Multivariate Statistical Analysis of the Effects of Rye Telomeric Heterochromatin on the Agronomic Traits of Hexaploid Triticale

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Summary

Two pairs of sister lines of hexaploid triticale (*X Triticosecale* Wittmack) differed by the presence (++) or absence (–) of telomeric heterochromatin on chromosome arms 7 RL (cv. Drira) and 6 RS (cv. Rosner) were used in order to study the effects of telomeric heterochromatin loss on twelve agronomic traits. The following multivariate statistical techniques were used : multivariate analysis of variance, partial correlation, multiple regression analysis and canonical correlation. The loss of telomeric heterochromatin was accompanied by significant changes in the means of the twelve traits as a whole as evidenced by the results of the multivariate analysis of variance and in the regression of yield on the other traits. Many more partial correlation coefficients were changed in the Drira lines than in the Rosner lines ; most coefficients became larger in the Rosner line lacking heterochromatin while the opposite was true in the corresponding Drira line. The traits most affected differed from cultivar to cultivar. There were also changes in the regression of seed yield on the other traits with number of spikes contributing significantly only in the lines lacking telomeric heterochromatin with a concomitant loss of the significant contributions in these lines of spike length, number of spikelets per spike and the derived variable spike density. It is concluded that the loss of telomeric heterochromatin has significant effects on the expression and the relationships between agronomic traits and groups of traits in hexaploid triticale and that for some traits these effects can be cultivar and chromosome specific.

Key Words : multivariate statistics, telomeric heterochromatin, canonical correlation, partial correlation, multivariate analysis of variance, hexaploid triticale.

Introduction

Hexaploid triticale (*X Triticosecale* Wittmack) is the amphiploid between tetraploid wheat and diploid rye (Kaltsikes 1974a). It has been created for the purpose of combining in one species the desirable properties of its parents. From the very early days of its creation two problems stood out as the main obstacles on its way to becoming a commercially successful crop. First it showed a varying percentage of spikelet sterility and second the seeds formed were not plump but showed

varying degrees of shrivelling. Both problems were traced, to a great extent, to the presence of heterochromatin on eleven of the fourteen telomeres of the rye chromosomes of triticale. Thus Merker (1976), Kaltsikes and Roupakias (1976) and Roupakias and Kaltsikes (1977) have shown that the loss of rye telomeric heterochromatin from one chromosome at a time led to an improvement in the pairing of chromosomes in triticale while Thomas and Kaltsikes (1974, 1976) showed that the chromosomes present as univalents in triticale were mostly rye chromosomes with heterochromatin at both telomeres. These findings were later extended to triticale combining more than one chromosome pair lacking telomeric heterochromatin even though the effects of heterochromatin loss were not additive (Kaltsikes and Gustafson 1980, 1985, 1986, Kaltsikes *et al.* 1983, Kaltsikes *et al.* 1983). Kernel shrivelling was also traced to the presence of rye telomeric heterochromatin (Bennett 1977, Thomas *et al.* 1980, but see also the results of Kaltsikes *et al.* 1975 and Varghese and Lelley 1973).

Rye telomeric heterochromatin affects agronomic traits also as well as their inter-relationships (Bebeli and Kaltsikes 1992, Bennett and Gustafson 1982, Gustafson and Bennett 1982, Kaltsikes and Bebeli 1993a, b). In all these studies the statistical methods used for the analysis of the data were univariate. Multivariate statistical methods exist for the analysis of data sets combining information on many traits and some of them have been used in triticale and rye (Kaltsikes 1973, 1974b).

In this paper we present results of multivariate analyses of twelve agronomic traits in two pairs of sister lines of triticale which lack telomeric heterochromatin on rye chromosome arms 7 RL and 6 RS and show that the loss of heterochromatin is associated with significant changes in the expression and interrelationships of the various traits and groups of traits.

Materials and Methods

The materials used consist of two pairs of sister lines of hexaploid triticale. One pair originated in the cultivar Drira and consists of one line lacking (7 RL–) and the other possessing (7 RL++) telomeric heterochromatin on rye chromosome arm 7 RL (Merker 1976). The other originated in the cultivar Rosner and involved chromosome arm 6 RS (Kaltsikes and Roupakias 1976), the lines being designated as 6 RS– and 6 RS++.

Seeds from these lines were germinated in Jiffy 7

Table 1. Mean values for several agronomic traits in two pairs of sister lines differing in telomeric heterochromatin

Line	Heading date	Tillers per plant	Plant weight (g)	Plant height (cm)	Spike weight (g)	Seed weight (g)	Spike number	Spike length (cm)	trait			
									Spikelets per spike	Seeds per spike	Harvest index (%)	Spike density
6 RS++	117.48	10.79	62.19	108.17	30.43	21.45	15.31	12.85	24.58	49.17	34.49	1.93
6 RS--	116.73	7.49	52.15	114.17	25.80	18.04	12.42	12.24	24.46	50.99	34.59	2.00
7 RL++	110.37	6.99	69.44	101.67	37.70	28.29	18.33	14.82	27.20	60.44	40.74	1.84
7 RL--	116.37	13.19	65.83	107.85	31.20	21.41	17.04	13.33	24.80	50.34	32.52	1.87

pots and then transplanted in the field at distances of 20 cm between rows and from plant to plant. Plants that did not survive were replaced by common wheat plants so that a uniform plant stand existed. The plants were individually randomized. The numbers of plants per line contributing data are given at the bottom of the various tables. The whole experiment was repeated twice and the results combined after it was determined that the data were homogeneous.

The following measurements were taken on a per plant basis :

1. Number of days to heading (referred to as heading date). This was determined as the number of days from January 1st to the day when the peduncle was clearly seen on the primary tiller in each plant.
2. Number of tillers per plant.
3. Plant height in cm.
4. Plant weight (in grams) at harvest.
5. Spike weight (in grams) at harvest.
6. Seed weight per plant (grams).
7. Number of spikes per plant.
8. Spike length in cm.
9. Number of spikelets per spike.
10. Number of seeds per spike.
11. Harvest index (the weight of seeds per plant divided by plant weight).
12. Spike density. The number of spikelets per spike divided by the length of the spike.

The data sets were first analyzed using MANOVA (Multivariate Analysis of Variance) to ascertain whether statistically significant differences existed between the pairs of lines and then the following methods were also used : partial correlation analysis, multiple regression analysis and canonical correlation (Cooley and Lohnes 1971).

The differences between the partial correlation coefficients of the two lines of each set were tested for statistical significance according to Morrison (1976). Multiple regression equations were compared using the method described by Zar (1974) while multiple regression coefficients were compared by the use of the t-test.

The mean values of the traits analyzed are given in Table 1.

Results

1. Multivariate analysis of variance

For each cultivar the two lines differing by the presence or absence of telomeric heterochromatin were highly statistically different one from the other in the multidimensional space delineated by the twelve traits studied (Table 2). This was true for all criteria used for testing the significance of the differences.

2. Partial correlation analysis

The two cultivars reacted differently to the loss of telomeric heterochromatin as far as the partial correlations between the traits were concerned. In Drira (Table 3) 28 of the 66 correlation coefficients (approximately 42 %) changed significantly in the line lacking telomeric heterochromatin ; of these only nine (approximately 32 %) became larger in the - line. Most of the changes occurred in the relationships of seed weight, spike weight and harvest index with the other traits.

In contrast, in the Rosner lines of the 17 coefficients (approximately 26 %) which changed significantly ten (approximately 59 %) became larger in the -- line (Table 4). The relationships of heading date, spike number and harvest index with the other traits were affected the most as a result of the loss of telomeric heterochromatin.

In both cases the number of coefficients changing significantly was higher than that expected on the basis of chance.

Table 2. Multivariate analysis of variance for twelve traits of two pairs of sister lines differing in telomeric heterochromatin

Line	Wilk's lambds	Pillai's trace	Hottelling Lawley trace	Roy's greatest root
7 RL++ vs 7 RL--	.2316 .0001	.7684 .0001	3.3186 .0001	3.3186 .0001
6 RS++ vs 6 RS--	.6531 .0001	.3469 .0001	.5311 .0001	.5311 .0001

N=106 and 79 for 7 RL++ and 7 RL--, respectively

N=81 for both 6 RS lines

Upper figure is the value of the statistic while the lower figure is the level of significance.

Table 3. Partial correlation coefficients among various agronomic traits in the Drira lines 7 RL++ and 7 RL--

Trait		Tiller /plant	Plant height	Plant weight	Spike weight	Seed weight	Spike number	Spike length	Spikelets /spike	Seeds /spike	Harvest index	Spike density
Heading date	++	-.4796	-.1725	.0620	.0505	-.1906	.0808	-.1410	.1049	.2700	-.1003	-.1050
	--	-.5446	<u>.2642</u>	-.0360	-.0334	.0674	.1000	-.2640	.2461	-.1784	-.3213	-.2420
Tillers/plant	++		-.2585	.0790	.0312	-.7397	.3560	-.1250	.1295	.0230	-.1434	-.1010
	--		-.0048	.2980	<u>.3488</u>	-.2538	.1267	-.0620	.0451	-.2314	-.1378	-.0070
Plant height	++			.0350	.0525	-.0673	.2429	-.3220	.3247	.3517	-.2460	-.2950
	--			<u>.3990</u>	<u>.4112</u>	-.3792	-.1592	-.1550	.1397	.1502	<u>.1073</u>	-.1170
Plant weight	++				.5839	-.1305	.2862	-.1920	.2374	-.0032	-.7137	-.2390
	--				-.9548	.9231	.5132	.1020	-.1056	.1729	-.1859	<u>.0720</u>
Spike weight	++					.8380	.1086	.4770	-.4933	-.0729	.5178	.4600
	--					<u>.9298</u>	<u>.4816</u>	<u>.0670</u>	-.0661	.2117	-.1546	<u>.0340</u>
Seed weight	++						-.1671	-.3890	.3745	.2239	-.1612	-.3480
	--						-.3589	<u>.0380</u>	-.0332	-.0038	<u>.2277</u>	<u>.0580</u>
Spike number	++							-.0370	.0415	.0070	.1515	-.0250
	--							-.0950	.1211	-.0112	-.0411	-.1150
Spike length	++								.9908	.3472	-.4284	-.9840
	--								<u>.9924</u>	-.2191	-.1540	-.9880
Spikelets/spike	++									-.3025	.4788	.9810
	--									<u>.2381</u>	<u>.1753</u>	<u>.9900</u>
Seeds/spike	++										.2505	.3210
	--										.2489	-.2110
Harvest index	++											-.4610
	--											-.1890

N=106 and 78 for the ++ and the -- lines, respectively

Correlation coefficients which are underlined are statistically different from their counterpart at $p=0.05$.**Table 4.** Partial correlation coefficients among various agronomic traits in the Rosner lines 6 RS++ and 6 RS--

Trait		Tiller /plant	Plant height	Plant weight	Spike weight	Seed weight	Spike number	Spike length	Spikelets /spike	Seeds /spike	Harvest index	Spike density
Heading date	++	-.5601	.0536	-.0780	-.0653	.1563	.0820	-.3020	.2734	-.0109	-.2518	-.2180
	--	-.6077	-.0982	-.0590	-.0638	.1057	.1319	<u>.1210</u>	-.1210	-.4258	.0101	<u>.1230</u>
Tillers/plant	++		-.0127	.0160	.2071	.0815	.2700	-.0930	.0814	-.1085	-.1731	-.0030
	--		-.1089	-.2280	.0823	.0323	.3609	-.0530	.0490	.0643	-.1481	-.0190
Plant height	++			.1260	.0840	-.1418	.1186	-.2350	.2068	.2935	-.0132	-.2150
	--			.0920	.0733	-.1421	-.0874	<u>.1020</u>	-.0783	.2155	.0377	.1100
Plant weight	++				.1851	.5716	.4416	-.0660	.0626	.2889	-.6834	-.0800
	--				<u>.6209</u>	-.2047	.2513	-.0920	.1002	.5379	-.8408	-.0420
Spike weight	++					.2851	.0593	-.2000	.1877	.0851	.1976	-.1960
	--					<u>.8624</u>	.3640	-.1230	.1492	-.4960	<u>.6375</u>	-.2050
Seed weight	++						-.0857	.3630	-.3722	.1339	.4724	.3300
	--						-.4284	.1310	-.1739	.3879	-.2859	.2070
Spike number	++							.0400	-.0053	-.2383	.2854	0
	--							<u>.4000</u>	-.4010	-.0824	.0795	.3980
Spike length	++								.9938	-.0666	-.0734	-.9760
	--								.9896	-.0387	-.0231	-.9780
spikelets/spike	++									.1226	.0645	.9730
	--									.0915	.0207	.9890
Seeds/spike	++										.3800	-.0720
	--										<u>.6728</u>	-.1380
Harvest index	++											-.0660
	--											.0430

N=81 for both lines

Correlation coefficients which are underlined are statistically different from their counterpart at $p=0.05$.

3. Multiple regression analysis

Turning to the multiple regression of seed yield on the other traits it can be seen from Table 5 that with the exception of line 6 RS++ the regression equations used explain almost all the variation in yield as evidenced by the values of the R^2 . Harvest Index, a derived

variable, did not contribute significantly to the prediction of yield in the two lines of Drira (lines designated as 7 RL) but did significantly so in the case of the Rosner lines (designated as 6 RS). The number of spikes per plant contributed significantly only in the case of the lines lacking telomeric heterochromatin while spike

Table 5. The regression of seed yield on agronomic traits in hexaploid triticale lines differing in telomeric heterochromatin

Line	Trait												R ²
	constant	Heading date	Tillers /plant	Plant height	Plant weight	Spike weight	Spike number	Spike length	Spikelets /spike	Seeds /spike	Harvest index	Spike density	
7 RL ++	153.2448	-.2033 -.0422	-.0706 -.0161	-.0188 -.0124	-.0320 -.0940	<u>.8158</u> 1.1550	-.1141 -.0507	<u>-9.3868</u> -.8250	<u>4.4534</u> .5781	<u>.0830</u> .0666	-.0708 -.0483	<u>-59.7966</u> -.3568	.9881
7 RL --	-13.2710	.0533 .0157	-. <u>1429</u> -.0567	-. <u>0799</u> -.0648	<u>.0295</u> .5053	<u>.6971</u> .9541	-. <u>2125</u> -.1027	.6821 .0789	-.3210 -.0560	-.0014 -.0013	.0819 .0552	7.2455 .0715	.9802
6 RS ++	-210.4069	.3539 .0916	.1107 .0441	-.0689 -.0552	<u>.1863</u> .5709	<u>.1615</u> .2070	-.1175 -.0547	<u>13.6146</u> 1.8963	<u>-6.9126</u> -1.5485	.1076 .0956	<u>.3701</u> .2866	<u>80.0420</u> .6550	.8882
6 RS --	-28.8191	.0857 .0172	.0207 .0064	-.0215 -.0211	-.0547 -.1666	<u>.9393</u> 1.3258	-. <u>3769</u> -.1629	1.8391 .1566	-1.3416 -.2632	<u>.0933</u> .1096	-. <u>1204</u> -.0846	16.4962 .1763	.9882

N=106, 78, 81 and 81 for lines 7 RL++, 7 RL--, 6 RS++ and 6 RS--, respectively

Coefficients underlined are statistically significant at least at $p=0.05$.

The second row of coefficients in each line represents the standard regression coefficients which are directly comparable to each other as to their importance in predicting the dependent variable.

length, number of spikelets per spike and spike density contributed in the lines possessing heterochromatin. Spike density, a derived variable, contributed to yield prediction only in the lines possessing heterochromatin.

The regression equations with all variables included in the model were statistically different from one another for each pair of lines (F values of 3.15 with 12 and 120 degrees of freedom for the Drira lines and 15.9231 with 12 and 138 degrees of freedom for the Rosner lines). This indicates that the relationship between yield and the other traits changed significantly as a result of the loss of the telomeric heterochromatin from chromosome arms 7 RL and 6 RS.

In order that the various regression coefficients could be compared directly as to their influence in predicting the dependent variable they were converted to their standard form and are also given in Table 5 on the second row of each triticale line. It can be seen from this table that the trait influencing the most seed yield was spike weight in the Drira lines. In the Rosner line possessing telomeric heterochromatin (6 RS ++) spike length contributed the most to yield prediction. The loss, however, of telomeric heterochromatin from chromosome 6 RS in Rosner brought the situation back to the usual with spike weight becoming again the predominant trait in predicting seed yield.

4. Canonical Correlation

The number of significant canonical correlations found between the two sets of variables, one dealing with plant traits and the other with seeds, yield and harvest index, differed in each pair of lines. There were three such correlations in the line 7 RL ++ but only two in its sister line (two of which are presented in Table 6). In the Rosner lines again there were three more significant canonical correlations in the line possessing telomeric heterochromatin and two in the line lacking it. It can also be seen in Table 5 that while in the 7 RL lines the line with the heterochromatin had the greater, numerically, coefficients in both canonical variates the opposite was true in the 6 RS lines.

Discussion

The plant genome is a coordinated entity which responds to internal and external stimuli during the life cycle of the organism. Any qualitative or quantitative changes in the composition of the genome may alter the way it functions and responds to the environment and have consequences in the expression of the various traits of the organism.

Constitutive telomeric heterochromatin is part of the genomic makeup of hexaploid triticale capable of undergoing excision from certain telomeres by as yet unexplained factors (Kaltsikes *et al.* 1983). This excision can have many consequences affecting cytological and agronomic traits (Kaltsikes and Bebeli 1993 b). Most of these changes have been studied using univariate statistical methods which rely on the differences of one trait at a time. We report in this study the results of the application of multivariate statistical techniques on the expression and interrelationships of traits in pairs of hexaploid triticale lines differing by well defined pieces of rye telomeric heterochromatin.

The effects of the loss of telomeric heterochromatin from chromosome arms 6 RS and 7 RL were seen as large differences between the pairs of lines in a twelve dimensional space as evidenced by the highly significant values of the statistics used in the multivariate analysis of variance (Table 2).

To examine the possible changes in the relationships between traits that are affected by their sequences in ontogenesis one has to utilize statistical methods that maintain all other variables constant and allow only those of interest to vary. Such a method is the partial correlation analysis. In both varieties changes in the correlation coefficients exceeding those expected on the basis of chance were observed. More coefficients became larger in the 6 RS - line than in the 7 RL - line while Drira had more significant changes than Rosner. These results indicate the tendency of the loss of the telomeric heterochromatin to be associated with signifi-

Table 6. Coefficients of the two sets of variables for the first two significant canonical factors in two pairs of lines of hexaploid triticale

Variable	Line	Canonical		Variate		Line	Canonical		Variate		
		1	2	1	2		1	2			
First Set											
Heading	7 RL ++	-.052	.386			6 RS ++	-.021	.298			
	7 RL --	-.278	.801			6 RS --	-.106	.093			
Tillers	7 RL ++	.003	-.423			6 RS ++	.182	.482			
	7 RL --	-.086	.707			6 RS --	-.085	.122			
Height	7 RL ++	.081	-.047			6 RS ++	.501	.607			
	7 RL --	.212	-.304			6 RS --	.852	.879			
Ear number	7 RL ++	.593	-.039			6 RS ++	.722	.390			
	7 RL --	.421	.902			6 RS --	.150	-.867			
Ear length	7 RL ++	.598	.435			6 RS ++	.223	-.514			
	7 RL --	.461	-.300			6 RS --	.120	-.461			
Spikelets	7 RL ++	-.217	.806			6 RS ++	.400	-1.242			
	7 RL --	-.011	-.276			6 RS --	-.032	.009			
Second set											
Seed weight	7 RL ++	-.565	-1.774			6 RS ++	.195	1.018			
	7 RL --	.569	1.333			6 RS --	-.035	1.576			
Seed number	7 RL ++	.166	1.050			6 RS ++	.231	-1.618			
	7 RL --	.327	-.475			6 RS --	.083	-1.507			
Plant weight	7 RL ++	1.266	.367			6 RS ++	.642	.434			
	7 RL --	.025	.194			6 RS --	.970	-.340			
Harvest index	7 RL ++	.314	.777			6 RS ++	.866	.597			
	7 RL --	.152	-1.144			6 RS --	.732	.689			
Canonical coefficient	7 RL ++	.919★★★	.550★★★			6 RS ++	.866★★★	.597★★★			
	7 RL --	.889★★★	.498★★			6 RS --	.936★★★	.661★★★			

Degrees of freedom for the coefficients of the 7 RL lines 24 for the first coefficient and 15 for the second. The corresponding values for the 6 RS lines are 18 and 10, respectively.

cant changes in the partial correlation coefficients between traits. This tendency, however, is modified by the residual genotype of the lines involved and by the chromosome on which the telomeric heterochromatin was located.

Triticale is mainly grown for seed production. Its grain yield, therefore, is of economic interest. To study the effects of the loss of telomeric heterochromatin on yield the method of multiple regression was utilized. In this method, yield is expressed as a function in which each of the other traits studied contributes according to its coefficient. The traits studied accounted for almost all the variability observed in yield in all lines but 6 RS ++. It can also be seen from Table 5 that the loss of telomeric heterochromatin from both chromosomes was associated with significant changes in the overall relationship of yield to the other traits studied.

Turning to the influence of individual traits on yield, spike traits contributed the most in each pair of lines, spike weight in Drira ++ and spike length in Rosner ++. In the lines lacking heterochromatin, spike weight was the leading trait.

It can be seen from these results that the removal of telomeric heterochromatin was accompanied by changes in the relative importance of the traits influencing the expression of yield with spike weight becoming the most important trait in determining grain yield.

The variables studied can also be grouped according to whether they are directly related to yield or not

(Table 6) and the correlations between the two sets of variables calculated. This is called canonical correlation and represents the maximum correlation between linear functions of the two sets of variables. There may be additional pairs of such functions but each one is uncorrelated with all the others already located. The loss of telomeric heterochromatin was accompanied by a decrease from three to two in the numbers of such significant canonical correlation in both varieties. In this case also the numerical changes in the canonical coefficients were different in Drira from those in Rosner.

As noted in the introduction the loss of telomeric heterochromatin from chromosome arms 6 RS and 7 RL was accompanied by many changes in the various traits both in their mean expression and in their relationships and that the two members of each set were thus differentiated one from the other in many ways. These effects of the heterochromatin were modulated by the genotype of the cultivar and the chromosome carrying the heterochromatin that was lost.

The results of this study show that the differences continue to be present when multivariate statistical methods are employed for their study. It is our opinion that the well characterized materials employed here with respect to the loss of the telomeric heterochromatin provide the means for the study of its effect. Other factors as well influence the traits studied here, each possibly having a small effect in comparison with the large effects of heterochromatin. When the background

genotype is altered extensively, in addition to changes in the presence of heterochromatin, then the effects of the two factors can be confounded and difficult to separate. This may account for the differences in opinion expressed in the literature regarding the effects of telomeric heterochromatin (Varghese and Lelley 1983, Gupta and Reddy 1991).

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