Theor Appl Genet (1985) 69:443–446

Role of D-genome chromosomes in photosynthesis expression in wheats

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Received June 20, 1984; Accepted August 24, 1984
Communicated by R. Riley

Summary. The role of D-genome chromosomes in the expression of net photosynthesis in wheats was analysed with the nullitetrasomic and ditelosomic lines of the bread wheat cultivar 'Chinese Spring'. The two arms of chromosome 3 D and the short arm of chromosome 6 D control major mechanisms of photosynthesis. The effect of chromosome 6 D can be thoroughly compensated by that of its homoeologues of genomes A or B, contrary to what can be observed for chromosome 3 D. Chromosome 7 D is responsible for the low photosynthesis of flag leaves developed under high irradiances in genotypes possessing the D-genome, as the likely result of ontogeny or of a loss in adaptability to irradiance.

Key words: *Triticum* – D-genome – Photosynthesis – Flag leaves – Irradiation

Introduction

The flag leaf plays a major role in determining the grain yield of wheats (Thorne 1965; Lupton 1968; Planchon 1976). Marked differences can be observed for the rate of net photosynthesis per unit leaf area: the highest values have been reported for primitive or wild diploid wheats (Evans and Dunstone 1970; Khan and Tsunoda 1970; Dunstone et al. 1973; Planchon 1974). In the course of evolution in wheats, the decrease in the net photosynthesis rate per unit leaf area paralleled the increase in leaf size, in relation to the ploidy level (Evans and Dunstone 1970; Planchon and Fesquet 1982). These latter two authors could show the negative specific effect of the D-genome on net photosynthesis expression, which is particularly significant for genotypes with small leaves. The differences are fully exteriorised at the flowering stage for flag leaves developed under high irradiances (Dunstone et al. 1973). They are attenuated during the seed filling stage (Austin 1982) and are not expressed in the leaves of young plants developed under low irradiances (Gaudilliere 1979).

The aim of the investigations reported here was to assess the role of the various chromosomes of the D-genome in photosynthesis expression, particularly at the flowering stage, in flag leaves developed under high irradiances.

Materials and methods

Plant culture

The investigations were carried out using two kinds of aneuploids of the bread wheat spring cultivar 'Chinese Spring' developed by Sears, where the D-genome chromosomes are found in the nullitetrasomic and ditelosomic types. The nullitetrasomics were eventually selected: the modifications in the D-genome chromosomes involve either the double occurrence of a pair of D chromosomes, which is compensated for by the absence of the homoeologous A or B pair, or the absence of a pair of D chromosomes, compensated for by the double occurrence of the homoeologous A or B pair. For the seven pairs of D chromosomes, there are, theoretically, 14 D-nullisomics which can be A- or B-tetrasomics, and 14 D-tetrasomics which can be A- or B-nullisomics. Actually, only 23 combinations, out of 28 theoretically, are available. The absence or the double occurrence of a pair of D-genome chromosomes should therefore allow the role of the various chromosomes in the expression of the characters considered to be assessed through the decrease or the exteriorisation observed.

D-genome ditelosomics have a pair of telocentric chromosomes which possess either one long or one short arm. DL ditelosomics have the long arms for the pair considered, whereas DS ditelosomics display short arms. The use of

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ditelosomics should therefore allow to determine which arm bears the genes responsible for the character considered. Only 11 D ditelosomics, out of 14 possibilities, were actually available. These aneuploids were supplied by Professor Sears, then multiplied and analysed cytologically by Y. Cauderon (Coudret and Cauderon 1984).

The plants were grown in pots containing a sand-soil-peat mixture under unlimited water supply conditions. The amounts of nitrogen applied were relatively low (equivalent to 50 kg N_2/ha). The first series of measures was carried out, at the four-leaf stage, on the third leaf of plants grown under controlled conditions (temperatures: day 22 °C, night 18 °C; irradiance: 40 W · m² (PAR), using a 400 W Philips HPLR lamp). The second series of measurements was made on the flag leaves of plants grown under natural conditions. The flag leaf, during its growth from the end of May to the beginning of June, was submitted to high irradiances (viz. an average of 300 W · m^{-2} (PAR) at noon). The measurements were performed on the flag leaf blade of the various genotypes at the stage corresponding to the maximum net photosynthetic rate, between ear emergence and flowering. Six replicates were grown separately for each genotype. However, so as to limit the number of determinations, only four plants per genotype were analysed, with the exception of the aneuploids which appeared to differ markedly from the 'Chinese Spring' control.

Gas exchange

Photosynthesis measurements were carried out with a device including a CO_2 analyser, an assimilation chamber, and an air conditioning system. The CO_2 concentration in the airstream was measured by infra-red gas analysis (Schlumberger Analyzer Type ANIR 12). The various measurements were performed in an assimilation chamber at 22 °C. The CO_2 concentration in the airstream was 320 ppm and the relative humidity 75%. The light intensity during the measurements was 150 W · m² (PAR) and the flow of air through the chamber was in the range 48–70 dm^{-3} h^{-1}, in relation to the size of the leaf. Leaf areas were assessed by a planimetric method.

Results

The data obtained for D ditelosomics and nullitetrasomics are listed in Tables 1 and 2, respectively. The relationship between net photosynthesis and flag leaf area (Planchon and Fesquet 1982; Austin 1982) is shown by the regression straight lines in Figs. 1 and 2. Such a relationship could not be established for the third leaf.

The analysis of the data obtained for the ditelosomics clearly shows the marked effect of chromosomes 3 D and 6 D on the rate of net photosynthesis. The long arm of chromosome 3 D (lacking in ditelosomics 3 DS) and the short arm of chromosome 6 D (lacking in ditelosomics 6 DL) are involved in the expression of this trait (Table 1). The absence of these chromosome arms brings about a marked drop in net photosynthesis, as could be observed on young plants under low irradiances and at the flowering stage on flag leaves developed under high irradiances (Fig. 1). In the case of young plants developed under low irradiances, the

Table 1. Net photosynthesis (P_N) and leaf area (S) of the D-genome ditelosomics

	1			2		
	P_N		S	P_N		S
	$\bar{x}$	$s_{\bar{x}}$		$\bar{x}$	$s_{\bar{x}}$	
'Chinese Spring'	430	12	0.200	514	10	0.190
1 DL	430	11	0.174	471	9	0.188
2 DL	472	10	0.122	552	12	0.176
2 DS	390	11	0.161	597	12	0.136
3 DL	300	13	0.180	347	10	0.259
3 DS	317	12	0.172	372	11	0.204
4 DL	433	10	0.200	590	12	0.144
4 DS	403	9	0.155	475	9	0.218
5 DL	403	12	0.222	389	10	0.252
6 DL	230	11	0.205	241	12	0.261
6 DS	410	9	0.210	466	11	0.227
7 DS	417	10	0.213	437	10	0.229

(1) The measurements were carried out at the four-leaf stage on the third leaf of plants developed under controlled conditions including low irradiances (40 W · m^{-2} PAR)

(2) The measurements were carried out at the flowering stage on the flag leaf of plants grown under high irradiances

P_N: Net photosynthesis 10^{-9} kg m^{-2} s^{-1}; S: leaf area dm²; $\bar{x}$: mean; $s_{\bar{x}}$: standard error; 4 replicates for all genotypes

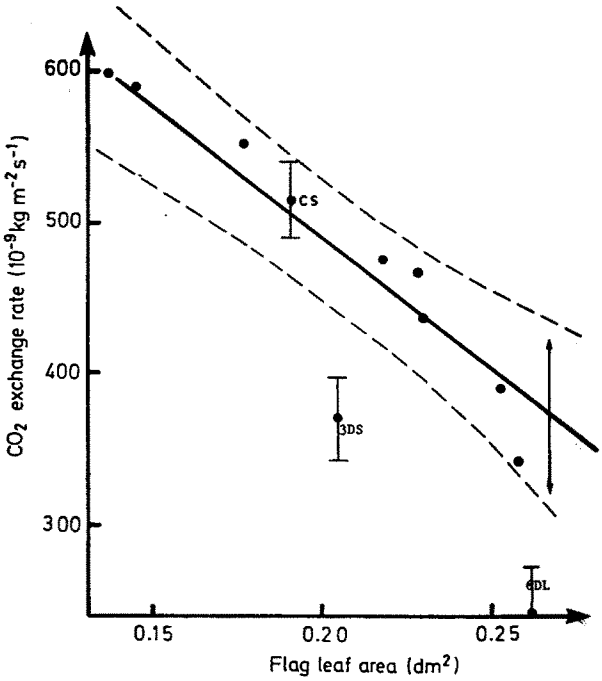


Fig. 1. Relationships between CO_2 exchange rate and flag leaf surface for the ditelosomics of 'Chinese Spring'. Regression line y = 859–1,862 x, correlation coefficient r = 0.96 for all genotypes except for *3 DS, 3 DL, 6 DL.* ⌇ Confidence interval for the regression line at the 5% threshold; ⌶ Confidence interval for the genotypes at 5% threshold

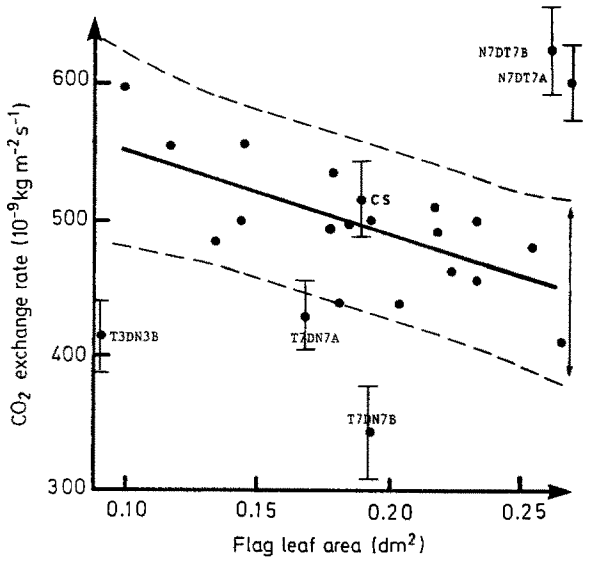
Table 2. Net photosynthesis (P_N) and leaf area (S) of the D-genome nullitetrasomics

	1			2		
	P_N		S	P_N		S
	$\bar{x}$	$s_{\bar{x}}$		$\bar{x}$	$s_{\bar{x}}$	
'Chinese Spring'	390	11	0.200	514	10	0.190
N 1D T 1B	405	10	0.172	478	12	0.254
T 1D N 1A	410	9	0.168	454	13	0.233
T 1D N 1B	410	9	0.183	437	12	0.204
N 2D T 2A	430	10	0.166	554*	9	0.146
N 2D T 2B	400	12	0.110	500	11	0.183
T 2D N 2B	470	10	0.176	462	8	0.224
N 3D T 3A	405	10	0.165	437*	11	0.182
N 3D T 3B	284	10	0.163	508	10	0.218
T 3D N 3A	390	10	0.161	483	13	0.135
T 3D N 3B	530	11	0.159	414*	9	0.093
N 4D T 4A	475	11	0.159	498	7	0.145
T 4D N 4B	368	9	0.133	492	13	0.178
N 5D T 5A	501	11	0.129	595*	8	0.101
N 5D T 5B	429	10	0.183	552	12	0.118
T 5D N 5A	410	10	0.168	498	11	0.194
T 5D N 5B	421	11	0.141	450	10	0.262
N 6D T 6A	350	10	0.117	532	12	0.178
N 6D T 6B	410	9	0.135	491	9	0.219
T 6D N 6A	340	10	0.174	499	10	0.234
N 7D T 7A	440	12	0.167	598*	10	0.269
N 7D T 7B	415	11	0.159	624*	11	0.262
T 7D N 7A	455	12	0.195	427*	9	0.169
T 7D N 7B	422	9	0.160	342*	12	0.193

(1) The measurements were carried out at the four-leaf stage on the third leaf of plants developed under controlled conditions including low irradiances (40 $W \cdot m^{-2}$ PAR)

(2) The measurements were carried out at the flowering stage on the flag leaf of plants grown under high irradiances

P_N: Net photosynthesis 10^{-9} kg m^{-2} s^{-1}; S: leaf area dm^2; $\bar{x}$: mean; $s_{\bar{x}}$: standard error; 4 replicates for all genotypes except; * (6 replicates)



short arm of chromosome 3 D also seems to be involved in the expression of photosynthesis.

The analysis of the data obtained for the nullitetrasomics shows the occurrence of a satisfactory compensation between chromosome 6 D and its homoeologues 6 A and 6 B, as well as between chromosome 3 D and its homoeologue 3 A (Table 2).

However, the absence of chromosome 3 D is poorly compensated by the occurrence of its homoeologue 3 B, as shown by the resulting decrease in net photosynthesis. On the contrary, the double occurrence of chromosome 3 D in the absence of its homoeologue 3 B improves the rate of net photosynthesis for the third leaf developed under low irradiances. This latter phenomenon appears to be reversed for the flag leaf developed under high irradiances, as shown by the low photosynthesis rate of nulli-3 B-tetra-3 D (Fig. 2). Complex relationships between homoeologues 3 D and 3 B are likely to involve interaction or even regulation phenomena between the genes borne by these two types of homoeologous chromosomes.

The specific negative effect of the D-genome on photosynthesis, which was reported previously for flag leaves developed under high irradiances (Planchon and Fesquet 1982), is to be assigned to chromosome 7 D. As a matter of fact, the double occurrence of chromosomes 7 D brings about a drop in net photosynthesis with respect to the Chinese Spring genotype, whereas the CO_2 exchange rate is markedly increased in the absence of chromosome 7 D (Table 2 and Fig. 2). This effect of chromosomes 7 D cannot be observed on young plants under low irradiances and displays a symmetry with respect to the 'Chinese Spring' cultivar in the presence of a double pair of chromosomes 7 D or in their absence, independently of the homoeologues 7 A or 7 B. This effect does appear to be of the same kind as that observed at the flowering stage between genotypes, with or without the D-genome, on the flag leaf developed under high irradiances (Planchon and Fesquet 1982).

Conclusion

Although the chromosomal location of proteic factors (Konzak 1977) and yield components (Morris 1978) on the D-genome has been widely investigated, very little data concern physiological processes.

Fig. 2. Relationships between CO_2 exchange rate and flag leaf surface for the nullitetrasomics of 'Chinese Spring'. Regression line $y = 613 - 618\,x$, correlation coefficient $r = 0.65$ for all genotypes except for the nulli *3 B* tetra *3 D* somic and the combination with chromosome *7 D*. ⌇ Confidence interval for the regression line at the 5% threshold; ⌶ Confidence interval for the genotypes at 5% threshold

Both arms of chromosome 3 D and the short arm of chromosome 6 D appear to control the major mechanisms of photosynthesis. The homoeologues of the chromosomes of the various genomes of wheats compensate the effects of chromosome 6 D in nullitetrasomics, contrary to what is observed from chromosome 3 D and its homoeologue 3 B. The interactions between these latter two homoeologues are modified during plant development and depend on the growth irradiance, although homoeologous chromosomes of group 3 are known to be very closely related for a number of other genes (Sears 1954).

Chromosome 7 D seems to be responsible for the decrease in net photosynthesis of flag leaves developed under high irradiances which could be observed in the genotypes possessing the D-genome (Planchon and Fesquet 1982). The different effects observed on flag leaves as compared to third leaves may result from ontogeny or from a loss in adaptability, under high irradiances, in genotypes possessing the D-genome. This involvement of chromosome 7 D is in agreement with the difference observed between *Triticum* species by Dunstone et al. (1972).

In the experiments reported here, the differences in spectral composition of the light in which the leaves were grown might provide an alternative explanation. However the possible involvement of a red coloration of the nullitetras 7 D–7 A and 7 D–7 B originating from the 'Chinese Spring' × 'Hope' cross can be rule out undoubtely (Sears 1984).

These data corroborate those obtained by Fortini et al. (1973) who reported an unfavourable effect of chromosome 7 D on leaf RuDP carboxylase activity.

Acknowledgements. The investigations reported here received financial support from the "Institut National de la Recherche Agronomique". The authors are grateful to Professor Sears, University of Missouri-Columbia, for seed supply and additional information on 'Chinese Spring' aneuploids, and to Dr. Y. Cauderon for the multiplication and the cytological control of the various genotypes.

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