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Full Length Article

Biomass and Phosphorus Accumulation, Partitioning and Remobilization during Grain Development in Wheat under Phosphorus Deficiency

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Abstract

We investigated the effect of phosphorus (P) deficiency on biomass and P accumulation, partitioning and remobilization in wheat over the course of grain development period in a pot study. Wheat cultivar NIA-Sunder was grown with P (60 mg kg^{-1} soil) and without P (only native soil P *i.e.*, 2.23 mg kg^{-1} soil) following completely randomized design. Plants were harvested at anthesis and subsequently every 5 days after anthesis (DAA) up to maturity and partitioned into various organs. The leaves, chaff, flag leaves and stems acted as a P source whereas grains acted as a P sink during grain development. The period of 15 – 35 DAA was the rapid phase of P accumulation in grains under both P treatments. Wheat plants remobilized 2.30 and 1.52 g $plant^{-1}$ of pre-anthesis accumulated biomass towards grain, contributing 60.22 and 53.73% of grain yield under adequate and deficient P, respectively. Likewise, 13.27 and 6.99 mg $plant^{-1}$ of pre-anthesis accumulated P was remobilized to grain which contributed 84.70 and 70.56% of grain P contents in P-fertilized and P-deficient plants, respectively. However, the post-anthesis P uptake amounted to only 9 and 18% of total P accumulation at maturity under adequate and deficient P, respectively. The results suggested that P remobilization from vegetative tissues was a key mechanism contributing significantly to grain P contents during grain development phase as post-anthesis P uptake from soil was typically low. Moreover, P deficiency considerably diminished biomass and P remobilization in wheat thereby influencing grain yield. © 2019 Friends Science Publishers

Keywords: Biomass remobilization; Pre-anthesis P accumulation; Post-anthesis P uptake; Remobilization efficiency; Wheat

Introduction

Phosphorus (P) is a vital element for plant growth and is among the major drivers for global crop productivity (Stewart *et al.*, 2005; Zhu *et al.*, 2017). It is a non-renewable element required for numerous physiological and biochemical processes within plants (Fageria *et al.*, 2013) and is an essential constituent of key biological molecules such as phosphate esters, ATPs, DNA, RNA, and phospholipids (Watanabe *et al.*, 2006). It is the second most limiting nutrient for sustainable crop productivity after nitrogen (Brady and Weil, 2008) and its deficiency can be found in nearly 67% arable soils around the globe. In Pakistan, more than 90% soils are deficient in bio-available P primarily due to high calcium carbonate contents, high base saturation and low organic matter (Irfan *et al.*, 2018). Although total P contents are abundant in most soils of the arid and semi-arid regions worldwide, but the plant available P fraction in the soil solution is seriously low ranging from 0.1 – 10 μM only (Halvin *et al.*, 2005; Hinsinger *et al.*, 2011). Plants have evolved an array of morphological, physiological and molecular adaptive mechanisms to cope with P-deficiency, such as altered root architecture (Aziz *et al.*, 2005), higher root-shoot ratio and root elongation (Irfan *et al.*, 2017), enhanced carboxylate exudation (Aziz *et al.*, 2011), better Pi uptake capacity (Shen *et al.*, 2005), recycling of internal Pi (Abel *et al.*, 2002), reprioritizing metabolic P utilization (Aziz *et al.*, 2015) and remobilizing P from vegetative to reproductive organs (Abbas *et al.*, 2018).

In cereals, accumulation of P into grains is derived from two sources; post-anthesis P acquisition by plant roots that is transferred directly to grains, and remobilization of P stored in vegetative parts prior to anthesis (Santiveri *et al.*, 2004). Phosphorus uptake occurs throughout the plant growth period and continues until physiological maturity. During grain development, significant P remobilization occurs from leaves and stems to developing grains (Batten, 1992). Similarly, the reserves assimilated in vegetative parts before anthesis may buffer grain yield against adverse conditions to current assimilation. Phosphorus is a relatively mobile element in plants which can move easily among various organs (Marschner, 1995). Under stressed conditions, cycling of mineral nutrients *i.e.*, re-translocation from shoot to roots *via* phloem, and recycling *i.e.*, translocations of cycled nutrients back to the shoot via xylem are significant mechanisms for plant growth. Phosphorus is

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either transported directly *via* phloem or recycled through the roots to ear *via* xylem (Marschner, 1995). However, the extent of circulation and translocation of P among various tissues modified at different developmental phases in wheat is still unclear.

During vegetative and early reproductive phases in wheat, carbon (C) and P are primarily assimilated in the stems and leaves (Dordas, 2009). The effective stem reserve storage is usually determined by the growing conditions from seed germination to anthesis. Much of these reserves are remobilized to developing grains representing a significant contribution to final grain yield (Dordas, 2009). Remobilization of stored C and P generally depends on three factors: (a) ability of a genotype to store assimilates in vegetative parts until anthesis, (b) sink strength which is generally dependent on spike length, number of grains per spike and grain size, and (c) the efficiency with which the stored reserves are remobilized to grain which is influenced by the genotype and environment (Fageria and Baligar, 1999; Prystupa *et al.*, 2004; Pampana *et al.*, 2007). Phosphorus accumulation at anthesis differed among crop genotypes, but the genotypic variations for total P contents at anthesis are primarily associated with the differences in biomass accumulation. Accumulation of P under optimal growing conditions is high while it declines under stress due to reduced carbon assimilation (Blum, 1998).

At maturity, wheat grains are major sinks of P constituting upto 90% of the total shoot P while 20 – 90% of this being remobilized from other organs (Batten and Wardlaw, 1987). Most of the P uptake occurs by anthesis and remobilization can account upto 56 – 63% of total grain P accumulation at maturity (Masoni *et al.*, 2007). Contribution of pre-anthesis assimilates remobilization to grain yield varied from 7 – 57% (Ehdaie and Waines, 2001), while contribution of P remobilization to grain P contents ranged from 11 – 100% (Papakosta, 1994) depending upon genotypes, P availability and climate. Phosphorus partitioning among plant organs is also altered under P deficiency *i.e.*, more preference is given to reproductive organs at the expense of P contents of vegetative organs (Dordas, 2009). Phosphorus uptake and remobilization during grain development in wheat has received much less attention in contrast to nitrogen. Therefore, the overall objectives of the present study were to investigate the extent of biomass and phosphorus accumulation and their partitioning in wheat plants over the course of grain development under P-fertilized and P-deficient conditions. Moreover, the effect of P-fertilization on remobilization of pre-anthesis accumulated biomass and phosphorus in vegetative tissues and their contribution to grain yield and grain P contents was also investigated.

Materials and Methods

Plant Material and Site Description

Uniform and healthy seeds of wheat cultivar NIA-Sunder were obtained from Plant Breeding and Genetics Division of Nuclear Institute of Agriculture (NIA) Tandojam, Sindh – Pakistan. The experiment was conducted in net-house during Rabi, 2016–17 under natural conditions at NIA, Tandojam (Latitude 25° 25' 19.8" North and Longitude 68° 32' 27.8" East). The climate of the study area was arid with 136 mm average annual precipitation. The mean daily maximum and minimum temperatures during experiment were 27 and 9.8°C, respectively, mean relative humidity was 54.9%, and mean sunshine was 8.0 h day^{-1}, while mean evaporation was 2.7 mm day^{-1}. The maximum total rainfall (3.0 mm) was recorded in January, 2017. The meteorological data for the whole crop growth period (15 November, 2016 – 01 March, 2017) is illustrated in Fig. 1. Bulk soil (15 cm surface layer) was collected from experimental farm area of NIA, Tandojam. A composite sample of respective soil was air dried and grinded to pass through 2 mm sieve and analyzed for various soil physico-chemical characteristics (Table 1). Briefly, the selected soil was silt loam in texture characterized as alkaline in reaction, high in available potassium while low in organic matter, nitrogen, and available phosphorus.

Pot Experiment

Plastic pots (19 cm diameter, 30 cm depth) inner lined with polythene sheet were filled with seven kilogram of thoroughly mixed soil. Experiment was designed following completely randomized design with factorial arrangements. Soil in each pot was moistened with canal water prior to sowing of seeds for attaining appropriate moisture for seed germination. Five seeds in each pot were manually sown and after seedling emergence; three plants were maintained and allowed to grow till maturity. Plants were grown at two phosphorus levels; deficient P (without external P addition or only native soil P *i.e.*, 2.23 mg kg^{-1}) and adequate P (addition of P at the rate of 60 mg kg^{-1} soil). The required quantities of P according to treatment plan and potassium at the rate of 30 mg kg^{-1} soil were applied at the time of wheat sowing while, nitrogen was applied at the rate of 70 mg kg^{-1} soil in three equal splits *viz*., at sowing, two, and five weeks after sowing. The fertilizer Urea (46% N), triple super phosphate (TSP, 46% P_2O_5) and sulphate of potash (SOP, 50% K_2O) were used as the source of nitrogen, phosphorus and potassium, respectively. Pots were irrigated according to plant requirements during the entire crop period. Plants were harvested at anthesis and thereafter every 5 days after anthesis (DAA) upto maturity from both P levels. At each harvest, plants were divided into stems, leaves, flag leaves, chaff and grains.

Phosphorus Assay and Estimation of Remobilization Characteristics

Plant material was dried in a forced air-driven oven at 70°C for 72 h and grinded to pass through a 0.42 mm screen using Wiley's mill (3383L10, Thomas Scientific, USA) fitted with

Table 1: Selected physico-chemical characteristics of soil used in experiment (0-15 cm surface soil)

Soil characteristics	Unit	Value	Method/ Reference
Physical characteristics			
Sand	%	22.22	Bouyoucos (1962)
Silt	%	55.83	~
Clay	%	21.95	~
Textural class	-	Silt loam	~
Chemical characteristics			
pH $_{(1:2.5)}$	-	8.10	Anderson and Ingram (1993)
EC $_{(1:2.5)}$	dS m^{-1}	0.56	~
Organic matter	%	0.83	Nelson and Sommers (1982)
Oxidizable Organic Carbon	%	0.36	~
Total Organic carbon	%	0.48	~
Kjeldahl nitrogen	%	0.04	Jackson (1962)
AB-DTPA extractable phosphorus	mg kg^{-1}	2.23	Soltanpour and Workman (1979)
AB-DTPA extractable potassium	mg kg^{-1}	250	~
AB-DTPA extractable zinc	mg kg^{-1}	0.995	~
AB-DTPA extractable iron	mg kg^{-1}	40.24	~

AB-DTPA = ammonium bicarbonate-diethylene triamine penta acetic acid

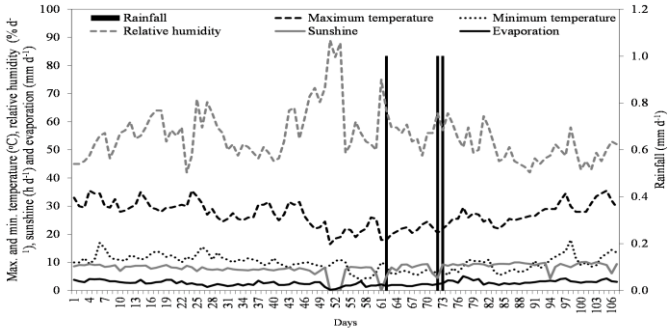

Fig. 1: Daily maximum and minimum temperatures (°C day^{-1}), RH (% day^{-1}), sunshine (hours day^{-1}), evaporation (mm day^{-1}) and rainfall (mm day^{-1}) during whole wheat growing period from crop sowing to harvesting

stainless steel blades. The total P concentration in plant material was determined following yellow color method as described by Chapman and Pratt (1961). Briefly, the plant material (0.3 g each) was wet digested in 10 mL of di-acid mixture of nitric acid and perchloric acid (5:1, *v/v*) in a conical flask, kept overnight and then placed on a hot plate until a clear solution was obtained. After digestion, volume was made upto 100 mL with distilled water and then filtered. The 10 mL of clear filtrate and 10 mL of ammonium-vanadomolybdate reagent were used to develop yellow color. Total P concentration was determined by reading light absorption at 470 nm wavelength using spectrophotometer (U-2900UV/VIS, Hitachi, Japan).

The various characteristics related to biomass and phosphorus remobilization within the wheat plants were derived according to Cox *et al.* (1986), Papakosta (1994) and Ercolia *et al.* (2008).

Phosphorus Contents (PCt)

$$\text{PCt (mg plant}^{-1}) = \text{P concentration in plan tissue (mg g}^{-1}) \times \text{Dry matter (g plant}^{-1})$$

Biomass Remobilization (BR)

$$\text{BR (g plant}^{-1}) = \text{Dry matter at anthesis} - (\text{Dry matter of leaves} + \text{culms} + \text{chaff at maturity})$$

Biomass Remobilization Efficiency (BRE)

$$\text{BRE (\%)} = \frac{\text{Biomass remobilization}}{\text{Dry matter at anthesis}} \times 100$$

Contribution of Biomass Remobilization to Grain Yield (CBRG)

$$\text{CBRG (\%)} = \frac{\text{Biomass remobilization}}{\text{Grain yield at maturity}} \times 100$$

Phosphorus Remobilization (PR)

$$\text{PR (mg plant}^{-1}) = \text{P contents at anthesis} - (\text{P contents of leaves} + \text{culms} + \text{chaff at maturity})$$

Phosphorus Remobilization Efficiency (PRE)

$$\text{PRE (\%)} = \frac{\text{Phosphorus remobilization}}{\text{P contents at anthesis}} \times 100$$

Contribution of Phosphorus Remobilization to Grain P Contents (CPRG)

$$\text{CPRG (\%)} = \frac{\text{Phosphorus remobilization}}{\text{Grain P contents at maturity}} \times 100$$

Statistical Analysis

The data relating to biomass production, P accumulation and remobilization characteristics of wheat under adequate and deficient P treatments was analyzed statistically using computer software STATISTIX 8.1 (Analytical Software, Inc., Tallahassee, FL, USA) according to the methods of Steel *et al.* (1997). Graphical presentation of data was carried out using Microsoft Excel (Redmond, WA, USA). A completely randomized design with two factors was employed for analysis of variance and least significant difference test at $P \leq 0.05$ was used to separate differences among treatment means.

Results

Dry Matter Partitioning in Wheat Plants during Grain Development

The data pertaining to dry matter production by various partitioned plant parts *i.e.*, stems, flag leaves, leaves, chaff, and grains throughout the grain development period is given in Table 2. Wheat plants were harvested at anthesis and every 5 days after anthesis (DAA) up to 45 DAA from adequate and deficient P treatments. Stem dry biomass continued to accumulate from anthesis to maturity and was recorded maximum (5.07 and 4.72 g plant^{-1}) on 30 DAA under adequate and deficient P supply, respectively. The highest dry biomass of flag leaves under adequate P (1.23 g plant^{-1}) and deficient P (1.11 g plant^{-1}) was observed on 25 DAA. Likewise, leaves dry matter during grain development period reached to maximum (2.02 and 1.77 g plant^{-1}) on 25 DAA at adequate and deficient P, respectively. The chaff dry matter ranged from 1.05 g palnt^{-1} at anthesis to 2.75 g plant^{-1} on 20 DAA under adequate P and 0.64 g plant^{-1} at anthesis to 2.41 g plant^{-1} on 25 DAA under P deficiency. Grain weight continued to increase with time and was influenced greatly by the P levels. Maximum grain weight under adequate P (4.31 g plant^{-1}) was recorded on 45 DAA which was statistically identical to 4.23 g palnt^{-1} on 40 DAA. Similarly higher grain weight of 3.46 g plant^{-1} was recorded on 45 DAA under P deficiency that was at par to grain weight on 35 and 40 DAA. Averaged over all harvestings from anthesis to maturity, dry matter partitioning to various parts of wheat plants under both P treatments was in the order of stem > grain > chaff > leaves > flag leaves.

Tissue P Concentration and Redistribution during Grain Development

Phosphorus concentration [P] located into different vegetative tissues (*i.e.*, stems, flag leaves, leaves and chaff) continued to decline throughout the period of grain development under both P supplies, however [P] in grains continued to increased till maturity (Table 3). The [P] in above ground vegetative parts was higher in P-fertilized plants compared to P-deficient plants and followed a similar pattern of reduction under both P treatments. The mean [P] in vegetative tissues was in the order of flag leaves (2.04 and 1.66 mg g^{-1}) > stems (2.01 and 1.50 mg^{-1}) > chaff (1.87 and 1.47 mg g^{-1}) > leaves (1.68 and 1.14 mg g^{-1}) under adequate and deficient P, respectively. Under adequate P supply, [P] in stems, flag leaves, leaves and chaff decreased gradually from anthesis to 25 DAA and then declined sharply till maturity. In P-deficient plants, [P] in vegetative tissues decreased gradually from anthesis to 30 DAA and then reduced sharply upto 45 DAA. The [P] in grains was higher on 15 – 25 DAA and was relatively lower in subsequent days until maturity in both P treatments.

The various aboveground plant parts growing with P addition had around 2-fold higher P contents than plants with P-deficiency (Table 4). Stem P contents continued to increase gradually from anthesis to 20 DAA and then declined until maturity under both P levels. The flag leaves, other leaves and chaff accumulated maximum P contents on 15 – 20 days of grain development and then illustrated a decreasing trend until maturity under both P treatments. The significant increase in grain P contents was observed at both P levels which continued to increase upto maturity. The mean grain P contents of P-fertilized plants were almost 1.5-fold higher compared with those of P-deficient Plants (11.62 *vs.* 8.26 mg plant^{-1}). The average P contents in aboveground parts followed the order of grain (11.62 and 8.26 mg plant^{-1}) > stems (7.76 and 4.47 mg plant^{-1}) > chaff (3.86 and 2.54 mg plant^{-1}) > leaves (2.93 and 1.76 mg plant^{-1}) > flag leaves (2.13 and 1.49 mg plant^{-1}) under adequate and deficient P, respectively.

Biomass and Phosphorus Accumulation in Wheat at Anthesis and Maturity

Phosphorus deficiency caused significant ($P \leq 0.05$) reduction of biomass production and P accumulation in wheat plants at anthesis and maturity (Fig. 2 and 3). The biomass of aboveground parts (stem + leaves) of P-fertilized plants at anthesis was 7.76 g plant^{-1} as compared to 5.36 g plant^{-1} in P-deficient plants. At maturity, straw biomass in P-fertilized plants was 5.47 g plant^{-1} while it was 3.84 g plant^{-1} in P-deficient plants. Grain yield was reduced in relation to P deficiency (2.84 g plant^{-1}) and increased in response to P addition (3.85 g plant^{-1}). Total aboveground biomass (straw + grain) at maturity was 9.31 g plant^{-1} in P-fertilized and 6.68 g plant^{-1} in P-deficient plants. The P contents in vegetative parts at anthesis were 2-fold higher in P-fertilized plant as compared to P-deficient plants. Similar pattern was also observed for straw and grain P contents at maturity. The straw P contents at anthesis varied from 24.39 mg plant^{-1} under adequate P to 12.60 mg plant^{-1} under P deficiency. At maturity, grain and straw P contents were 15.72 and 11.13 mg plant^{-1} in P-fertilized, while 9.79 and 5.62 mg plant^{-1} in P-deficient plants, respectively.

Table 2: Dry matter partitioning (g plant^{-1}) in various plant parts of wheat cultivar NIA-Sunder during grain development period under adequate and deficient P levels. Values are means of three replicates

	Stem dry matter		Flag leaves dry matter		Leaves dry matter		Chaff dry matter		Grain dry matter	
DAA	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$
00	2.36 j	1.54 k	0.76 j	0.60 k	1.28 hi	1.15 i	1.05 k-m	0.64 m	-	-
05	2.92 i	2.04 jk	1.01 d-g	0.82 ij	1.76 a-e	1.51 e-h	1.93 d-h	0.92 lm	-	-
10	3.22 hi	2.96 i	1.14 a-d	0.99 e-h	1.86 a-c	1.65 c-f	1.99 c-g	1.74 f-j	-	-
15	4.14 d-f	3.58 gh	1.17 a-c	1.06 b-f	1.99 ab	1.75 b-e	2.46 a-c	2.15 b-f	0.59 fg	0.33 g
20	4.45 cd	3.90 e-g	1.21 ab	1.04 c-f	2.00 ab	1.74 b-e	2.75 a	2.34 a-e	0.94 f	0.63 fg
25	4.99 ab	4.49 b-d	1.23 a	1.11 a-e	2.02 a	1.77 a-e	2.66 ab	2.41 a-d	1.66 e	1.41 e
30	5.07 a	4.72 a-c	1.14 a-d	1.03 c-f	1.83 a-d	1.61 c-g	2.61 ab	2.33 a-e	2.85 cd	2.64 d
35	4.27 c-e	3.83 e-g	0.93 f-i	0.87 g-j	1.69 c-e	1.57 d-g	1.86 e-i	1.57 g-k	4.06 a	3.20 bc
40	3.79 e-g	3.63 f-h	0.85 h-j	0.80 ij	1.62 c-g	1.40 f-i	1.49 g-k	1.32 j-l	4.23 a	3.23 bc
45	3.82 e-g	3.60 gh	0.84 h-j	0.79 ij	1.40 f-i	1.37 g-i	1.45 h-l	1.40 i-l	4.31 a	3.46 b
Mean	3.90	3.43	1.03	0.91	1.74	1.55	2.02	1.68	2.66	2.13
$LSD_{0.05}$ (T)	0.37		0.11		0.19		0.37		0.33	
$LSD_{0.05}$ (P)	0.16		0.05		0.09		0.17		0.18	
$LSD_{0.05}$ (T × P)	0.52		0.15		0.27		0.53		0.47	

DAA = days after anthesis; T = time (*i.e.*, DAA); P = phosphorus levels; T × P = interaction between time and P levels. Means sharing identical letter(s) in the same column indicate non-significant differences (LSD test, $P \leq 0.05$)

Table 3: Phosphorus concentration [P] (mg g^{-1}) in various analyzed plant parts of wheat cultivar NIA-Sunder during grain development period under adequate and deficient P levels. Values are means of three replicates

	[P] in stem		[P] in flag leaves		[P] in leaves		[P] in chaff		[P] in grains	
DAA	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$
00	2.72 ab	1.70 c-e	2.89 a	2.72 a-c	2.71 a	1.74 c	2.91 ab	2.66 bc	-	-
05	2.64 ab	1.58 d-f	2.99 a	2.80 ab	2.28 b	1.62 cd	3.09 a	2.61 cd	-	-
10	2.91 a	1.56 d-f	2.51 b-d	2.30 d-f	2.27 b	1.65 cd	2.79 bc	2.24 e	-	-
15	2.84 a	1.74 c-e	2.48 c-e	2.20 ef	2.25 b	1.60 cd	2.41 de	1.94 f	5.14 a	4.56 bc
20	2.45 b	1.62 d-f	2.01 f	1.43 g	1.70 cd	1.14 e-g	2.34 e	1.85 f	4.70 a-c	4.42 b-d
25	2.05 c	1.38 e-g	2.16 f	1.49 g	1.36 d-f	1.03 fg	1.79 f	1.50 g	4.69 a-c	4.36 b-e
30	1.87 cd	1.30 f-h	2.08 f	1.39 gh	1.41 c-e	0.85 gh	1.51 g	1.35 g	4.85 ab	3.91 d-f
35	1.17 g-i	1.02 h-j	1.45 g	0.98 ij	0.97 g	0.58 h	0.79 h	0.65 hi	4.33 b-e	3.90 d-f
40	1.04 g-j	0.91 i-k	1.11 hi	0.70 jk	0.95 g	0.55 h	0.69 h	0.56 h-j	4.17 c-e	3.83 ef
45	0.76 jk	0.64 k	0.77 jk	0.58 k	0.86 gh	0.61 h	0.41 ij	0.32 j	4.00 d-f	3.57 f
Mean	2.01	1.50	2.04	1.66	1.68	1.14	1.87	1.47	4.55	4.08
$LSD_{0.05}$ (T)	0.26		0.21		0.24		0.17		0.39	
$LSD_{0.05}$ (P)	0.11		0.10		0.11		0.78		0.21	
$LSD_{0.05}$ (T × P)	0.36		0.30		0.34		0.25		0.55	

DAA = days after anthesis; T = time (*i.e.*, DAA); P = phosphorus levels; T × P = interaction between time and P levels. Means sharing identical letter(s) in the same column indicate non-significant differences (LSD test, $P \leq 0.05$)

Table 4: Phosphorus contents (mg plant^{-1}) in various plant parts of wheat cultivar NIA-Sunder during grain development period under adequate and deficient P levels. Values are means of three replicates

	P contents in stem		P contents in flag leaf		P contents in leaves		P contents in chaff		P contents in grains	
DAA	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$	$P_{adequate}$	$P_{deficient}$
00	6.36 de	2.56 hi	2.19 d	1.63 e	3.46 b-d	2.00 f-h	3.05 gh	1.70 ij	-	-
05	7.70 d	3.23 hi	3.01 a	2.29 d	4.00 a-c	2.44 e-g	5.96 ab	2.39 hi	-	-
10	9.41 c	4.64 fg	2.85 ab	2.26 d	4.21 ab	2.71 d-f	5.51 bc	3.91 ef	-	-
15	11.76 a	6.20 e	2.90 ab	2.34 cd	4.51 a	2.81 de	5.91 ab	4.11 de	3.04 fg	1.52 g
20	10.90 ab	6.27 e	2.44 cd	1.49 e	3.40 cd	1.99 f-h	6.42 a	4.33 de	4.38 ef	2.85 fg
25	10.22 bc	6.17 e	2.64 bc	1.64 e	2.75 d-f	1.83 g-i	4.78 cd	3.63 e-g	7.79 d	6.11 de
30	9.46 c	6.12 e	2.37 cd	1.43 e	2.58 e-g	1.36 h-l	3.95 ef	3.13 f-h	13.86 b	10.31 c
35	5.00 ef	3.88 f-h	1.34 e	0.85 fg	1.64 h-j	0.90 j-l	1.45 jk	1.00 j-l	17.53 a	12.48 b
40	3.89 f-h	3.29 g-i	0.92 f	0.56 gh	1.55 h-k	0.77 l	0.98 j-l	0.74 kl	17.50 a	12.39 bc
45	2.93 hi	2.31 i	0.65 f-h	0.45 h	1.21 i-l	0.83 kl	0.60 l	0.45 l	17.24 a	12.20 bc
Mean	7.76	4.47	2.13	1.49	2.93	1.76	3.86	2.54	11.62	8.26
$LSD_{0.05}$ (T)	0.97		0.24		0.55		0.59		1.52	
$LSD_{0.05}$ (P)	0.44		0.11		0.24		0.26		0.81	
$LSD_{0.05}$ (T × P)	1.38		0.33		0.77		0.83		2.14	

DAA = days after anthesis; T = time (*i.e.*, DAA); P = phosphorus levels; T × P = interaction between time and P levels. Means sharing identical letter(s) in the same column indicate non-significant differences (LSD test, $P \leq 0.05$)

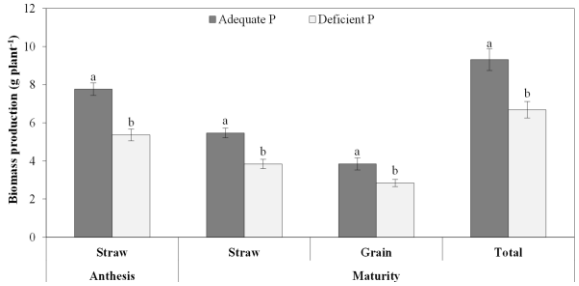

Fig. 2: Biomass production of wheat cultivar NIA-Sunder at the time of anthesis (*i.e.,* straw) and maturity (*i.e.,* straw, grain and total) under adequate and deficient P levels. Values are means of three replicates. For each parameter, bars not sharing identical letter(s) indicate significant differences among each other at two P levels (LSD test, $P \leq 0.05$). LSD values for straw biomass at anthesis = 1.27; straw biomass at maturity = 0.97; grain yield at maturity = 0.89; total biomass at maturity = 1.98

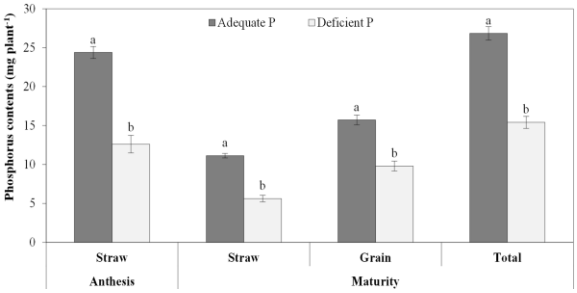

Fig. 3: Phosphorus contents of wheat cultivar NIA-Sunder at the time of anthesis (*i.e.,* straw) and maturity (*i.e.,* straw, grain and total) under adequate and deficient P levels. Values are means of three replicates. For each parameter, bars not sharing identical letter(s) indicate significant differences among each other at two P levels (LSD test, $P \leq 0.05$). LSD values for straw P contents at anthesis = 2.48; straw P contents at maturity = 1.01; grain P contents at maturity = 1.77; total P contents at maturity = 3.20

Biomass and Phosphorus Remobilization

The data regarding biomass and P remobilization under adequate and deficient P supply has been illustrated in Fig. 4 and 5. Biomass remobilization and the contribution of pre-anthesis assimilated biomass to grain yield were higher in P-fertilized plants as compared to P-deficient plants. Biomass remobilization in plants with adequate P was 34% higher those of P-deficient plants (2.30 *vs.* 1.52 g plant^{-1}). Biomass remobilization efficiency was not affected significantly with P treatments and varied from 29.57% in P-fertilized plants to 28.44% in P-deficient plants. The contribution of pre-anthesis assimilated biomass to grain weight was 11% higher in plants growing with adequate P (60.22%) compared to P-deficient plants (53.73%). Phosphorus remobilization was 47% higher in P-fertilized plants than P-deficient plants (13. 27 *vs.* 6.99 mg plant^{-1}). The P remobilization efficiency in P-deficient plants was slightly higher than P-fertilized plants (54.72 *vs.* 53.31%). The remobilization of pre-anthesis accumulated P contributed 84.70 and 70.56% to grain P contents at maturity under adequate and deficient P, respectively.

Discussion

The prime objectives of the present study were to investigate how phosphorus deficiency influences the biomass and P accumulation, partitioning into various plant tissues and remobilization in wheat during grain development. In current study, phosphorus deficiency caused significant decline in dry matter assimilation and further partitioning into various plant tissues as reported in earlier investigations (Demotas-Mainard and Jeuffory, 2001; Prystupa *et al.,* 2004). Elliot *et al.* (1997) have reported that biomass production and allocation of assimilates to reproductive organs is directly influenced by the P supply (Elliot *et al.,* 1997). Prevailing growth conditions and genotypes also contribute greatly to influence dry biomass between anthesis to maturity in winter wheat (Dordas *et al.,* 2008). Wheat is known to remobilize its pre-anthesis storage of assimilates to grain up to 73% (Papakosta and Gagianas, 1991) and 57% (Ehdaie and Waines, 2001). We found in present study that remobilization of pre-anthesis assimilates contributed 60.24 and 53.67% of grain yield at adequate and deficient P, respectively. The contribution of pre-anthesis assimilates to grain is important to sustain grain yield under unfavorable circumstances limiting photosynthesis, nutrients and water uptake (Yoshida, 1972; Arduini *et al.,* 2006). Remobilization of assimilates facilitates the plants to withstand restricted production of photosynthates under stress conditions (Farooq *et al.,* 2011, 2014). A key factor regarding the roles of assimilate reserves in grain filling is the loss of carbon either from vegetative tissues or developing grains that is associated with respiration. Phosphorus deficiency may impair mitochondrial respiration and alter carbon metabolism in many plants (Vance *et al.,* 2003). About one third of the reduction of carbohydrates from stem during grain filling could be attributed to respiratory losses in wheat (Wardlaw and Willenbrink, 1994). The carbon reserves in leaves and stems are the prominent contributor to grain filling in wheat as taller plants owing to their higher storage capacity have greater potential to support grain filling for a longer period (Blum, 1998).

At anthesis, phosphorus concentration [P] in aboveground vegetative tissues of P-deficient plants was significantly lower than P-fertilized plants. While the [P] located in various plant parts continued to decline throughout the grain development under both P supplies. The reduction in [P] followed the order as flag leaves < stems < chaff < leaves, whereas [P] in grains increased. The decline in [P] of vegetative tissues during the period from anthesis to maturity is the indication of P remobilization towards grain (Julia *et al.,* 2016). Papakosta (1994) stated that the reduction in [P] is usually slow during early plant growth and becomes extensive at later stages. Thus, delay in P remobilization until the later stages of senescence could be a key mechanism

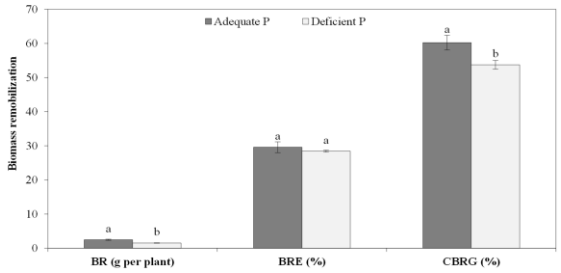

Fig. 4: Biomass remobilization (BR), biomass remobilization efficiency (BRE) and contribution of biomass remobilization to grain yield (CBRG) of wheat cultivar NIA-Sunder under adequate and deficient P levels. Values are means of three replicates. For each parameter, bars not sharing identical letter(s) indicate significant differences among each other at two P levels (LSD test, $P \leq 0.05$). LSD values for BR = 0.49; BRE = 1.58; CBRG = 6.07

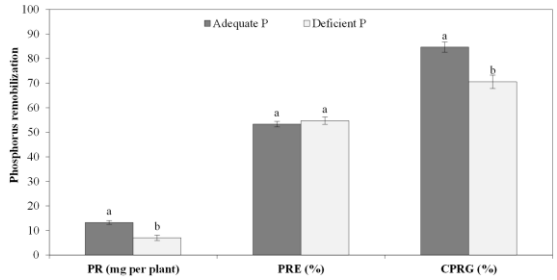

Fig. 5: Phosphorus remobilization (PR), phosphorus remobilization efficiency (PRE) and contribution of phosphorus remobilization to grain P contents (CPRG) of wheat cultivar NIA-Sunder under adequate and deficient P levels. Values are means of three replicates. For each parameter, bars not sharing identical letter(s) indicate significant differences among each other at two P levels (LSD test, $P \leq 0.05$). LSD values for PR = 2.38; PRE = 3.41; CPRG = 3.98

responsible for ensuring continuous accumulation of biomass and photosynthates throughout the grain filling. The synchronization of P decline from vegetative tissues seems prudent to facilitate main photosynthetic organs such as flag leaves to carry on function optimally for as long as possible (Bertheloot *et al.,* 2008). Wheat plants employed such types of strategies in relation to nitrogen allocation for photosynthetic tissues during grain development (Bertheloot *et al.*, 2008; Wang *et al.*, 2016).

The period of 15 – 35 DAA was the rapid phase of P accumulation in grains under both P treatments. However, the P contents of aboveground parts were increased by 48% (at anthesis) and 43% (at maturity) with P addition. In contrast, peak loading of P into rice grains occurs from 6 – 15 days after flowering (Wang *et al.,* 2016). The measure of the ability of a crop to transport P from vegetative tissues to grain can be expressed as remobilization efficiency (Muurinen *et al.,* 2007). The P remobilization in current study was noticed higher in P-fertilized than P-deficient plants. Although the P remobilization efficiency was statistically identical in both treatments but the contribution of pre-anthesis P remobilization to grain was greatly influenced by the P treatments and recorded higher in P-fertilized plants (70.53 *vs.* 84.69%). Dordas (2009) estimated the contribution of assimilated P translocated to seed in the range of 63.1 – 87.2% in wheat. The efficiency of a genotype to remobilize P reserves (source) to grains (sink) during grain development is a genetic controlled trait and may vary among different genotypes (Abbas *et al.,* 2018). Therefore, this phenomenon might be the reason behind non-significant effect of P supplies on remobilization efficiency. In some cases, remobilization efficiency becomes stable across genotypes and environments. When post-anthesis P uptake is ceased, early senescence and limited photosynthetic activity results in enhanced remobilization from vegetative tissues (Barbottin *et al.,* 2005; Kong *et al.,* 2013). This suggests that wheat tend to rely heavily on remobilization of P from vegetative organs during grain development indicating that post-anthesis P uptake from soil is typically low. Similar findings have also been reported in other crops such as durum wheat and rice (Masoni *et al.,* 2007; Dordas, 2009; Julia *et al.,* 2016). In contrast, flooded rice appears to be different in which post-flowering P uptake from soil during grain filling is a critical contributor (40 – 70%) to the grain P contents (Julia *et al.,* 2016).

Conclusion

Phosphorus accumulation in wheat grains originates from two sources *i.e.,* post-anthesis P uptake from soil by plant roots, and P remobilization from aerial parts. In current study, the period of 15–35 DAA was the rapid phase of P accumulation in wheat being grains as a strong P sink while vegetative parts (flag leaves < stems < chaff < leaves) acts as a source of P during grain development. Post-anthesis P uptake contributed only 9–18% of total P contents at maturity. Therefore, P remobilization from vegetative tissues was a key mechanism which contributed greatly to grain P contents during grain development as post-anthesis P uptake from soil was diminutive. Phosphorus deficiency also decreased wheat grain yield by reducing the remobilization of pre-anthesis accumulated biomass and P reserves in different tissues.

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