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Genetic analysis of plant height and its components in diallel crosses of bread wheat (*Triticum aestivum* L.)

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Abstract

An incomplete diallel cross study comprising of seven bread wheat (*Triticum aestivum* L.) cultivars was carried out with parents and F_1 progeny to determine heterosis, combining ability, gene action, and correlations for plant height and its components. The results showed that heterosis and heterobeltiosis occurred in plant height, spike length, peduncle length, length of the second internode from the top to bottom, length of the third internode from the top to bottom, length of the second basal internode and length of the first basal internode, but their values varied among crosses and characters. Estimates of the genetic components of variation as well as ratio of GCA/SCA showed that all the characters were predominantly controlled by additive gene action. Plant height and its components were governed by partial dominance with additive type of gene action. Narrow sense heritability estimates for all the characters were higher, varying from 76.62% to 95.08%. Plant height might be controlled by four groups of dominant genes, while its components might be controlled by one or two/ three groups of genes. The correlation analysis showed that lengths of internodes were positively and significantly associated with plant height, and path analysis indicated that peduncle length had the highest effect on plant height, followed by length of the second internode from the top to bottom. The estimates of general combining ability pointed out that the best general combiners for the plant height and its components were Ningmai 8 and Yangmai 9, which appeared to be promising parents for wheat breeding program. Results concluded that selection for plant height and its components would be effective in early generation. The results obtained from this study might be helpful for wheat breeders trying to develop new varieties with semi-dwarf and lodging resistance.

Keywords: combining ability, diallel cross, gene action, heterosis, plant height, *Triticum aestivum* L.

Abbreviations: AD_additive-dominance; GCA_ general combining ability; HBS_heterobeltiosis; HS_ heterosis; LFBI_ length of the first basal internode; LSBI_ length of the second basal internode; LSI_ length of the second internode from the top to bottom; LTI_ length of the third internode from the top to bottom; PH_ plant height; PL_ peduncle length; SL_ spike length; SCA_specific combining ability; Vr_array variance; Wr_array covariance.

Introduction

Plant height is a very important character for high and stable yield in wheat production; therefore, at present the reduction in height is one of the principle breeding objectives for wheat in China. Plant height is composed of the lengths of various internodes and the spike. Li et al. (1997) and Wen et al. (2007) found that there were relatively high levels of heterosis and heterobeltiosis of plant height and its components, but their values varied among crosses and characters. In most of the diallel studies of wheat, plant height, spike length and peduncle length seemed to be controlled by the partial dominance with additive gene effects (Khan et al., 2000; Subhani *et al*., 2000; Chaudhry et al., 2001; Khan and Habib, 2003; Riaz and Chowdhry, 2003). However, over dominance was also noted for plant height by Nazeer et al. (2004); Saleem et al. (2005), for spike length by Bakhsh et al. (2003); Inamullah et al. (2006), and for peduncle length by Allah et al. (2010). Wei and Wu (1990) reported that the spike length was a qualitative character affected by one main allele with some modifying factors, while the lengths of various internodes were quantitative characters, and they had their own independent genetic patterns and were controlled by many genes. Related studies by some researchers showed that plant height was positively correlated with length of various internodes, particularly, peduncle length contributing a great deal to plant height (Yang et al., 1999; Zhao and Wang, 2003). Thus it would be useful in the planning of breeding programs of wheat to understand the inheritance not only of the total height but also of the different internodes composing it. The objective of this research was to investigate the heterosis, combining ability, gene action and correlations for plant height and its components in a 7×7 incomplete diallel cross experiment in wheat. This information would 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

Heterosis

Analysis of variance revealed highly significant differences ($P \leq 0.01$) among the genotypes for plant height and its components (Table 2). Heterosis was evident in the F_1 hybrids for all the characters (Table 3). The mean values of 21 crosses for PH, SL, PL, LSI, LTI, LSBI and LFBI were equal to 100.2, 9.6, 36.6, 24.4, 16.1, 9.4 and 4.0 cm, respectively. The variations among crosses were also clearly observed for seven characters. Among the traits, LFBI had the largest coefficient of variation (CV = 33.7%), the variations for PH, PL, LSI, LTI and LSBI were medium (CV was about 16%), and SL had the least variation (CV = 9.6%). In case of relationships of plant height with its components, all the components were positively and significantly correlated with PH and correlation coefficient varied from 0.71 to 0.97. Heterosis (HS) of PH and its components occurred in 21 crosses, but the values varied among crosses (Table 3). The average HS of all crosses for PH was 7.5% (CV = 54.7%), all the components had positive HSs on the average, and the means for SL, PL, LSI, LTI, LSBI and LFBI were 3.5%, 8.4%, 7.9%, 6.0%, 5.6% and 0.8%, respectively. It indicated that heterosis in plant height was mainly due to heterosis in its upper middle internode. Results are in agreement with the findings of Carrillo et al., (1985) and Wen et al. (2007), but inconsistent with those of Li et al. (1997) who demonstrated that positive heterosis for length of the basal internode and the third internode were larger than those of other characters. The average HBS of PH and its components was negative, the HBS of SL was the largest (- 3.8%) and that of LFBI was the least (- 14.1%) (Table 3). The HS of PH was significantly correlated with those of PL (r=0.73), LSI (r=0.82), LTI (r=0.58) and LSBI (r=0.51), and the HBS of PH was closely associated with those of PL (r=0.73), LSI (r=0.82), LTI (r=0.73), LSBI (r=0.73) and LFBI(r=0.63). However, the HS and HBS of SL were less and insignificantly correlated with those of PH (Table 3). Therefore, the HS and HBS of PL, LSI, LTI and LSBI contributed a lot to the corresponding ones of PH. In this experiment, the positive heterosis for lengths of the upper middle internode were larger than those of the basal internode, and the phenotypic and heterotic relationships of plant height with lengths of the upper middle internode were more remarkable. This may imply that heterotic performance of plant height in wheat could be largely limited by reducing the HS and HBS for lengths of the upper middle internodes. However, the negative heterosis for lengths of PL, LTI, LSBI and LFBI was found in the cross of Ningmai 9×Yangmai 11, and it means that it is possible to develop new wheat cultivars or hybrid combinations with short stature through selection of appropriate parents for crossing. This was confirmed by Abdullah et al. (2002); Cui et al. (2002) and Wen et al. (2007).

Combining ability

The combining ability analysis of variance (Table 4) showed that both general (GCA) and specific combining ability (SCA) variances were highly significant for all the characters except LFBI for SCA, indicating the importance of both additive and non-additive gene effects. However, the magnitude of GCA variances were several times greater than SCA (15.02 to 110.07), which in turn indicated that larger amount of genetic variation for these traits was mainly due to the additive gene action. Therefore, selection for these traits in early generations would be effective to developing the semi-dwarf varieties in a wheat breeding program. In addition, the preponderance of additive genetic variation for plant height and its components in F_1 generation indicated that the parents involved in these crosses could be selected based on their GCA values. These results were in agreement with earlier findings (Knezevic et al., 1993; Cui et al., 2002) who reported the predominance of additive genetic effects for PH, and Yucel et al., (2009) and Dagustu, (2008) who observed additive gene effects for SL and PL, respectively. However, Hasnain et al. (2006); Farooq et al. (2006); Ilker et al. (2009) illustrated a higher importance of non-additive gene actions for the genetic control of PH, and Chowdhry et al. (2005) demonstrated that the non-additive effects were more important for the genetic control of PL, while Iqbal and Khan (2006) observed non-additive gene effects for SL.

General combining ability and performance of parents

GCA effects can be considered as the numerical values assigned to the parents in relation to their mean performance in cross-combinations. Table 5 showed the relative values of GCA effects of all the parents for the seven characters. The GCA effects of Sumai 3 and Wangshuibai for PH were positive and highly significant. They also had positive and obvious GCA effects on SL and lengths of internodes. Ningmai 8, Ningmai 9, Yangmai 5, Yangmai 9, and Yangmai 11 had negative and remarkable GCA effects for PH, and most of them also had negative and/or significant GCA effects on PL, LSI, LTI, LSBI, and LFBI. The GCA effects of Ningmai 8 and Yangmai 9 for all the characters were highly and negatively significant, indicating that these two parents were best general combiners for PH and lengths of internodes. Short stature behavior is preferred, because these plants do not lodge and are more fertilizer responsive; therefore, negative combining ability effects are preferred for plant height in case of wheat. Thus parents Ningmai 8 and Yangmai 9 could be utilized to reduce plant height in wheat. The positive and significant correlation between GCA and parental performance (Table 5) suggested the possibility of further selection of parents for plant height and its components on the basis of *per se* performance.

Specific combining ability

The values of SCA effects in the diallel crosses for six characters except for length of the first basal internode were shown in Table 6. The magnitude of SCA effects varied among crosses and characters. Most of the crosses had positive and/or significant SCA effects for PH, and the value of Yangmai 5×Yangmai 9 was the largest (7.4833) followed by Ningmai 8×Wangshuibai,(6.3526) and of Ningmai 9×Yangmai 11 was the smallest (– 2.9926). The 16 crosses had positive value of SCA effects for PL and four of them were significant. The relative values of SCA effects for other components were smaller, and five of the crosses were significant for LSI, three crosses were significant for SL, two crosses were significant for LTI, and only one cross was significant for LSBI. The two crosses of,Ningmai 9×Yangmai 11 and Yangmai 9×Yangmai 11 showed negative SCA effects for PH and its components, and they may be used in future breeding program for development of semi-dwarf wheat varieties.

Assessment of the plant height and its components for Additive-Dominance model

The data were assessed for Additive-Dominance (AD) model by exploiting various adequacy parameters given in Table 7. According to Mather and Jinks (1982) the data will be only valid for genetic interpretation if the value of regression coefficient (b) must deviate significantly from zero but not from the unity. The value of b departed significantly from zero but not from unity for all the traits, suggesting the absence of non-allelic interactions in genetic behavior of all the traits which in turn attested the data valid for AD model for all the traits. The appropriateness of the model data analysis was also verified by the analysis of variance of (Wr

Table 1. Genetic background and characteristics of the seven parents

parents	Pedigree	PH (cm)	SL (cm)	PL (cm)	LSI (cm)	LTI (cm)	LSBI (cm)	LFBI (cm)
Ningmai 8	Yangmai 5/Yang 86-17	72.7	8.3	27.0	16.7	11.1	6.8	2.5
Ningmai 9	Yang 86-17/Xifeng	81.1	8.7	29.7	18.6	12.9	7.6	3.6
Yangmai 5	Yangmai 4/st1472-506	90.2	8.1	34.2	20.9	15.2	8.8	3.0
Yangmai 9	Jian 3/Yangmai 5	73.2	10.6	21.4	20.5	11.6	6.6	2.6
Yangmai 11	Y.C/Yangmai 5//85-85	89.0	8.5	32.7	22.0	14.2	8.5	3.1
Sumai 3	Funo/Taiwan wheat	114.1	9.3	47.3	27.7	16.4	9.7	3.7
Wangshuibai	Landrace	134.5	11.6	44.6	31.2	23.5	14.0	9.6

where PH=Plant height; SL=Spike length; PL=peduncle length; LSI=Length of the second internode from the top to bottom; LTI=Length of the third internode from the top to bottom; LSBI=Length of the second basal internode and LFBI=Length of the first basal internode

Table 2. Analysis of variance for plant height and its components in a 7×7 diallel cross of wheat

Source of variation	df	PH	SL	PL	LSI	LTI	LSBI	LFBI
Replications	2	212.2089**	0.4027^{NS}	26.3912**	25.6697**	4.7644**	1.6345**	1.4438^{NS}
Genotypes	27	917.8551**	3.0774**	146.2847**	52.2860**	27.4978**	10.8766**	8.1164**
Error	54	5.9367	0.1463	1.2664	0.5187	0.6599	0.3528	0.5271

** Significance at P≤0.01, NS=not-significa

+ Vr) and (Wr - Vr). The lack of significant variation in the (Wr - Vr) arrays for all the traits suggested that any kind of epistasis was not involved in the phenotypic expression of the traits. Although the values of regression coefficient (b) proved the fitness of the data of LSBI and LFBI for AD model, mean square values of (Wr + Vr) for the two traits indicated no significant deviation, thus emphasizing partial validity of the two traits. The other five traits exhibited full adequacy for AD model.

Graphical (Vr/Wr) representation for the plant height and its components

The Vr/Wr graph (Fig. 1) showed that regression line intercepted Wr-axis above the point of origin suggesting that PH was governed 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 interaction. The results seems to be compatible with those of Khan et al. (2000); Subhani et al. (2000); Chaudhry et al. (2001); Khan and Habib (2003); Allah et al. (2010); Bakhsh et al. (2003); Riaz and Chowdhry (2003). However over dominance for PH was indicated by Kashif and Khaliq (2003); Nazeer et al. (2004); Saleem et al. (2005), and epistasis for PH was presented (Fan et al., 1999). It was also apparent from the graphic illustration that parent Wangshuibai being closest to the origin possessed most of the dominant genes while parent Ningmai 8 and Yangmai 11 carried most of the recessive genes being farthest from the origin. The other two parents i.e. Ningmai 9 and Yangmai 9 also had relatively high frequency of recessive genes for PH. Graphic presentation of data (Fig. 2) indicated the additive type of gene action with partial dominance for SL as point of intercept on Wr-axis was positive. The epistasis was absent as regression line followed the unit slope. Similar results have also been reported by Subhani et al. (2000); Kashif and Khaliq (2003); Allah et al. (2010); and Gurmani et al. (2007), while Bakhsh et al. (2003); Inamullah et al. (2006) observed over dominance for SL. Distribution of array point along the regression line illustrated that Wangshuibai contained maximum dominant genes for SL as it was situated more near to point of origin. Ningmai 8 lay most apart from the origin so it contained most recessive genes for SL. From Vr/Wr graph for PL (Fig.3), it was evident that the regression line cut the Wr-axis above the origin, indicating partial dominance with additive gene action. The regression line did not deviate significantly from unit slope, suggesting the absence of epistasis. The results are in agreement with the earlier findings of Khan et al. (2000); Khan and Habib (2003). However,Allah et al. (2010) reported that in the inheritance of PL over dominance was involved. The distribution of array points on the regression line made it clear that parent Wangshuibai possessed maximum dominant genes because it was located nearest to the origin followed by parent Yangmai 5 whereas parent Yangmai 9 contained maximum recessive genes. The graphical representation revealed that partial dominance with additive gene action was found for other components as all the regression lines cut the Wr-axis above the origin (Fig.4-7). As all the regression lines did not deviate significantly from unit slope, the absence of epistasis was concluded. From the relative position of array points on the regression line it was apparent that Wangshuibai contained maximum dominant genes while Yangmai 11 possessed most recessive genes for LSI (Fig. 4). The maximum dominant genes for LTI were present in parent Sumai 3 whereas the most recessive genes were present in parents Ningmai 8 and Yangmai 11 (Fig.5). Parent

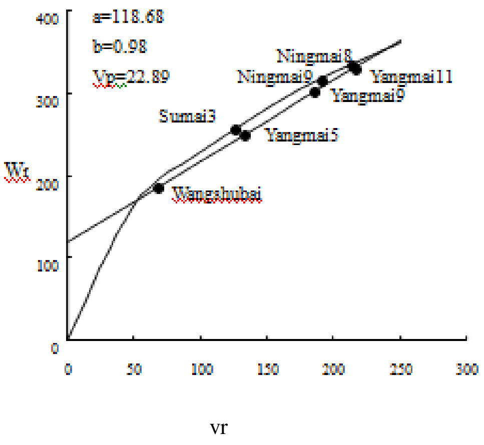

Fig 1. Vr versus Wr graph for pH

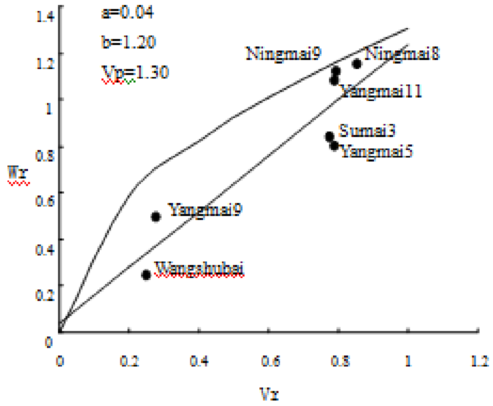

Fig 2. Vr versus Wr graph for SL

Wangshuibai contained maximum dominant genes while Ningmai 8 possessed most recessive genes for LSBI (Fig. 6). Fig. 7 indicated most dominant genes were present in parent Yangmai 9 for LFBI while parent Wangshuibai had maximum recessive genes for this trait. As the characters exhibited additive gene action with partial dominance in the absence of epistasis (Fig 1-7), the selection for PH and its components in early generations would be beneficial. Correlation analysis of the genotypes showed recessive gene control（r=0.6535）for LFBI, and dominant gene control（r= -0.8902，-0.9403，-0.6515，-0.7805，-0.6267，-0.8067）for PH, SL, PL, LSI, LTI and LSBI, respectively.

Genetic components of variation for the plant height and its components

Genetics of plant height and its components was evaluated by the calculation of genetic components of variation D, H_1, H_2 and F (Table 8). All the characters the additive variation (D) was highly significant, which proved that additive genetic effects were prominent in determination of these characters. Li et al. (1993) also observed significant additive component of variation for these characters in barley. Dominance components (H_1 and H_2) were also highly significant for all the traits. However, the greater magnitude of additive component for these characters suggested that additive gene effects were more pronounced than dominance effects in controlling the genetic mechanism of these characters. This advocated that selection can be helpful for the improvement of these traits. Zhang and Xu. (1997); Farooq et al. (2010); and Hussain et al. (2008) also reported that additive gene action played a predominant role in the inheritance of PH and PL, respectively, and Madic et al. (2009) showed additive effect genes prevailed in the inheritance of LSBI in barley. The ratio of dominance-additive indicated the degree of dominance ($H_1/D^{0.5}$). The value of degree of dominance ($H_1/D^{0.5}$) for all the characters were less than unity which confirmed the greater contribution of additive genes in the inheritance of these characters and indicated presence of partial dominance for these traits. The Vr/Wr graphs also supported the genetic components (Fig. 1-7). The estimates of $H_2/4H_1$ were smaller than 0.25 for PH, LSI, LSBI and LFBI, and moreover, significant values of F components for these four traits suggested that there were asymmetrical distribution of dominant and recessive alleles in the parents. The magnitude of $H_2/4H_1$ was smaller than 0.25 for SL, PL and LTI, but non-significant value of F components for these three traits indicated that there were equal frequencies for positive and negative alleles in the parents. Significant environmental component (E) for PH (4.4345), LSI (0.4723), LTI (0.2688), LSBI (0.1329) and LFBI (0.1866) indicated that these characters were highly affected by environmental variations (Halloran.1975; Hussain et al., 2008). The number of gene group differentiating the parents (k) was 3.5476 for PH, suggesting the inheritance of PH was controlled approximately by four groups of genes, PL and LSI by three groups of genes, LSBI by two groups of genes, and SL and LFBI by one group of genes, respectively. Our results are inconsistent with early reports. Li (1999) reported that PH and SL were controlled by only one group of gene, and Halloran (1975) found that at least two groups of dominant genes influenced plant height expression; whereas Li et al. (2005) reported that PH was controlled by five groups of genes, SL by ten groups of genes and PL by six groups of genes, respectively. Estimates of narrow sense heritability (h^2_N) showed high heritability for all the characters except for SL (76.62%). Such high heritable values for PH, SL and PL were also reported by other researchers (Yu et al., 2001; Li et al., 2005; Novoselovic et al., 2004; Hussain et al., 2008). Higher narrow sense heritability for basal internode length was also reported by Cui et al. (2002), Wen et al. (2007). High heritability represented fixable and additively heritable variation, which indicated that selection response should be rapid for these characters. This offers a lot of scope for improvement of these characters through individual plant selection. Hayman (1957) reported that epistasis can decrease or increase degree of dominance which in turn effect on heritability estimates.

Correlation and Path analysis

Correlation coefficients between plant height and its components were shown in Table 9. In general, correlation coefficients at genotypic level were higher than those of phenotypic level. It might be due to depressing effect of environment on character association as reported earlier for wheat crop (Proda and Joshi, 1970). The SL and lengths of internodes were positively and significantly associated with PH, and the genotypic correlation coefficients between SL,

Table 3. Phenotypic values (PV, cm), heterosis (HS, %) and heterobeltiosis (HBS, %) of plant height and its components in 7 x 7 diallel of wheat.

F_1 hybrids	PH			SL			PL			LSI			LTI			LSBI			LFBI		
	PV	HS	HBS	PV	HS	HBS	PV	HS	HBS	PV	HS	HBS	PV	HS	HBS	PV	HS	HBS	PV	HS	HBS
Ningmai8×Ningmai9	80.1	4.2	- 1.3	9.0	5.1	2.9	29.3	3.6	- 1.1	17.8	0.9	- 4.3	12.7	4.5	- 1.6	7.6	4.9	- 0.4	3.7	22.9	3.6
Ningmai8×Yangmai5	88.1	8.2	- 2.3	8.1	- 1.6	- 2.9	31.9	4.4	- 6.7	21.3	13.3	1.9	15.5	16.1	- 1.5	8.3	6.9	- 4.8	3.0	10.0	- 0.7
Ningmai8×Yangmai9	77.6	6.4	6.0	9.5	0.6	- 10.0	26.2	8.5	-2.7	19.2	3.3	- 6.2	12.9	7.3	2.1	7.0	- 0.6	- 3.7	2.8	7.4	2.6
Ningmai8×Yangmai11	83.5	3.9	- 5.1	8.4	0.5	- 0.4	30.9	3.4	-5.7	20.3	4.6	- 8.0	13.3	3.6	- 6.7	8.0	3.8	- 6.4	2.7	- 1.3	- 11.4
Ningmai8×Sumai3	97.1	3.9	- 15.0	8.6	- 2.6	- 7.5	36.9	- 0.6	-22.0	23.2	4.3	- 16.4	15.8	13.3	- 4.1	9.2	11.5	- 4.8	3.5	11.5	- 7.8
Ningmai8×Wangshuibai	116.0	12.0	- 13.8	11.0	8.2	- 7.0	40.2	12.4	- 9.8	26.7	11.6	- 14.3	19.9	14.2	- 15.3	12.0	16.4	- 13.4	6.2	3.1	- 35.3
Ningmai9×Yangmai5	92.4	7.8	2.4	8.8	4.3	0.8	35.3	10.5	3.2	21.6	9.3	3.3	14.9	5.7	- 2.4	8.7	6.7	- 0.2	3.1	- 6.2	2.0
Ningmai9×Yangmai9	82.1	6.5	1.3	9.9	2.8	- 6.3	28.4	11.4	- 4.2	20.3	3.8	- 0.9	13.2	3.8	2.6	7.4	- 1.1	1.0	2.9	- 7.0	- 18.5
Ningmai9×Yangmai11	84.5	0.3	- 3.6	8.5	- 0.6	- 2.0	30.8	- 1.3	- 6.0	20.4	0.4	- 7.3	13.0	- 4.5	- 8.8	7.9	- 1.5	- 6.7	3.0	- 9.5	- 15.7
Ningmai9×Sumai3	103.4	5.9	- 9.4	9.4	10.0	1.0	39.9	3.6	- 15.7	24.4	5.3	- 12.0	16.2	10.3	- 1.5	9.7	12.0	0.1	3.9	6.7	4.3
Ningmai9×Wangshuibai	116.8	8.4	- 13.1	11.0	9.0	- 4.6	40.2	8.3	- 9.9	28.2	13.1	- 9.7	20.0	9.8	- 15.0	11.0	3.8	- 19.9	6.2	- 5.6	- 35.2
Yangmai5×Yangmai9	95.9	17.3	6.3	8.9	- 4.9	- 15.9	35.0	25.9	2.3	24.1	16.5	15.3	15.7	12.5	2.9	8.9	11.0	1.8	3.3	15.2	8.6
Yangmai5×Yangmai11	99.4	17.1	13.0	9.0	8.9	11.2	37.3	11.4	13.8	24.4	13.8	11.0	16.3	10.5	6.8	9.3	8.2	6.7	3.1	2.0	1.3
Yangmai5×Sumai3	108.5	6.2	- 5.0	10.0	17.5	10.1	41.8	2.5	- 11.7	26.0	6.7	- 6.4	16.8	5.8	1.9	9.9	7.6	2.5	3.9	15.0	4.3
Yangmai5×Wangshuibai	120.7	7.4	- 10.2	10.0	4.3	- 11.3	43.2	9.6	- 3.2	28.4	8.9	- 9.0	20.1	3.5	- 14.8	12.0	9.5	- 11.1	6.4	1.4	- 33.2
Yangmai9×Yangmai11	85.3	5.8	- 3.1	10.0	4.5	- 5.9	28.9	6.8	- 11.7	22.0	3.6	- 0.1	13.3	- 1.2	- 6.7	8.0	0.6	- 6.6	3.0	5.0	- 1.6
Yangmai9×Sumai3	100.6	7.3	- 11.9	10.0	0.7	- 5.5	36.9	7.6	- 21.9	26.1	8.2	- 6.0	15.6	7.1	- 5.4	9.0	6.3	- 6.7	3.0	- 7.0	- 20.1
Yangmai9× Wangshuibai	111.5	7.3	- 17.1	10.0	- 8.4	- 12.4	39.8	20.7	- 10.7	27.6	6.9	- 11.5	17.8	- 1.6	- 24.5	11.0	2.3	- 22.3	5.2	- 14.8	- 45.4
Yangmai11×Sumai3	105.5	4.4	- 7.6	8.9	- 0.1	- 4.4	42.8	6.9	- 9.6	27.2	9.3	- 2.0	14.9	- 3.0	- 9.6	8.9	- 2.5	- 8.3	3.0	- 12.9	- 20.6
Yangmai11×7Wangshuibai	123.3	10.8	- 8.3	11.0	7.5	- 6.9	43.6	12.7	- 2.2	30.3	13.7	- 3.0	21.0	11.2	- 10.9	12.0	8.2	- 13.1	5.5	- 12.3	- 42.1
Sumai3× Wangshuibai	131.0	5.4	- 2.6	11.0	6.9	- 3.7	49.9	8.6	11.9	31.9	8.3	- 2.3	19.5	- 2.7	- 17.3	12.0	4.6	- 11.7	6.2	- 6.3	- 34.8
Over average	100.2	7.5	- 4.8	9.6	3.5	- 3.8	36.6	8.4	- 5.9	24.4	7.9	- 4.0	16.1	6.0	- 6.0	9.4	5.6	- 6.1	4.0	0.8	- 14.1
±s	15.6	4.1	7.7	0.9	5.8	6.7	6.2	6.4	9.1	3.8	4.5	7.8	2.7	6.1	8.1	1.6	5.0	7.4	1.3	10.4	17.6
CV(%)	15.6	54.7	161.7	9.6	169.2	173.4	16.9	76.0	155.2	15.8	57.5	197.5	16.7	101.4	134.2	17.5	88.6	120.9	33.7	1261.5	125.2
r with PH				0.71^{**}	0.09	0.32	0.96^{**}	0.73^{**}	0.73^{**}	0.97^{**}	0.82^{**}	0.82^{**}	0.95^{**}	0.58^{**}	0.73^{**}	0.97^{**}	0.51^{*}	0.73^{**}	0.86^{**}	0.14	0.63^{**}

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

Table 4. Combining ability analysis for plant height and its components in a 7×7 diallel cross of wheat.

Source of variation	df	PH	SL	PL	LSI	LTI	LSBI	LFBI
GCA	6	1309.8241^{**}	3.7436^{**}	204.2643^{**}	72.9142^{**}	38.0301^{**}	15.5158^{**}	11.7994^{**}
SCA	21	19.1310^{***}	0.2493^{***}	4.3322^{***}	1.5757^{***}	0.9190^{***}	0.2283^{*}	0.1072^{NS}
Error	54	1.9789	0.0488	0.4221	0.1729	0.2200	0.1176	0.1757
GCA/SCA		68.47	15.02	47.15	46.27	41.38	67.96	110.07

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

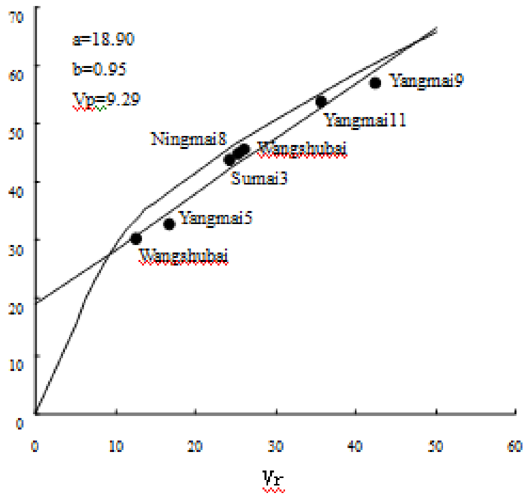

Fig 3. Vr versus Wr graph for PL

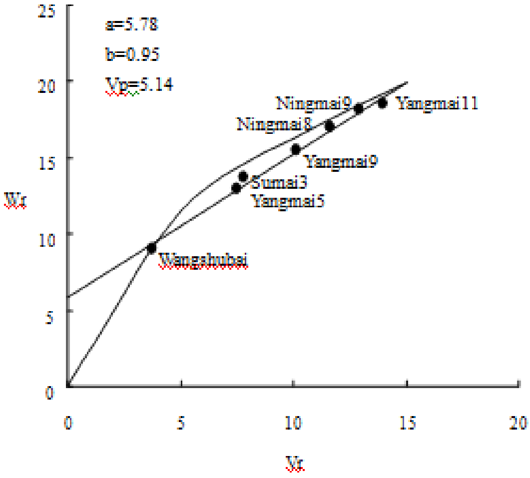

Fig 4 . Vr versus Wr graph for LSI

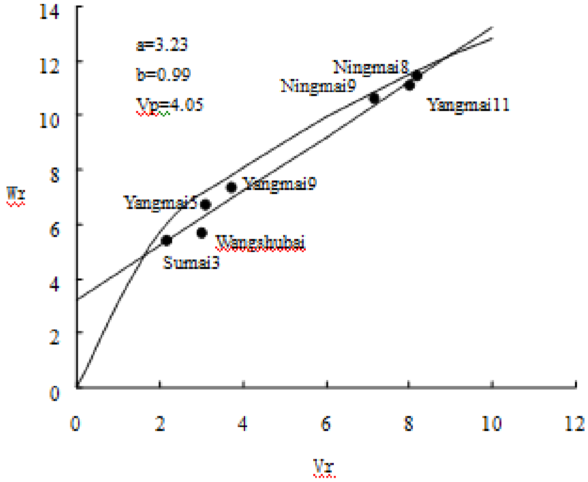

Fig 5. Vr versus Wr graph for LTI

PL, LSI, LTI, LSBI, LFBI and PH were 0.6847, 0.9486, 0.9735, 0.9562, 0.9707 and 0.8495, respectively. Among the internodes, SL and lengths of adjacent internodes were positively associated with each other. These results were in agreement with the previous reports by Zhao and Wang (2003). These strong positive correlations among the traits should provide wheat breeders with insights on possible impacts of selection for one trait on others. From the results of the correlation analysis, it could be concluded that the plant height can be decreased by selecting progenies with low PL, LSI, LTI, LSBI and LFBI values.

Genetic correlation analysis simply measures the correlation between two traits, and cannot elucidate the related mechanisms among them. Path analysis can dissect the correlation coefficient into direct and indirect effects, and quantify the relative contribution of each component to the overall correlation. Path analysis of direct and indirect effects of SL and lengths of internode on PH revealed that PL had the greatest direct effect（0.4258）, followed by LSI（0.2191）(Table 10). Moreover, the basal internodes had larger indirect effect on PH through upper internodes, particularly through PL. Similar results were also reported by Yang et al. (1999); Zhao and Wang (2003). A decrease in the plant height of wheat genotypes using PL and LSI as selection criteria is possible, although the influence of other traits cannot be omitted. However, PL was not as short as possible, and it was positively associated with 1000-grain weight, number of grain per spike and grain yield per plant (Yao et al. 203). Therefore, selection for longer PL had a positive effect on grain yield under the same PH.

Materials and methods

Plant materials

The present research work was conducted in the field area of Jiangsu Academy of Agricultural Sciences, Nanjing during crop season 2009-2010. The parental material comprised of seven wheat varieties of diverse genetic background Ningmai 8, Ningmai 9, Yangmai 5, Yangmai 9, Yangmai 11, Sumai 3 and Wangshuibai. The parents were chosen based on their broad genetic background and great variations for plant height and its components (Table 1). These genotypes were crossed in an incomplete diallel fashion during April, 2009.

Experimental design

The seeds of 21 F_1 crosses along with their parents were planted in the field during November 2009 in a randomized complete block design with three replications. Two rows of 2 m length served as an experimental unit. Plant to plant and row-to-row spacing kept were 5 cm and 25 cm, respectively. Other cultural and agronomic practices were kept uniform for whole experiment. Ten main stems from each parent and hybrid were selected randomly during milk stage in the middle of May 2010 and data were recorded for plant height (PH), spike length (SL), peduncle length (PL), length of the second internode from the top to bottom (LSI), length of the third internode from the top to bottom (LTI), length of the second basal internode (LSBI) and length of the first basal internode (LFBI).

Statistical analysis

Based on the average values over the 10 stems and 3 replications, heterosis (HS) and heterobeltiosis (HBS) of

Table 5. Estimates of general combining ability (GCA) and mean for plant height and its components in a 7×7 diallel cross of wheat

Parents	PH		SL		PL		LSI		LTI		LSBI		LFBI	
	GCA	mean	GCA	mean	GCA	mean	GCA	mean	GCA	mean	GCA	mean	GCA	mean
Ningmai 8	-11.1263^{**}	72.66	-0.5648^{**}	8.33	-4.2251^{**}	26.95	-3.2439^{**}	16.71	-1.5714^{**}	11.39	-0.9862^{**}	6.84	-0.5774^{**}	2.45
Ningmai 9	-7.3382^{**}	81.07	-0.2344^{*}	8.70	-2.6851^{**}	29.66	-2.3580^{**}	18.61	-1.2347^{**}	12.91	-0.7837^{**}	7.61	-0.2193	3.57
Yangmai 5	-0.2608	90.23	-0.5096^{**}	8.12	0.6004	34.19	-0.3872	20.92	0.2857	15.22	0.0445	8.75	-0.3370	3.04
Yangmai 9	-9.8230^{**}	73.23	0.3830^{**}	10.57	-5.4759^{**}	21.38	-1.2113^{**}	20.46	-1.4799^{**}	12.61	-1.0022^{**}	7.30	-0.7059^{**}	2.69
Yangmai 11	-3.3230^{**}	88.01	-0.3937^{**}	8.47	-0.8607^{*}	32.73	-0.2872	22.01	-0.7743^{**}	14.20	-0.3925^{**}	8.51	-0.5981^{**}	3.08
Sumai 3	9.6081^{**}	114.13	0.0726	9.28	6.1467^{**}	47.29	2.5620^{**}	27.72	0.5046^{*}	16.44	0.3919^{*}	9.66	-0.1122	3.74
Wangshuibai	22.2633^{**}	134.45	1.2470^{**}	11.58	6.4997^{**}	44.56	4.9257^{**}	31.19	4.2701^{**}	23.54	2.7282^{**}	14.02	2.5500^{**}	9.56
r(GCA, mean)	0.9967^{**}		0.9801^{**}		0.9684^{**}		0.9958^{**}		0.9962^{**}		0.9991^{**}		0.9955^{**}	

*, ** Significance at $P \leq 0.05$ and $P \leq 0.01$ levels, respectively. r correlation coefficient

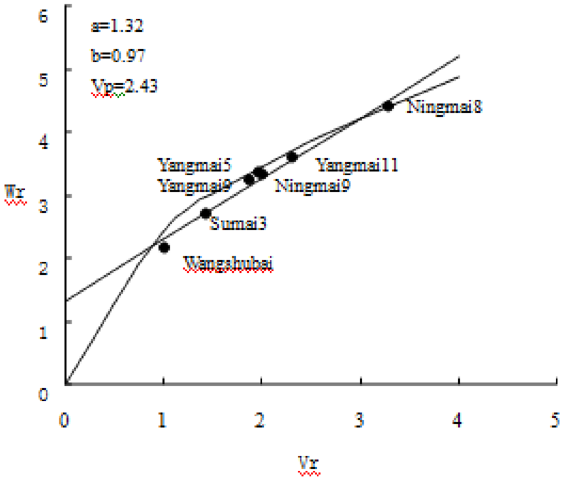

Fig 6. Vr versus Wr graph for LSBI

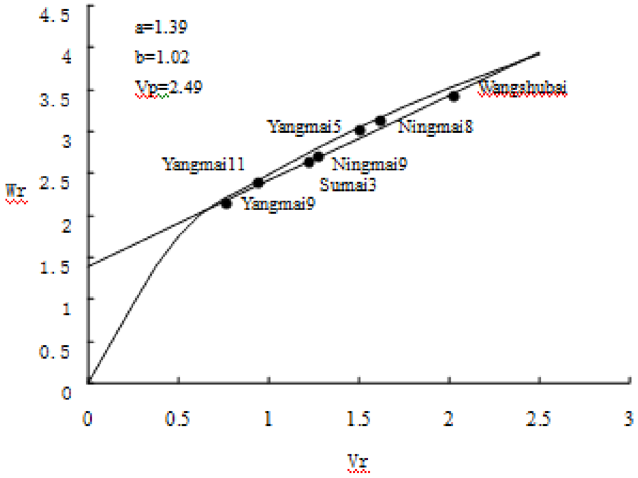

Fig 7. Vr versus Wr graph for LFBI

Table 6. Estimates of specific combining ability (SCA) for plant height and its components in a 7×7diallel cross of wheat

F_1 hybrids	PH	SL	PL	LSI	LTI	LSBI
Ningmai 8×Ningmai 9	0.0574	0.2418	0.3232	-0.4775	-0.3563	-0.0030
Ningmai 8×Yangmai 5	1.0400	-0.3464	-0.3790	1.0618*	0.8767	-0.0744
Ningmai 8×Yangmai 9	0.0689	0.1844	0.0073	-0.2375	0.0589	-0.3344
Ningmai 8×Yangmai 11	-0.5311	-0.1123	0.0321	-0.1082	-0.2700	-0.0041
Ningmai 8×Sumai 3	0.1211	-0.4386	-0.9419	-0.0208	0.9678	0.4415
Ningmai 8×Wangshuibai	6.3526**	0.5736*	1.9984*	1.1655*	1.3756*	1.0485*
Ningmai 9×Yangmai 5	1.4752	-0.0001	1.4477	0.4592	-0.0500	0.1230
Ningmai 9×Yangmai 9	0.8274	0.2406	0.6773	-0.0368	0.0956	-0.1937
Ningmai 9×Yangmai 11	-2.9926	-0.3527	-1.5945	-0.8408	-0.9033	-0.2333
Ningmai 9×Sumai 3	2.6563	0.0244	0.4781	0.3132	1.0611	0.7089
Ningmai 9×Wangshuibai	3.4311	0.5232	0.4351	1.7095**	1.1256	-0.0641
Yangmai 5×Yangmai 9	7.4833**	-0.4908	3.9518**	1.8258**	0.9919	0.5215
Yangmai 5×Yangmai 11	4.5367*	0.4225	1.6066	1.2051*	0.8763	0.3419
Yangmai 5×Sumai 3	0.6656	1.1462**	-0.9008	-0.1108	0.0941	0.1141
Yangmai 5×Wangshuibai	0.2304	0.0184	0.1295	-0.0579	-0.3548	0.3444
Yangmai 9×Yangmai 11	-0.0244	0.4466	-0.6771	-0.4008	-0.3615	-0.0048
Yangmai 9×Sumai 3	2.2911	0.0203	0.3521	0.8366	0.6630	0.2707
Yangmai 9×Wangshuibai	0.5426	-0.9942**	2.8525**	0.0129	-0.8693	-0.1756
Yangmai 11×Sumai 3	0.7444	-0.3197	1.5669	1.0192	-0.7359	-0.4922
Yangmai 11×Wangshuibai	5.8893**	0.4158	2.0040*	1.7221**	1.6219**	0.5081
Sumai 3×Wangshuibai	0.6415	0.3195	1.2932	0.5362	-1.1804	-0.0896

*, ** Significance at $P \leq 0.05$ and $P \leq 0.01$ levels, respectively.

Table 7. Adequacy test of additive-dominance model for the plant height and its components

Parameters	PH	SL	PL	LSI	LTI	LSBI	LFBI
Joint regression (b)	0.981±0.042	1.197±0.229	0.948±0.078	0.946±0.045	0.999±0.059	0.970±0.061	1.019±0.055
Test for b=0	23.251**	5.221**	12.091**	21.245**	17.055**	15.860**	18.698**
Test for b=1	0.455^{NS}	0.860^{NS}	0.666^{NS}	1.205^{NS}	0.009^{NS}	0.499^{NS}	0.354^{NS}
Mean squares of Wr + Vr between arrays	35098.901**	0.778*	1226.632**	142.886**	75.690**	5.494^{NS}	2.467^{NS}
Mean squares of Wr - Vr between arrays	82.254**	0.102^{NS}	11.918^{NS}	0.637^{NS}	0.997^{NS}	0.140^{NS}	0.028^{NS}
Fitness of the data to Additive-Dominance model	Full	Full	Full	Full	Full	Partial	Partial

*, ** Significance at $P \leq 0.05$ and $P \leq 0.01$ levels, respectively, NS=not-significant

plant height and its components were calculated according to the following formulae: HS = (F_1-MP)×100%, and HBS = (F_1-HP)/HP×100%. Here, MP means mid-parent value, F_1 is the mean value of F_1 hybrids, and HP represents the mean value of the higher parent in a cross. To estimate significant differences among parents and F_1 hybrids, the data was subjected to analysis of variance using SAS software. The estimates of general and specific combining ability were calculated using Method II, Model I of Griffing's (1956). Two scaling tests were applied following Mather and Jinks (1982) for testing the validity of additive-dominance model. Further, Hayman (1954) method was used for the estimations of the gene action. Genetic correlation coefficients and path coefficients between plant height and its components were calculated, using the data processing system (Tang and Feng, 2002).

Table 8. Estimate of genetic parameters of plant height and its components

Parameter	PH	SL	PL	LSI	LTI	LSBI	LFBI
D	519.3928**±3.9921	1.6458**±0.1094	85.4828**±1.4202	25.9370**±0.3039	16.1613**±0.2591	5.7654**±0.0762	5.9880**±0.0396
F	-74.6724**±9.5767	0.0556±0.2625	-3.9771±3.4070	-7.6749**±0.7290	-1.0946±0.6215	-1.3541**±0.1829	1.2095**±0.0951
H_1	49.7000**±9.6106	0.8822**±0.2635	14.1305**±3.4190	4.1021**±0.7316	2.7993**±0.6237	0.5192**±0.1835	0.3160**±0.0954
H_2.	44.3294**±8.4083	0.8084**±0.2322	10.7588**±3.0127	3.5266**±0.6446	2.6308**±0.5496	0.4618**±0.1617	0.2180**±0.0841
$(H_1/D)^{1/2}$	0.3093	0.7321	0.4066	0.2149	0.4162	0.3001	0.2297
E	4.4345±1.4116**	0.0518±0.0387	0.7212±0.5022	0.4723±0.1075**	0.2688±0.0916**	0.1329±0.0270**	0.1866±0.0140**
$H_2/4H_1$	0.2230	0.2291	0.1904	0.2149	0.2350	0.2224	0.1725
K	3.5476	0.1803	2.0977	2.7068	0.8554	1.6096	0.1443
h^2_N (%)	95.08	76.62	93.16	92.66	90.39	93.53	95.08

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

Table 9. Phenotypic (p) and genotypic (g) correlation coefficient between plant height and its components in wheat

Characters	SL	PL	LSI	LTI	LSBI	LFBI
PH	0.6752**	0.9432**	0.9708**	0.9496**	0.9625**	0.8416**
	0.6847**	0.9486**	0.9735**	0.9562**	0.9707**	0.8495**
SL		0.4531*	0.7088**	0.7072**	0.7119**	0.7594**
		0.4666*	0.7224**	0.7221**	0.7234**	0.7850**
PL			0.9088**	0.8153**	0.8402**	0.6571**
			0.9133**	0.8322**	0.8613**	0.6688**
LSI				0.9021**	0.9102**	0.7587**
				0.9153**	0.9269**	0.7683**
LTI					0.9830**	0.9087**
					0.9917**	0.9261**
LSBI						0.9234**
						0.9395**

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

Table 10. Path coefficient analysis between Plant height and its components

Characters	Direct effects	Indirect effects					
		SL	PL	LSI	LTI	LSBI	LFBI
SL	0.0532		0.1930	0.1553	0.1241	0.0688	0.0809
PL	0.4258	0.0241		0.1991	0.1430	0.0812	0.0700
LSI	0.2191	0.0377	0.3870		0.1583	0.0879	0.0808
LTI	0.1755	0.0376	0.3472	0.1976		0.0950	0.0968
LSBI	0.0966	0.0379	0.3578	0.1994	0.1725		0.0983
LFBI	0.1065	0.0404	0.2798	0.1662	0.1594	0.0892	

Conclusion

Overall, significant genetic variations were observed for plant height and its components investigated in this study. Heterosis occurred in the F_1 hybrids for all the characters, but their values varied among crosses and characters. Significant GCA and SCA effects for all the characters imply the role of both additive and non-additive gene actions in the genetic control of these characters. The ratios of GCA/SCA imply the higher contribution of additive gene effects to the inheritance of all the characters. The preponderance of additive gene action in explaining genetic variations in these characters indicates the possibility for their genetic improvement through accumulating favorable alleles from parents with highly negative GCA values in the target genotype using conventional breeding methods. The additive-dominance model was fully adequate for PH, SL, PL, LSI and LTI, but LSBI and LFBI showed partial adequacy of AD model. Additive genes coupled with high narrow sense heritability were involved in the inheritance of PH and its components, suggesting selection for these characters will be effective in early segregating generations. Ningmai 8 and Yangmai 9 appeared to be promising parents for wheat breeding, because they possesed obvious and negative GCA effects for lengths of various internodes and plant height. The two crosses of Ningmai 9 × Yangmai 11 and Yangmai 9 × Yangmai 11 showed negative SCA effects for PH and its components, which may yield desirable semi-dwarf types in the segregating population.

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