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PARTITIONING OF ASSIMILATES DURING VEGETATIVE STAGES OF THE FOUR VARIETIES OF WHEAT

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Abstract

Four varieties of wheat viz., C591, C273, Pak-81 and Pirsabak-85 partitioned different proportions of assimilates to the different organs having different functions. Varieties C591 and C273 grew taller, reached anthesis stage earlier and partitioned more assimilates to stem and less to spike and leaves resulting in smaller spikes, while Pak-81 and Pirsabak-85 partitioned more assimilates to spikes and leaves and thus they had larger spikes than the tall varieties. Upto anthesis the 4 varieties produced about the same total biomass indicating that Pak-81 and Pirsabak-85 had lower net assimilation rate since their total green leaf areas were greater than C591 and C273.

Introduction

Shortly after emergence till seed growth initiation the roots, stem and leaves are the main sinks which compete for assimilate (Stoy, 1969). Movement of assimilates to various sinks according to their changing demands, known as partitioning, is important for developing the photosynthetic machinery for absorption of nutrients, developing yield potential in terms of sink capacity and for realizing the yield in terms of fulfilling the sink capacity. The photosynthetic machinery is important for plant growth and for realizing the potential grain size, grain number and hence it determines the yield of wheat crop. Leaf area duration during seed filling correlates with grain yield (Evans *et al.*, 1975). Partitioning to leaves increases growth because it accelerates leaf area expansion which according to Kramer (1980) affects growth more than photosynthesis per unit leaf area. Partitioning to roots is necessary since growth of the above ground plant parts depend upon root function (Murarta *et al.*, 1965). Roots and shoots interact with each other (Wardlaw, 1980). Partitioning to stem is also important to place the leaves at different height in the canopy for efficient absorption of light and carbon dioxide. Vertical separation of leaves in relation to leaf size affect the solid angle occlusion and hence the skylight pattern within a canopy. Size and vertical separation of leaves also affect gaps geometry and umbra and penumbra within the canopy (Loomis & Williams, 1969). Partitioning of assimilates is affected by factors like light, moisture availability and nutrient (Evans & Wardlaw, 1976). Partitioning also depend upon genetic make-up. Thus the distribution of dry matter within the plant depend not only on environmental conditions but on the type of species and varieties.

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In order to increase the yield, an optimum combination of physiological, morphologic and agronomic characteristics are required for balanced photosynthetic and absorption machinery and for proper storage capacity for economic end products. Too much partitioning to leaves increases leaf area beyond optimum leaf area index causes shading of the lower leaves which in turn reduces total gross photosynthesis. The present report describes the partitioning of assimilates in the above ground plant parts of wheat plant upto anthesis.

Materials and Methods

The experiment was conducted in 1991-92 at Malkandher farm of the NWFP Agricultural University, Peshawar located about 1200 km north of the Indian ocean at 34.01 oN latitude, 72.3 oE longitude and 450 m altitude. The soil of the experimental site is low in organic matter and nitrogen and alkaline in nature. Wheat varieties comprising of 2 tall viz., C591 and C273 and two dwarf viz., Pak-81 and Pirsabak-85 were planted in 1.5m by 3m plots, having five rows 5m long and 30cm apart, on 24 November, 1991, in a well prepared field using a randomized complete block design with four replications. The crop emerged on 6 December, 1991. At anthesis 5 representative tillers were harvested and separated into spikes, leaves and stems with leaf sheaths. The number of green leaves were counted. The plant components thus separated were dried in an oven at $70^{o}C$ for 48 hours and weighed to record data on spike, leaf and stem with sheath mass. Leaf and stem mass were added to calculate vegetative mass at anthesis. Weight of all the 3 plant components were compiled to calculate the total above ground mass at anthesis. Spike mass at anthesis was divided by vegetative mass at anthesis to calculate reproductive-vegetative mass ratio at anthesis.

Time when 50 -75 % of the spikes emerged in the plots were recorded for calculation of days to spike emergence. Similarly, anthesis time was recorded when anthers were visible in 50 - 75 % of the spikes for the calculation of days to anthesis. The complete loss of green colour from the glumes was used as a criterion for physiological maturity. Days to anthesis was calculated as a difference between date of emergence and of anthesis, which was considered as the vegetative period. Days to maturity was calculated as a differences between date of emergence and dates of maturity. Seed filling duration was calculated as a difference between days to maturity and days to anthesis.

At physiologic maturity, 5 representative plants were selected from each main plot and a representative tiller from each plant was used to record data on plant height, spike base height, peduncle node height and height of all the nodes. From these measurements the spike length, peduncle length and other internodes length were calculated.

The following linear model was used for the analysis of the data:

where, Y_{ij} is an observation of the ith block and jth treatment μ p is the over all mean is the effect of the ith block

t is the effect of the jth treatment

c is the random effect which is $(0,r^2)$

The variety sum of square was partitioned into the following orthogonal single degree of freedom contrasts:
Tall varieties vs short varieties.
C591 vs C273
Pak-81 vs Pirsabak-85

Results

***Days to phenological stages and seed filling duration*:** Days to various phenological stages and seed filling duration in 4 wheat varieties are given in Table 1. Statistical analysis of days to spike emergence data revealed that there are significant differences among the days to spike emergence in 4 wheat varieties. Tall wheat varieties viz., C591 and C273 took 109 and 110 days respectively for the emergence of spikes. Single degree of freedom contrast between the two tall varieties revealed that the difference between the days to ear emergence in two varieties are not significant. Dwarf wheat

Table 1. Days to various phenological stages and seed filling duration in four wheat varieties planted at the NWFP Agricultural University, Peshawar, in 1991-92

Varieties	Type	Ear emergence	Anthesis	Maturity	Seed fill duration
			Days		
C591	Tal	109	112	153	41.5
C273	Tall	110	112	153	41.2
Pak-81	Dwarf	113	114	155	40.7
Pirsabak-85	Dwarf	115	117	156	39.2

Analysis of Variance table

Source of Variation	DF	Mean Squares			
Replications	3	4.2292*	8.5625**	0.0000	8.5625**
Varieties	3	31.5625**	24.2292**	9.0000**	4.0625*
Tall vs. dwarf	1	85.5625**	60.0625**	25.0000**	7.5625*
C591 vs C273	1	1.1250	0.1250	0.0000	0.1250
Pak-81 vs Pk-85	1	8.0000**	12.5000**	2.0000**	4.5000*
Error	9	0.6736	0.8403	0.0000	0.8403
Coefficient of variation		0.73	0.81	0.00	2.2529

* Significant at the 5 % level of probability
** Significant at the 1 % level of probability

Table 2. Dry mass of the three main plant parts at anthesis stage of the four wheat varieties planted at the NWFP Agricultural University in 1991-92. Per cent mass of the three main plant parts are given in parenthesis.

Varieties	Type	Dry mass of plant components at anthesis			
		Leaves	Stem+LS	Spike	total
			Grams per tiller		
C591	Tall	463 (16.4)	1861 (65.9)	498 (17.6)	2822
C273	Tall	455 (16.7)	1820 (66.7)	453 (16.6)	2728
Pak-8	Dwarf	523 (18.4)	1723 (60.8)	590 (20.8)	836
Pirsabak-85	Dwarf	499 (17.6)	1769 (62.4)	565 (19.9)	2833

Analysis of Variance table

Source of Variation	DF	Mean squares			
Replications	3	11985.0*	75108.9	4844.9	180174.7
Varieties	3	4043.0	14470.9	15600.9**	10542.7
Tall vs. dwarf	1	10816.0	35910.3	41412.3**	13924.0
C591 vs C273	1	112.5	3362.0	4140.5	17672.0
Pak-81 vs Pk-85	1	1200.5	4140.5	1250.0	32.0
Error	9	2390.6	37934.7	2032.3	64452.4
Coefficient of variation		10.09	10.86	8.57	9.05

*Significant at the 5 % level of probability

**Significant at the 1 % level of probability

varieties viz., Pak-81 and Pirsabak-85 took 113 and 115 days respectively for emergence of ears. The difference between these two varieties was statistically significant. Statistical analysis of the tall vs dwarf varieties revealed that the differences between the days to spike emergence are significant.

Both the tall varieties reached anthesis stage 112 days after sowing. The dwarf varieties, Pak-81 and Pirsabak-85 reached anthesis stage 2 and 5 days later than the tall varieties. The single degree of freedom contrast shows that the differences between days to anthesis of the tall and dwarf varieties are significant and the difference between the days to anthesis of the two dwarf varieties is also significant. Both the tall varieties took 153 days to reach maturity stage. Cultivars Pak-81 and Pirsabak-85 took 155 and 156 days respectively to reach maturity with no significant difference. The tall varieties matured earlier than the dwarf varieties. Differences between the days to maturity in the tall and dwarf varieties are significant. Seed filling duration in C591 was longer than other varieties and that in Pirsabak-85 shorter than other varieties.

Dry mass of plant parts at anthesis and partitioning: The Dry mass of the plant parts at anthesis stage in 4 wheat varieties are given in Table 2. Leaf mass in tall varieties was less than the dwarf varieties. Pak-81 showed higher leaf mass of 523 mg/tiller, followed by Pirsabak-85 with 499/tiller ANOVA shows that the difference between leaf mass in tall varieties was not significant and the difference between leaf mass in dwarf varieties was also not significant. However, the differences between the tall and dwarf varieties was significant. Spike weight in dwarf varieties was also greater than those of tall varieties. Spike weight of Pak-81 was 591 mg/tiller followed by Pirsabak-85 which had an average spike weight of 565 mg/tiller and C273 showed the lowest spike mass of 453 mg/tiller.

Dry mass of stem + leaf sheaths in tall varieties was greater than the dwarf varieties. Due to tallness C591 had greater stem + leaf sheath mass of 1861 mg/tiller followed by C273. Cultivar Pak-81 had the lowest stem + leaf sheaths mass, which was 1723 mg/tiller. Dry weight of flag leaf and penultimate leaf of dwarf varieties was greater than the corresponding weight in tall varieties (Table 3). Tillers in Pak-81

Table 3. Dry mass of leaves, vegetative mass, reproductive-vegetative mass ratio, planted at the NWFP Agricultural University in 1991-92

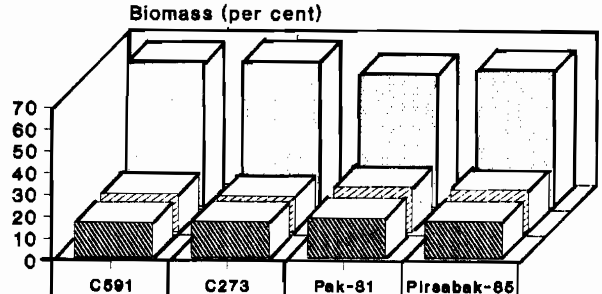
Varieties	Type	Dry mass of plant components at anthesis top 2 leaves	Vegetative mass	Rep-Veg ratio	Leaves-stem ratio
		Grams per tiller			
C591	Tall	249	2324	0.2140	0.2481
C273	Tall	290	2275	0.2014	0.2520
Pak-8	Dwarf	318	2246	0.2626	0.3037
Pirsabak-85	Dwarf	292	2267	0.2492	0.2827

Analysis of Variance table

Source of Variation	DF	Mean squares			
Replications	3	4396.8	135590.9	0.000505	0.001593
Varieties	3	3225.0	4298.9	0.003318**	0.002791*
Tall vs. dwarf	1	4989.8	7310.3	0.009274**	0.007455*
C591 vs C273	1	3384.7	4704.5	0.000319	0.000029
Pak-81 vs Pk-85	1	1300.5	882.0	0.000360	0.000887
Error	9	1113.5	48835.4	0.000248	0.000881
Coefficient of variation		11.62	9.70	6.79	10.93

* Significant at the 5 % level of probability

** Significant at the 1 % level of probability



	C591	C273	Pak-81	Pirsabak-85
Stem+leaf sheaths	66.05	66.71	60.72	62.63
Spike	17.65	16.57	20.8	19.92
Leaves	16.3	16.71	18.48	17.05

Fig.1. Dry matter partitioning up to anthesis stage in the four wheat varieties planted at the NWFP Agricultural University, Peshawar in 1991-92

partitioned 318 mg mass followed by Pirsabak-85 and C273 which partitioned 292 and 290 mg biomass to the top two leaves. Dry weight in two top leaves of C591 was 249 mg/tiller. Vegetative mass in tall varieties at anthesis was greater than the dwarf varieties, but the differences was not significant. C591 produced highest vegetative mass upto anthesis (2324 mg/tiller) followed by C273 (2275 mg/tiller). Pak-81 produced lowest vegetative mass at anthesis (2246 mg/tiller). Fig.1 shows the partitioning of assimilates in different plant organs upto anthesis stage. Tall varieties partitioned more mass to stems while the dwarf varieties partitioned more assimilates to spikes and to leaves.

***Plant height, spike length, peduncle length and internodes lengths*:** Plants of tall varieties grew taller and attained greater heights of 117 to 119 cm as compared to dwarf varieties which attained heights of 92-98 cm (Tables 4, Fig.2). Peduncles in the tall varieties were taller than those of the dwarf varieties. Similarly, the internodes below peduncle in the tall varieties were longer then their corresponding internodes in the dwarf varieties except the internodes near the ground-level which were of about the same length in all the 4 varieties. The dwarf varieties produced longer spikes than the tall varieties. Among the dwarf varieties Pirsabak-85 produced longer spikes than Pak-81.

Discussion

Thoooough the differences in time to phenological stages are not very large, the tall varieties of wheat viz., C591 and C273 reached heading, anthesis and maturity stages earlier than the dwarf varieties viz., Pak-81 and Pirsabak-85. The variation in days to different phenological stages in the 4 varieties may be due to their response to photo-periods and thermoperiods (Table 5). Due to rapid changes in photo-periods

Table 4. Plant height, spike length, and peduncle length and peduncle-plant height ratios of the four wheat varieties planted at the NWFP Agricultural University, Peshawar, in 1991-92

Varieties	Type	Plant Height	Spike length	Peduncle length	Peduncle-plant height ratio
		Centimeters			
C591	Tall	119.38	8.08	49.50	0.4147
C273	Tall	116.78	8.75	44.63	0.3814
Pak-81	Dwarf	91.78	9.18	35.00	0.3811
Pirsabak-85	Dwarf	97.90	10.13	38.13	0.3894

Analysis of Variance table

Source of Variation	DF	Mean squares			
Replications	3	68.26	1.29*	12.14	0.00001
Varieties	3	749.49**	2.94**	169.35**	0.00100
Tall vs. dwarf	1	2159.92**	6.12**	441.00**	0.00065
C591 vs C273	1	13.52	0.91	47.53	0.00221
Pak-81 vs Pk-85	1	75.03	1.80*	19.53	0.00014
Error	9	30.24	0.19	14.60	0.00061
Coefficient of variation		5.16	4.94	9.14	6.32

*Significant at the 5 % level of probability
**Significant at the 1 % level of probability

and thermoperiod and due to steep rise in diurnal temperature in the spring season of Peshawar valley as compared to other wheat growing area having greater latitudes, the differences in time to various phenological stages in the 4 varieties are small. Though the tall varieties matured 2 to 3 days earlier than the dwarf varieties, the tall varieties had 1 to 2 days longer seed filling durations than the dwarf varieties because the differences in days to maturity of the tall and varieties was less than the differences in their days to anthesis. The maturity of wheat varieties in Peshawar valley is accelerated due to rapid rise in temperature during later part of seed filling duration in spring season.

All the four varieties produced about the same total biomass up to anthesis but the different varieties partitioned different proportions of dry matter to the different organs whose functions are different. The dwarf varieties partitioned 20-21% assimi-

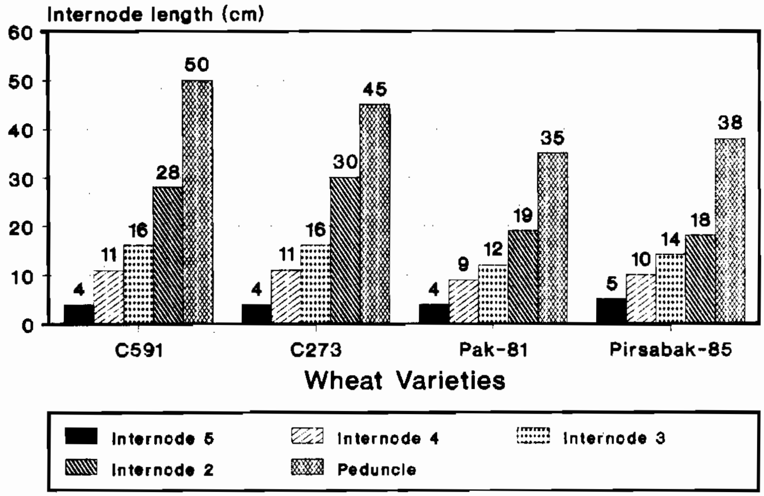


Fig.2. Vertical distribution of internodes lengths in the four wheat varieties planted at the NWFP Agricultural University, Peshawar in 1991-92

lates to spikes more than the tall varieties which partitioned 17-18% assimilates to spikes. Takahashi *et al.*, (1989) also reported that semidwarf cultivars had a higher rate of partitioning to ears than the tall cultivars. However, Takahashi *et al.*, (1988) reported that seasonal pattern of dry matter partitioning was almost identical in the semidwarf and tall cultivars. The increased grain yield in the dwarf cultivars is due to greater allocation of assimilates to the developing ears (Borrell *et al.*, 1991). Reproductive - vegetative mass ratios at anthesis (Table 3) also indicate that the dwarf varieties partitioned more assimilates to reproductive parts, which sets potentia. for

Table 5. Photoperiods and temperatures of the Malkandher Farm for the 1992-1993 wheat growing season.

Month	Temperature Maximum	Minimum	Average	Change in temperature from previous month	Photoperiod during the month	Photoperiod average change per day
		Degree C			Minutes	Seconds
November	22.91	8.41	15.66	---	42	84
December	20.07	5.96	13.01	- 2.65	6	12
January	27.26	4.11	10.68	- 2.33	32	62
February	19.60	5.29	12.44	+ 1.76	55	110
March	22.00	9.50	15.25	+ 2.81	66	132
April	27.00	14.00	20.50	+ 5.25	58	116
May	32.00	16.00	24.00	+ 2.50	42	8[illegible]

economic yield. In the dwarf varieties there is less competition between the stem and the developing spike, resulting into greater partitioning of assimilates to the spike (Youssefian *et al.*, 1992; Fischer & Stockman, 1986). The tall varieties partitioned more assimilates to vegetative parts particularly to stems. Stem acts as a support to place leaves in different strata of crop canopy. Leaves are the main photosynthetic machinery. Investment in leaf production is good for greater assimilation of carbon. Though the dwarf varieties partitioned less assimilates to vegetative parts than the tall varieties, the dwarf varieties partitioned 17-18% dry matter to leaves which is more than the tall varieties which partitioned about 16 % dry matter to leaves. The leaf-stem ratios in the 4 varieties (Table 3) also indicate greater partitioning to leaves in the dwarf varieties. The four varieties also partitioned different proportion of assimilates to the leaves placed at different vertical positions on the tiller. Varieties C273 and Pak-81 partitioned more dry matter to the flag leaf and penultimate leaf both of which are important due to placement in space and due to proximity to spike.

Tall varieties grew taller than the dwarf varieties due to comparatively greater sensitivity to gibrellic acids (Youssefian *et al.*, 1992). The dwarf varieties having dwarfing genes from Norin-10 are less sensitive to gibrellic acid. The differences in height of tillers are due to differences in elongation rates. Dwarf character is desirable because it imparts resistance to lodging and make the varieties responsive to fertilizers. Regardless of the differences in plant, the peduncle length was 41-38% of the plant height. Natrova (1991) reported peduncle relative length of 36-38%. Our results showed that the tall cultivars had longer peduncles than the dwarf cultivars and dwarf cultivars producing more grain yield (results not reported here), contradict those of Ma *et al.*, (1988) who reported that the length of the first internode below the spike was closely related to grain yield and Bessonova (1987) who reported that the length of the topmost internode was positively correlated with grain weight/ear.

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