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THE INFLUENCE OF ADDITIONS OF RYE CHROMOSOMES ON PLANT DRY MATTER AND ROOT SIZE IN BREAD WHEAT

ABSTRACT

The toleration of poor soil and high efficiency of mineral nutrients use of rye has been successfully transferred to triticale, but only one rye chromosome (1RS) has been used in wheat breeding. We started studies on identification of other rye chromosomes potentially useful in improvement of wheat, with special emphasis on root characters. We analyzed dry matter, length and number of roots (seminal and adventitious roots separately), together with plant dry matter, in two sets of disomic wheat-rye addition lines (CS-'Blanco' and CS-'Imperial'). Plants were grown in hydroponic culture. In relation to the 'Chinese Spring' (CS) wheat, all the addition lines showed decrease of plant and root size parameters. The chromosomes 5R and 7R were best tolerated in wheat, but they caused a decrease of root proportion in plant. The 4R addition was the least viable one, but the root/plant ratio was higher than in wheat. The results were influenced mainly by interaction between homoeology group and cultivar of origin of rye chromosomes. The highest interactions of this kind were found in the 5R and 6R additions.

Key words: addition lines, chromosome, root system, rye, wheat

INTRODUCTION

The growing popularity of low input cultivation systems in agriculture creates demand for new wheat cultivars with improved nutrient use efficiency (Ceccarelli 1996). Marked differences have been reported among wheat cultivars in uptake as well as in utilization of mineral nutrients (Fageria and Baligar 1999, Le Gouis *et al.* 2000). The root size and structure characteristics have profound effects on plants ability to acquire and sorb nutrients in soil (Jungk 2001). They are related to the ability of roots to penetrate high density soil layers, to tolerate temperature and moisture extremes as well as toxicity and deficiencies of elements. Additionally, the ability to modify the rhizosphere pH and the nutrient uptake kinetics are also affected by root morphology (Baligar *et al.* 2001). A remarkable level of variation has been reported in the morphological traits of roots of barley, oats and wheat (Górny 1992). However, this kind of variation is little applicable in plant breeding because of difficult observation of roots *in situ* (Zobel 1986). The progress in marker assisted selection makes new prospects of controlling root characters in a breeding process, but it requires a profound knowledge on genetics of the charac-

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ters. The analysis of wheat-rye addition lines may be helpful in integration and verification of genetic maps. The existing literature on location of the root development genes is rather scarce and concerns mainly *Arabidopsis thaliana* and rice. Only a few root mutants have been isolated in cereals other than maize and rice (Hochholdinger *et al.* 2004). On the other hand, the area for studies is large, because root characters are conditioned by about 30% of plant genes, and one-third of those (10% of the total) are expected to determine only the root traits (Zobel 1986). It implies, that the genes for root system are located on all chromosomes of a plant.

In the typical Polish soil conditions rye is the cereal species with the most efficient root system (Starzycki 1976). The value of rye genome has been confirmed in triticale, the species showing a remarkable improvement, in relation to wheat, in uptake and use of mineral nutrients, particularly on poor soils (Ciepły and Oracka 2001). Therefore, rye chromosomes should be considered a valuable source of variation in root traits for wheat. The existing breeding materials of wheat support the idea, as even the substitution of a whole single chromosome arm (1BS or 1AS by 1RS) proved to be highly useful in raising yield potential (Rabinovich 1998). The wide distribution of 1RS.1BL translocation among wheat cultivars seems to be related to higher root biomass causing wide adaptation of wheat with this introgression (Ehdaie *et al.* 2003).

The wheat-rye addition lines are a convenient material for research on localization of genes determining root characters in wheat, rye and triticale and their investigation should bring information on usefulness of rye chromosomes or their fragments in wheat breeding. In this study we have determined the influence of particular rye chromosomes from two sets of wheat-rye addition lines on the size of root system.

MATERIALS AND METHODS

The experiment was performed with two sets of disomic addition lines of the hexaploid wheat cv. ‘Chinese Spring’ carrying chromosomes from rye cultivars ‘Blanco’ and ‘Imperial’. The ‘Chinese Spring’ – ‘Blanco’ set (CSB), established by Lukaszewski (1988), was complete. The available set ‘Chinese Spring’ – Imperial (CSI, established by Driscoll and Sears, 1971) was lacking the 4R chromosome addition, but its genetic material was present in two ditelosomic lines CSI 4RL and CSI 4RS. As controls, the parental wheat and rye cultivars and their amphiploids were used. The both CSB and CSI sets were received from A. J. Lukaszewski, University of California, Riverside, USA and propagated in IHAR-Radzików. The seed used in the experiment was collected from bagged spikes of plants with cytogenetically verified chromosome constitution, in order to avoid spontaneous losses of added chromosomes. The divergent plants (mainly those with better vigor) were additionally verified for carrying rye chromosomes (with the C-banding method).

Seedlings were kept in 4°C for 30 days and were planted on plastic tanks containing 40 l of the modified Hoagland no. 2 solution at reduced level of mineral elements. The medium contained the following salts: $Ca(NO_3)_2{\cdot}4H_2O$ – 475 mg × l^{-1}, KNO_3 - 305 mg × l^{-1}, $MgSO_4{\cdot}7H_2O$ – 245 mg × l^{-1}, $NH_4H_2PO_4$ – 60 mg× l^{-1},

H_2BO_3 – 1.43 mg × $l^{-1,}$ $MnCL_2{\cdot}4H_2O$ – 0.90 mg × l^{-1}, $CuSO_4{\cdot}5H_2O$ – 0.04 mg × l^{-1}, $ZnSO_4{\cdot}7H_2O$ – 0.11 mg × l^{-1}, $Na_2MoO_4{\cdot}2H_2O$ - 0.04 mg × l^{-1}, EDTA Fe-Na - 0.007 mg × l^{-1}.

The nutrient solution was renewed every 4 days and aerated for 10 minutes every hour. The experiments were carried out in a growth chamber supplied with the fluorescent lamps (MASTER TLD 58W/865, PHILIPS), at radiance 350 mmol × m^2 × s^{-1} and 16h day length. The temperatures ranged between 18°C (day) and 13°C (night). Air humidity was kept at 70%. The plants were harvested after 17, 30 and 38 days of growth, in three replicates of four plants each. It corresponded to the growth phases of seedling, beginning of shooting and advanced shooting, respectively. The following measurements were made: dry matter (105°C) of plant (PM), seminal and adventitious roots dry matter (SRM and ARM), length (according to Tennant 1975) and number of seminal and adventitious roots (SRL, ARL, SRN, ARN, respectively). The length of roots was analyzed only for the first two harvests. From the collected data, three other values characterizing root system were calculated: RM – total root dry matter (ARM + SRM), RM/PM – root dry matter to plant dry matter ratio and ARM/RM – ratio of adventitious roots dry matter to total root dry matter.

Data were processed in two ways. The first one was a single factorial analysis of variance procedure (ANOVA), including both sets of additions, separately for each of the three times of harvest. The differences were tested using the Tukey`s test. The data on figures are presented in relative values; for each of the measured traits the differences between results obtained for the additions and the results for 'Chinese Spring' were divided by relevant LSD values. Therefore, all the resulting differences higher than 1 or lower than –1 are significant. Additionally, a two factorial analysis of variance was performed for the 2nd and 3rd harvest time, in order to determine significance of interaction between chromosome homoeology group and donor rye cultivar (procedure VARCOMP for Type 1 sum of squares, SAS 9.1).

RESULTS

The statistically significant differences have been stated with the single -factorial ANOVA for all the investigated characters of both sets, together with the parental forms, in all three times of harvest (Fig. 1). The Table 1 contains means for the 'Chinese Spring' wheat and LSD values for the investigated traits. The results for the 1st harvest were frequently very divergent from those of the following two harvests. It suggested influence of differences in amount of nutrients delivered from seed at germination. Among the addition lines, the thousand kernel weight varied from 13.6 g (CSI 4R) to 46.3 (CSI 7R). Significant coefficients between the seed mass and the studied parameters were found for the main characteristics in the seedling stage, the results of the next two harvests were not influenced, with the exception of SRM for the 3rd harvest (Table 2). Thus, the descriptions below concern mainly the results of harvests 2 and 3.

The two-factorial analysis of variance, performed for the harvests 2 and 3, revealed almost no effect of donor rye cultivar on the investigated traits. The effect of homoeology group of the added chromosome was higher for the majority of the

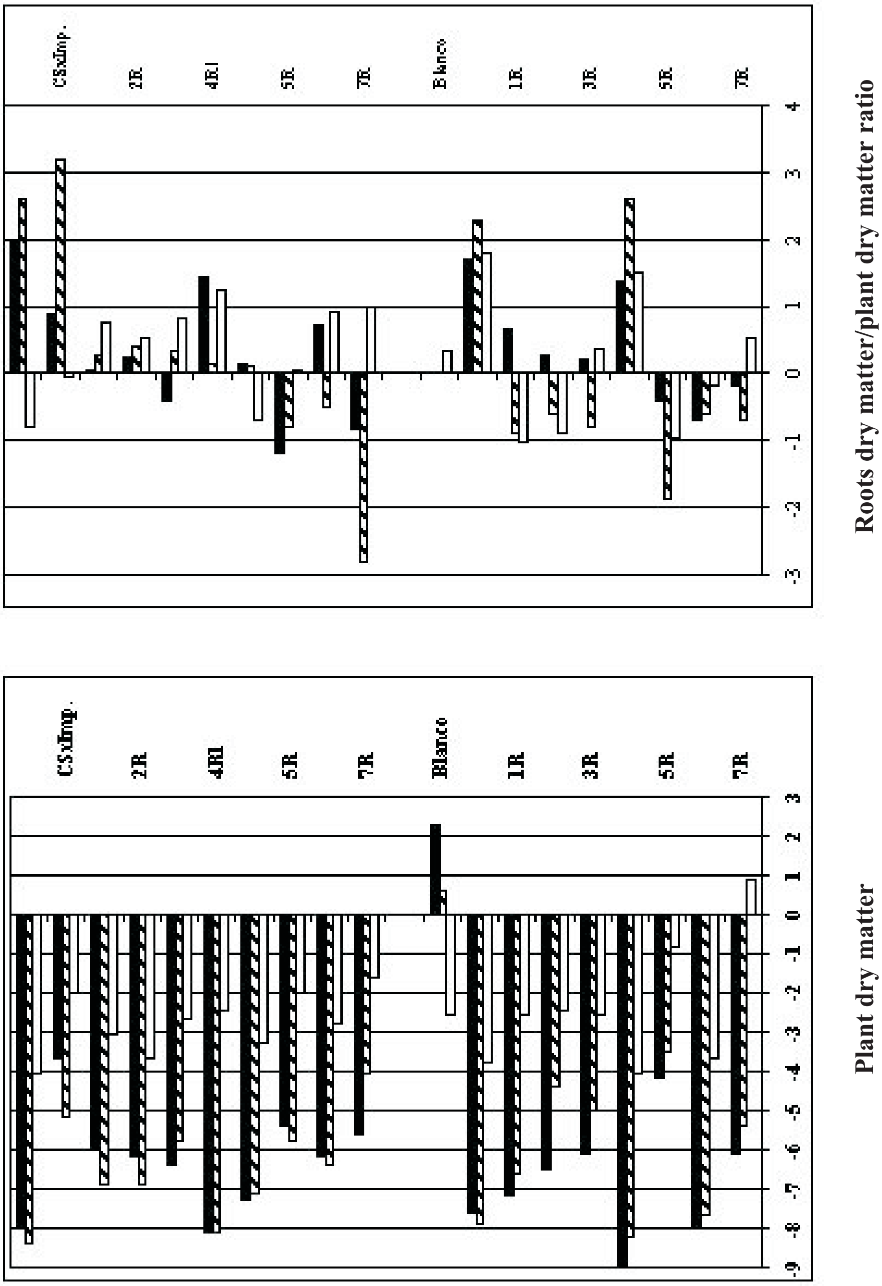
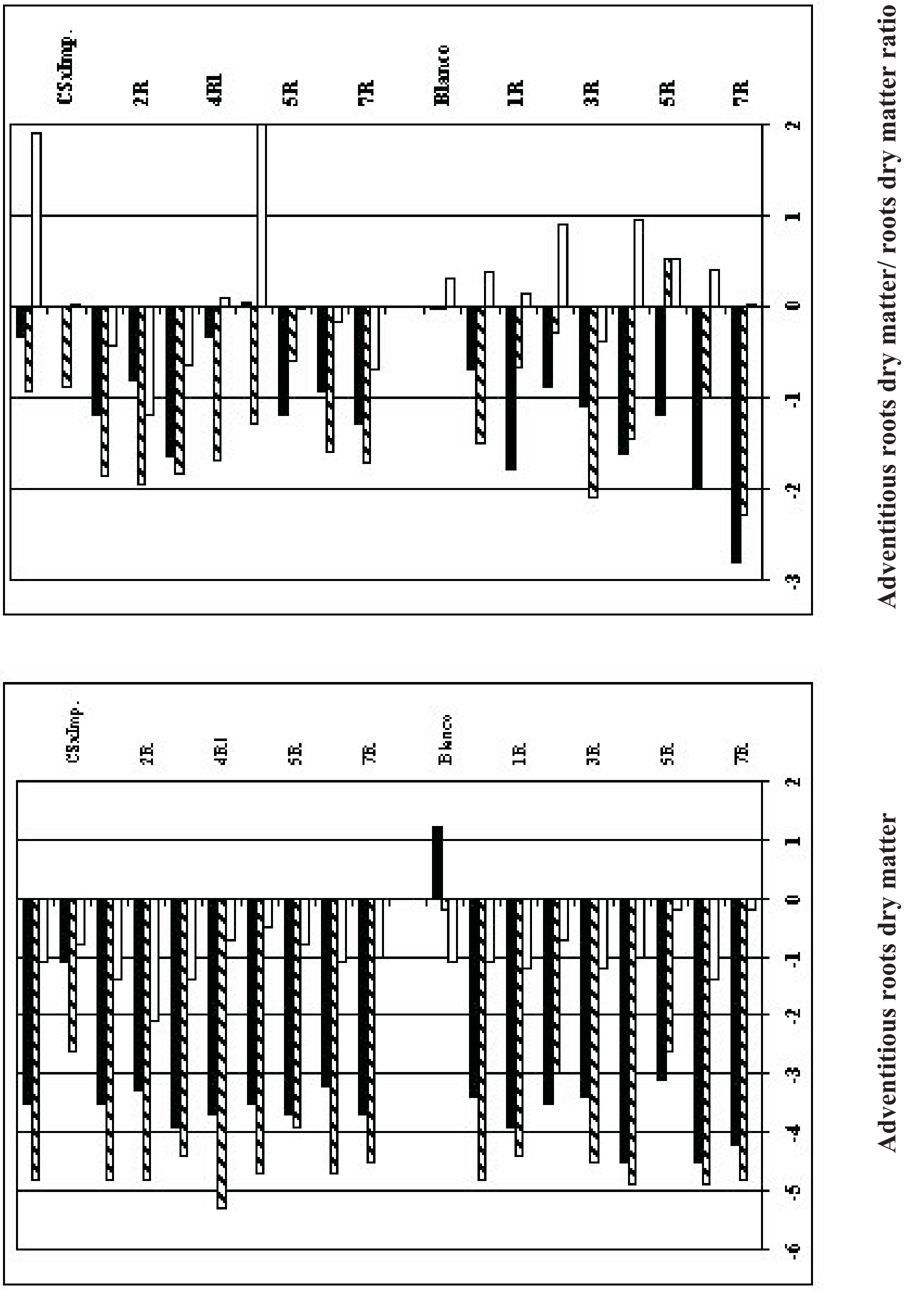


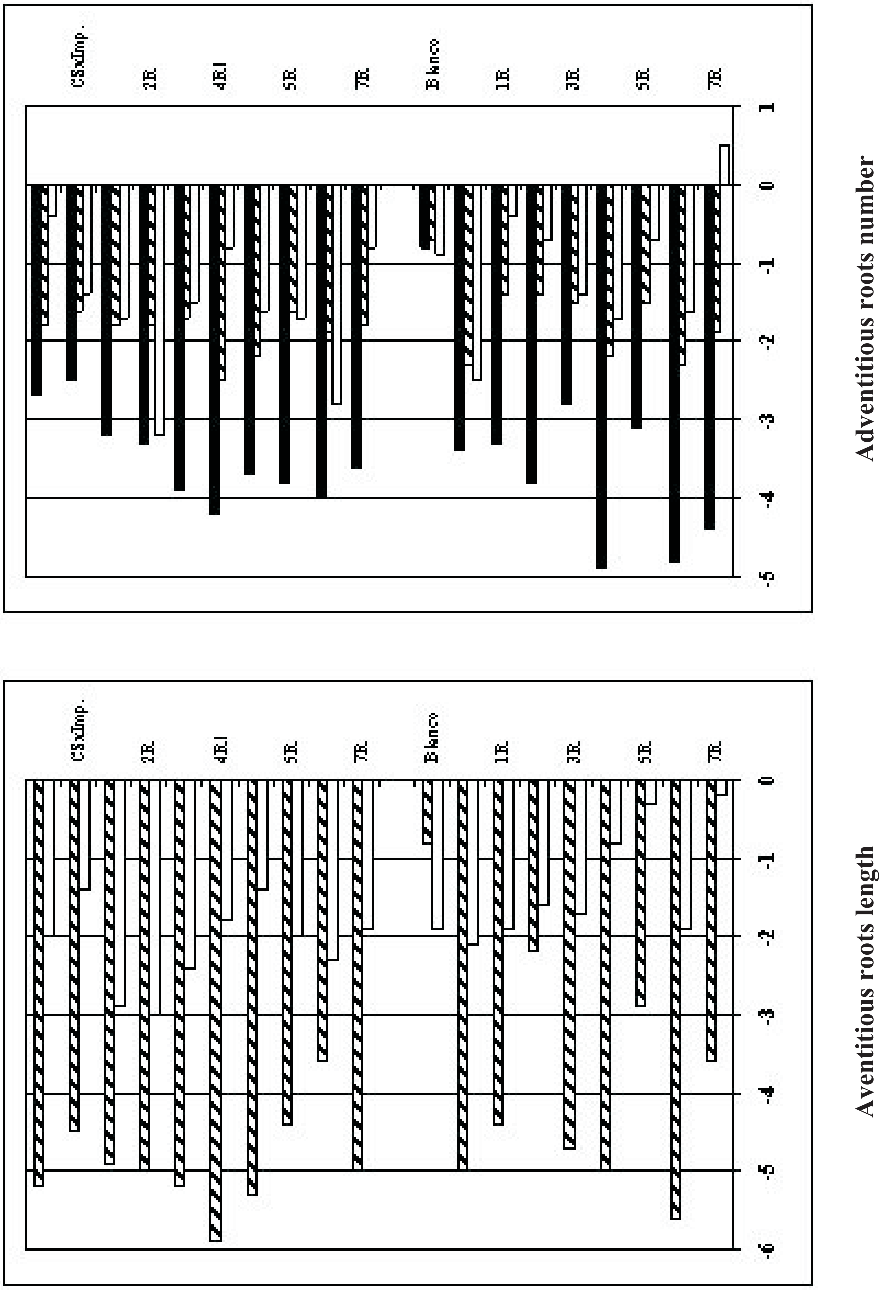
Fig.1. The influence of chromosome additions from 'Blanco' and 'Imperial' rye cultivars to the 'Chinese Spring' wheat on root system. Deviations from the wheat standard are expressed in the LSD units. Time of harvest: I – white, II – hatched, III – black



Adventitious roots dry matter/ roots dry matter ratio

Adventitious roots dry matter

Fig.1. The influence of chromosome additions from ‘Blanco’ and ‘Imperial’ rye cultivars to the ‘Chinese Spring’ wheat on root system. Deviations from the wheat standard are expressed in the LSD units. Time of harvest: I – white, II – hatched, III – black (continued)



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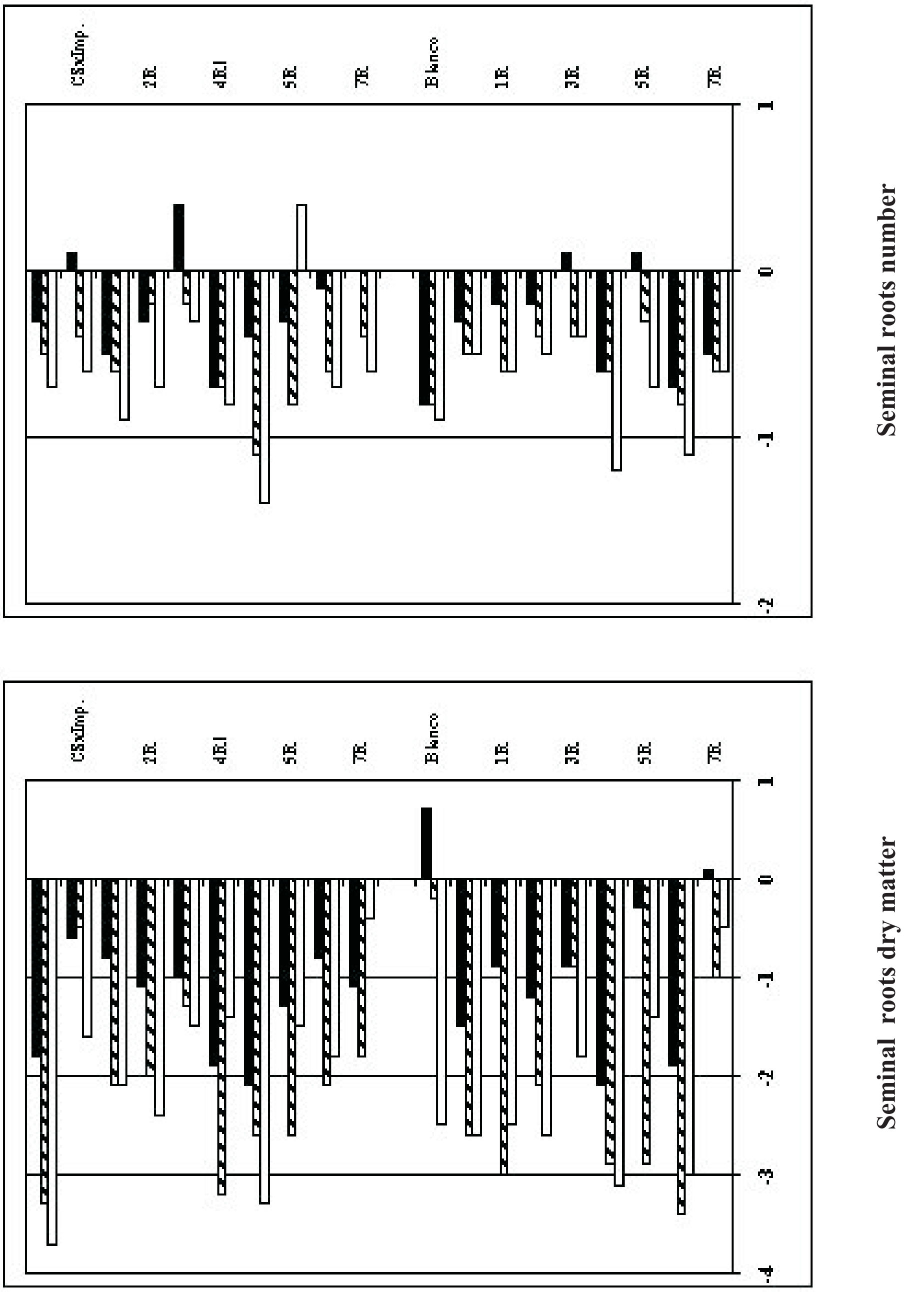

Seminal roots number

Seminal roots dry matter

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characters (0 – 56% of total variance). The dominant part of variance (up to 99% for seminal roots length) constituted interaction between chromosome and cultivar (Table 3).

Table 1

The mean values for the investigated traits of the 'Chinese Spring' wheat and the corresponding LSD-values

Traits	Times of harvest (days after planting)					
	17		30		38	
	mean	LSD	mean	LSD	mean	LSD
PM - plant dry matter [g]	0.279	0.042	1.377	0.129	2.82	0.285
RM - total roots dry matter [g]	0.082	0.013	0.338	0.035	0.613	0.115
SRM - seminal roots dry matter [g]	0.065	0.012	0.129	0.025	0.16	0.057
SRL - seminal roots length [cm]	800	116	1407	189		
SRN - seminal roots number	5.5	1.3	5.5	1.4	5.1	1.6
ARM - adventitious roots dry matter [g]	0.018	0.006	0.209	0.033	0.454	0.093
ARL - adventitious roots length [cm]	125	37	944	134		
ARN - adventitious roots number	6.4	1.4	30.3	9.4	41.8	7.5
RM/PM - ratio [%]	29.7	3.8	24.6	2.9	21.8	5.8
ARM/RM - ratio [%]	21.8	8.1	61.7	12.5	73.9	16.8

Table 2

Correlation coefficients between kernel weight and the investigated traits of the wheat-rye addition lines

Traits	Times of harvest [days after planting]		
	17	30	38
PM - plant dry matter	0.46	ns	ns
RM - total roots dry matter	0.55	ns	ns
SRM - seminal roots dry matter	0.6	ns	0.56
SRL - seminal roots length	ns	ns	
ARM - adventitious roots dry matter	ns	ns	ns
ARL - adventitious roots length	ns	ns	

Plant and root mass of 'Blanco' surpassed those of 'Chinese Spring'. The 'Imperial' rye donor and the both amphiploids showed lower dry matter. length and number of roots than the wheat acceptor of chromosomes. but the proportion of roots in a plant was significantly higher.

Generally. the addition lines had lower values of number. length and dry matter of seminal and adventitious roots as well as dry matter of the whole plant when compared to the 'Chinese Spring' wheat control.

Among the investigated characters. plant dry matter is a trait expressing plant vigor in the best way. therefore it is useful as a background for analysis of other traits of the root system. The tolerance for added rye chromosomes was dependent on time of harvest. addition homoeology group together with the rye donor cultivar. In the CSB set. the highest decrease of total plant dry matter was found for the 4R and 6R additions. The result for 5R. although significantly lower than the pure wheat record. was the least different from the wheat control. In the CSI set. the highest vigour of the 5R addition was confirmed and the 7R was almost on the same level. Both added arms of 4R exerted negative influence similar to the whole 4R of the CSB set. The highest interactions between rye cultivar and homoeology group were recorded for the 6R and 5R chromosomes: the 5R from 'Imperial' and 6R from 'Blanco' exerted more negative influence on plant mass than the 5R from 'Blanco' and 6R from 'Imperial'.

Table 3

Percentage contribution of addition set, added chromosome homology group and their interaction to total variance of the investigated traits

Variance components	Set		Chromosome		Interaction		Error	
Traits harvest	2	3	2	3	2	3	2	3
PM - plant dry matter	0	0	19	35	78	61	3	4
RM - total roots dry matter	0	0	26	0	69	94	5	6
SRM - seminal roots dry matter	0	0	56	0	39	86	5	14
SRL - seminal roots length	0		0		99		1	
SRN - seminal roots number	0	0	10	4	31	46	59	50
ARM - adventitious roots dry matter	9	0	24	0	63	95	4	5
ARL - adventitious roots length	2		0		97		1	
ARN - adventitious roots number	0	0	17	9	13	81	70	10
RM/PM - ratio	0	0	3	5	89	74	8	21
ARM/RM - ratio	13	15	38	3	45	71	4	11

The proportion of roots in plant dry matter of the wheat control was 29.7% at the first harvest and dropped gradually to 21.8% at the last one. Among the addition lines. the decrease was observed from 25.7% (CSB 1R) – 34.5% (CSI 4RL) in the seedling phase to 14.9% (CSI 5R) - 30.2% (CSB 4R) at advanced shooting. The influence of the additions on root dry matter was generally similar to that observed for the whole plant. As the RM/PM ratios show. only in the additions 4R. 5R and 7R the root mass decrease was not parallel to that of total plant. In the CSB 4R and CSI 4RL lines the root mass decrease was lower than in whole plant. The negative effect of the additions on roots was more distinct than on whole plant in the 5R and 7R addition lines.

The effects of the additions on seminal roots dry matter were most pronounced at the first harvest. The most negative and significant effects were those of the additions of 4R for both sets and 6R in the CSB set (but it could be a result of lower kernel weight). The 3R. 7R and 5R additions caused the lowest decrease of seminal roots dry matter. and this prevalence was extended to the following harvests' results.

The differences observed for length of seminal roots were almost identical to those for the dry matter (data not presented in the Fig. 1). In the number of seminal roots. significant differences from 'Chinese Spring' were met only in the groups 4R and 6R at the early growth phases. Occasionally. the results for the 3R and 5R additions were even higher than for the wheat control. Particularly the 3R chromosome increased the number of seminal roots in both sets (up to 110% of the wheat check in the shooting phase for CSI).

For the ‘Chinese Spring’ wheat. the proportion of adventitious roots in total dry mass of roots changed from 21.8% in the first harvest time to 73.9% in the third one. The rye additions showed the increases from 12.1(CSI 2R)- 38.1% (CSI 4RS) in seedling to 27.4% (CSB 7R) – 74.7% (CSI 4RS) in shooting. The lowest negative influence on length of adventitious roots was recorded in 2R. 5R and 7R of the CSB set. and 6R and 5R of the CSI set. The lowest results were those for CSB 6R. CSB 4R and CSI 4RL. The lowest number of adventitious roots was observed in the 4R and 6R additions. The differences were most distinct at the last harvest. especially in the CSB set. where they were statistically significant. The 3R. 5R and 1R of CSB additions were the least divergent from the control. in the CSI set the differences between various additions were not significant.

DISCUSSION

The influence of addition of the whole alien genome on plant vigor may be roughly assessed in the CSB and CSI octo-alloploids as the 61% and 36% decrease of plant dry matter. respectively. in relation to the ‘Chinese Spring’ wheat control. Decrease of root dry matter was 62% for the CSB alloploid and only 14% for the CSI alloploid (at the end of the experiment). In the CSI. the root system was distinctly less susceptible to addition of the rye genome than shoots. This shows the importance of varietal differences of the rye genome donors. The performance of donors *per se* was not parallel to that of their alloploids. However. the results for rye may not be reliable. because the ‘Blanco’ and ‘Imperial’ were represented in the experiment by progenies of small groups of individuals derived from the cultivars populations and the inbreeding depression level was beyond control. The distinct superiority of the ‘Blanco’ rye over the ‘Imperial’ one in plant and root dry matter may be related to a lower number of inbreeding events during maintenance of the ‘Blanco’ set. which was established more recently.

For a single added pair. only 1/7 of the whole rye genome effect could be ascribed to intergeneric incompatibility of non-coadapted genes. but the differences were much higher. The pairs of rye chromosomes added to hexaploid wheat caused a 30-90% decrease of plant or root dry matter. Therefore. the majority of vigor decrease could be attributed rather to the disturbed gene ratio effects. related to aneuploidy. than to the intergeneric incompatibility.

The magnitude of effects exerted by the added chromosomes on size of plants. roots and their fractions was differentiated among the addition lines. depending on homoeology group as well as cultivar-specific genes carried by the added chromosomes. The extreme effects were noted on the same chromosomes in both sets. The 5R-s were best tolerated and the 4R-s. were most detrimental. The highest interaction effects. related to the varietal background of rye chromosomes. were recorded for the 6R and 5R additions in their plant dry matter. Other rye cultivar specific differences were stated in seminal roots mass of the groups 6R. 7R and 5R. in adventitious roots length of 2R. 6R. 7R and 5R. and adventitious roots number in 3R.

According to the earlier results of Lahsaiezadeh *et al.* (1983). the 5R chromosome from the CSI addition set caused also the lowest decrease of yield and was followed by the chromosomes 7R and 1R. In their drought stress experiment the yield of 5R addition line was even higher than the yield of the 'Chinese Spring' wheat control. The cited authors' results for the 4R addition confirm also our results. Only the results for the 2R line are divergent. It was the lowest yielding line in the cited publication. but average or a little above it in our comparisons of plant and root dry matter. The CSI 2R results are more in agreement with those of Shakir and Waines (1993). announcing high productivity of this line under drought conditions.

The number of seminal roots in the addition lines was not significantly different from that of 'Chinese Spring'. The number of adventitious roots was growing depending on an addition and it was the main component of the above mentioned differences stated for the whole root system. The differences observed in dry matter and length of seminal and adventitious roots were generally parallel to those found for the whole plants and roots.

The chromosomes 5R and 7R are known as carriers of genes controlling tolerance to some micronutrient deficiencies: Zn. Mn and Fe (for 7R) and Cu (for 5R) (Cakmak *et al.* 1997. Schlegel *et al.* 1993. 1997. Graham *et al.* 1987). therefore engineering of these chromosomes seems to be much important for nutrient-effective wheat. Recent work of Mohammadi *et al.* (2003) revealed also location of major genes controlling yield and drought tolerance on the chromosomes 7R. 3R and 5R of the same CSI set of addition lines. The positive effect of the 3R chromosome was evident also in studies of Anioł (2004) on aluminum toxicity tolerance. In our studies. the influence of 3R on plant and root size was not as distinct as it could be expected. However. noticeable effects were recorded on dry matter. length and number of seminal roots. The 3R addition of 'Blanco' was also the least different from the wheat control in adventitious roots number.

CONCLUSIONS

Rye chromosomes of the 5th and 7th groups of homoeology may serve as the most promising sources of genes influencing plant vigor in wheat. Their influence on volume of root system is less pronounced. but it does not exclude important positive effects on root efficiency. as the results of other authors suggest. The 3R is also worth of attention as a potential source of abiotic stress tolerance. particularly in early growth stages. The cultivar of origin of a rye chromosome is much important and the 5R from 'Blanco' or 6R from 'Imperial' are distinctly superior over the same chromosomes from the other cultivar. The high significance of chromosome – cultivar interaction. found in this relatively small material of two sets of addition lines. suggests that a much greater volume of useful variation remains undiscovered on chromosomes of rye populations.

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THE INFLUENCE OF D(R) SUBSTITUTIONS ON PLANT DRY MATTER AND ROOT SIZE IN HEXAPLOID TRITICALE

ABSTRACT

Two sets of disomic substitution lines, derived from the cultivars ‘Presto’ and ‘Rhino’ of triticale, with rye chromosome pairs replaced by their wheat D-genome homoeologues, were tested in hydroponic culture. The size of root system (dry matter, length, number of seminal and adventitious roots) was investigated together with total plant dry matter. The results were influenced mainly by the growth stage and interaction between homoeology group of exchanged chromosomes and varietal background. In relation to the controls (unchanged cultivars), only the ‘Rhino’ 2D(2R) showed a significant increase of plant dry matter. No significant negative effect on plant mass was stated for the 3D(3R) in ‘Presto’ and the both 1D(1R) substitutions. Tolerance of the 4D(4R), and 5D(5R) disomic substitutions was poor; 7D(7R) was absent as not able to survive. The majority of changes noticed for the root system parameters were parallel to the changes in plant dry matter. Besides, some effects specific to root system were found in adult plants. Relationships are discussed between the obtained results and the earlier ones on disomic rye additions to hexaploid wheat.

Key words chromosome substitution, root system, rye, triticale, wheat

INTRODUCTION

Considering the importance of rye root characters in determination of this crop usefulness in low-input agriculture we performed studies on co-operation of particular rye chromosomes with genomes of wheat, in respect of possible effects on plant mass as well as on root mass, length and number. In the earlier experiment the influences have been described of whole rye chromosome disomic additions in wheat (Oracka and Łapiński, 2005). A significant differentiation was stated among the addition lines in the magnitude of effects exerted by chromosomes of different homoeology groups interacting with donor cultivars (‘Blanco’ or ‘Imperial’) of rye chromosomes. It applied to dry matter of plants and roots as well as number and size of seminal and adventitious roots. The chromosomes 5R and 7R were best tolerated in wheat and the effect of 4R was most detrimental. The 3R chromosome seemed interesting as a possible source of genes controlling number and mass of seminal roots.

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The D(R) chromosome substitution lines of hexaplod triticale make a unique opportunity of verification of the above statements on different genetic background. In the wheat addition lines, it is impossible to separate incompatibility effects of foreign rye genes and aneuploidy effects of supernumerary chromosomes. In a substitution line of triticale, the effects may be attributed to introduction of a foreign D-genome wheat chromosome as well as to removal of the corresponding rye chromosome. Only a complex investigation of both addition and substitution lines gives opportunity to notice genic effects, significant for genetic mapping and breeding applications. The results for substitution are expected to be „reversed" when compared to those of the corresponding addition lines, i.e. the rye chromosomes best tolerated in wheat should be the most lacking for vigor when substituted in triticale by the wheat homoeologous chromosomes.

In this study, we investigated effects of two sets of D(R) substitution lines carrying single chromosome pairs of the bread wheat D-genome replacing their corresponding rye homoeologues.

MATERIAL AND METHODS

The analyzed sets of substitution lines of hexaplod triticales 'Rhino' and 'Presto' were received from their author, A.J. Lukaszewski, University of California, Riverside, USA (Lukaszewski, 1990). The 'Rhino' set consisted of the substitutions 1D(1R), 2D(2R), 3D(3R), 4D(4R), 4D''(7R'), 5D(5R), 6D(6R); the 4D pair (designed as 4D'') was able to substitute only for single 4R or 7R, (4R' and 7R' mean monosomics). In the 'Presto' set the substitutions 1D(1R), 2D(2R), 3D(3R), 4D(4R), 5D(5R), and 6D(6R) were present. The 7D(7R) disomic substitutions were absent as unobtainable. The lines were propagated from bagged spikes in Radzików.

Seed germination, planting and growth conditions were the same as described in the previous publication on the addition lines of wheat (Oracka and Łapiński, 2005). The whole plants were harvested after 14, 29 and 41 days of growth. It corresponded to the growth phases of a) seedling at beginning of tillering, b) beginning of shooting and c) advanced shooting, respectively. Plants were separated into roots (seminal and adventitious) and shoots. The following measurements were made: dry matter (105°C) of plants (PM), fresh matter, dry matter, number and length (assessed according to Tennant, 1975) of seminal and adventitious roots (SFM, SDM, SN, SL, AFM, ADM, AN, and AL, respectively). From the collected data, five other values were calculated for root system: RM – total root dry matter (ADM + SDM), RM/PM – root dry matter to plant dry matter ratio and ADM/RM – ratio of adventitious roots dry matter to total roots dry matter, seminal root radius (SR) and adventitious root radius (AR). The SR and AR parameters were calculated from root fresh matter (FM) and its length (L) according to the formula (Ningping and Barber, 1985): R=(FM/3.14*L)1/2 .

$$R \quad \frac{FM}{3.14 \quad L} \quad 0.5$$

The experiment was designed as three replicates of four plants for each time of harvest. Data were processed in two ways. The first one was a single-factorial analysis of variance (ANOVA), together for both sets of substitutions, separately for each of the three times of harvest. The differences were tested using the Tukey`s test.

Additionally, a two-factorial analysis of variance was performed for the 2nd and 3rd harvest time, in order to determine contribution of the homoeology group of exchanged chromosomes, triticale cultivar, and their interaction to the total variance (procedure VARCOMP for Type 1 sum of squares, SAS 9.1).

RESULTS

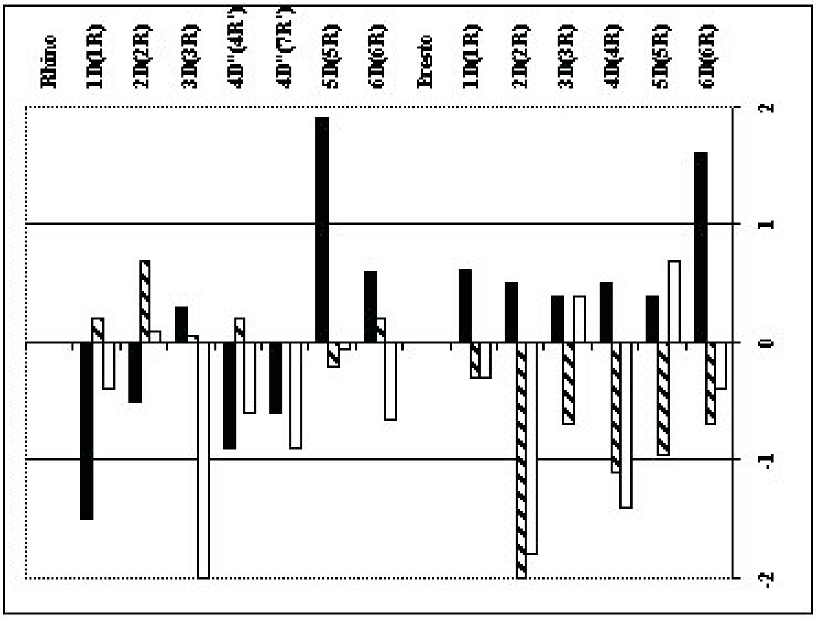
Thousand kernel mass (TKM) was examined in the investigated material, in order to avoid consideration of possible differences related to variable nutrition of seedlings in early growth phases. The TKM was 38.2 g in the complete ‘Rhino’ and 59.1 g in the complete ‘Presto’. Among the substitution lines the TKM varied between 27.5 g (‘Rhino’ 1D(1R)) and 53.9 g (‘Presto’ 4D(4R)). None of the simple correlation coefficients calculated between the TKW and all mass, length and number parameters proved to be significant at the =0.05 probability level for all times of harvest.

Table 1

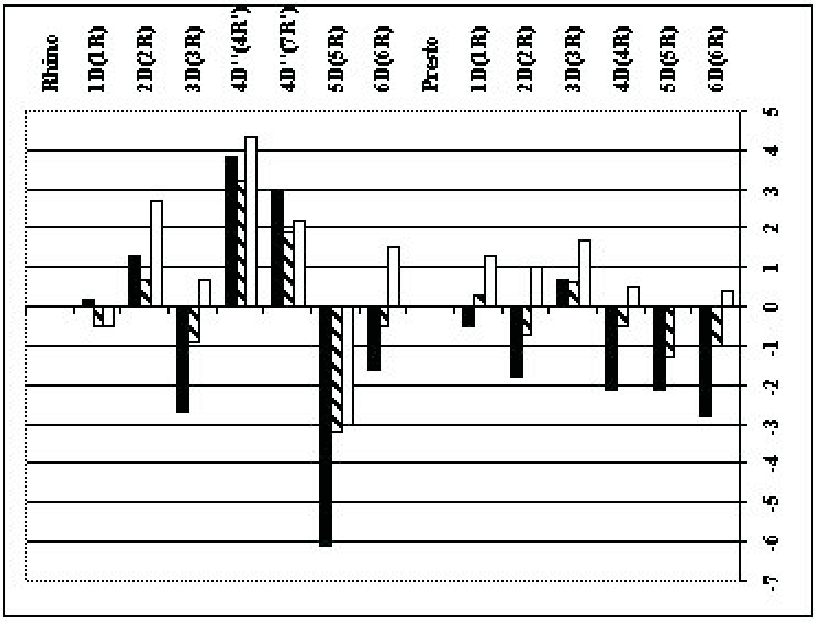
The means for the investigated traits of ‘Presto’ and ‘Rhino’ and the corresponding LSD values for their substitution lines

Traits	Time of harvest (days after planting)								
	14			29			41		
	mean		LSD	mean		LSD	mean		LSD
	'Presto'	'Rhino'		'Presto'	'Rhino'		'Presto'	'Rhino'	
PM - plant dry matter [g]	0.0753	0.105	0.016	0.49	0.703	0.143	1.581	1.986	0.24
RM - total roots dry matter [g]	0.0204	0.027	0.005	0.137	0.149	0.042	0.298	0.376	0.067
SDM - seminal roots dry matter [g]	0.015	0.023	0.004	0.077	0.065	0.031	0.16	0.1	0.05
SL - seminal roots length [m]	1.48	1.78	0.40	15.09	10.11	3.22			
SR - seminal root radius [mm]	0.23	0.21	0.02	0.18	0.2	0.03			
SN - seminal roots number	4.6	5.6	0.7	5.4	5.6	1.3	5.3	5	1
ADM - advent. roots dry matter [g]	0.0054	0.004	0.002	0.06	0.084	0.031	0.138	0.276	0.047
AL - adventitious roots length [m]	0.42	0.21	0.10	7.64	5.18	1.87			
AN - adventitious roots number	3.5	3.4	0.8	11.6	11.6	1.5	19	26	6.1
AR - adventitious root radius [mm]	0.24	0.24	0.03	0.24	0.27	0.03			
RM/PM - ratio [%]	27.103	25.4	3	27.993	21.25	4.85	18.83	18.91	2.88

A highly significant differentiation of plant mass and root system size parameters has been revealed with the single-factorial analysis of variance among the investigated D(R) substitution lines. The results are presented in Fig. 1 in relative values; for each of the measured traits the differences between results obtained for a substitution line and the results for Rhino or Presto controls were divided by the relevant LSD values. Therefore, all the resulting differences higher than 1 or lower than –1 are significant. Table 1 contains means of the controls and the LSD values for the investigated traits.

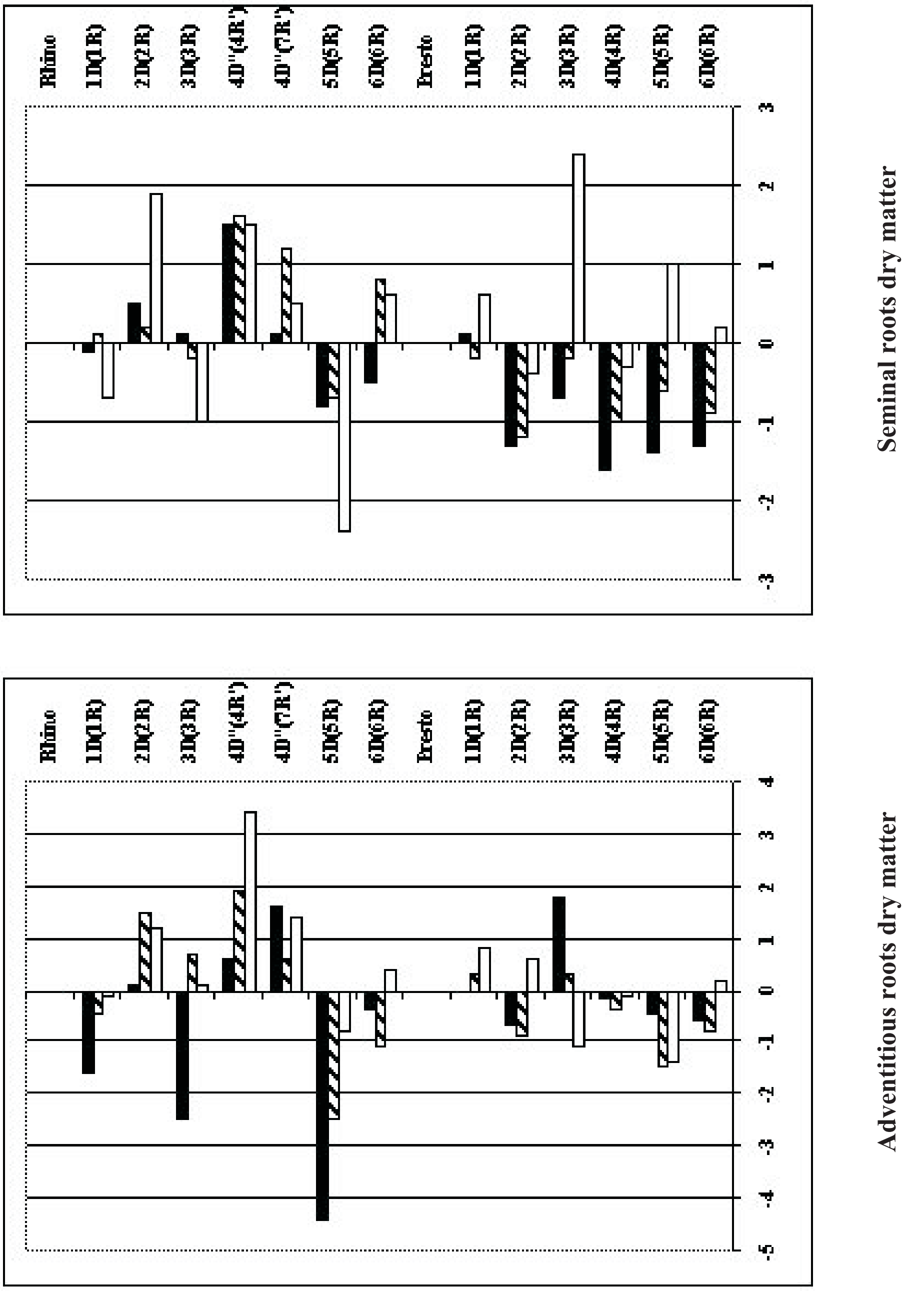


Root dry matter/plant dry matter ratio



Plant dry matter

Fig. 1. Effect of rye chromosomes substitutions by their wheat D homoeologues on plant dry matter and root characteristics in hexaploid triticales 'Presto' and 'Rhino', expressed in the LSD units.
Times of harvest: I - white, II - hatched, III – black



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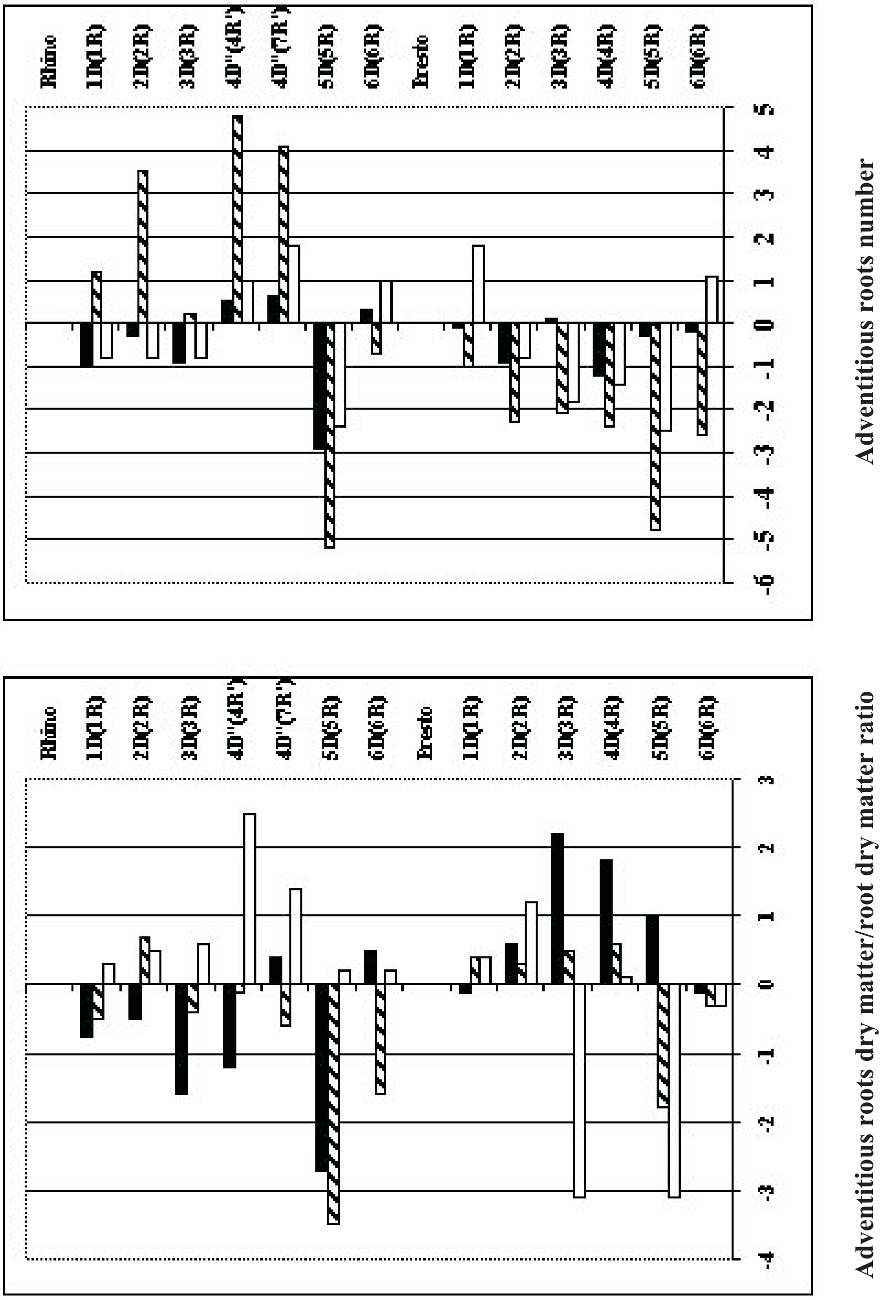
Times of harvest: I - white, II - hatched, III – black. (continued)



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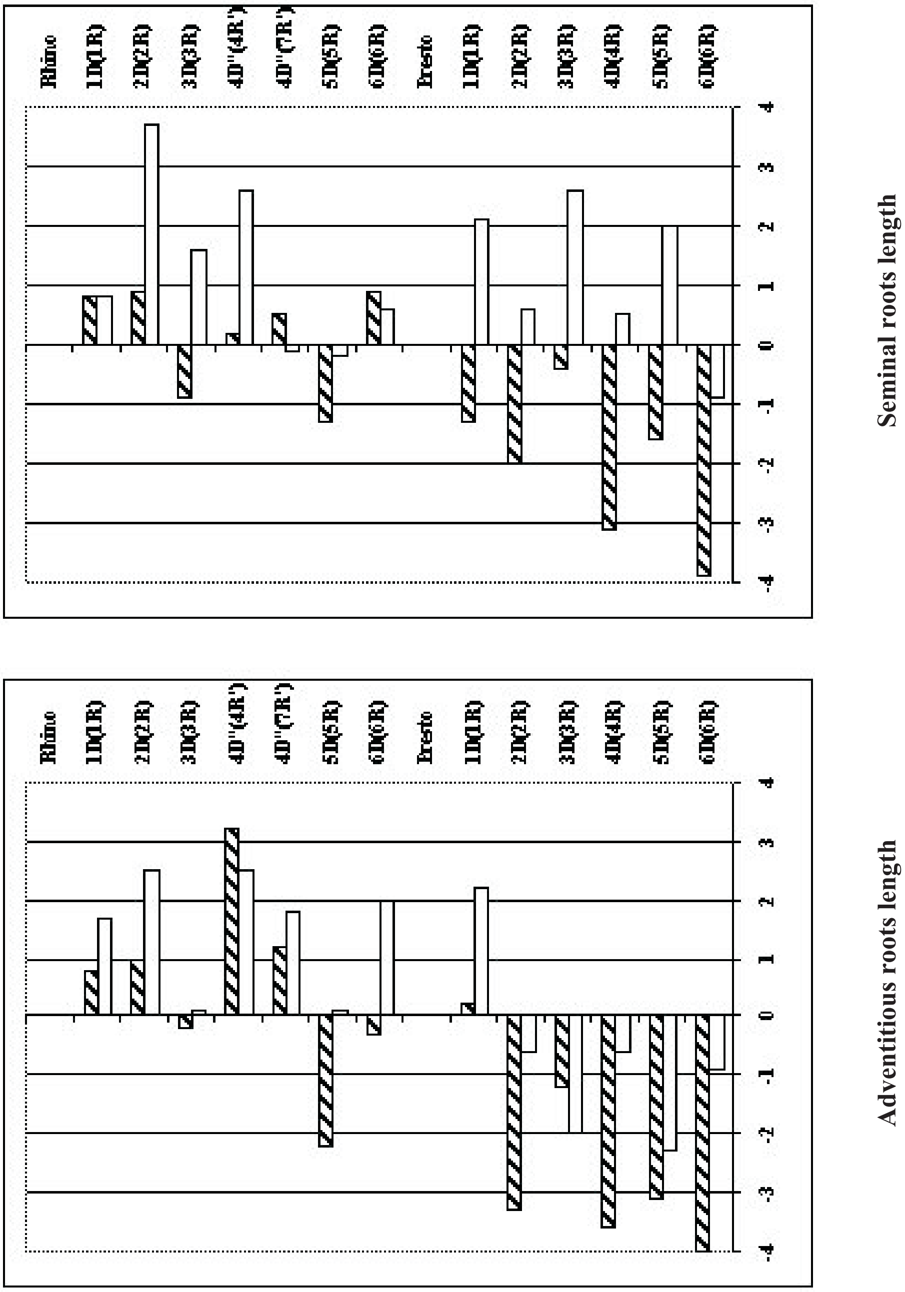

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Times of harvest: I - white, II - hatched, III – black. (continued)

Generally, the highest differentiation was noticed for harvest the 1st and the 2nd, the 3rd harvest results departed less from the controls.

The two-factorial analysis of variance, performed for harvest 2nd and 3rd, showed, that the differences between lines were shaped mainly by the interaction between homoeology group of exchanged chromosomes and varietal background (Table 2).

Table 2

Percentage contribution of homology group of exchanged chromosomes (chromosome), varietal background (set) and their interaction to total variance

Variance components	Set		Chromosome		Interaction		Error	
Traits Harvest	2	3	2	3	2	3	2	3
PM - plant dry matter	21	0	21	7	55	92	3	1
RM - total roots dry matter	0	0	1	0	95	97	4	3
SDM - seminal roots dry matter	0	5	0	3	85	91	15	1
SL - seminal roots length	0		0		98		2	
SR - seminal root radius	0		15		80		5	
SN - seminal roots number	0	0	0	2	67	29	33	69
ADM - adventitious roots dry matter	0	6	19	0	76	79	4	15
AL - adventitious roots length	0		45		53		2	
AN - adventitious roots number	27	0	44	0	29	91	0	9
AR - adventitious root radius	19		17		51		13	
RM/PM - ratio	3	0	0	15	73	73	24	12
ADM/RM - ratio	0	39	75	0	19	56	6	5

Plant dry matter (PM): At the seedling stage, increase of plant dry matter was frequent in the substitution lines, but at the following harvests it dropped down below the control level. Among the disomic substitutions, only the 2D(2R) of 'Rhino' significantly and stable increased plant dry matter when compared to the triticale standard with the complete rye genome (115% at the 3rd harvest). For all other disomic substitutions, with exception of the 1D(1R) ones and the 'Presto' 3D(3R), significant decreases of adult plant dry matter were recorded. The lowest result was that for 5D(5R) in 'Rhino' (27% of the control at the 3rd harvest). Both rye-monosomic-wheat-disomic substitutions in the homoeology groups 4 and 7 were highly beneficial for plant vigour (146% and 135% of controls, respectively).

The proportion of roots in total plant dry matter (RM/PM) changed in 'Rhino' from 25.5% at the 1st harvest to 18.9% at the 3rd harvest. The corresponding results for 'Presto' were 27.1% and 18.8%. Among the substitution lines, the changes ranged from 19.6% - 29.1% at the 1st harvest to 14.6% - 24.4% at the 3rd one. The majority of the substitution lines were similar to the controls. The retardation effects of substitutions on dry matter of roots were smaller than on shoots in adult plants of 'Rhino' 5D(5R) and 'Presto' 6D(6R). An opposite relationship was recorded in early growth stages of the lines 'Presto' 2D(2R) and 'Rhino' 3D(3R), and in adult plants of 'Rhino' 1D(1R).

Seminal roots dry matter (SDM) of the disomic substitution lines was generally increased at the seedling stage (to 105%-170% of the controls). The increases were significant for ‘Presto’ 3D(3R), 5D(5R) and ‘Rhino’ 2D(2R), only the mass of ‘Rhino’ 5D(5R) seminal roots was significantly below the control level. At the following stages, the substitution effects on seminal roots turned to be distinctly negative in ‘Presto’ 2D(2R), 4D(4R), 5D(5R) and 6D(6R). In ‘Rhino’, all disomic substitution effects were insignificant. The monosomic-disomic substitution 4D”(4R’) of ‘Rhino’ showed a stable positive effect at all times of harvest.

The seminal roots length (SL) differences were more distinct when compared to those of SDM. The increase at the seedling stage ranged between 106% - 183% of the controls, the differences were significant for ‘Presto’ 1D(1R), 3D(3R), 5D(5R) and ‘Rhino’ 2D(2R), 3D(3R). At the second harvest, the significant negative substitution effects on seminal roots were observed in almost all ‘Presto’ lines, with exception of 3D(3R). In ‘Rhino’, the differences were insignificant with exception of 5D(5R).

The seminal roots radius (SR) of seedlings of all disomic substitution lines was significantly decreased when compared to the control cultivars. The most thin seminal roots had ‘Rhino’ 5D(5R) and ‘Presto’ 1D(1R) (54% and 58% of the controls, respectively). The highest values of root thickness among the disomic substitutions were recorded for seedlings of 3D(3R) in the ‘Presto’ set (79%), and 6D(6R) in the ‘Rhino’ set (91% of the control). At the 2nd harvest, the seminal root radius had grown distinctly and reached at least the control level in all disomic substitution lines, with exception of ‘Rhino’ 2D(2R). The most striking was a seminal root thickness increase, up to 174% of the control, in ‘Presto’ 6D(6R).

Seminal roots number (SN) was the character least influenced by the substitutions; small but significant effects were recorded only for the 1st harvest and were positive in ‘Presto’ (2D(2R), 5D(5R), 6D(6R)) and negative in ‘Rhino’ 5D(5R).

The adventitious roots dry matter (ADM) of the ‘Presto’ set was generally similar to the control. The 3D(3R) substitution was significantly positive. The same substitution of the ‘Rhino’ set was among the three most negative ones (together with 1D(1R) and 5D(5R)).

The proportion of adventitious roots dry matter in the total roots dry matter (ADM/RM), was less dependent on plant vigour. This parameter changed in ‘Rhino’ from 14.8% in seedlings, through 56.4% at the 2nd harvest to 73.3% at shooting. The corresponding values for ‘Presto’ were much different: 26.6%, 43.9% and 46.2%. In the ‘Presto’ set of substitutions, the ADM/RM indices were frequently higher than in the control and they were frequently growing at subsequent harvests; significant increases were found in the 3D(3R), 4D(4R) and 5D(5R). For the ‘Rhino’ set oppositely, an increasing negative influence on ADM/RM was recorded for all the lines, except for 6D(6R) and 4D”(7R’).

Adventitious roots length (AL) was highly variable and not necessarily parallel to their dry matter. In the ‘Presto’ set, the substitutions’ effects at the seedling stage were predominantly negative (from 45% to 86% of the control) except for the 1D(1R) line (150%). At the next harvest, the frequency and magnitude of the negative effects generally rose (extremes: 31% in 5D(5R), 87% in 6D(6R)), significant decreases were recorded for the 2D(2R), 4D(4R) and 5D(5R). In the ‘Rhino’ disomics set the effects were positive (from 4% in 5D(5R) to 219% in 2D(2R) on seedlings and from 20% in 5D(5R) to 137% in 2D(2R) at the 2nd harvest). The effects of ‘Rhino’ 4D”(4R’) and 4D”(7R’) disomic-monosomic substitutions on adventitious roots length were distinctly positive at both times of harvest.

Adventitious roots radius (AR) of seedlings was much thinner than in the complete triticale in all disomic substitution lines. The parameter, in relation to the controls, ranged between 27% (3D(3R)) and 62% (5D(5R)) for the ‘Presto’ set and between 29% 5D(5R)) and 78% (3D(3R)) for the ‘Rhino’ set. At the 2nd harvest, the AR in ‘Rhino’ lines grew distinctly and reached the control level. In the ‘Presto’ set, a significant decrease of root thickness was maintained in the 6D(6R) line and significant increases above the ‘Presto’ level were recorded in the lines 3D(3R) (123%) and 4D(4R) (116%).

Adventitious roots number (AN) was much differentiated, unlike the seminal roots number. The most numerous significant differences were found for the first two harvests. In the first one, the range of variation was from 43% to 143% of the controls. Negative effects were stated for the 3D(3R), 4D(4R) and 5D(5R) of the ‘Presto’ set and 5D(5R) of the ‘Rhino’ set, the positive effects were recorded for the ‘Presto’ 1D(1R), 6D(6R) and the ‘Rhino’ 4D’’(7R’). Frequency and magnitude of effects on adventitious roots number increased at the 2nd harvest (the range from 34% to 159% of the controls) and next dropped down at the at the 3rd harvest, when only the ‘Presto’ 4D(4R) and ‘Rhino’ 5D(5R) maintained significance of decreases noted at the earlier stages.

DISCUSSION

Differentiation of the studied parameters among the investigated substitution lines was caused by overlapping and interaction effects of chromosome homoeology group, varietal background and growth stage of the plant. Similarly to the results obtained on the wheat addition lines, the homoeology group – varietal background interaction was the main factor shaping differences between the lines, however more variation was dependent on chromosome homoeology group or variety of origin. Reactions of root mass to the substitutions was generally less intense, in comparison to the respective reactions of plant mass. Root length showed the highest differences with the controls among the studied parameters. Thus, the earlier opinions have been confirmed on the value of root length in characterization of plant root system (Paponov *et al*.,1999; Lawlor, 2002).

The majority of effects of the substitutions were negative, causing decrease of mass, length and number parameters, in relation to the controls with the complete rye genome. Disomic substitution is a kind of change, which breaks coadaptation of genes within a genome, therefore some decrease of growth rate and plant mass is usually observed, even at higher ploidy levels, where other unchanged complete genomes exert a buffering effect.

Among the studied lines, the ‘Rhino’ 2D(2R) substitution is worth discussing in this context as the only disomic line increasing significantly total plant mass. The root mass, length and number parameters exceeded or were close to the control. In the ‘Presto’ set, toleration of the same substitution was poor and root growth was more retarded than that of the shoot.

The 2D(2R) substitution is well known to spring triticale breeders. In the eighties, the 2D(2R) substituted triticales prevailed among the lines bred in CIMMYT, Mexico (Ortiz-Monasterio *et al.*, 1993). Photoperiod insensitivity, earliness, better grain plumpness and fertility were their main advantages, but on marginal areas they performed worse than the lines with a complete rye genome. The Rhino cultivar, coming from this gene pool, contains the complete set of rye chromosomes, but has 2D(2R) substituted lines among the ancestors (Ammar Karim, personal communication). Therefore, the observed positive effects of the 2D(2R) can not be safely attributed only to the natural properties of unchanged 2D, the influence of artificial selection for coadaptation with the background chromosomes of 'Rhino' is highly probable.

No such stipulation is necessary in the case of 'Presto' 3D(3R) substitution. It is another one which exerted no negative effect on plant and root mass, however the increase was significant only at the seedling stage. The adventitious roots growth in 'Presto' 3D(3R) was intense and the resulting ADM/RM ratio showed a particularly distinct trend of increase. In 'Rhino', the same substitution was distinctly deleterious. The influence of 3D(3R) on seminal roots was dependent on varietal background. In the 'Presto' substitution the seminal roots grew much slower than the adventitious ones, in 'Rhino' 3D(3R) the opposite relationship was stated. In this context, the 3R rye chromosome seems less interesting than after the earlier (own and foreign) studies on wheat addition lines (Oracka and Łapiński, 2005). The 'Presto' 3D(3R) substitution seems much promising for triticale breeders. A work on improvement of its coadaptation with background of other chromosomes could yield with new cultivars containing this chromosomal change.

It is not excluded, that some 1D(1R) exchanges could be also applicable in triticale breeding. If not to consider seedling root parameters, no significant decreases were stated. The RM/PM proportion was decreased in adult plants of 'Rhino' 1D(1R), but the plant mass was at the control level.

Positive effects of the D(R) substitutions on plant mass and root system size parameters were met frequently at the seedling stage of other investigated lines, with exception of 'Rhino' 5D(5R) and 'Presto' 4D(4R). Intense development of seminal roots at early growth stages makes the young plant more resistant to drought stress conditions. Longer and thinner roots, recorded in seedlings of almost all the studied substitution lines, are considered a trait facilitating uptake of nutrients in cereals (Chapin,1980; Horst *et al.*, 1996). These positive effects of the substitutions disappeared in the more advanced stages, with exception of the 'Rhino' 2D(2R). The worst and most dramatically changed parameters of seminal roots length and thickness were recorded at the 2nd harvest in the 'Presto' 6D(6R).

Among the studied substitutions, 5D(5R) and 4D(4R) seem to be the most difficult for triticale breeding applications, if not to consider the 7D(7R) ones, which were absent as not able to survive. The 5D(5R) substitution was extremely deleterious in 'Rhino', however the total root growth was less retarded than that of shoots. The negative influence was particularly intense on the adventitious roots, as shows the lowest ADM/RM ratio.

In the 'Presto' 4D(4R) substitution, the mass, length and number parameters were also significantly lower than in the control, but the ADM/RM proportion was significantly higher. The results for 5D(5R) and 7D(7R) fit well to earlier results on plant and root size for hexaploid wheat disomic addition lines. In an addition set, genic content effect of a donor chromosome overlaps with an effect of increased dosage of chromosomes in a homoeology group within a polyploid. An ideal substitution set is free of the dosage influences, but a result is shaped by differences in genic content of both the replaced and replacing chromosomes. Joint analysis of addition and substitution sets gives more chances to extract the genic effects, which are potentially useful in breeding. However, the situation is far from the ideal, because of additional effects of interaction with variety or species background or structural differences of chromosomes participating in a substitution. The 5R and 7R additions were best tolerated in wheat background, which suggests that these chromosomes carried genes causing stable positive effects. The same way of explanation does not work for the 4D(4R) disomic substitutions, because the 4R disomic addition in wheat was the least tolerable. The lack of the disomic substitution in the 'Rhino' set and low vigour in the 'Presto' set could suggest rather good toleration of the 4R disomic addition, which was not the case. The dilemma of poor toleration of 4R addition together with poor toleration of disomic 4D(4R) substitution may be related to the large 4R/7R intragenomic translocation, which produces an additional effect of disturbed dosage of some genes. On the other hand, the other partner of the same reciprocal translocation – rye 7R, showed a predictable relationship between the addition and the 7D(7R) substitution.

The genetic diversity of donor and acceptor stocks must significantly restrict precision of comparison between the effects of substitutions and those of additions within the same groups of homoeology; only the value of 5R and 7R could be mutually confirmed. More precise conclusions could be drawn only when the wheat addition and triticale substitution stocks are produced from the same genotypes of wheat and rye.

Improvement of large disomic alien introgressions (like the substitutions of whole chromosomes or their arms) is possible with application of additional chromosome engineering. Usefulness of the 1RS.1BL translocation, widely distributed in hexaploid wheat, has been improved recently through induced precise intergenomic recombination of small chromosome fragments carrying troublesome rye genes, which decreased baking properties of flour. At the same time, the transgressive effect of the main body of the alien chromosome arm has been maintained (Lukaszewski, 2000). The method is applicable to those chromosome pairs, which maintained homoeology, presence of translocations hampers chromosome conjugation and severely restricts chances for success.

Large translocations on the substituted chromosomes bring a burden of lacking genes or disturbed gene ratios in the genome. The R-genome of rye is deeply reconstructed through at least six intragenomic interchromosomal exchanges (Devos *et al.* 1993), while the D-genome of bread wheat has maintained conservative gene order. Only the 1R chromosome has maintained full synteny with its common chromosomal ancestor. Other rye chomosomes participating in the substitutions are not syntenic and the 4R and 7R are those most restructured; the reciprocal translocation between these chromosomes is the largest one in the rye genome (it may explain why the 7R chromosome could be replaced by a pair of 4D ones in the 4D''(7R') substitution line.) Controlled restoration of the ancestral gene order in rye chromosomes other than 1R is a challenge for cytogeneticists. It may be easy for the chromosomes 3R and 5R, carrying single transocations, but difficult for 7R resulting from three chromosomal interchanges.

The results for both 4D''(4R') and 4D''(7R') disomic-monosomic substitutions indicated a high level of heterotic effects between the related chromosomes, which could not take part in a complete disomic substitution. The disomic substitutions of 4R or 7R were lacking some necessary rye genes and presence of additional single homoeologous rye chromosomes was sufficient for compensation. The heterotic effect of homoeologous chromosomes was high enough to overcome also the negative effect of trisomy. The difference of one compensing chromosme proved to be very important and made the disomic-monosomic substituted karyotypes incomparable in context of analysis of the remained euploid disomic substitutions.

CONCLUSIONS

The comparison of effects of the same substitutions in the two investigated sets revealed highly significant differences related to varietal origin of the studied lines. These interaction differences were observed mainly in three groups of homoeology (2, 3 and 6). Thus, it may be expected, that much more of such important variation could be discovered in triticale after production of new sets of wheat-rye substitution lines on different genetic backgrounds (A similar conclusion was possible also in relation to various sets of wheat-rye addition lines, investigated earlier by the authors).

The 5R and 7R rye chromosomes revealed their high relevance for triticale in the substitution lines, they were also the best tolerated in wheat disomic addition lines, therefore they seem to be the most interesting candidates for further chromosome engineering.

High heterotic effects were found in the monosomic-disomic substitution lines between the homoeologous chromosomes 4D and 4R, and between 4D and 7R.

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