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REGULAR ARTICLE

Dry matter partitioning, grain filling and grain yield in wheat genotypes

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ABSTRACT

In an experiment with new hexaploid wheat lines existing lines and other tetraploids was conducted in the *Rabi* (post-rainy) 2001 and 2002 dry seasons. The data on yield and yield components shows that the tetraploids had more spikes plant^{-1} but fewer seeds spike^{-1} and a lower seed weight spike^{-1}. The most important yield component the 1000-grain yield was shown by the hexaploids. The new hexaploid lines DL-1266-1 and DL-1266-2 had the maximum grain growth rate at 5 – 15 days after anthesis (DAA). Line DL-1266-2 had the highest grain growth rate 0.09 g g^{-1} day^{-1}. Photosynthetic rate values showed that the hexaploids had a higher rate than the tetraploids. Generally, at 7 and 15 DAA, the photosynthetic rate was higher compared to 25 DAA and 35 DAA. It appears that in the high yielding hexaploids (DL-1266-1 & DL-1266-2) a better photosynthetic rate and better mobilization of photosynthates during grain filling contributes to their higher yield

Key Words: *wheat; CGR; grain yield; dry matter partitioning.*

INTRODUCTION

The success of food grain production in India over the years is attributed mainly to the performance of wheat (*Triticum aestivum* Linn.) crop. Wheat is the most important dry season crop in India and occupies about 50 % of the total area under food crops accounting for more than 70 % of total grain production in dry season. The development of new plant architecture with semi-dwarf wheat cultivars replacing traditional cultivars resulted in an increase in wheat yield from 1.0 Mg ha^{-1} in early 1960's to nearly 2.9 Mg ha^{-1} in late 1990's. This was a remarkable achievement, which led to the green revolution in India (Khush, 1999). To keep pace with the increasing population, it is estimated that India will need 109 million t of wheat by 2020 (Mishra 2006). To achieve this production has to increase to 4.0 Mg ha^{-1} from the present 2.9 Mg ha^{-1}. Efforts are being made to achieve this and the Indian Agricultural

Research Institute (IARI) initiated strategic research to develop new wheat plant types in 1994-95; these were developed by IARI by 2000. They have large spikes, more grains spike^{-1}, a higher 1000-grain weight, more biomass and increased sink size. Efficient assimilate partitioning is generally considered a factor in regulating plant productivity, but the basis of its control has not been fully exploited. Jenner (1974) affirmed that genotypic variation in grain weight of wheat results from the interaction between potential storage capacity/volume and the realization of this potential. Variation in grain filling is also the result of the interaction between assimilate availability to the grain, intermediate metabolism and the synthesizing chloroplasts (Jenner and Rathjen, 1978). In this experiment, dry matter (DM) partitioning in the plant and the efficiency of photosynthate translocation to seed during grain filling in the new wheat plant types developed at IARI and in other tetraploid wheat genotypes was examined.

MATERIALS AND METHODS

The experiment was conducted in pots at the Division of Plant Physiology, Indian Agricultural Research Institute, New Delhi during the dry seasons of 2001-02 and 2002-03. There were three hexaploids DL 1266-1, DL 1266-2 [new plant types] and PBW 343 and three tetraploids HD 4530, 8498 and PDW 233. Plants were grown in cement pots of size 30 cm x 30 cm x 50 cm containing soil with substantial farmyard manure. Standard plant protection measures and nutrient applications were undertaken to obtain optimum growth and development of the wheat genotypes.

GROWTH AND MORPHOLOGICAL CHARACTERS

At heading spikes were labeled and heading and flowering dates of individual spikes recorded. Ten to 12 labeled spikes were sampled at 7, 15, 25 and 35 days after anthesis (DAA) in each wheat line. Spikes were dried in an oven at 80 C to constant weight. They were then threshed and weighed to determine grain growth rate. To record growth analysis parameters, 5 pots were randomly selected for plant sampling at 5, 15, 25 and 35 DAA and at final harvest when spikes turned into yellow dry (55 DAA). Stem, leaves and spikes of the plants were separated and data pertaining to growth analysis were recorded. Plant height was recorded from base of the plant to the growing tip on 5 plants at different sampling dates. Average plant height was recorded in cm. Leaves, stems and spikes were separated and their dry weights determined. Leaf area was measured on a leaf area meter (LICOR 3100, USA) and expressed as cm^2 plant^{-1}. Leaf samples were dried at 80 C to constant weight and dry weights were recorded as g plant^{-1}. The dry weight data of the different plant parts, the total dry weight and leaf area were used to compute various growth parameters. Grain growth rate, absolute grain growth rate, relative growth rate of the spike and the absolute growth rate of the spike were recorded at intervals of 10 d from 5 to 35 d after anthesis and at maturity. Growth parameters and plant physiological traits were measured using formulae from various workers (Table 1, 2).

PHYSIOLOGICAL PARAMETERS

The photosynthetic rate of the flag leaf of all wheat lines was measured at 10, 20 and 30 DAA using a portable photosynthetic system, (LICOR 6200, USA). This closed system measures changes in CO_2 concentration over time. Measurements were made between 10:00 a.m. and noon. The leaf was enclosed in the assimilation chamber and net exchange of CO_2 between the flag leaf and the atmosphere was measured. The photosynthetic rate was expressed as μ mol CO_2 m^{-2} s^{-1}.

Statistical analysis: The experimental data was subjected to statistical analysis following completely randomized design as described by Panse and Sukhatme (1961). Duncan's Multiple Range Test (DMRT) was carried out using MSTAT-C (ver. 2.10) to determine significant difference among the genotypes.

Table 1. Growth indices formulae.

Equ. no.	Growth parameter	Reference
1	Grain growth rate (GRR) g g^{-1} day^{-1} = (log W1 – log W2)/(T2-T1)*	Zhu et al. (1988)
2	Absolute grain growth rate (AGGR) g day^{-1} = (W1 – W2)/(T2-T1)	Radford (1967)
3	Crop growth rate (CGR) g g^{-1} day^{-1} = (log W1 – log W2)/(T2-T1)	Zhu et al. (1988)
4	Absolute ear growth rate (AEGR) g day^{-1} = (W1 – W2)/(T2-T1)	Radford (1967)
5	Relative growth rate (RGR) g g-1 day-1 = (log W1 – log W2)/(T2-T1)	Blackman (1919)
6	Net assimilation rate (NAR) g cm-2 day-1 = [(W2-W1) (log L2 – log L1)]/(T2-T1)	Watson (1952); Radford (1967)

* W1 and W2 are dry weights of sample and L2 and L1 are the total leaf area at time T1 and T2, respectively.

Table 2. Genotypic differences in morphological characters at harvest of wheat genotypes

Genotype	Plant height cm	Tiller number N $plant^{-1}$	Spike number N $plant^{-1}$	Spike length cm
Hexaploid				
DL 1266-1	104.7 a*	4.6 c	3.8 bc	16.5 a
DL 1266-2	100.2 a	4.9 c	3.7 c	17.3 a
PBW 343	89.1 d	9.0 a	6.0 a	15.5 a
Average	98.0	6.2	4.5	16.4
Tetraploid				
PDW 233	87.0 bc	8.6 ab	5.8 a	8.3 b
HD 4530	97.2 ab	7.7 b	5.6 a	7.3 b
HI 8498	81.7 cd	7.7 b	5.0 ab	8.5 b
Average	88.6	8.0	5.5	8.1
Trial Avg.	93.3	7.1	5.0	12.3

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

RESULTS AND DISCUSSION

LEAF DRY WEIGHT

Leaf dry weight showed significant differences among genotypes and mean leaf dry weight increased from 5 to 25 DAA (Table 3). It decreased at later stages. Generally, hexaploids had significantly higher values than tetraploids at all growth stages except at 5 DAA. Among tetraploids, PDW-233 had a significantly ($P < 0.05$) lower value. At 15 and 25 DAA and at harvest, DL-1266-2 and PDW-233 had significantly higher and lower values, respectively. All the hexaploids and tetraploids did not differ significantly among themselves at 25 and 35 DAA and at final harvest.

PLANT STEM DRY WEIGHT

Data on stem dry weight showed significant differences among genotypes at all DAA after anthesis, except at 25 DAA (Table 4). Among genotypes, stem dry weight was significantly ($P < 0.05$) higher in hexaploids than tetraploids at all stages. At 5 DAA, DL-1266-2, a hexaploid had a significantly ($P < 0.05$) higher stem dry weight than all other

genotypes, irrespective of their being hexaploid or tetraploid but it was on par with DL-1266-1. Hexaploid PBW-343 and tetraploids PDW-233, HD-4530 and HI-8498 were not significantly different. There was a similar trend at 15 DAA. Line DL-1266-2 had a significantly ($P < 0.05$) higher stem dry weight (9.57 g plant^{-1}) followed by DL-1266-1 (9.31 g plant^{-1}). At 25 DAA there was no significant difference among genotypes. At 35 DAA, the hexaploid genotypes were not significantly different from each other. Similarly the tetraploids were not different. At harvest the hexaploid DL-1266-1 had a significantly ($P < 0.05$) higher stem dry weight than all other genotypes except DL-1266-2. Both were significantly ($P < 0.05$) different to all other genotypes, whether hexaploid or tetraploid. There were no significant differences among the tetraploids and these were no different from the hexaploid PBW-343.

Table 3. Leaf dry weight of hexploid and tetraploid trial entries at 5 sampling dates.

	Leaf weight per plant [g plant^{-1}]				
Genotype	5 DAA	15 DAA	25 DAA	35 DAA	Harvest
Hexaploid					
DL 1266-1	2.84 a*	3.59 b	4.23 ab	2.45 a	1.98 a
DL 1266-2	2.86 a	4.28 a	4.99 a	2.27 ab	1.99 a
PBW 343	2.62 ab	3.49 b	3.30 bc	2.12 bc	1.96 a
Average	2.77	3.79	4.17	2.28	1.98
Tetraploid					
PDW 233	2.09 a	2.31 d	2.59 c	1.81 c	1.59 b
HD 4530	2.33 bc	2.94 c	3.21 bc	1.83 c	1.68 b
HI 8498	2.22 c	2.85 c	3.06 bc	1.82 c	1.67 b
Average	2.21	2.70	2.95	1.82	1.65
Trial Avg.	2.49	3.24	3.56	2.05	1.81

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

Table 4. Stem dry weight of hexploid and tetraploid trial entries at 5 sampling dates.

	Stem dry weight per plant [g plant^{-1}]				
Genotype	5 DAA	15 DAA	25 DAA	35 DAA	Harvest
Hexaploid					
DL 1266-1	6.6 a*	9.3 a	12.2 ab	13.1 a	15.7 a
DL 1266-2	7.0 a	9.6 a	12.4 ab	13.5 a	15.5 a
PBW 343	5.8 b	8.6 b	11.9 b	13.2 a	14.2 b
Average	6.5	9.2	12.2	13.3	15.1
Tetraploid					
PDW 233	5.2 c	8.5 b	11.8 b	12.7 b	13.5 b
HD 4530	5.2 c	8.4 b	11.9 b	12.6 b	13.5 b
HI 8498	5.1 c	8.6 b	11.7 b	12.4 b	13.2 b
Average	5.2	8.5	11.8	12.5	13.4
Trial Avg.	5.8	8.8	12.0	13.1	14.3

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

SPIKE DRY WEIGHT

The data on spike dry weight showed significant ($P < 0.05$) differences among genotypes at all stages (Table 5). The data further indicate that spike dry weight increased continuously from 5 DAA until harvest in all genotypes. At 5 DAA, the hexaploid DL-1266-2 had a significantly ($P < 0.05$) higher spike dry weight than all other genotypes except the hexaploid DL-1266-1. However, there were no significant differences among any of the tetraploids and these were no different from each other and with hexaploid PBW-343. Spike dry weight was significantly higher in the hexaploids than the tetraploids at all stages until harvest. At 15 DAA, the hexaploid DL-1266-2 had a significantly ($P < 0.05$) higher spike dry weight than all other genotypes, except DL-1266-1. There were no significant differences among the tetraploid genotypes. At 25 and 35 DAA and at harvest the tetraploids were not significantly different. However, the hexaploids did differed significantly at these stages. The line DL-1266-2 had a significantly ($P < 0.05$) higher spike dry weight at all stages. At harvest DL-1266-2 had a significantly higher spike dry weight of 27.9 g plant^{-1}.

TOTAL PLANT DRY WEIGHT

The total plant dry weight was significantly different among genotypes at all stages (Table 6). Among genotypes, the hexaploids had higher total dry weights at all the stages than the tetraploids. In all genotypes total dry weight increased continuously from 5 DAA until harvest. At 5 DAA, the hexaploid DL-1266-2 had significantly ($P < 0.05$) higher total dry weight than all other genotypes both hexaploid and tetraploid except for DL-1266-1. None of the tetraploid genotypes differed significantly from each or the hexaploid PBW-343. At 15 DAA, again hexaploids DL-1266-2 followed by DL-1266-1 had significantly ($P < 0.05$) higher total dry weights than all other genotypes. At this stage the tetraploid genotypes did not differ significantly from each other. Similarly the hexaploids DL-1266-1 and PBW-343 were also no different from each other. There was a similar trend at 25 and 35 DAA. Hexaploid line DL-1266-1 and DL-1266-2 had significantly ($P < 0.05$) higher total dry weights than all other genotypes. A lower total dry weight of 24.1 g plant^{-1} was recorded in HI-8498 at 25 DAA and 28.1 g plant^{-1} in PDW-233 at 35 DAA. At harvest the hexaploids DL-1266-2 and DL-1266-1 continued to maintain high total dry weights.

RELATIVE PLANT GROWTH RATE

Mean relative growth rate (RGR) decreased continuously from 5 – 15 DAA to 25 – 35 DAA (Table 7). At 35 DAA – harvest it increased slightly all hexaploid and tetraploid genotypes of both. The relative growth rate was significantly ($P < 0.05$) higher in the tetraploids at 5 – 15, 15 – 25 and 25 – 35 DAA. It was significantly ($P < 0.05$) higher among hexaploids at 35 DAA to harvest. At 5 – 15 DAA, the tetraploids had a significantly ($P < 0.05$) higher RGR compared to the hexaploids. Among genotypes, tetraploids showed no significant differences but the hexaploids differed significantly ($P < 0.05$). The new plant types have lower RGR. At 15 – 25 DAA there were no significant differences between tetraploids and hexaploids. However, by 25 – 35 DAA genotypes differed significantly ($P < 0.05$) within groups. At this time, the hexaploid DL-1266-2 had the lowest RGR at 0.010 g g^{-1} day^{-1}. The other hexaploids were not different from the tetraploid PDW-233. From 35 DAA to harvest the hexaploids DL-1266-1 and DL-1266-2 had a significantly higher RGR than any other genotype.

NET ASSIMILATION RATE

The net assimilation rate (NAR) decreased continuously from 5 – 15 DAA to 25 – 35 DAA in all genotypes irrespective of ploidy (Table 8). Generally, the tetraploids had a higher NAR at all stages than the hexaploids. At 5 – 5 DAA, the tetraploid PDW-233 was no different from all other tetraploids or the hexaploid PBW-343. A significantly lower NAR was recorded in the hexaploids DL-1266-1 and DL-1266-2 compared with all other genotypes. At 15 – 25 DAA, the tetraploids had a significantly higher NAR than the hexaploids but were not different from each other. The hexaploid PBW-343 had a

significantly lower NAR than all other genotypes. At 25 – 35 DAA, the tetraploid HI-8498 had a significantly higher NAR than all other genotypes irrespective of ploidy. At this stage the hexaploid DL-1266-1 had a lower NAR than all other genotypes.

Table 5. Spike dry weight of hexploid and tetraploid trial entries at 5 sampling dates.

	Spike dry weight per palnt t [g plant^{-1}]				
Genotype	5 DAA	15 DAA	25 DAA	35 DAA	Harvest
Hexaploids					
DL 1266-1	7.76 a*	12.46 a	16.99 b	21.58 b	25.56 b
DL 1266-2	7.80 a	13.55 a	18.89 a	24.56 a	27.89 a
PBW 343	5.38 b	8.79 b	11.46 c	14.45 c	16.23 c
Average	6.98	11.60	15.78	20.20	23.23
Tetraploids					
PDW 233	4.35 b	6.53 c	8.65 d	11.13 d	12.45 d
HD 4530	4.27 b	6.35 c	8.51 d	10.85 d	12.01 d
HI 8498	4.23 b	6.25 c	8.22 d	10.56 d	12.08 d
Average	4.28	6.38	8.46	10.85	12.08
Trial Avg.	5.63	8.99	12.12	15.52	17.65

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

Table 6. Total plant dry weight of hexploid and tetraploid trial entries at 5 sampling dates.

	Total plant dry weight [g plant^{-1}]				
Genotype	5 DAA	15 DAA	25 DAA	35 DAA	Harvest
Hexaploid					
DL 1266-1	15.7 a*	22.1 b	29.9 b	32.9 ab	38.3 a
DL 1266-2	16.3 a	24.2 a	32.9 a	34.2 a	39.4 a
PBW 343	11.8 b	19.8 c	26.7 c	29.6 bc	32.3 b
Average	14.6	22.0	29.8	32.2	36.7
Tetraploid					
PDW 233	10.0 bc	18.3 cd	25.6 cd	28.1 c	31.2 b
HD 4530	9.9 bc	17.6 d	25.2 cd	28.4 c	32.0 b
HI 8498	9.7 c	17.3 d	24.1 d	28.8 c	31.6 b
Average	9.9	17.7	25.0	28.4	31.6
Trial Avg.	12.2	19.9	27.4	30.3	34.1

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

Table 7. Relative plant growth rate of hexaploid and tetraploid wheat genotypes.

	Relative growth rate [g g^{-1} day^{-1}]			
Genotype	5 – 15 DAA	15 – 25 DAA	25 – 35 DAA	35 - Harvest
Hexaploid				
DL 1266-1	0.034 c*	0.030 b	0.009 c	0.015 ab
DL 1266-2	0.039 c	0.031 b	0.004 d	0.014 ab
PBW 343	0.052 b	0.029 b	0.010 c	0.009 d
Average	0.042	0.030	0.008	0.013
Tetraploid				
PDW 233	0.061 a	0.034 a	0.008 c	0.011 cd
HD 4530	0.058 a	0.036 a	0.013 b	0.012 bc
HI 8498	0.059 a	0.034 a	0.016 a	0.012 bc
Average	0.059	0.035	0.012	0.012
Trial Avg.	0.050	0.032	0.010	0.012

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

Table 8. Net assimilation rates of hexaploid and tetraploid wheat genotypes.

	Net assimilation rate [mg cm^{-2} day^{-1}]		
Genotype	5 – 15 DAA	15 – 25 DAA	25 – 35 DAA
Hexaploid			
DL 1266-1	1.97 b*	2.07 b	0.88 c
DL 1266-2	2.13 b	2.02 bc	0.33 d
PBW 343	2.67 a	1.90 c	0.85 c
Average	2.26	2.00	0.69
Tetraploid			
PDW 233	3.06 a	2.31 a	0.90 c
HD 4530	2.68 a	2.29 a	1.06 b
HI 8498	2.75 a	2.11 b	1.42 a
Average	2.83	2.24	1.13
Trial Avg.	2.54	2.12	0.91

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

ABSOLUTE SPIKE GROWTH RATE

Spike absolute growth rate (AGR) data indicated significant ($P < 0.05$) differences among genotypes at all growth stages (Table 9). For all entries spike AGR decreased from 5 – 15 DAA to 25 – 35 DAA, increased at 25 – 35 DAA and then decreased s. Among hexaploids, spike AGR was maximal at 5 – 15 DAA and decreased there after and again at 25 – 35 DAA, it increased until 35 DAA to harvest. At 5 – 15 DAA, the hexaploid DL-1266-2 had a significantly ($P < 0.05$) higher AGR than all other genotypes. At this stage the lowest AGR, 0.20 g day^{-1}, was in the tetraploid HI–8498. At 15 – 25 DAA the hexaploid DL-1266-2 had a significantly higher AGR than all other genotypes. The hexaploid PBW-343 and the tetraploids PDW-233 and HD-4530 were not significantly different. At 25–35 DAA, the

hexaploids DL-1266-2 and DL-1266-1 had a significantly ($P < 0.05$) higher AGR than all other genotypes. At 35 DAA – harvest, the hexaploid DL-1266-1 had a significantly ($P < 0.05$) higher AGR. The lowest AGR of 0.12 g day^{-1} was registered in tetraploid HI-8498 and in the hexaploids it was PBW-343 (0.18 g day^{-1}). The new plant types, at all growth stages, had a significantly higher AGR than any other genotype.

RELATIVE SPIKE GROWTH RATE

spike relative growth rate (RGR) data indicated significant ($P < 0.05$) differences among genotypes at all growth stages (Table 10). Spike RGR was significantly ($P < 0.05$) higher in the hexaploids than tetraploids at all growth stages except at 25 – 35 DAA. The hexaploid new plant type DL-1266-2 had a growth rate that was higher than the other genotypes except PDW-233 and HI-8498. The RGR decreased from 5 – 15 DAA until 35 DAA – harvest in all genotypes. At 5 – 15 DAA, the hexaploids DL-1266-1 and DL-1266-2 had a higher RGR. There were no significant differences among the tetraploids. There was a significantly ($P < 0.05$) lower RGR in the tetraploid HI-8498 than in all other genotypes at this stage. At 15 – 25 DAA, all the genotypes tetraploid and hexaploid, were not significantly different. At 25 – 35 DAA genotypes DL-1266-2, PDW-233 and HI-8498 all displayed as higher RGR. At this stage the hexaploid PBW-343 had a significantly lower RGR than all other genotypes, except for HD-4530. At 35 DAA – harvest, hexaploid DL-1266-1 had a significantly ($P < 0.05$) higher RGR. The tetraploid genotypes had a low RGR and were not significantly different from each other or from the hexaploid PBW-343.

There were significant differences among genotypes in total DM accumulation and its distribution among plant parts. Generally the hexaploids accumulated more biomass and allocation of assimilate to the grain was more giving a higher grain yield.

MEAN SEED WEIGHT

The mean seed weight data showed significant ($P < 0.05$) differences among genotypes at all stages (Table 11). In all genotypes, hexaploid and tetraploid seed weight increased continuously from 5 DAA until harvest. At all stages the hexaploids had a significantly higher seed weight than the tetraploids. At 5 DAA and at all stages of growth, the hexaploids DL-1266-1 and DL-1266-2 had significantly ($P < 0.05$) higher seed weights. All other genotypes did not differ significantly among each other. At 15 DAA, genotypes DL-1266-1 and DL-1266-2 again had significantly higher seed weights over all other genotypes except HI-8498. At this stage, the lowest seed weight (11.8 mg grain^{-1}) was in the tetraploid HD-4530. At 25 DAA, and later stages, the hexaploids DL-1266-1 and DL-1266-2, which were not significantly different, had significantly higher seed weights than all other genotypes. At harvest, DL-1266-1 and DL-1266-2 had significantly higher seed weights of 60.2 mg grain^{-1} and 61.3 mg grain^{-1} than all other genotypes. All the other genotypes had much lower mean seed weights and were not significantly different from each other.

ABSOLUTE SEED GROWTH RATE

At all stages seed absolute growth rate (AGR) showed significant differences among genotypes (Table 12). In all genotypes seed AGR increased from 5 – 15 DAA to 15 – 25 DAA and then decreased until 35 DAA – harvest. Among genotypes, the mean AGR was higher in hexaploids than tetraploids at all growth stages. At 5 – 15 DAA, the hexaploids DL-1266-1 and DL-1266-2 had a significantly ($P < 0.05$) higher AGR than all other genotypes. There was no difference in AGR of among the tetraploids. There was a similar trend, at other growth stages. The hexaploid DL-1266-2 had a significantly ($P < 0.05$) higher AGR than all other genotypes. At 15–25 DAA, highest AGR was in DL-1266-1 and DL-1266-2 (mean 2.20 mg day^{-1}). At 35 DAA – harvest, DL-1266-1 and DL-1266-2 were significantly ($P < 0.05$) superior to all other genotypes, irrespective of ploidy level. Tetraploid genotypes did not differ significantly among themselves or from the hexaploid PBW-343.

Table 9. Absolute growth rate for spikes of hexaploid and tetraploid wheat genotypes.

	Absolute growth rate [g day^{-1}]			
Genotype	5 DAA	15 DAA	25 DAA	35 DAA
Hexaploid				
DL 1266-1	0.520 b*	0.450 b	0.470 b	0.400 a
DL 1266-2	0.570 a	0.530 a	0.570 a	0.330 b
PBW 343	0.340 c	0.270 c	0.300 c	0.180 c
Average	0.480	0.420	0.440	0.300
Tetraploid				
PDW 233	0.220 d	0.210 cd	0.250 cd	0.130 d
HD 4530	0.210 d	0.220 cd	0.230 d	0.120 d
HI 8498	0.200 d	0.200 d	0.230 d	0.120 d
Average	0.210	0.210	0.240	0.120
Trial Avg.	0.343	0.312	0.341	0.213

* Means within columns followed by the same letter are not significantly different at P = 0.05.

Table 10. Relative growth rate for spikes of hexaploid and tetraploid wheat genotypes.

	Relative growth rate [g g^{-1} day^{-1}]			
Genotype	5 – 15 DAA	15 – 25 DAA	25 – 35 DAA	35 - Harvest
Hexaploid				
DL 1266-1	0.054 a*	0.031 ab	0.024 bc	0.017 a
DL 1266-2	0.054 a	0.033 a	0.026 a	0.013 b
PBW 343	0.049 b	0.027 b	0.023 c	0.012 bc
Average	0.052	0.030	0.024	0.014
Tetraploid				
PDW 233	0.041 c	0.028 ab	0.025 ab	0.011 bc
HD 4530	0.040 c	0.029 ab	0.024 bc	0.010 c
HI 8498	0.039 c	0.027 b	0.025 ab	0.011 bc
Average	0.040	0.028	0.025	0.011
Trial Avg.	0.046	0.070	0.025	0.011

* Means within columns followed by the same letter are not significantly different at P = 0.05.

Table 11. Average seed weight of hexploid and tetraploid trial entries at 5 sampling dates.

	Average seed weight [mg seed^{-1}]				
Genotype	5 DAA	15 DAA	25 DAA	35 DAA	Harvest
Hexaploid					
DL 1266-1	6.3 a*	15.6 a	37.6 a	54.9 a	60.2 a
DL 1266-2	6.4 a	16.4 a	38.5 a	56.1 a	61.3 a
PBW 343	5.2 b	13.2 bc	30.6 b	45.3 b	49.6 b
Average	6.0	15.0	35.5	52.1	57.0
Tetraploid					
PDW 233	5.2 b	12.3 bc	28.7 b	40.4 b	43.7 b
HD 4530	5.1 b	11.8 c	26.1 b	36.5 b	39.5 b
HI 8498	5.3 b	14.3 ab	26.6 b	37.1 b	40.3 b
Average	5.2	12.8	27.1	38.0	41.2
Trial Avg.	5.6	13.9	31.3	45.0	49.1

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

Table 12. Absolute growth rate for seed of hexaploid and tetraploid wheat genotypes.

	Absolute growth rate [g day^{-1}]			
Genotype	5 DAA	15 DAA	25 DAA	35 DAA
Hexaploid				
DL 1266-1	0.930 a*	2.200 a	1.730 a	0.530 a
DL 1266-2	0.990 a	2.210 a	1.770 a	0.510 a
PBW 343	0.790 b	1.740 b	1.470 b	0.430 b
Average	0.900	2.050	1.660	0.490
Tetraploid				
PDW 233	0.710 bc	1.640 b	1.170 c	0.330 c
HD 4530	0.670 c	1.430 b	1.030 c	0.310 c
HI 8498	0.700 c	1.430 b	1.060 c	0.310 c
Average	0.690	1.500	1.080	0.320
Trial Avg.	0.798	1.780	1.370	0.405

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

GRAIN GROWTH RATE

In all genotypes grain growth rate (GGR) decreased continuously from 5 – 15 DAA to 35 DAA – harvest (Table 13). At all growth stages the GGR was higher in the hexaploids. At 5 – 15 DAA, there was no difference among hexaploid genotypes or with the tetraploid PDW 233. The lowest GGR was in the tetraploid HI-8498. At 15 – 25 DAA, the situation was similar with a higher GGR all of the hexaploids and the tetraploid PDW 233. There was a significantly lower RGR of 0.08 g g^{-1} day^{-1} in the tetraploid HI-8498 compared with all other genotypes. Again at 25 – 35 DAA the hexaploids had a significantly higher GGR. By 35 DAA – harvest there were no significant differences among genotypes.

GRAIN FILLING AND GROWTH

Analysis of spike growth and development among the wheat genotypes showed that the mean spike AGR increased from 5 – 15 DAA to 25 – 35 DAA. Among genotypes, the hexaploids had a higher AGR at the early stages at 5 DAA and at 15 DAA and maintained a higher rate until harvest. Hexaploids, especially the new plant types, had a higher spike AGR. This increase in rate was due to increased seed and chaff weight. When spike growth of was analyzed in terms of RGR, the spike RGR was higher in the hexaploids at 5 – 15 DAA. Thereafter, it fell in both hexaploids and tetraploids until 35 DAA – harvest. The mean RGR decreased from 5 – 15 DAA to 35 DAA – harvest. At the rapid grain growth phase (7 to 14 DAA) hexaploid spike AGR was not different from the tetraploids. This might be because of a substantial increase in hexaploid seed weight compared to the tetraploids at the end of the rapid growth phase.

The higher spike AGR at 25 – 35 DAA in tetraploids infers that they had slow initial grain fill at this stage and the spike might have filled up all its spikelets as envisaged with the increase in weight of the spike. Spike relative growth rates were higher in hexaploids than tetraploids. Thus they had faster spike growth than the tetraploids. They also had relatively higher seed growth. The absolute grain growth rate of hexaploids and tetraploids were found to be at high however, with the passage of time, the hexaploids, especially the new plant types continued to increase more rapidly than the tetraploids. The mean seed growth rate of seed (Table 13) in the genotypes was higher initially and then declined over time. Although the hexaploids (especially the new plant types) initially had a higher relative grain growth rate, they were similar to the tetraploids at 25 – 35 DAA and at 35 DAA – harvest. This infers that the hexaploids had higher grain filling rates (ear RGR of ear) and could fill all the spikelets in the spike and increase grain weight. The hexaploids with higher grain filling rates initially and at the rapid growth stage (15 DAA) and might have filled all spikelets and increased seed weights. Sayed and Gadallah (1983) reported that wheat grain yield was more closely related to the rate than the duration of grain filling. The correlations between yield and seed AGR with yield and the RGR of seed and yield were significantly ($P < 0.05$) and strongly positive. Gebeyehou et al. (1982) found that both the rate and duration of grain fill were positively associated with final grain weight. In this work the hexaploids with higher rates of spike growth also had increased chaff weight, and seed weight. The tetraploids increased seed weight more than chaff weight. Though chaff weight was higher in the hexaploids, it had a lower contribution to spike weight. This gave higher yields in the hexaploid new plant types. Darroch and Baker (1990) reported significant genotypic differences in both the rate and duration of grain fill in spring wheat.

YIELD AND YIELD COMPONENTS

The 1000-seed weight is an important yield determinant parameter and it gives an idea of grain fill and size (Tables 14 and 15). Analysis of hexaploid and tetraploid wheat with different grain sizes showed that DL-1266-2 had a higher 1000 seed weight (55.4 g) than the tetraploids, which ranged from 44 to 46 g. The yield determining attributes like seed number spike^{-1} and grain number plant^{-1} showed that because they had a higher seed weight the hexaploids had higher 1000 seed weight than the tetraploids. Despite a 3% higher seed number plant^{-1} the tetraploids had a 32% reduction in seed yield plant^{-1} (Table 16) compared with the hexaploids (DL-1266-2). In the other attributes grain spike^{-1} and 1000 seed weight they showed reductions of 9% and 12% respectively.

Complex phenomena govern plant yield. Yield is the ultimate manifestation of plant morphological, physiological, biochemical processes and growth parameters and is the result of efficient conversion of solar energy. Increased yield can be realized by adapting existing varieties to grow better in their environment or by altering the relative proportion of different plant parts to increase the economic yield (Humphries and Bond, 1969). In this

work, the hexaploids, especially the new plant types, had higher grain yields than the tetraploids.

Evans (1978) reported that wheat grain yield is determined by three components spikes unit area^{-1}, kernels spike^{-1} and kernel weight of kernels. The yield data and yield components showed that the tetraploids had more spikes plant^{-1} but fewer seeds spike^{-1} and a lower seed weight spike^{-1}. The hexaploids, particularly the new plant types had fewer tillers plant^{-1} but more seeds spike^{-1} by virtue of longer spikes and higher seed weights spike^{-1}. The 1000 seed weight was also higher in the hexaploids. The higher grain yield from the new plant types was mainly due to the more grains spike^{-1} and heavier individual grain weights. Increases in both the components might have helped by increased assimilate distribution to developing grain and less to stems giving a higher grain yield. Spiertz and Van de Haar (1978) also reported that the higher the yield components the better the grain yield and harvest index (HI).

The seed yield gram^{-1} of total DM produced was much higher in the hexaploids than in the tetraploids. Thus the hexaploids had a higher seed yield plant^{-1} by virtue of having a higher 1000 seed weight. Seed yield differed significantly between ploidy level and among genotypes. The hexaploids had a significantly higher seed yield than the tetraploids. In the hexaploids the maximum grain yield was from DL-1266-2 at 17.5 g plant^{-1}. In the tetraploids the maximum grain yield of 12.5 g plant^{-1} was from HD-4530.

Seed number spike^{-1} also varied significantly among genotypes. The genotypes DL-1266-2 and PDW-233 respectively had the highest seed number spike^{-1} in the hexaploids and tetraploids. Seed weight spike^{-1} data showed significant differences among genotypes. Genotypes DL-1266-2 DL-1266-1, PBW-343 and HI-8498 had significantly higher seed weights spike^{-1}. The lowest seed weights were recorded by HD-4530 and BW-343. The 1000 seed weight data indicated that it was highest in the hexaploids DL-1266-2 of and DL-1266-1, which were significantly superior to all other genotypes, irrespective of ploidy level. The remaining genotypes were not significantly different. Hexaploids DL-1266-1 and DL-1266-2 had significantly more chaff spike^{-1} than all other genotypes. The lowest chaff weight of 1.12 g spike-1 was from the tetraploid HD-4530.

The harvest index (HI) results showed it was higher among hexaploids than tetraploids. There was no significant difference in HI in the hexaploids. The tetraploid PDW-233 had the lowest HI (45.5).

FLAG LEAF PHOTOSYNTHETIC RATE

Flag leaf photosynthetic rate was recorded at 5, 15, 25 and 35 DAA and indicated significant ($P < 0.05$) differences among genotypes at all stages. Generally, mean values indicated that the flag leaf photosynthetic rate was higher in hexaploids than tetraploids at all stages. The hexaploid genotype DL-1266-2 had a significantly higher flag leaf photosynthetic rate than all other genotypes, hexaploid or tetraploid at 7 DAA. The tetraploid HD-4530 had a significantly ($P < 0.05$) a lower flag leaf photosynthetic rate than all other genotypes. At 15 DAA, there was no significant difference among hexaploids DL-1266-1 and DL-1266-2 and the tetraploid PDW-233. The hexaploid PBW-343 and the tetraploids PDW-233 and HI-8498 of tetraploids were not significantly different from each other. At 25 DAA, hexaploid DL-1266-1and DL-1266-2 were not significantly different from the tetraploid HD-4530 of. At this stage the maximum photosynthetic rate was in the hexaploid DL-1266-2 at (21.2 μ mol CO_2 m^{-2} s^{-1}) and the minimum 16.89 μ mol CO_2 m$_{-2}$ s$_{-1}$ was in the hexaploid PBW-343. In all genotype, irrespective of ploidy level, the photosynthetic rate decreased continuously from 7 to 35 DAA in all genotypes. At 35 DAA, there was no significant difference among hexaploids among genotypes. The lowest photosynthetic rate at 10.0 μ mol CO_2 m^{-2} s^{-1} was in the tetraploid HD-4530.

The photosynthetic rate data indicated higher values in the hexaploids than in the tetraploids. Such variability among genotypes could be attributed to structural and

anatomical differences in the mesophyll and carboxylation resistance in the species. Sharma-Natu and Ghildiyal (1993) also reported species differences in photosynthetic rate. The photosynthetic rate was higher at 7 and 15 DAA compared to 25 and 35 DAA. There was a higher demand for photosynthate at seed filling, which coincided with 7 and 15 DAA and hence the photosynthetic rate was higher at these stages. A strong dependence of flag leaf photosynthesis, in wheat, on the assimilate requirement for developing seed was reported by Birecka and Dakic-Wlodkowska (1963) and King et al. (1967).

Table 13. Relative growth rate for seed of hexaploid and tetraploid wheat genotypes.

	Relative growth rate [g g^{-1} day^{-1}]			
Genotype	5 - 15 DAA	15 - 25 DAA	25 - 35 DAA	35 - Harvest
Hexaploid				
DL 1266-1	0.091 a*	0.088 a	0.041 a	0.009 a
DL 1266-2	0.093 a	0.086 a	0.037 abc	0.009 a
PBW 343	0.092 a	0.084 ab	0.039 ab	0.009 a
Average	0.092	0.086	0.039	0.009
Tetraploid				
PDW 233	0.086 ab	0.085 a	0.034 bc	0.008 a
HD 4530	0.079 b	0.079 bc	0.033 c	0.009 a
HI 8498	0.077 b	0.077 c	0.033 c	0.008 a
Average	0.081	0.080	0.033	0.008
Trial Avg.	0.086	0.083	0.036	0.009

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

Table 14. Seed yield and yield components of hexaploid and tetraploid wheat genotypes.

Genotype	Yield g $plant^{-1}$	Seed number per spike N $spike^{-1}$	Seed weight per spike g $spike^{-1}$	1000 Seed Weight g	Chaff per spike g $spike^{-1}$	Harvest index %
Hexaploid						
DL 1266-1	16.5 ab*	70.0 ab	3.8 ab	54.3 a	2.8 a	57.0 ab
DL 1266-2	17.5 a	73.0 a	3.9 a	55.4 a	2.7 a	58.9 a
PBW 343	16.5 ab	63.0 c	2.6 bc	46.9 b	1.5 bc	50.7 abc
Average	16.8	68.7	3.5	52.2	2.4	55.5
Tetraploid						
PDW 233	11.1 c	65.0 bc	3.4 abc	45.0 b	1.4 c	45.5 c
HD 4530	12.5 abc	60.0 bc	2.0 c	45.6 b	1.1 c	49.7 bc
HI 8498	12.2 bc	63.0 b	3.3 bc	46.7 b	2.0 bc	48.6 bc
Average	12.0	62.7	2.9	45.8	1.5	47.9
Trial Avg.	14.4	65.7	3.2	49.0	1.9	51.7

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

Table 15. Seed yield and harvest index of hexaploid and tetraploid wheat genotypes.

Genotype	Seed yield	Dry matter yield	Harvest index
	g plant^{-1}		%
Hexaploid			
DL 1266-1	16.5 ab*	38.3 a	57.0 ab
DL 1266-2	17.5 ab	39.4 a	58.9 a
PBW 343	16.5 ab	32.3 b	50.7 abc
Average	16.8	36.7	55.5
Tetraploid			
PDW 233	11.1 c	31.2 b	45.5 c
HD 4530	12.5 abc	32.0 b	49.7 bc
HI 8498	12.2 bc	31.6 b	48.6 bc
Average	12.0	31.6	47.9
Trial Avg.	14.4	34.1	51.7

* Means within columns followed by the same letter are not significantly different at $P = 0.05$.

Table 16. Performance of trail entries relative to hexaploid line DL-1266-2

Genotype	Yield	Seed yield per plant	Number of seeds per spike	100-seed weight	Total dry matter yield	Harvest index
Hexaploid						
DL 1266-1	94	99	96	98	97	97
DL 1266-2	100	100	100	100	100	100
PBW 343	94	111	86	85	82	86
Average	96	103	94	94	93	94
Tetraploid						
PDW 233	70	103	86	84	79	83
HD 4530	64	104	89	81	81	77
HI 8498	71	102	82	82	80	84
Average	68	103	86	82	80	81
Trial Avg.	82	103	90	88	87	88

Among genotypes, the new hexaploid plant types had a significantly higher number of spikes and longer spikes compared to the tetraploids. During evolution and domestication of wheat, hexaploids have been found to have a lower biological yield than tetraploids (Bamakhramah et al., 1984). However, in this work the tetraploids had a lower biological yield than the hexaploids. This study investigated new hexaploids, which were bred to match the plant ideotypes developed by Donald (1968) with a single culm, a strong stem, dwarf stature and a large spike. This resulted in higher biomass production due to a heavier stem and thicker, broader leaves. Considering the hexaploids other than the two new plant types DL-1266-1 and DL-1266-2 the others hexaploids had lower total DM production, which is in agreement with the results of Bamakhramah et al. (1984).

Dobben (1962) reported that the HI of cereal cultivars tended to rise progressively with little change in biological yield. The growth, development and biomass production in plant largely depends on photosynthates produced by the leaves. The flag leaf is the principal source of photo-assimilates for grain filling (Rawson et al., 1976). The RGR represents the increase in DM unit DM^{-1} already present unit $time^{-1}$ and it was a maximum in the tetraploids at 5 – 15 DAA in this study. Plants with a higher RGR have the opportunity to acquire a larger share of limiting resources such as moisture than slower growing plants (Poorter, 1989). The RGR of genotypes in this study decreased from 5 – 15 DAA to 25 – 35 DAA. Simane et al. (1993) reported similar results.

The NAR in this study decreased with advanced growth, in all genotypes, from 5 – 15 DAA to 25 – 35 DAA. Tetraploids had a higher NAR than hexaploids. This contrast with the results of Pramod Kumar et al. (1998) who found a positive association between NAR and grain yield. In this study there was a negative correlation between the NAR at 5 – 15 DAA and yield.

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