

Manganese influx and its utilization efficiency in wheat

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Manganese deficiency in wheat has become an important nutritional disorder particularly in alkaline calcareous soils where rice-wheat rotation is followed. This experiment was aimed to study the mechanism of Mn efficiency during various developmental stages in six wheat cultivars grown at two Mn levels viz. 0 and 50 mg Mn kg⁻¹soil (Mn applied as MnSO₄.H₂O) in pots. The Mn vegetative efficiency calculated on the basis of shoot dry weight at anthesis indicated HD 2967 and PBW 550 (bread wheat) as Mn efficient and durums as Mn inefficient. The efficient cultivars recorded highest values for influx, uptake, shoot dry weight, leaf area/plant, SPAD index, F_v/F_m ratio and root length that explained their higher efficiencies whereas inefficiency of durum cultivars was attributed to their smaller roots and lower influx. Under Mn deficiency, PDW 314 and PDW 291 retained 68% and 64%, respectively, of total Mn uptake in vegetative parts (stem and leaves) and lowest in grains 7% and 5%, respectively, whereas PBW 550, BW 9178 and HD 2967 retained 29, 37 and 34% in vegetative parts, and 21, 17 and 15 % in grains, respectively at maturity. Higher utilization efficiency of efficient genotypes also indicated that increased Mn uptake with Mn supply produced more efficiently grains in efficient genotypes but vegetative parts in inefficient genotypes. Hence Mn efficiency of a cultivar could be explained by longer roots, higher uptake, influx and efficiency index during vegetative phase and higher grain yield and utilization efficiency during generative phase.

Keywords: Manganese acquisition, Manganese kinetics, Rhizosphere, Root growth, Wheat grain

Manganese is an essential micronutrient involved in several processes like photosynthesis (water splitting reaction), CO₂ assimilation, nitrogen metabolism and enzymatic reactions that play an important role in crop growth and yield¹. Manganese availability issue is predominant over soil Mn content for better crop yield on calcareous soils¹. Reduction of Mn⁴⁺ form (plant unavailable form) to Mn²⁺ (plant available form) is either biological or chemical in nature². Manganese deficiency is difficult to overcome by fertilizers as the added Mn is quickly converted to unavailable oxidized form³. Mn deficiency can be overcome by foliar application of 0.5-1% (w/v) MnSO₄.H₂O solution, but it has to be applied repeatedly (3-4 times) and it may also prove less efficient under severe Mn deficiency conditions. Wheat is the staple food crop of 35% of the world's population and the most important cereal in food security prospective. The crop is highly sensitive to Mn deficiency as revealed by high decline in yield⁴. In Punjab state of India, rice-wheat cropping system

has exhausted most of the micronutrient reserves. Leaching losses of manganese (Mn) after rice cultivation is the primary factor of upcoming Mn deficiency in wheat that has imposed a threat on yield⁵.

In these circumstances the effective means to increase yield will be screening of wheat cultivars which can grow well on soils low in available Mn. Identification of Mn efficient genotypes can help in incorporating their efficiency characters or genes into high yielding cultivars^{6,7}.

Tolerance to Mn deficiency in crops can be described by the mechanisms namely: superior root geometry⁸, better uptake kinetics leading to higher influx and uptake^{8,9}, chemical mobilization by root exudates leading to more solubilization of plant unavailable form of Mn into available form¹⁰, superior internal utilization resulting in better photosynthetic activities¹¹, seed Mn content leading to better seedling growth and enhanced yield¹², and population of Mn oxidizing and reducing microorganisms in the rhizosphere¹³.

Manganese accumulates in plant organs where intensive chemical reactions take place and which are in active vegetation. Phloem mobility of Mn is very

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low and it can reach glumes directly via xylem in mature wheat plants or can be first transferred from xylem to phloem and then reach the glumes via phloem in young plants¹⁴. On the contrary, good reproductive phase mobilization of Mn to barley grains at harvest stage with an increased spike Mn concentration accompanied by decreased Mn concentration in the other plant parts including older leaves has been reported¹⁵. Manganese moves readily from roots, stems and petioles to developing sinks, including seeds in lupin¹⁶. Under Mn deficiency, Mn content of stem, peduncle and flag leaf decreases and that of glumes increases towards maturity¹⁷.

The study on Mn uptake efficiency during vegetative phase and its consequences on Mn utilization efficiency during the generative phase in wheat are relatively scanty. The present study has been planned to assess the Mn efficiency of six wheat cultivars with a hypothesis that differential Mn influx resulting from corresponding depletion of Mn in the rhizosphere; and superior Mn partitioning to grains at maturity could influence the Mn uptake efficiency during vegetative phase and Mn utilization efficiency during generative phase, respectively.

Materials and Methods

A greenhouse pot experiment was carried out with six wheat cultivars (PDW 291, PDW 314, PBW 550, PBW 636, HD 2967 and BW 9178) grown on Mn deficient soil (1.56 g cm⁻³ bulk density, pH 8.4 and 1.50 mg kg⁻¹ soil DTPA-extractable Mn) with two Mn treatments (0 and 50 mg Mn kg⁻¹ soil, applied as MnSO₄.H₂O). Treatments were replicated thrice for each of three harvest stages (tillering, anthesis and maturity) in plastic pots (5 plants/pot) containing 9 kg soils. The experiment was laid out in a completely randomized design.

Before harvesting the plants at tillering and anthesis stage, SPAD index and F_v/F_m ratio of the topmost fully expanded leaves were recorded. Ten observations from each pot were recorded for SPAD index using SPAD 502 (Konica Minolta) and F_v/F_m ratio with Junior-PAM Chlorophyll Fluorometer (Walz Mess-und Regeltechnik). Maximum length and width of a leaf was measured and leaf area calculated by multiplying leaf length and width with a constant (0.81).

To study Mn dynamics in the rhizosphere, roots were carefully separated from soil at tillering and anthesis by washing and floating over sieves. After cleaning roots of any foreign material, they were kept

between two filter papers to remove surface water and fresh root weight was recorded for the sub samples. Weighed samples of roots were preserved in 20% ethanol for measurement of root length by Win Rhizo Basic V. 2009c software. Mean root radius (r₀) was calculated from fresh root weight (FRW) and root length (RL) from the formula: r₀ = √FRW/(π.RL).

The net Mn influx (I_n) is the net amount of Mn taken up per unit root length or root surface area per unit time. Assuming that, young plants have exponential root growth, the average Mn influx (I_n) was calculated from formula¹⁸:

$$I_n = \frac{U_2 - U_1}{RL_2 - RL_1} \cdot \frac{\ln(RL_2 / RL_1)}{t_2 - t_1}$$

where U is Mn content in nmol plant⁻¹, RL is root length per plant in cm; t is time of harvest in seconds; subscripts 1 and 2 refer to first and second harvest at tillering and anthesis, respectively.

Concentration difference between bulk soil and root surface (ΔC_L) is the difference in Mn concentration between the average bulk soil solution, (\bar{C}_L) and the concentration at the root surface (C_{L0}) needed to drive a given flux (I_n) by diffusion. ΔC_L was calculated from the formula of¹⁹ based on the steady state model of²⁰:

$$\Delta C_L = \bar{C}_L - C_{L0} = -\frac{I_n}{4\pi D_L \Theta f} \left(1 - \frac{1}{1 - \pi r_0^2 RL_v} \ln \frac{1}{\pi r_0^2 RL_v} \right)$$

where r₀ is mean root radius in cm, RL_v is root length density in soil, D_L is diffusion coefficient of Mn in water 25 °C = 7.1*10⁻⁶ cm² s⁻¹, f is impedance factor calculated from formula of Barraclough and Tinker²² where, f = 1.58θ - 0.17 and θ is volumetric water content of the soil. Initial soil solution Mn concentration (C_{L0}) was measured by inductively coupled argon plasma atomic emission spectrophotometer. Soil solution was recorded for displacement technique²³ at soil water content equivalent to 60% of the maximum water holding capacity of the soil. The treated soil was incubated for 24 h before the collection of soil solution samples.

Shoots were washed with distilled water, dried at 70 °C and weighed to record their shoot dry matter yield. The dried samples were milled, digested in diacid mixture (HNO₃ and HClO₄ in 2:1 ratio) and aqueous extracts were prepared. These extracts were analyzed for Mn content using Atomic Absorption Spectrophotometer (Varian Spectra AA 20 plus).

To study Mn partitioning at maturity, plants harvested at maturity were separated into leaves, stem, peduncle, chaff and grains. All samples were washed with distilled water and dried at 70 °C to a constant weight and weighed to record dry weight and Mn concentration. The following parameters were calculated:

Mn uptake in shoot (nmol plant^{-1}) = [Concentration (mg kg^{-1}) \times dry matter (mg plant^{-1})]/54.9

Mn uptake in plant part at maturity (μg) = [Concentration ($\mu\text{g g}^{-1}$) \times dry matter (g)]

Partitioning of a nutrient within a plant at different growth stages was calculated by Partition quotient (PQ) representing the proportional mineral content in a tissue relative to the proportional dry weight of that tissue. Mathematically, PQ^{24} is the ratio between percent nutrient uptake in each plant part and percent shoot dry matter of each plant part multiplied by 100

Manganese efficiency = [(Dry weight at low Mn level/experimental mean dry weight at low Mn)]/[(Dry weight at high Mn level/experimental mean dry weight at high Mn)]²⁵

Mn utilization efficiency (MnUE) = grain weight (g) at high Mn-grain weight (g) at low Mn/total plant uptake ($\mu\text{g/g}$) at high Mn- total plant uptake ($\mu\text{g/g}$) at low Mn)²⁶.

For statistical analysis, the data were subjected to analysis of variance (ANOVA) to evaluate difference between the treatment means. Standard error of difference (SED) Least significant difference (LSD) from ANOVA table was used for all comparisons

where significant F-probabilities ($P \leq 0.05$) were found as per Singh *et al*²⁷.

Results

Under Mn deficiency, all the cultivars showed Mn deficiency symptoms that were more severe in durum cultivars. Shoot dry weight (SDW) and root length (RL) were significantly reduced under Mn deficiency compared to the Mn treated plants irrespective of growth stage and cultivar (Table 1). Compared to high Mn, PDW 291 and PDW 314 retained 22 and 39% RL and 20 and 12% SDW respectively, under Mn deficiency at tillering but the corresponding values were 5 and 2% and 4 and 3% respectively, at anthesis indicating that effect of Mn deficiency is more severe at anthesis in durum cultivars. Gain in RL and SDW from tillering to anthesis was more in bread wheat cultivars than durum.

The leaf area, an indicator of vegetative growth, was markedly affected with Mn deficiency (Table 2). The leaf area on an average decreased from 92.1 to 63.6 cm^2 at tillering and 92.7 to 17.1 cm^2 at anthesis under low Mn. The severe Mn deficiency from tillering to anthesis stage hampered the growth of all cultivars but it was more pronounced for PDW 314, PDW 291 and PBW 636 as most of the leaves showed senescence.

The SPAD index, an indicator of chlorophyll content, was low in durum cultivars in comparison to bread cultivars at both the stages under Mn deficiency but at high Mn the value was not much lower than

Table 1—Plant parameters of wheat cultivars as affected by Mn application at different stages of growth

Wheat cultivar	Mn levels (mg kg^{-1})	Root length (cm)		SDW (mg plant^{-1})		Mn uptake (nmol plant^{-1})	
		Tillering	Anthesis	Tillering	Anthesis	Tillering	Anthesis
PBW 550	0	594	1050	133	612	15.6	112.0
	50	2197	3514	976	4060	838.0	963.0
BW 9178	0	191	1970	137	544	23.0	107.0
	50	1418	9350	993	6386	475.0	898.0
HD 2967	0	204	1877	206	820	29.7	146.0
	50	702	7193	901	5385	219.0	887.0
PBW 636	0	423	796	304	494	55.7	81.3
	50	1557	5209	1166	6508	274.0	1000.0
PDW 291	0	319	370	176	239	25.4	34.0
	50	800	7082	852	4587	223.0	644.0
PDW 314	0	247	320	88	148	13.3	19.1
	50	1109	11294	714	4273	412.0	683.0
LSD (0.05)	Treatment	45.2	205	34.5	81.6	15.6	20.8
	Cultivars	78.7	355	59.7	141	27.0	36.0
	Interaction	111.3	502	84.5	200	38.2	50.9

Table 2—Photosynthetic contributing traits of wheat cultivars as affected by Mn application at different stages of growth

Wheat cultivar	Mn levels (mg kg ⁻¹)	Leaf Area (cm/plant)		SPAD index		F _v /F _m ratio	
		Tillering	Anthesis	Tillering	Anthesis	Tillering	Anthesis
PBW 550	0	44.2	21.9	29.80	23.2	0.41	0.37
	50	187.6	587.4	44.77	42.6	0.67	0.77
BW 9178	0	44.5	19.3	30.80	17.2	0.39	0.34
	50	174.9	264.7	42.30	47.0	0.59	0.71
HD 2967	0	63.6	62.7	31.90	29.0	0.37	0.36
	50	161.1	240.0	45.13	47.6	0.65	0.76
PBW 636	0	92.1	33.0	30.47	23.8	0.57	0.42
	50	205.1	310.1	43.27	49.0	0.61	0.72
PDW 291	0	42.5	22.4	24.43	13.6	0.31	0.19
	50	92.8	322.1	46.27	40.8	0.72	0.79
PDW 314	0	25.3	27.1	26.37	24.4	0.47	0.32
	50	140.3	337.1	42.83	41.4	0.60	0.72
LSD (0.05)	Treatment	11.45	48.92	1.68	1.43	0.023	0.023
	Cultivars	19.83	84.73	NS	2.48	0.040	0.041
	Interaction	28.04	119.83	4.12	3.51	0.057	0.058

other cultivars (Table 2). The cultivar HD 2967 retained highest SPAD value of 71 (tillering) and 61 (anthesis) % under low Mn whereas, corresponding values were 53 and 23% for PDW 291. The ‘chlorophyll a’ fluorescence emission, F_v/F_m ratio, declined (on an average by 34%) under low Mn. The durum cultivars had higher absolute and relative values of F_v/F_mratio than bread cultivars (Table 2).

All the cultivars had lower concentration of Mn under low Mn. As reported above, both the biomass accumulation and Mn concentration decreased under low Mn that resulted in reduced Mn uptake in plants. The Mn uptake of all the cultivars significantly decreased under low Mn (Table 1). The Mn uptake was lowest for PDW 314 and highest for PBW 636 at tillering and HD 2967 at anthesis under low Mn. The increase in Mn uptake from tillering to anthesis was 86, 79 and 78% for PBW 550, HD 2967 and BW 9178 whereas the corresponding values were 25, 30 and 31% for PDW 291, PDW 314 and PBW 636, respectively. The influx of Mn was highest for HD 2967 and lowest for PDW 314 (Table 3). The influx is directly proportional to the concentration gradient between bulk soil and root surface i.e. the depletion of Mn in the rhizosphere. The cultivar HD 2967 followed by PBW 550 recorded higher depletion of Mn in the rhizosphere compared to other cultivars.

The Mn vegetative efficiency calculated on the basis of SDW at anthesis indicated HD 2967 and PBW 550 as Mn efficient and durums as Mn inefficient (Table 4). This was further supported by all the parameters viz. RL, leaf area/plant, SPAD index, F_v/F_m ratio, Mn uptake

and influx. Under Mn deficiency, the efficiency of cultivar was highly correlated to Mn influx (r = 0.92), Mn uptake (r = 0.92), shoot dry weight (r = 0.93) and root length (r = 0.67) at anthesis but to Mn influx (r = 0.92) and SPAD value (r = 0.77) at tillering.

Due to severity of Mn deficiency the biomass accumulation at maturity was significantly reduced in all the cultivars (Table 5). Under low Mn, the cultivar PBW 550 accumulated highest dry matter whereas BW 9178 accumulated under high Mn. The uptake of Mn was also affected under Mn deficiency (Table 6). All the cultivars had significantly less uptake under low Mn. The relative Mn uptake in grain compared to the non-grain parts was highest in cv. PBW 550 (27.3%) followed by BW 9178 (20.6%) while for the two durum cv. PDW 291 and PBW 314 it was only 7.8 and 5.8% , respectively (Fig. 1). The partitioning data on uptake depicted that despite low retention of Mn in vegetative parts of PBW 550, BW 9178 and HD 2967, the maximum retention of Mn was in chaff under low Mn and for durums the maximum retention was in vegetative parts.

The partition quotient data (which explains the accumulation of Mn in different plant parts irrespective of their individual dry weight) also revealed that the durums retained higher proportion of Mn in their stem and peduncle compared to grain in both Mn treatments (Fig. 2).

The grain yield was severely hampered under Mn deficiency (Table 5). The cultivar BW 9178 and HD 2967 yielded highest under high Mn but PBW 550 and BW 9178 under low Mn. The grain yield of both durums was very less under Mn deficiency.

Mn efficiency index based on grain yield varied from 0.80 to 1.33 (Table 4). Although the absolute yield of both durum cultivars was less but their relative yield (yield at low Mn / yield at high Mn) was more as compared to other genotypes. The cultivars HD 2967 and BW 9178 recorded low efficiency index (≤ 0.82) whereas durums recorded high index (≥ 1.12).

The increase in grain yield per unit increase in Mn uptake with Mn application i.e. utilization of Mn in grain production was highest for BW 9178 (50.3 g mg^{-1}) and lowest for PDW 314 (5.6 gm g^{-1}). Higher utilization efficiency of efficient genotypes indicated that increased Mn uptake with Mn supply produced more efficiently grains in efficient genotypes (Table 4).

Correlation analysis supported the results that efficiency of a cultivar is related to Mn influx, uptake and utilization efficiency as yield was significantly and positively related to Mn influx ($r = 0.92$), total Mn uptake at maturity ($r = 0.97$), grain Mn uptake ($r = 0.99$), Mn vegetative efficiency ($r = 0.85$) and utilization efficiency ($r = 0.73$) but negatively to yield efficiency index ($r = -0.34$) under low Mn and their corresponding values under high Mn were $r = 0.93, 0.97, 0.98, 0.73, 0.85$ and -0.72 respectively.

Discussion

Mn deficiency severely hampers the plant growth in terms of SDW and RL due to its role in several metabolic processes of growth and development viz. in most of the redox reactions fundamental for cellular processes and in protein and enzymes for structural and catalytic enzyme activities^{28,29}. The reduction in SDW and RL under Mn deficiency has also been reported in wheat^{7,30} and rice³¹. The

reduction in root growth under low Mn might be due to the role of Mn in regulating the level of auxins particularly indole acetic acid (IAA) through IAA oxidases³². The shoot dry weight is intimately linked with the photosynthetic efficiency of a plant that further depends on the area of photosynthetic tissue i.e. the leaf area. The leaf area reduction under Mn deficiency in rice³¹ and in wheat³³ has been reported. The measures of photosynthetic efficiency viz. F_v/F_m ratio and SPAD index were significantly reduced in all the cultivars under Mn deficiency, indicating the critical role of the Mn^{2+} as a co-factor in the photosynthetic light dependent reactions³⁴.

Manganese deficiency significantly reduced the uptake of Mn in wheat plants^{35,36}. The higher influx of Mn in cultivars HD 2967 followed by PBW 550 could be explained due to higher Mn acquisition by each root segment leading to higher uptake of Mn in compared to the other cultivars. The Mn efficiency data also supported the fact that higher Mn efficiency is based on higher influx due to more depletion of Mn in the rhizosphere. The cultivars HD 2967 and PBW 550 recorded highest values for influx, uptake, shoot

Table 4—Manganese efficiency indexes of different wheat cultivars under Mn deficiency

Cultivar	Mn vegetative efficiency	Mn efficiency index (maturity)	Mn utilization efficiency ($\text{g}^2/\mu\text{g}$)
PBW 550	1.63	1.3	25.2
BW 9178	0.92	0.8	50.3
HD 2967	1.65	0.8	24.2
PBW 636	0.82	1.1	20.2
PDW 291	0.63	1.1	16.1
PDW 314	0.37	1.3	5.6

Table 3—Depletion of Mn in the rhizosphere and its related parameters

Cultivar	Mn applied (mg kg^{-1} soil)	Mn influx ($10^{-17} \text{ mol cm}^{-1} \text{ s}^{-1}$)	Mean root radius 40 days post tillering (0.01 cm)	Root length density (cm cm^{-3}) 40 days post tillering	Depletion of Mn in the rhizosphere
PBW 550	0	3.48	1.24	0.9	4.67
	50	5.07	1.41	3.0	5.33
BW 9178	0	3.22	1.39	1.7	3.77
	50	3.37	1.27	8.1	3.04
HD 2967	0	4.45	1.20	1.6	5.52
	50	6.37	1.18	6.2	6.25
PBW 636	0	1.28	1.34	0.7	1.75
	50	1.56	1.51	4.5	1.47
PDW 291	0	0.71	1.48	0.3	1.06
	50	4.27	1.35	6.1	3.97
PDW 314	0	0.57	1.57	0.3	0.84
	50	3.03	1.14	9.8	2.74

DL = 7.10E^{-06} ; Teta = 0.25; F = 0.225

dry weight and root length that explain their higher efficiencies whereas inefficiency of durum wheat is attributed to their smaller roots and lower influx. The cultivar PBW 636 recorded highest SDW, RL and Mn uptake as compared to efficient cultivars at tillering but from tillering to anthesis there was a setback to its growth as a result percent increase in SDW and RL was very less that further affected the Mn uptake and influx. Thus, lower Mn influx and uptake at anthesis is responsible for inefficiency of PBW 636. The lower shoot yield of durum cultivars could be explained by their lower Mn uptake owing to their poor root growth^{8,37}. The correlation data also supported that higher uptake and influx led to high Mn efficiency of a cultivar during vegetative phase.

The biomass accumulation, Mn uptake and grain yield of all genotypes declined under Mn deficiency. The decline in yield under low Mn has also been reported earlier in wheat³⁵ and rice^{31,38}.

The nutrient efficiency in terms of relative yield (yield efficiency index) at low Mn revealed durum cultivars (PDW 314 and PDW 291) to be efficient than other cultivars but at the same time these cultivars had very low absolute yield and Mn uptake. Therefore, this index of nutrient efficiency can be useful only when the genotypes under study have same yields under non limiting nutrient availability^{39,7}. The data of correlation also supported

the fact as yield efficiency index was found to be negatively related to efficiency of a cultivar.

The cultivars with high Mn vegetative efficiencies were also having high utilization efficiencies i.e. these cultivars utilized the increased uptake of Mn for producing grains. This result was in concomitant of the higher partitioning of Mn uptake in grain rather than vegetative parts in these cultivars viz. PBW 550, BW 9178 and HD 2967 at maturity.

Hence, durum inefficiency could be explained by their lower root growth leading to lower uptake, influx and efficiency index during vegetative phase and their lower utilization efficiency during the generative phase. On the other hand in HD 2967 and

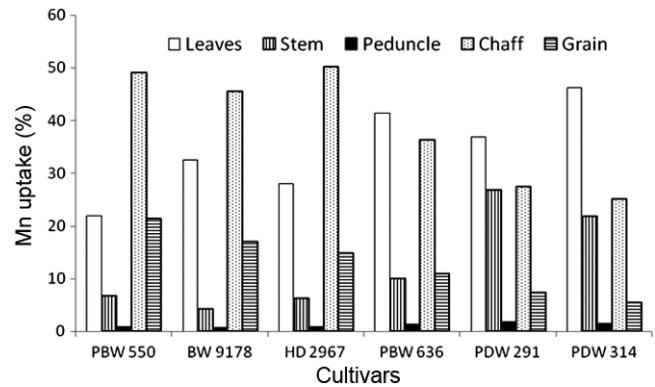


Fig.1—Partitioning of Mn (uptake) in various plant parts of different wheat cultivars at maturity under Mn deficiency

Table 5—Dry weight/pot (g) accumulated in various plant parts of different wheat cultivars at maturity as influenced by Mn application

Cultivar	0 mg Mn kg ⁻¹ soil						50 mg Mn kg ⁻¹ soil					
	Leaves	Stem	Peduncle	Chaff	Grain	Total	Leaves	Stem	Peduncle	Chaff	Grain	Total
PBW 550	1.01	0.54	0.14	2.87	1.65	6.21	4.25	8.23	1.02	27.91	16.84	58.3
BW 9178	1.23	0.35	0.15	2.55	1.46	5.73	4.75	6.04	1.06	34.55	24.03	70.4
HD 2967	1.47	0.66	0.16	2.27	1.28	5.83	6.67	9.79	1.81	32.94	21.54	72.7
PBW 636	1.40	0.65	0.10	1.27	0.71	4.13	5.48	9.09	1.01	17.37	8.56	41.5
PDW 291	1.43	0.72	0.07	1.00	0.54	3.76	5.99	10.22	1.48	12.78	6.52	37.0
PDW 314	1.45	0.75	0.06	0.82	0.44	3.52	6.61	10.63	1.14	10.34	4.61	33.3

CD (5%) Mn application = 0.405, Cultivars = 0.701, Mn application x Cultivars = 0.992

Table 6—Mn uptake (µg pot⁻¹) in various plant parts of different wheat cultivars at maturity as influenced by Mn application

Cultivar	0 mg Mn kg ⁻¹ soil						50 mg Mn kg ⁻¹ soil					
	Leaves	Stem	Peduncle	Chaff	Grain	Total	Leaves	Stem	Peduncle	Chaff	Grain	Total
PBW 550	11.2	3.4	0.4	25.0	10.9	51.0	128	81.6	3.7	251	188	653
BW 9178	16.0	2.1	0.3	22.4	8.4	49.0	186	52.2	3.5	320	235	798
HD 2967	13.1	2.9	0.4	23.4	6.9	46.7	241	72.5	6.9	381	182	883
PBW 636	13.2	3.2	0.4	11.6	3.5	31.9	147	89.8	4.4	173	66.8	481
PDW 291	6.6	4.8	0.3	4.9	1.3	17.9	112	120	7.4	130	37.2	406
PDW 314	6.8	3.2	0.2	3.7	0.8	14.7	105	141	6.4	110	22.8	385

CD (5%) Mn application = 3.88, Cultivars = 6.72, Mn application x Cultivars = 9.51

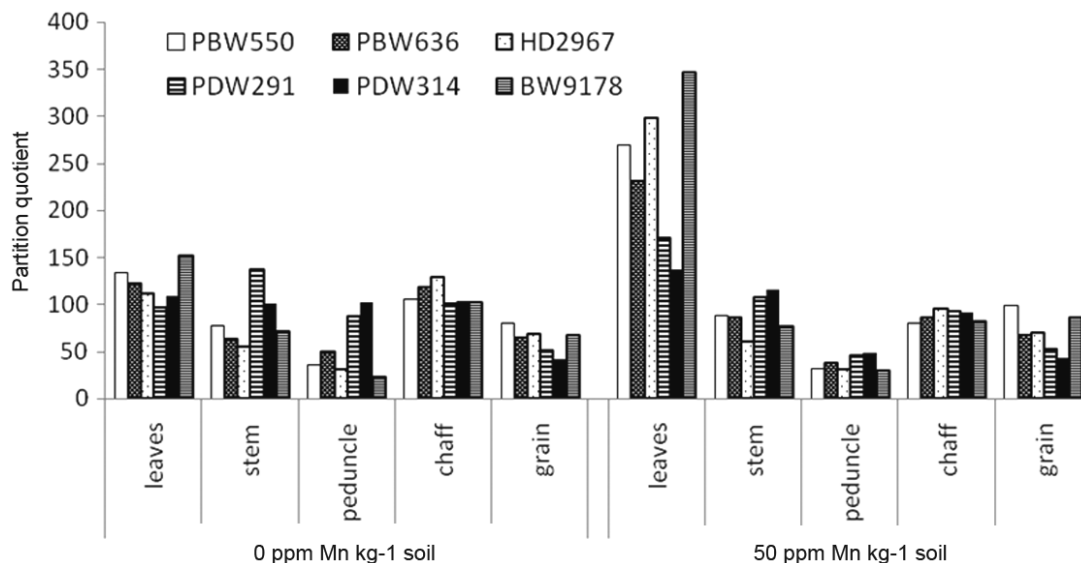


Fig. 2—Influence of Mn application on partition quotient of Mn in plant parts at maturity

PBW 550, longer roots, higher uptake, influx and efficiency index during vegetative phase and accumulation of less Mn in their vegetative parts and higher in grain leading to higher grain yield and utilization efficiency accounted for higher efficiency of these cultivars. It has been reported that Mn inefficient cultivars retained higher proportion of Mn in vegetative parts under Mn deficiency and lower partitioning to the grain and had the lowest grain yield. While Mn efficient cultivars facilitated superior Mn partitioning to the grain, lesser retention in vegetative organs^{40,41}.

Under Mn deficiency, Mn influx could explain 81% variation in yield and significantly influence total Mn uptake ($r = 0.79$) and grain Mn uptake ($r = 0.75$), that further could explain 94 and 98% variation in yield. Notably, BW 9178 out yielded HD 2967 during generative phase which can be explained by its lower retention of Mn in chaff relative to the grain in both treatments leading to its higher utilization efficiency that could explain 53% of variation in yield.

Manganese has very low phloem mobility so any remobilization from leaves to grains could probably not account for higher grain Mn accumulation in a cultivar. The other possibility could be continued uptake by roots and supply to the grains via xylem. Significant positive correlation of Mn influx with grain Mn uptake ($r = 0.75$) in the present study supported the fact that higher direct Mn supply to grain via xylem. The relative uptake in grain relative to the non-grain organs i.e. higher partitioning to grains also explained the higher grain yield of PBW

550 and BW 9178 and lower grain yield of the durum cultivars.

Conclusions

Mn efficiency of wheat cultivars depends upon uptake of each root segment i.e. the influx which in turn depends on depletion of Mn in the rhizosphere during vegetative phase and higher utilization efficiency of acquired Mn during reproductive phase that governs the ultimate grain yield.

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