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Inheritance of internode and culm length in hexaploid Triticale

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Summary. A diallel cross of twelve cultivars of hexaploid Triticale was made in order to study genic action types for total culm length and for the length of its different segments. Culm length, and four partial lengths of the culm were studied in the F_1 and F_2 generations. The analysis was made according to the Griffing, Hayman and Jinks models. Heterosis in culm length is mainly due to its upper half. Spanish cultivars have, in general, positive GCA and transmit greater height in crosses, whereas the Mexican ones show a negative GCA effect and have a tendency to decrease in height when crossed. Additivity greatly influences the inheritance of culm length, this influence being lower at the first plant internodes. The environmental component has also a large influence in the phenotypic expression of Triticale height. Dominance is only partial for the five traits studied. The predominant kind of interaction seems to be of the duplicate type. All correlations between culm length and its components are high and positive, especially the genetic ones.

Key words: Diallel cross – Triticale – Culm length – Internode length

Introduction

The introduction of genes reducing height without altering the yield components has resulted in yield increases of varieties of wheat, barley and other cereals. The early bred varieties of triticale had the inconvenience of susceptibility to lodging and, therefore, they did not tolerate the high doses of nitrogen fertilizers necessary for reaching high yields (Zillinsky 1973; Kiss 1973). The reduction of height in triticale is at present one of the principle breeding objectives for this cereal (Cimmyt 1980).

In previous work on the inheritance of height in triticale, additive effects seemed to be more important than non-additive ones (Reddy 1976; Rao and Joshi 1979). However, with respect to first straw internode length, Kaltsikes and Lee (1973) found that non-additive effects were more important than additive ones.

It would be useful in the planning of breeding programs of Triticale to understand the inheritance not only of the total height but also of the different segments composing it.

In the present work we have tried to study the types of genic action for total culm length and for the length of its different segments.

Material and methods

Twelve varieties of hexaploid Triticale were included in a diallel cross (Table 1). The number given to each cultivar in Table 1 is used in all tables and graphics for identification purposes. Plant height was studied in generations F_1 and F_2, only nine parents were used in the F_2 studies due to difficulties in obtaining enough seed in the crosses involving the cultivars 'Pissarev', 'M 1605' and 'C 120'. Backcrosses of the F_1 with both parents were obtained for five varieties: 'Cachirulo', 'M 1635', 'Armadillo PPV-13' and 'Bronco 90'. The 12 parents, the 66 F_1, the 36 F_2 and 20 backcrosses were sown in a randomized block with four replications. The separation between rows was 0.6 m, and each row contained 15 plants at 0.1 m intervals. Six plants per replication, taken at random, were studied and the measurements were made in centimeters for:
- culm length (CL). Distance between the tillering node and the start of the main ear.
- first straw internode length (1NL). Distance between the first node from top and the start of the main ear, sometimes called the peduncle or neck.
- two internodes length (2NL). Distance between the second node and the start of the main ear.

– three internodes length (3NL). Distance between the third node and the base of the main ear.

– four internodes length (4NL). Distance between the fourth node and the base of the main ear.

The analysis of data were made according the techniques of Hayman (1954a, 1958); Jinks (1954, 1956) and Griffing (1956). Individual effects for both combining abilities, general and specific, were estimated according to Method 4, Modell II. For the analysis of variance of the diallel we used the model proposed by Hayman (1954b), and modified by Morley Jones (1965) in the case of non-reciprocals. Parameters for testing epistasis were estimated according to the model of Jinks and Morley Jones (1958) and Mather and Jinks (1971).

Results and discussion

Combining ability and heterosis

Average data for the culm length and its parts are shown in Table 1 for the 12 parents. From the ordering of the parents it seems that the architecture of height is similar in almost all of them. The cultivar 'Pissarev' has a relatively short first straw internode and in the cultivars 'M 1635', 'C 120' and 'Bronco 90' the peduncle comprises an important part of the total culm length.

There exists an almost total concordance between the ordering of culm lengths and the GCA effects (Table 2): the taller the cultivar, the greater the effect of the GCA. This concordance applies to the five traits studied.

Highly significant, positive or negative, GCA was shown by all the cultivars for the traits CL, 2NL and 3NL, but not by all cultivars for the other traits (Table 2). Cultivars of Spanish origin have in general positive GCA and transmit greater height when crossed, whereas the Mexican ones show negative GCA effect and have a tendency to decrease in height when crossed.

Table 1. Origin and mean performance or the 12 parents included in the diallel analysis. CL = culm length; 1 NL = neck length; 2 NL = neck plus one internode; 3 NL = neck plus two internodes; 4 NL = neck plus three internodes

Variety	Origin	CL	1 NL	2 NL	3 NL	4 NL
1. 'Cachirulo'	Spain	118.75 (1)	47.67 (2)	81.58 (1)	99.71 (1)	112.04 (1)
2. 'Pissarev'	URSS	114.12 (2)	37.58 (9)	66.25 (6)	86.79 (4)	102.96 (3)
3. 'M 1635'	Spain	111.92 (3)	48.58 (1)	79.83 (2)	95.38 (2)	107.38 (2)
4. 'M 1605'	Spain	110.21 (4)	43.00 (6)	72.13 (3)	88.04 (3)	101.33 (4)
5. 'C 110'	Spain	86.46 (7)	39.25 (8)	62.33 (7)	74.50 (7)	83.58 (7)
6. 'C 120'	Spain	93.00 (6)	43.37 (4)	68.21 (5)	81.50 (6)	90.92 (6)
7. 'U. Manitoba'	Mexico	78.63 (11)	35.79 (10)	54.50 (11)	67.04 (10)	76.04 (10)
8. 'Armadillo 1972-1'	Mexico	73.21 (12)	35.45 (12)	51.83 (12)	63.88 (12)	71.92 (12)
9. 'Cinnamon'	Mexico	75.54 (10)	35.79 (11)	55.38 (10)	66.00 (11)	73.04 (11)
10. 'Badger'	Mexico	80.00 (9)	39.45 (7)	58.67 (9)	70.42 (9)	78.37 (9)
11. 'Armadillo PPV-13'	Mexico	85.04 (8)	43.17 (5)	61.46 (8)	73.71 (8)	82.96 (8)
12. 'Bronco 90'	Mexico	100.50 (5)	44.20 (3)	68.33 (4)	82.92 (5)	94.42 (5)

Table 2. Estimates of general combining ability effects (g_i) and specific combining ability variances (σ^2_{si}) for five characters of height in a 12 × 12 diallel set of triticale

Variety	CL		1 NL		2 NL		3 NL		4 NL	
	g_i	σ^2_{si}	g_i	σ^2_{si}	g_i	σ^2_{si}	g_i	σ^2_{si}	g_i	σ^2_{si}
'Cachirulo'	14.2**	25.6	3.8**	4.1	9.0**	13.0	10.4**	12.6	12.3**	16.5
'Pissarev'	13.4**	21.7	−0.2	4.0	3.1**	11.9	6.2**	14.3	8.3**	13.6
'M 1635'	8.6**	35.3	4.2**	6.6	7.0**	17.2	8.2**	21.9	8.6**	27.3
'M 1605'	4.5**	52.5	−0.7*	8.7	1.2**	21.4	1.5**	29.1	2.8**	35.1
'C 110'	− 3.3**	5.7	0.5	3.2	0.1	5.5	− 1.2**	4.8	− 1.9**	5.6
'C 120'	2.0**	3.5	2.3**	3.2	3.1**	8.1	3.3**	8.2	2.9**	5.9
'U. Manitoba'	− 7.7**	21.5	−2.4**	3.4	−4.9**	10.1	−5.8**	13.1	6.5**	19.3
'Armadillo 1972/1'	−10.2**	10.0	−3.7**	2.6	−6.3**	5.7	−7.2**	6.4	−8.4**	8.1
'Cinnamon'	− 9.5**	34.5	−2.6**	7.1	−5.1**	18.4	−6.4**	23.2	−7.7**	26.5
'Badger'	− 5.4**	29.5	−0.9**	4.8	−3.6**	13.5	−4.1**	19.4	−4.7**	26.6
'Armadillo PPV-13'	− 9.0**	15.6	−1.0**	3.5	−4.4**	8.2	−6.1**	12.1	−7.1**	13.2
'Bronco 90'	2.3**	32.6	0.7	5.8	1.0*	13.3	1.2**	20.2	1.6**	22.2
	S.E. = 0.45		S.E. = 0.30		S.E. = 0.35		S.E. = 0.37		S.E. = 0.40	

**, * Significant at the 1% and 5% levels, respectively

The fact that 'Cinnamon' transmited the largest reduction in height and has a relatively high variance for its GCA (Table 2) indicates that the transmission is not uniform and that the specific combinations with other parents can give values higher or lower than expected depending on the GCA effects. The same is true for parents 'M 1605' and 'M 1635', which transmited greater height. However, the two parents with the highest and lowest GCA, 'Cachirulo' and 'Armadillo 1972-1', respectively, are rather uniform in the transmission of greater or lower height.

As shown by item **b** in the variance analysis (Table 3), heterosis is significant in the F_1 for culm length. It is also significant for 1NL and 2NL, but not for the other two traits, meaning that heterosis in culm length is mainly due to heterosis in its upper half.

Validity of assumptions

The assumptions of the model (Hayman 1954a) must be met in order to be able to estimate the variance components. Assuming from the beginning that the parents are homozygous, that there is diploid segregation and that the reciprocal effects are non significant, the absence of epistasis and multiple allelism remains to be tested as well as the independent distribution of genes in the parents. To prove the last assumption two tests are recommended by Mather and Jinks (1971): the variance analysis of (Wr–Vr) and the slope of the regression of Wr on Vr. The significant heterogeneity for (Wr–Vr) and the slope of the regression significantly different from 1 indicate the failure of one or more assumptions.

Significant variance at the 5% level of the arrays for culm length in F_1 was found in the analysis of variance (Wr–Vr). For the other traits the variance was non significant. For all traits, with the exception of 1NL, the slope of the regression of Wr on Vr was not significantly different from 1.

Additivity

All the estimations indicate the great influence of additivity in the inheritance of culm length. Item **a** in the variance analysis, that estimates additivity effects (Table 3), and the genetic parameter D are highly significant (Table 4). The influence is greater in F_1, where the difference between the parameters D for additivity and H_1 for dominance is highly significant, showing that the heritability also has a high value (Table 4). These results are in agreement with the findings of Reddy (1976) and Rao and Joshi (1979) for triticale and of Gyawali et al. (1968); Bitzer et al. (1971) and Amaya et al. (1972) for wheat. The important role of additive effects in the total genetic variability is a decrease in the first plant internodes in such a way that the 1NL additive and non additive effects seem to have similar importance.

The environmental component, E, has also a great influence in the phenotypic expression of triticale height (Table 4). This has been found to be the same for wheat by different authors (Halloran 1975). The relative influence of the environment is lower for great values of the height component. In spite of the importance of the environmental influence, it seems that the hereditable component establishes the relative order in height in the triticale cultivars used in this work.

Dominance

Dominance is only partial for the five traits studied (Figs. 1 and 2), peduncle length being the trait showing the higher average ($\sqrt{H_1/D}$ in Table 4) but still within

Table 3. The mean squares for the analysis of variance of the F_1 (12 × 12) and F_2 (9 × 9) diallel crosses of Triticale

	Source	D.F.	CL	1 NL	2 NL	3 NL	4 NL
F_1	a	11	4,160.4**	307.8**	1,339.6**	2,007.8**	2,785.1**
	b	66	112.5**	24.6**	56.1**	70.1**	83.6**
	b_1	1	525.1*	110.7*	246.2**	258.9	332.1
	b_2	11	60.7*	15.6	25.5*	32.9	37.8
	b_3	54	115.5*	24.8**	58.9**	74.2**	88.3**
	E	231	26.1	8.4	14.2	17.4	20.8
F_2	a	8	2,829.8**	239.3**	1,043.1**	1,611.9**	2,159.3**
	b	36	103.7**	18.8**	50.9**	69.5**	84.6**
	b_1	1	43.6	1.7	47.9	42.7	23.7
	b_2	8	46.2*	14.2	31.4**	43.1**	45.9*
	b_3	27	123.0**	20.8**	56.8**	78.3**	98.3**
	E	132	29.7	7.4	13.1	19.0	23.6

**, * Significant at the 1% and 5% levels, respectively

Table 4. Estimates of the genetic components of variation for culm lenght and their components in F_1 (12×12) and F_2 (9×9) diallel crosses of Triticale

	CL		1 NL		2 NL		3 NL		4 NL	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
D	266.5**	257.5**	21.6**	28.0**	86.6**	109.7**	134.3**	159.7**	195.6**	212.6**
H_1	82.4	234.4	14.1	117.7	41.5	108.4	47.8	206.6	57.6	177.6
H_2	78.3	282.6	23.5	64.1	43.1	118.5	47.5	215.1	56.6	204.9
F	−30.0	18.5	1.7	51.6	−12.3	46.3	−7.3	30.2	−2.5	7.9
h^2	47.8	7.6	7.8	0.1	24.7	9.8	24.5	9.1	33.0	6.9
E	26.1**	29.7**	8.4**	7.4**	14.2**	13.1**	17.4**	19.0**	20.8**	23.6**
$D-H_1$	184.1**	23.1	7.5	−89.7	45.1	1.3	86.6**	−46.6	137.9**	35.0
$\sqrt{H_1/D}$	0.56	0.95	0.81	2.05	0.69	0.99	0.60	1.14	0.54	0.91
H_1-H_2	4.13	−48.24	−9.43	53.6	−1.65	−10.1	0.31	−8.80	0.98	−27.30
$H_2/4H_1$	0.24	0.30	0.42	0.14	0.26	0.27	0.25	0.26	0.25	0.29
Dom./Rec.	0.82	1.01	1.10	2.63	0.81	1.54	0.91	1.18	0.98	1.04
Her. s.e.	0.77	0.49	0.27	0.39	0.66	0.38	0.71	0.45	0.74	0.54

**, * Significant at the 1% and 5% levels, respectively

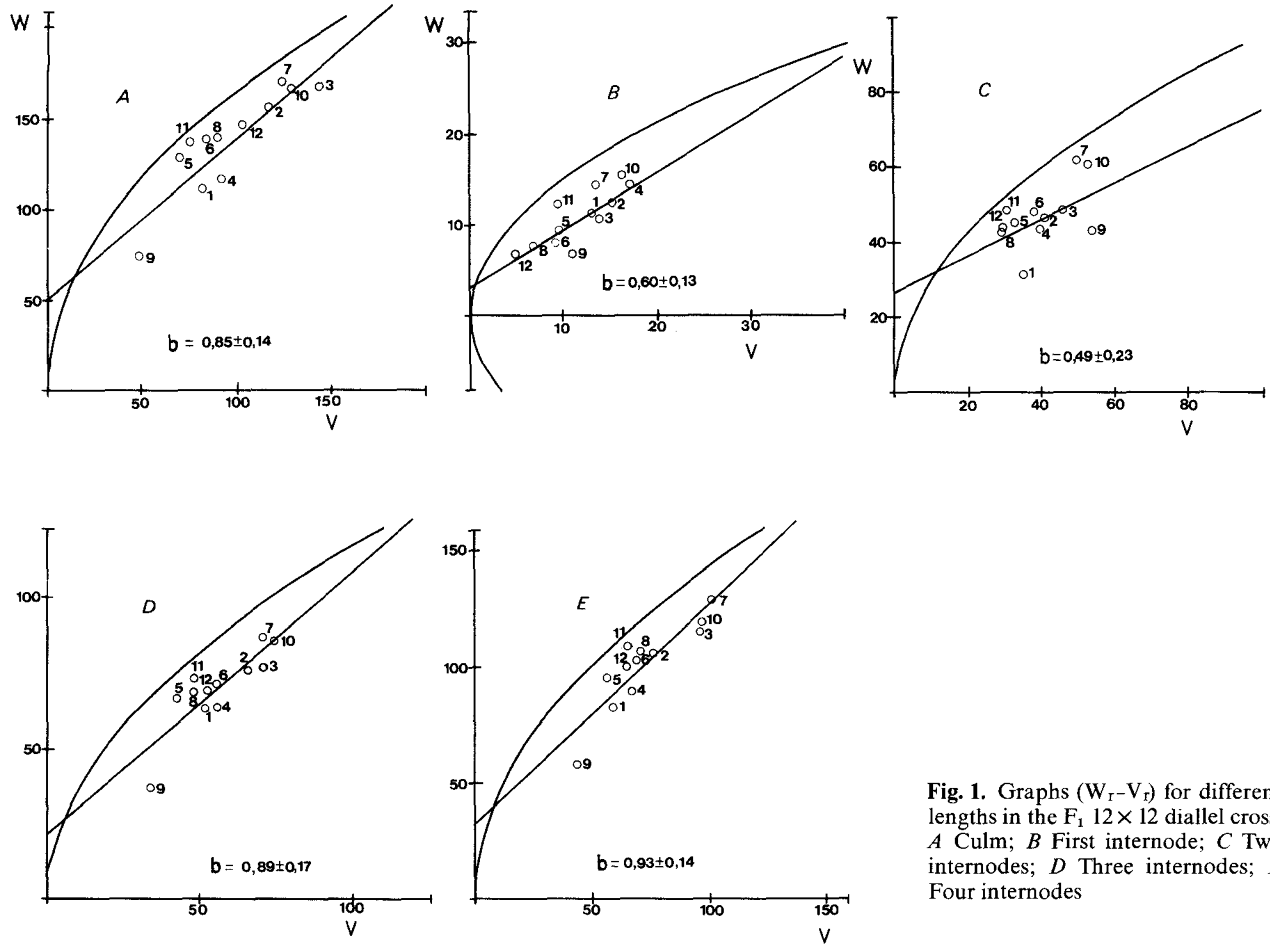

Fig. 1. Graphs (W_r-V_r) for different lengths in the F_1 12×12 diallel cross. *A* Culm; *B* First internode; *C* Two internodes; *D* Three internodes; *E* Four internodes

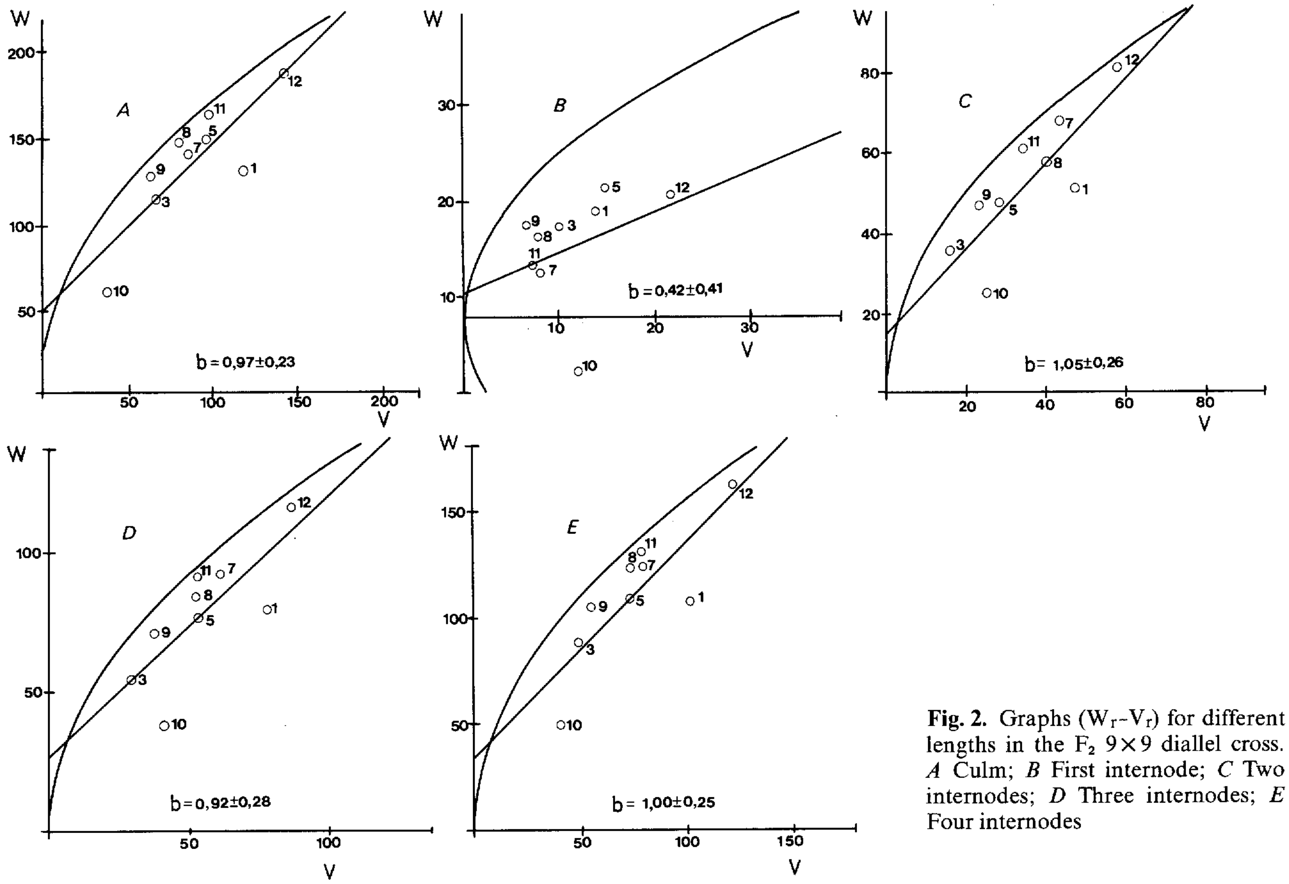

Fig. 2. Graphs (W_r–V_r) for different lengths in the F_2 9×9 diallel cross. *A* Culm; *B* First internode; *C* Two internodes; *D* Three internodes; *E* Four internodes

the common characteristic of incomplete and possible small dominance, as the regression line reaches the Wr axis well above the origin (Fig. 1). This low level of dominance could be responsible for the differences in the array distributions of F_1 and F_2 (Figs. 1 and 2), some arrays having the greater number of dominant genes in F_1, have the greater number of recessive ones in F_2 and vice versa. 'Cinnamon' (9) and 'Cachirulo' (1) are the parents with the higher number of dominant genes, and 'M 1635' (3) and 'Badger' (10), the parents with the higher number of recessive ones (Fig. 1). No association has been found between dominance and greater height or between recessivity and lesser height.

In the 6×6 diallels obtained by separating the parents in accordance with their origin, the relative positions of the 12×12 diallel are maintained (Fig. 3). The Spanish cultivar 'M 1605' (4) shows a higher degree of dominance, and the cultivar 'Badger' (10), being the more recessive in the 12×12 diallel, is in a dominant situation in the 6×6 one.

There exists a slight asymmetry in the distribution of genes between the parents. In the F_1 the number of recessive genes is a little higher than the number of dominants (Table 4) with the exception of peduncle length. The number of dominant genes is higher in the F_2. Regarding genes with positive or negative action estimated by the value of $H_2/4\,H_1$, this value is in the F_1 close to 0.25, indicating balance, but in the F_2 there is a small imbalance. 1NL is the trait more distant of the general performance in both generations (F_1: 0.42; F_2: 0.14).

Epistasis

For five of the parents the tests for epistasis (Table 5) seem to confirm some of the previous results. With the exception of the cross 'C 110'×'Armadillo PPV-13', the parameter ($\{\hat{d}\}$) estimating additivity is significant for culm length. Only half of the crosses are significant for additivity for peduncle length. Dominance is less important for this trait, the corresponding parameter ($\{\hat{h}\}$) being significant only in less than half the crosses.

The predominant kind of interaction seems to be of the duplicate type (Mather 1967), especially in the crosses involving the variety 'C 110'.

Correlations

All correlations between culm length and its components are high and positive, especially the genetic correlations (Table 6). The correlation with 1NL is

Table 5. Estimates of the additive, dominance and interaction parameters for the mean length of culm (upper) and neck (bottom) in a 5×5 diallel cross of Triticale

		1	3	5	11	12
1	$\hat{m}$		85.42±14.08**	122.01±13.76**	121.16±13.85**	114.49±15.58**
	$\{\hat{d}\}$		3.42± 1.06**	16.15± 1.09**	16.86± 0.97**	9.13± 1.08**
	$\{\hat{h}\}$		42.80±31.80	-36.24±33.01	- 44.09±29.64	- 0.90±33.17
	$\{\hat{i}\}$		29.92±14.04*	-19.40±13.72	- 19.26±13.81	- 4.86±15.54
	$\{\hat{j}\}$		29.25± 6.83**	- 1.89± 8.13	- 8.45± 4.97	32.25± 5.40**
	$\{\hat{l}\}$		0.75±18.36	25.77±20.15	25.39±16.28	- 3.63±18.03
3	$\hat{m}$	37.57± 7.92**		86.53± 6.50**	96.40± 8.03**	142.71± 7.63**
	$\{\hat{d}\}$	- 0.46± 1.07		12.73± 1.05**	13.44± 0.92**	5.71± 1.05**
	$\{\hat{h}\}$	10.79±18.84		40.53±15.09*	19.63±19.17	-55.18±19.80*
	$\{\hat{i}\}$	10.56± 7.85		12.66± 6.42	2.08± 7.97	-36.50± 7.56**
	$\{\hat{j}\}$	5.15± 4.90		- 6.80± 2.82	- 10.96± 4.93*	23.24± 5.83**
	$\{\hat{l}\}$	5.69±11.33		-26.18± 9.16**	- 14.70±11.59	12.68±13.13
5	$\hat{m}$	39.06± 6.75**	36.18± 4.30**		15.41±11.29	47.88±11.34**
	$\{\hat{d}\}$	4.21± 0.91**	4.67± 0.97**		0.71± 0.95	- 7.02± 1.07**
	$\{\hat{h}\}$	10.30±16.50	24.53±10.35**		198.46±27.85**	121.68±25.24**
	$\{\hat{i}\}$	4.40± 6.69	7.74± 4.19		70.34±11.25**	45.60±11.29**
	$\{\hat{j}\}$	- 5.66± 4.51	- 4.23± 3.05		- 17.76± 7.44*	10.28± 5.20
	$\{\hat{l}\}$	- 1.32±10.10	-15.07± 6.39*		-126.24±17.16**	-77.56±14.74**
11	$\hat{m}$	34.68± 6.80**	41.88± 6.56**	24.63± 5.30**		102.59± 9.13**
	$\{\hat{d}\}$	2.25± 1.07*	2.71± 0.86	1.96± 0.65*		- 7.73± 0.95**
	$\{\hat{h}\}$	28.51±16.36	11.66±14.27	50.02±13.07**		-32.12±20.39
	$\{\hat{i}\}$	10.74± 6.75	4.00± 6.51	16.58± 5.26**		- 9.82± 9.09
	$\{\hat{j}\}$	2.24± 4.28	- 7.41± 2.88**	- 4.42± 3.57		- 5.20± 4.32
	$\{\hat{l}\}$	-19.06± 9.87	- 4.49± 8.05	-31.58± 8.14**		24.20±11.83
12	$\hat{m}$	52.18± 9.49**	52.26± 6.59**	34.89± 5.54**	35.44± 6.10**	
	$\{\hat{d}\}$	1.73± 0.88	2.19± 0.94*	- 2.48± 0.75	- 0.23± 0.76	
	$\{\hat{h}\}$	-12.96±20.67	- 7.57±15.52	19.50±13.11	13.62±13.93	
	$\{\hat{i}\}$	- 6.24± 9.45	- 5.86± 6.52	6.84± 5.49	8.92± 6.05	
	$\{\hat{j}\}$	9.62± 3.93*	4.97± 3.98	7.12± 3.36*	0.53± 3.27	
	$\{\hat{l}\}$	5.36±11.69	- 0.43± 9.35	-12.56± 8.00	- 5.13± 8.19	

**, * Significant at the 1% and 5% levels, respectively

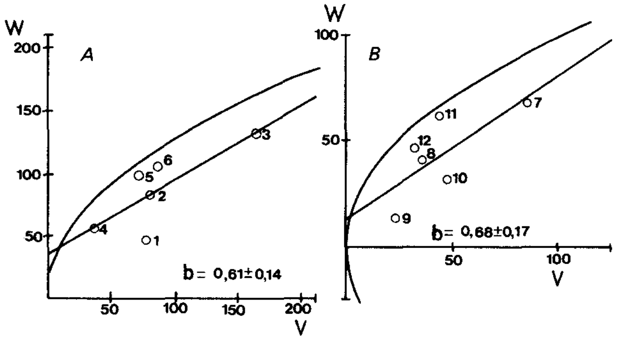

Fig. 3. Graphs (W_r-V_r) for culm length in F_1 6×6 diallel cross. *A* Spanish varieties; *B* Mexican varieties

Table 6. Correlation coefficients between culm length and their components in F_1 (12×12) and F_2 (9×9) generations of a diallel cross of Triticale

	1 NL		2 NL		3 NL		4 NL	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
r_P	0.53	0.63	0.85	0.86	0.92	0.93	0.97	0.96
r_G	0.70	0.89	0.93	0.96	0.97	0.98	0.99	1.00
r_g	0.78	0.91	0.94	0.97	0.98	0.99	0.99	1.00
r_s	0.45	0.86	0.87	0.92	0.94	0.97	0.96	1.00
r_e	0.39	0.48	0.67	0.74	0.79	0.85	0.90	0.90

somewhat smaller, this being mainly due to the low value of the environmental correlation. This is perhaps an indication of the environment acting in a different way on the upper and lower internodes. For this reason peduncle length would not be a good index for culm length selection.

Almost all the analyses made involving 1NL suggest a different performance for this trait from that of the lower internodes. This could be an indication of the existence of different genetic systems in Triticale for the lengths of the lower internodes than for the lengths of the upper internodes, mainly for the uppermost internode or peduncle.

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