphological traits for the basal internode.

Stem diameter and culm wall thickness are normally distributed with transgressive segregation in the double haploid (DH) population (Hai et al., 2005). Culm wall thickness of the second basal internode resulted from contribution of both additive and non-additive gene effects with a potential for transgressive segregation in the F_2 generation (Wang et al., 1998). Culm diameter of the second basal internode may result from additive and dominant genes and the degree of dominance is partial dominance (Cui et al., 2002b). The objective of this research was to investigate the combining ability, gene action for morphological traits of the second basal internode in a 7×7 incomplete diallel cross experiment in wheat. This information can be of great importance in the selection of desirable parents for an effective breeding program to develop the new wheat varieties with lodging resistance.

Results and discussion

Combining ability analysis

Analysis of variance revealed the highly significant differences ($P \leq 0.01$) among the genotypes for the three morphological traits of the second basal internode (Table 2). Both general (GCA) and specific combining ability (SCA) variances were highly significant for all the traits (Table 2), indicating the importance of both additive and non-additive gene effects. However, the magnitude of GCA variances were about three to seven times greater than SCA values, which indicated that most of the observed genetic variation for these traits are due to the additive gene action. Therefore, selection for these traits in

Table 1. Genetic background and basal internode properties of the seven parents.

parents	Pedigree	CD (cm)	CWT (mm)	Cw cm ⁻¹ (mg/ cm ⁻¹)
Ningmai 8	Yangmai 5/Yang 86-17	4.537 <i>aA</i>	0.563 <i>abA</i>	22.493 <i>abAB</i>
Ningmai 9	Yang 86-17/Xifeng	3.873 <i>cC</i>	0.480 <i>abA</i>	20.337 <i>bcAB</i>
Yangmai 5	Yangmai 4/st1472-506	4.363 <i>abAB</i>	0.501 <i>abA</i>	24.223 <i>abA</i>
Yangmai 9	Jian 3/Yangmai 5	4.093 <i>bcABC</i>	0.503 <i>abA</i>	25.530 <i>aA</i>
Yangmai 11	Y.C/Yangmai 5//85-85	4.330 <i>abABC</i>	0.586 <i>aA</i>	22.740 <i>abAB</i>
Sumai 3	Funo/Taiwan wheat	4.067 <i>bcBC</i>	0.527 <i>abA</i>	22.337 <i>abAB</i>
Wangshuibai	Landrace	3.917 <i>cBC</i>	0.475 <i>bA</i>	17.830 <i>cB</i>

where: CD=culm diameter; CWT=Culm wall thickness; Cw cm⁻¹=culm weight per cm. A-C, a-c, a-b and A-B, a-c Values followed by different upper or lower case letters within the same column are significantly different at the 0.01 and 0.05 probability levels, respectively.

Table 2. Mean squares from preliminary analysis and combining ability in 7 × 7 diallel cross of wheat.

Source of variation	df	CD	CWT	Cw cm ⁻¹
Replications	2	0.0060 ^{NS}	0.0039 ^{NS}	7.7217 ^{NS}
Genotypes	27	0.1329 ^{**}	0.0064 ^{**}	15.6329 ^{**}
Error	54	0.0178	0.0018	4.4156
GCA	6	0.1321 ^{**}	0.0046 ^{**}	12.8806 ^{**}
SCA	21	0.0192 ^{**}	0.0014 ^{**}	3.0197 [*]
Error	54	0.0059	0.0006	1.4719
GCA/SCA		6.88	3.29	4.27

^{*}, ^{**} Significance at P≤0.05 and P≤0.01 levels, respectively, NS=not-significant.

early generations should be effective to develop the lodging-resistant lines in wheat breeding program. In addition, the preponderance of additive genetic variation for these traits in F₁ generation indicated that these parents involved in these crosses could be selected on the basis of their GCA values (Topal et al., 2004). These results were in agreement with earlier findings (Cui et al., 2002a).

General combining ability and performance of parents

Table 3 shows the relative values of GCA effects of all the parents for the three traits. To produce the best progeny, parental lines with the highest GCA for a specific trait should be used (Barnard et al., 2002). Ningmai 8 was the best general combiner for CD, CWT, and fourth best for Cw cm⁻¹, suggesting that this genotype would be the best candidate as one of the parents to improve any of these traits. The GCA effects of Yangmai 5 for all the traits were positive and highly significant, indicating that this genotype is also a good candidate for improving any of these traits. Yangmai 9 had the greatest GCA value for Cw cm⁻¹. The positive and significant correlation between GCA and parental performance (Table 3) suggested that selection of parents for CD and Cw cm⁻¹ could be made on the basis of their performance by itself.

Specific combining ability

The SCA values in the diallel crosses for the three traits are shown in Table 4. The magnitude of SCA effects varied among crosses and traits. The best specific cross to produce progeny with desirable morphological traits of the second basal internode was Yangmai 9 × Yangmai 11. The Ningmai 8 × Yangmai 5 cross was the best for improving both CWT and Cw cm⁻¹, and the Ningmai 9 × Sumai 3 cross the best for improving Cw cm⁻¹.

Adequacy tests for additive-dominance (AD) model

The results of the regression analysis for all the traits are presented in Table 5. The regression coefficient (b) for all the traits departed significantly from zero and not from unity except CWT, suggesting the absence of non-allelic interactions.

The regression coefficient for CWT did not depart significantly from zero, but departed significantly from unity, which suggested presence of epistasis. Hence, the data for CWT did not fulfill the diallel assumptions and were not suitable for additive-dominance model. The suitability of the data for the model was also tested with the analysis of variance of (Wr + Vr) and (Wr - Vr) (Table 5), which showed no evidence for dominance effects as either the mean square between arrays for (Wr + Vr), and the mean square between arrays for (Wr - Vr) were not significant, emphasizing a partial adequacy of the additive dominance hypothesis for Cw cm⁻¹.

Significant differences for (Wr + Vr) of CD indicated the presence of dominance, while the (Wr - Vr) was also highly significant, and probably resulted from the presence of non-allelic interactions. These results suggest that the CD data will be only partially suitable for the additive dominance model as regression coefficient (b) for the trait deviated significantly from zero but not from unity. Recently, many researchers used partially adequate data for genetic analysis (Yao et al., 2011a). The data for CWT was not suitable for further genetic analysis as the regression coefficient did not deviate significantly from zero and the mean square between arrays (Wr + Vr) was not significant. However, the mean square between (Wr - Vr) was significant. Therefore, this trait was not subjected to further genetic analysis.

Graphical (Vr/Wr) representation for the data

The Vr/Wr graph (Fig. 1) shows that the regression line intercepted Vr-axis above the point of origin, suggesting that CD was controlled by the additive gene action with partial dominance. The estimated regression line did not deviate significantly from unit slope, indicating the absence of non-allelic interactions. The distribution of array points along the regression line showed that Sumai 3 contained most dominant genes for CD as it was located nearer to the point of origin. Yangmai 11 was furthest away from the origin and thus it contained most recessive genes for CD. For Cw cm⁻¹ the regression line intercepted the Vr-axis below the origin (Fig.2), indicating Cw cm⁻¹ was controlled by over-dominant genes.

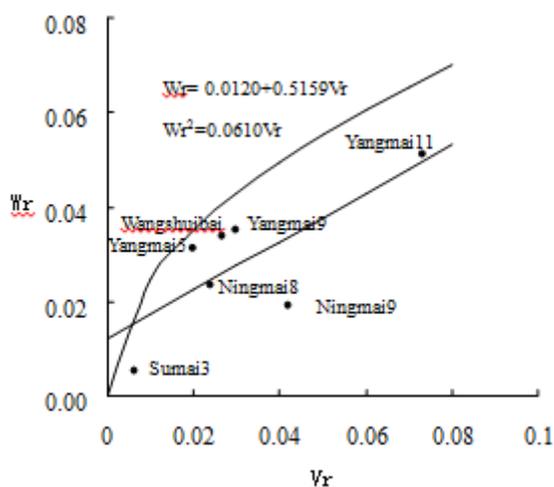


Fig 1. Vr versus Wr graph for CD.

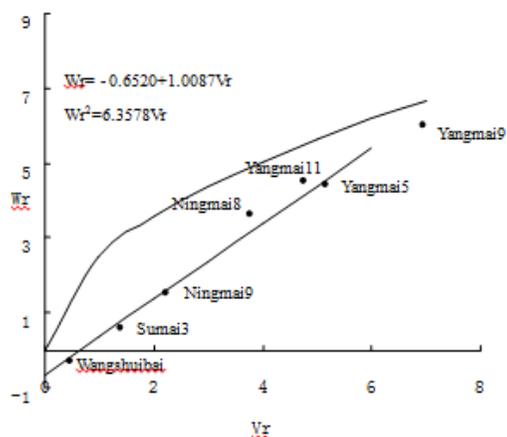


Fig 2. Vr versus Wr graph for $Cw\text{ cm}^{-1}$.

The Wangshuibai parent was located near the origin, indicating that it carried most dominant genes. In contrast, Yangmai 9 was located further away from the origin, indicating a relative abundance of recessive genes in this parent. The positive r -value ($r = 0.1626$) between parental values (Pr) with $(Wr + Vr)$ indicated that the parents with great CD may carry recessive genes, while negative r -value ($r = -0.2611$) between parental values (Pr) with $(Wr + Vr)$ indicated that the parents with high $Cw\text{ cm}^{-1}$ may carry dominant genes (Table 6).

Genetic components of the data

Genetics of CD and $Cw\text{ cm}^{-1}$ was evaluated by calculation of the genetic components of variation D , H_1 , H_2 and F (Table 6). The additive variation (D) was highly significant, supporting that additive genetic effects are prominent in determining the two traits. Similar results were also obtained for CD in barley (Guo and Xu, 1995). The dominance components (H_1 and H_2) were highly significant for $Cw\text{ cm}^{-1}$ but not for CD. Thus, inheritance of CD was primarily through additive gene actions, whereas the expression of $Cw\text{ cm}^{-1}$ was determined by additive genetic effects with partial dominance. The predominance of

additive effects (D) in the genetic mechanism for CD suggests that the genes for this trait have been fixed and the trait could be improved via the pedigree selection method from the F_2 generation. Although D , H_1 and H_2 were all highly significant for $Cw\text{ cm}^{-1}$, the D was greater than H_1 and H_2 , indicating that effects of additive gene are more important than dominance effects for this trait. Thus, selection can be useful for improving this trait. The average degree of dominance $(H_1/D)^{0.5}$ for the two traits was all less than unity, confirming that additive gene effects were greater than dominance effects and there was partial dominance for the two traits. Asymmetrical distribution of dominant genes for the two traits was confirmed by unequal estimates of H_1 and H_2 , which was further, supported by the value of $H_2/4H_1$ for CD (0.3829) and $Cw\text{ cm}^{-1}$ (0.4641). The F value, which estimates frequency of dominant alleles relative to recessive alleles in the parents, was negative for the two traits. This suggests the excess of recessive alleles present in the parents, which was further supported by the small values (< 1.0) of $[(4DH_1)^{0.5} + F] / (4DH_1)^{0.5} - F$. Significance for h^2 for the two traits indicated that dominance was unidirectional, suggesting that heterosis breeding could be rewarding for the two traits. Significant environmental component (E) indicated that the two traits were also highly affected by environmental conditions. The number of gene groups differentiating the parents (k) was 1.4 for CD and 6.7 for $Cw\text{ cm}^{-1}$, suggesting that the inheritance of CD was controlled approximately by two groups of genes, and $Cw\text{ cm}^{-1}$ by seven groups of genes. Estimates of narrow sense heritability (h^2_N) showed lower heritability for the two traits. Such lower heritable values for CD were also reported in rice by Liang et al. (2000). However, Cui et al. (2002a) estimated a moderate value of heritability for CD in wheat.

Materials and methods

Plant materials

This study was conducted in a field area of Jiangsu Academy of Agricultural Sciences, Nanjing, China, during the 2009-2010 season. The parental material comprised of seven wheat varieties: Ningmai 8, Ningmai 9, Yangmai 5, Yangmai 9, Yangmai 11, Sumai 3 and Wangshuibai. These parents were chosen based on their broad genetic background and large variation for morphological traits of the second basal internode (Table 1). A 7×7 diallel cross was made using these varieties. For each of the crosses, 15 female spikes were emasculated and bagged to avoid contamination with foreign pollen. Pollination with the pollen collected from the specific male parent was done when the ovaries became receptive. At maturity, the seeds from each cross were harvested and stored separately.

Experimental design

The seeds of 28 genotypes (7 parents and 21 F_1 hybrids) were sown in the field in November 2009 in a randomized complete block design with three blocks. Plant-to-plant and row-to-row spacing was 5 and 25 cm, respectively. Within each block, each genotype occupied a plot of two rows of 2-m-long. All the other cultural operations, including weeding, fertilizers and disease control, were carried out uniformly. Ten main stems from each of the parents and F_1 progeny during the milk stage, around the mid-May 2010, were randomly selected from each plot and assessed for culm length, diameter, wall thickness and

Table 3. Estimates of general combining ability (GCA) and mean for different traits in 7×7 diallel cross of wheat.

Parents	CD		CWT		Cw cm ⁻¹	
	GCA	mean	GCA	mean	GCA	mean
Ningmai 8	0.1971 <i>aA</i>	4.54	0.0210 <i>aA</i>	0.56	0.3715 <i>aAB</i>	22.49
Ningmai 9	- 0.1662 <i>eE</i>	3.87	0.0020 <i>aA</i>	0.48	- 0.9233 <i>bBC</i>	20.30
Yangmai 5	0.1016 <i>bAB</i>	4.36	0.0077 <i>aA</i>	0.50	0.8281 <i>aA</i>	24.22
Yangmai 9	- 0.0151 <i>cBC</i>	4.09	- 0.0017 <i>aA</i>	0.50	1.3185 <i>aA</i>	25.53
Yangmai 11	- 0.0090 <i>bBC</i>	4.33	0.0198 <i>aA</i>	0.59	0.2430 <i>aAB</i>	22.74
Sumai 3	- 0.0658 <i>dCD</i>	4.07	- 0.0020 <i>aA</i>	0.53	0.3896 <i>aAB</i>	22.34
Wangshuibai	- 0.0777 <i>dDE</i>	3.92	- 0.0468 <i>bB</i>	0.48	- 2.2274 <i>cC</i>	17.83
r(GCA, mean)	0.9643**		0.6767		0.9844**	

A-E, a-e, A-B, a-b and A-C, a-c Values followed by different upper or lower case letters within the same column are significantly different at the 0.01 and 0.05 probability levels, respectively. r coefficient of correlation. ** Significance at P<0.01 level.

Table 4. Estimates of specific combining ability (SCA) for different traits in 7×7 diallel cross of wheat.

F ₁ hybrids	CD	CWT	Cw cm ⁻¹
Ningmai 8×Ningmai 9	0.1083	- 0.0165	-1.8173
Ningmai 8×Yangmai 5	- 0.0494	0.0798	0.8312
Ningmai 8×Yangmai 9	- 0.0694	0.0135	-0.3092
Ningmai 8×Yangmai 11	- 0.0572	- 0.0306	-1.7403
Ningmai 8×Sumai 3	- 0.1787	- 0.0017	-0.1836
Ningmai 8×Wangshuibai	0.1165	- 0.0737	-0.0966
Ningmai 9×Yangmai 5	- 0.0094	0.0551	-0.3240
Ningmai 9×Yangmai 9	- 0.0328	0.0148	-1.1410
Ningmai 9×Yangmai 11	- 0.3872	0.0050	-1.7155
Ningmai 9×Sumai 3	0.1146	- 0.0018	1.0312
Ningmai 9×Wangshuibai	- 0.0502	0.0053	-0.2151
Yangmai 5×Yangmai 9	0.0261	- 0.0122	-1.0992
Yangmai 5×Yangmai 11	- 0.0183	- 0.0340	-0.6336
Yangmai 5×Sumai 3	- 0.0698	- 0.0079	-2.1269
Yangmai 5×Wangshuibai	- 0.0446	- 0.0381	-1.5966
Yangmai 9×Yangmai 11	0.1750	0.0047	0.8560
Yangmai 9×Sumai 3	- 0.1698	0.0082	-1.8873
Yangmai 9×Wangshuibai	- 0.0213	- 0.0287	-2.0203
Yangmai 11×Sumai 3	- 0.0309	- 0.0406	-0.1984
Yangmai 11×Wangshuibai	- 0.0824	0.0165	-0.8914
Sumai 3×Wangshuibai	0.0928	- 0.0060	0.4353
LSD(0.05)	0.0396	0.0516	2.5577

Table 5. Adequacy test of additive-dominance model for different traits in 7×7 diallel cross of wheat.

Parameters	CD	CWT	Cw cm ⁻¹
Joint regression (b)	0.5159±0.1967	0.1372±0.0989	1.0087±0.0602
Test for b=0	2.6228*	1.3873 ^{NS}	16.7558**
Test for b=1	2.4611 ^{NS}	8.7240**	0.1445 ^{NS}
Mean squares of W _T + V _r between arrays	0.0047*	0.0001 ^{NS}	103.2859 ^{NS}
Mean squares of W _r - V _r between arrays	0.0007**	0.0001*	16.9276 ^{NS}
Fitness of the data to Additive-Dominance model	Partial	Inadequate	Partial

*, ** Significance at P<0.05 and P<0.01 levels, respectively, NS=not-significant

dry weight per centimeter. Stem diameter was measured at the middle of the second internode using a vernier caliper. The culm wall thickness was measured at its center by a vernier caliper after the second internode was cut. The culm was then dried at 80°C for 24 h and weighed. Culm weight per cm (Cw cm⁻¹) was calculated according to culm dry weight and culm length.

Statistical analysis

To assess the differences among parents and F₁ progeny, the data were subjected to analysis of variance using the SAS

software. The general and specific combining ability values were estimated using Method II, Model I of Griffing's (1956). Two scaling tests (Mather and Jinks, 1982) were applied to test the validity of additive-dominance model. Further, the Hayman (1954) method was used for estimation of gene actions.

Conclusion

In general, significant genetic variations were observed for morphological traits of the second basal internode investigated in this study. Significant GCA and SCA effects for all the traits

Table 6. Components of variation for different traits in 7 × 7 diallel cross of wheat.

Components of variation	CD	Cw cm ⁻¹
<i>D</i>	0.0395**±0.0105	3.7534**±0.2332
<i>F</i>	- 0.0223±0.0251	- 2.6410**±0.5593
<i>H</i> ₁	0.0158±0.0252	1.7739**±0.5613
<i>H</i> ₂	0.0242±0.0222	3.2927**±0.4946
(<i>H</i> ₁ / <i>D</i>) ^{1/2}	0.6325	0.6875
<i>H</i> ₂ /4 <i>H</i> ₁	0.3829	0.4641
[(4 <i>DH</i> ₁) ^{0.5} + <i>F</i>]/(4 <i>DH</i> ₁) ^{0.5} - <i>F</i>	0.3828	0.3230
<i>h</i> ²	0.0331**±0.0149	22.2134**±0.3322
<i>E</i>	0.0215**±0.0037	2.6044±0.0824
<i>K</i>	1.3678	6.7462
<i>h</i> ² _{<i>N</i>} (%)	49.22	41.56
<i>r</i> (<i>Pr</i> , <i>Wr</i> + <i>Vr</i>)	0.1626	- 0.2611

*, ** Significance at P≤0.05 and P≤0.01 levels, respectively.

imply the role played by both additive and non-additive gene actions in the genetic control of these traits. The ratios of GCA/SCA indicate greater contributions to the inheritance of all the traits by the additive gene effects than the dominance effects. Parents with the best GCA values for CD, CWT and Cw cm⁻¹ were Ningmai 8 and Yangmai 5, while the best specific combination for all the traits was the cross between Yangmai 9 and Yangmai 11. The additive-dominance model was partially adequate for CD and Cw cm⁻¹, while CWT did not fit the additive-dominance model. The CD and Cw cm⁻¹ were controlled mainly by additive gene actions, but exhibited lower narrow sense heritability.

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