ORIGINAL ARTICLE

Inter-cultivar variations of phosphorus deficiency stress tolerance in hydrponically grown Brassica

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Abstract

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Phosphorus (P) plays a central role as reactant and effector molecule in plant cell metabolism but P is limiting for crop yield on >30% of the world's arable land. Fear of depletion of world reserves of rock P, consistently increasing prices of phosphate fertilizers coupled with their notoriously low utilization efficiency has made the P-application cost ineffective and unacceptable choice for amelioration of inorganic phosphate (Pi) deficiency. A solution culture experiment was conducted to evaluate ten Brassica cultivars for their relative efficiency to utilize deficiently (20 µM) and adequately (200 µM) supplied P, in Johnson's modified

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solution. Pi deficiency markedly reduced shoot dry matter (SDM), root dry matter (RDM) production. Control of whole plant dry matter by plant P content under P deficient conditions suggests an internal regulation in addition to the influence exerted by external P supply. There were large differences of plant growth among Brassica cultivars exposed to the same P concentration in the growth medium. The cultivars differed significantly (p<0.001) in their root, shoot growth and root to shoot ratio. The P concentrations and uptake in shoot and P utilization efficiency (PUE) also varied significantly among different Brassica cultivars. Shoot and root dry matter yields as well as total biomass production were found to have significant (p<0.01) relationships with their shoot P uptake and P utilization. Cultivars, which were efficient in both P-acquisition and P-utilization, were found to be effective in the production of more biomass under both adequate and deficient levels of P.

Key words : Brassica, P-use efficiency, growth response, P content, P stress factor

Phosphorus (P) is one of six essential macronutrients (N, P, K, Ca, Mg and S) required by plants. Plant roots acquire P as inorganic phosphate (Pi), primarily in the form of $H_2PO_4^{1-}$ and HPO_4^{2-} depending on soil pH, from the soil solution (Vance *et al*., 2003). The concentration of Pi in the soil solution is often low (2 to 10 µM; Raghothama, 1999) and consequently, the supply of Pi to the root surface by diffusion is slow (Fitter and Hay, 2002). The diffusion of Pi in soils is slow (10^{-12} to 10^{-15} m^2 S^{-1}) (Rausch and Bucher, 2002), hence P is one of the most unavailable and inaccessible macronutrients in the soil (Vance *et al*., 2003; Raghothama, 2000) and frequently limits plant growth. Paradoxically, although phosphorus is abundant in the lithosphere, limited Pi availability represents a general phenomenon in many natural and agricultural ecosystems and a major constraint for crop production on tropical and subtropical soils. For this reason, crops are supplied with inorganic P fertilizers. However, the non-renewable nature of inorganic P fertilizers means that cheap sources of P, such as phosphate rocks, will be exhausted within the next 60-90 years (Plaxton *et al*., 1999; Plaxton, 2004). In addition, excess P added to crops can pollute local watercourses, contributing to the process of eutrophication (Withers *et al*., 2001). Therefore, P fertilization should be minimized. This might be achieved by developing crops that either acquire P or use P more efficiently, so that less P fertilizer is required, or developing more precise methods to monitor crop P status, such that P fertilization can be managed efficiently. It includes exploitation of genetic differences of plants in absorption, translocation, assimilation and utilization of nutrients in a resource-poor environment (Gill *et al*., 2002; Hammond *et al*., 2004). Differential response of genotypes in nutrient-stress environment may be related to morphological root features, efficiency of ion uptake mechanism, nutrient movement across roots and delivery to the xylem nutrient utilization in metabolism and growth processes (Vose, 1984; Clark and Duncan, 1991; Akhtar *et al*., 2002; Gill and Ahmad, 2003).

Plants have developed numerous morphological, physiological, biochemical and molecular responses to cope with growth under Pi-limiting conditions, including changes in root morphology, improved Pi uptake efficiency, and changes in metabolism (Raghothama 1999; Plaxton, 2004; Vance *et al*., 2003). The ultimate goals of these adaptive changes are increased Pi availability in the rooting media, enhanced Pi uptake and maintenance of plant metabolism. To optimally exploit the soil Pi, plants respond with an increased root-shoot ratio and increased P-acquisition and utilization. Therefore, selection of plant genotype efficient in biomass accumulation under P stress (deficiency) is an important strategy in Low Input Sustainable Agriculture (LISA) systems.

Brassica is one of the major oil seed crops of many countries for edible oil production but P is limiting its production by affecting oil content and seed yield. Categorization of the existing Brassica cultivars for P-use efficiency may help not only in sustaining production but also in providing a database for breeders for their future ventures. Keeping this in view, we evaluated 10 commonly grown Brassica cultivars for their efficiency to utilize P and their relative tolerance to P-deficiency stress grown at deficient (20 µM) and adequate (200 µM) P levels in the growth medium.

Materials and Methods

Plant material and growth conditions

Seeds of ten Brassica cultivars were collected from Ayub Agriculture Research Institute (ARRI), Faisalabad, Pakistan. The cultivars of Brassica tested were as follows: 'B. S. A.', 'Brown Raya', 'Con-1', 'Dunkled', 'Peela Raya', 'Rainbow', 'Gold Rush', 'Toria', 'Toria Selection' and 'Sultan Raya'. The experiment was conducted in a greenhouse and the temperature during growth period varied from a minimum of 20ºC to a maximum of 25ºC with a mean value of 23ºC. Seeds were germinated in polyethylene-lined iron trays containing pre-washed riverbed sand and irrigated with distilled water for seed germination and seedling establishment. Seven-day-old uniform sized seedlings were transplanted in foam-plugged holes (one plant per hole) in thermopal sheets floating on continuously aerated 200-L half strength modified Johnson's Solution (Johnson *et al*., 1957) in two polyethylene lined iron tubs (1 x 1 x 0.3 m). The composition of the nutrient solution was; [in mM]: KNO_3 [2], NH_4NO_3 [1], $Ca(NO_3)_2.4H_2O$ [2], $MgSO_4.7H_2O$ [0.5], K_2SO_4 [0.5] and [in µM]: Fe (III)-EDTA [50], H_3BO_3 [25], $MnSO_4.H_2O$ [2], $ZnSO_4.7H_2O$ [2], $CuSO_4.5H_2O$ [0.5], KCl [50], H_2MoO_4 [0.5]. The solutions in these tubs were modified to maintain deficient (20 µM) and adequate (200 µM) P levels, respectively, using $NH_4H_2PO_4$ as P source. The pH of the solution was daily monitored and maintained at 5.5±0.5 using HCl or NaOH. The nutrient solutions were renewed at 5-day intervals to maintain nutrient concentrations being exhausted because of plant uptake. Ten Brassica cultivars were grown in each P nutrient level using completely randomized factorial design with six repeats of each cultivar. Whole plants harvested at 30 days after transplanting were washed with distilled water, blotted dry with tissue paper and separated into shoots and roots. The samples were dried at 70ºC for 48 hours in a forced air-driven oven to a constant weight and dry weights (g plant^{-1}) were recorded using an analytical balance. The shoot and root samples were ground to a 40-mesh for further analysis.

Measurement of various growth parameters

The shoot and root samples (0.5 g each) were digested in a mixture of nitric acid (HNO_3) and perchloric acid ($HClO_4$) (3:1) (Miller, 1998). Phosphorus concentrations in shoot and root were estimated by the vanadate-molybdate yellow color method (Chapman and Pratt, 1961) using a spectrophotometer. Phosphorus uptake (mg plant^{-1}) was calculated on a root and shoot dry weight basis by multiplying P concentration in the respective tissue with its dry matter, and on whole plant basis by adding the two.

$$\text{P-uptake} = \text{P concentration (mg g}^{-1}) \times \text{dry matter (g plant}^{-1})$$

Phosphorus stress factor (PSF) for shoot dry matter was calculated by the formula given below:

$$\text{PSF} = \frac{\text{SDM}_{(\text{adequate P})} - \text{SDM}_{(\text{deficient P})}}{\text{SDM}_{(\text{adequate P})}} \times 100$$

Where SDM is shoot dry matter (g plant^{-1}) in the respective treatment.

Phosphorus Utilization Efficiency (PUE) was calculated according to Siddique and Glass (1983).

$$\text{PUE (g}^2\text{SDM mg}^{-1}\text{ P)} = \frac{\text{SDM (g plant}^{-1})}{\text{P concentration(mg g}^{-1})}$$

Values of various parameters observed at low P-level, relative to their respective values observed under control (keeping control value at 100) were estimated by the following formula.

Relative values of various parameters

$$= \frac{\text{SDM}_{\text{deficient}}}{\text{SDM}_{\text{adequate}}} \times 100$$

Analysis of Zinc and Calcium concentration

Zinc ($\mu g\ g^{-1}$) and calcium concentration ($mg\ g^{-1}$) in shoots of cultivars were estimated using atomic absorption spectrophotometery (Hanlon, 1998).

Statistical Analysis

Data were subjected to statistical analyses according to standard procedures (Steel and Torrie, 1980) using 'MSTAT-C' (Russell and Eisensmith, 1983), and the methods described by Gomez and Gomez (1984). Completely randomized factorial design (factorial CRD) was employed for analysis of variance (ANOVA). The separation of treatment (P-level) means was done by using Duncan's New Multiple Range test (DMRT). The means of cultivars at each level of P were separated using DMRT at each cultivar level by employing completely randomized design.

Results and Discussion

Phosphorus deficiency in the growth medium caused sharp decrease in most of the parameters studied except root and shoot ratio, P utilization efficiency and Ca concentration in shoot. An overall picture of the effects of P-deficiency on Brassica growth in terms of relative values of various growth parameters and characters of P metabolism compared to their respective value observed under control (keeping control value as 100) is presented in Figure 1.

Biomass production

Production of SDM is generally considered a good indicator of ultimate economic yield (Romer and Schenk, 1998; Ahmad *et al.*, 2001; Alloush, 2003). Therefore, SDM was used as a selection criterion for evaluating cultivars for nutrient efficiency at seedling stage. Brassica cultivars and rate of P supply was found to have a significant ($p<0.01$) direct and interactive effect on shoot growth, root development and total biomass production (Figure 2). Highly significant variations in SDM production due to P level x genotype interaction is a clear indication of the existence of useful genetic differences for responsiveness to P application. Such genotype-by-environment interaction seems to be very important in crop cultivar development (Kang, 1998).

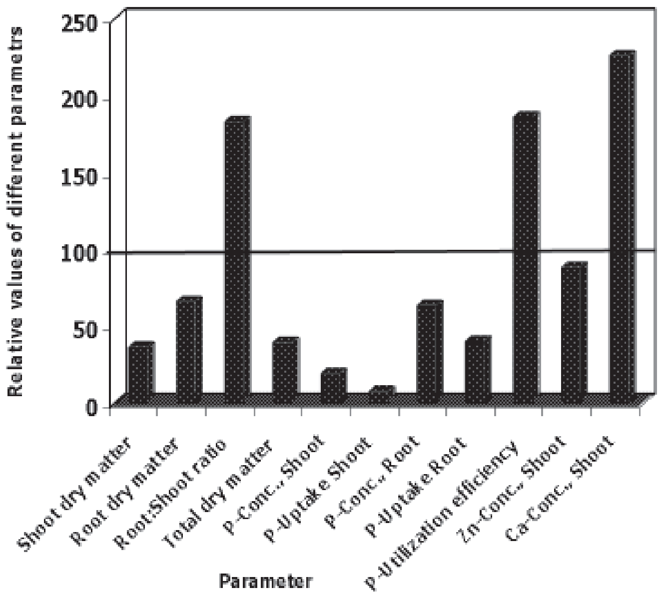

Figure 1. Values of various parameters observed at deficient P level, relative to their respective values observed under control, by considering control values as 100.

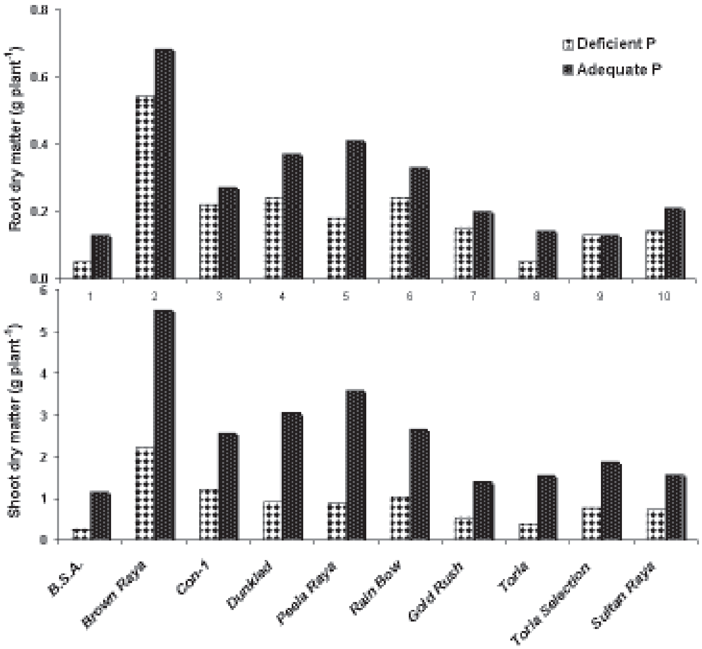

Figure 2. Root and shoot dry matter of Brassica cultivars with deficient and adequate levels of P.

Average production of SDM was found to be decreased about 2.8 fold in Brassica cultivars when P concentration in the rooting media was decreased from 200 µM to 20 µM. A similar trend of decrement of SDM of Brassica with a decrease level of P was observed by Jain *et al.* (1996) and Akhtar *et al.* (2002). Brown Raya yielded maximum SDM at both the P levels and proved to be highly efficient and responsive (Figure 2).

Phosphorus stress factor (PSF) or relative reduction in SDM due to P-deficiency can also be used as a useful parameter in assessing relative tolerance (Ahmad *et al*., 2001; Gill *et al*., 2002) of Brassica cultivars to low P conditions. The PSF or relative reduction in SDM due to P-deficiency was significantly ($p<0.01$) different among cultivars, indicating their relative tolerance to low P conditions (Figure 3). The genotypes showing relatively low PSF values such as Brown Raya, Con-1 and Sultan Raya may be considered suitable for growing under P-limiting conditions. Relative reduction in SDM of the cultivars ranged between 36% (Brown Raya) and 76% (B.S.A.) indicating a considerably wide genetic variation for adaptability to P-deficient conditions. Since PSF only indicates relative magnitude of reduction in SDM due to P-deficiency compared to control, it cannot be used as a sole criterion for selecting genotypes to be grown under P-deficiency stress. The P-tolerant selected cultivars on the basis of PSF should also be reasonably efficient under P-deficient as well as P-sufficient conditions. Phosphorus stress factor as a function of PUE of P-deficient Brassica cultivars revealed that genotypes such as Brown Raya and Con-1 showing lower PSF values are considered more efficient than other cultivars (Figure 5).

Dependence of SDM production by Brassica cultivars on various growth parameters and characters of P metabolism at stress and adequate P levels in the solution, determined in terms of 'r' values are presented in Table 3. Root dry matter, total dry matter, P-content in shoot and PUE had significant and positive effect on production of SDM in P-deficient environment. Shoot-P concentration, however, negatively affected SDM of genotypes exposed to P-deficient conditions.

Root dry matter of Brassica cultivars was decreased 1.5-times due to P deficiency (Figure 2) in agreement with Ahmad *et al.* (2001), who

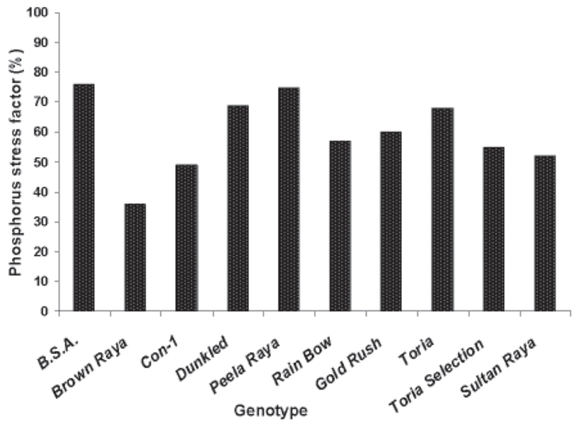

Figure 3. Relative reduction in shoot dry matter of Brassica cultivars due to P deficienty.

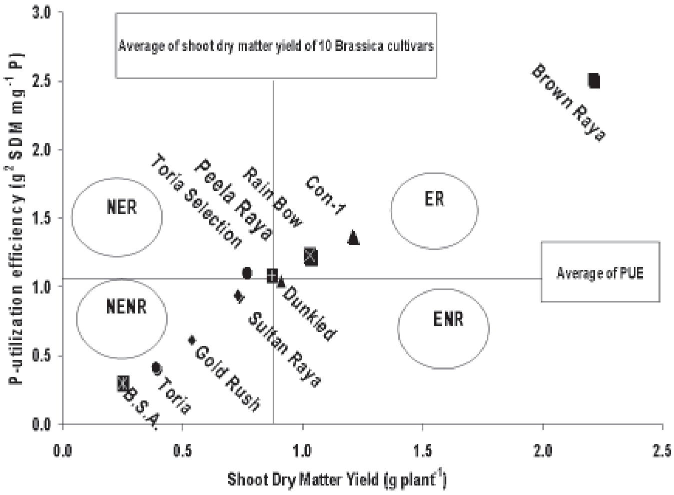

Figure 4. Classification of Brassica cultivars for P utilization efficiency.
ER: Efficient and Responsive
NER: Non-efficient but Responsive
ENR: Efficient but non-responsive
NENR: Non-efficient and non-responsive

reported similar reduction in root dry matter of cotton cultivars due to P-deficiency. Shoot P uptake and PUE had significant ($p<0.01$) and positive correlation with total dry matter production in Brassica cultivars (Table 3).

Phosphorus concentration and content in shoot and root

Various Brassica cultivars and rate of P supply had a significant ($p<0.01$) direct and interactive effect on shoot P concentration of Brassica genotypes. Shoot P concentration was significantly lowered (5-fold) in P-stressed Brassica cultivars compared to those grown with adequate P (Table 1). Considering 2.00 mg g^{-1} as the sufficiency limit of P in shoot at about its ontogenic stage, all the cultivars grown at 0.02 mM P level showed internal P-deficiency. Low P supply in growth medium caused P-deficiency in plants especially in P deficiency non-tolerant cultivars (Figure 6).

A decrease in P supply (10 fold) in the root medium decreased the P content about 15-fold in

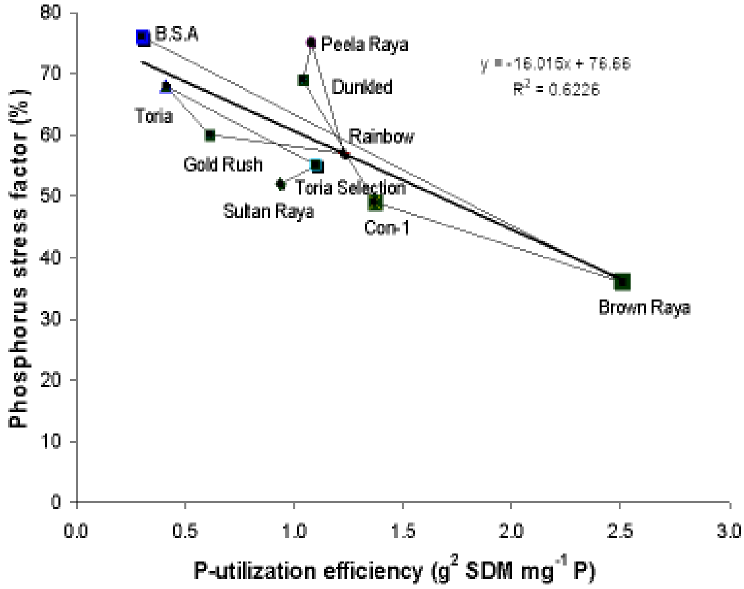

Figure 5. Phosphorus-stress factor as a function of P-utilization efficiency of P-deficient Brassica cultivars.

Table 1. Phosphorus concentration (mg g^{-1}) in shoots and roots, and P-uptake (mg $plant^{-1}$) in shoots, roots and whole plants of Brassica cultivars at deficient (20 µM) and adequate (200 µM) levels of P in nutrient solutions

Cultivar	Shoot P-conc. (mg g^{-1})		Shoot P-uptake (mg $plant^{-1}$)		Root P-conc. (mg g^{-1})		Root P-uptake (mg $plant^{-1}$)		Total P-uptake (mg $plant^{-1}$)	
	Deficient P	Adequate P	Deficient P	Adequate P	Deficient P	Adequate P	Deficient P	Adequate P	Deficient P	Adequate P
B.S.A.	0.85 NS	5.22 a	0.21 NS	5.94 d	2.54 NS	3.52 NS	0.13 NS	0.46 c	0.31 cd	6.40 c
Brown Raya	0.88	4.70 bc	1.95	25.75 a	1.60	3.20	0.87	2.20 a	2.82 a	27.95 a
Con-1	0.89	5.04 a	1.08	12.90 b	1.42	3.16	0.31	0.85 bc	1.39 b	13.75 b
Dunkled	0.88	3.63 f	0.80	11.04 bc	2.1	3.51	0.50	1.30 b	1.30 b	12.34 b
Peela Raya	0.79	4.06 e	0.70	14.52 b	2.61	4.06	0.46	1.67 ab	1.16 b	16.19 ab
Rain Bow	0.86	4.17 e	0.89	11.18 bc	2.06	3.51	0.49	1.16 ab	1.38 b	12.34 b
Gold Rush	0.88	4.96 ab	0.48	6.91 cd	2.44	3.28	0.37	0.65 bc	0.85 bc	7.56 bc
Toria	0.97	4.57 cd	0.38	7.09 cd	2.26	3.26	0.12	0.45 c	0.50 c	7.54 bc
Toria Selection	0.70	4.29 de	0.54	7.96 cd	2.38	3.26	0.31	0.42 c	0.85 bc	8.38 bc
Sultan Raya	0.78	4.16 e	0.58	6.48 d	2.29	3.58	0.32	0.75 bc	0.90 bc	7.23 c
Mean[2]	**0.85 B**	**4.48 A**	**0.76 B**	**10.98 A**	**2.17 B**	**3.43 A**	**0.39 B**	**0.99 A**	**1.15 B**	**11.97 A**
F-values for analysis of variance										
P-level (P)	395.380***		3130.193***		331.482***		93.813***		271.236***	
Cultivar (C)	8.579**		1117.574***		2.676NS		6.216**		7.964**	
P X C	7.362**		819.666***		1.031NS		5.689**		6.823**	

[1] Individaul treatment means in the same column with different letter(s) differ significantly according to Duncan's multiple Range test (P = 0.05):
**** Significant at P = 0.01: *** Significant at P = 0.001: NS Non-significant.**
[2] Avergae of all treatments (Treatment means)

Table 2. Shoot Ca and Zn concentration, Root: Shoot ratio and PUE of Brassica cultivars grown at deficient (20 µM) and adequate (200 µM) P levels

Cultivar	Shoot Ca-conc. ($mg\ g^{-1}$)		Shoot Zn-conc. ($\mu g\ g^{-1}$)		Root :Shoot ratio		PUE (g^2 SDM mg^{-1} P)	
	Deficient P	Adequate P	Deficient P	Adequate P	Deficient P	Adequate P	Deficient P	Adequate P
B.S.A	10.56 e	5.38 de	57 a-d	58 bcd	0.24 abc	0.11 NS	0.30 e	0.23 e
Brown Raya	19.10 a	6.28 cde	45 e	68 ab	0.28 ab	0.14	2.51 a	1.18 a
Con-1	16.85 bc	8.56 ab	65 ab	56 cd	0.19 bcd	0.12	1.37 b	0.51 bc
Dunkled	17.14 b	7.24 bc	55 b-e	53 d	0.26 abc	0.12	1.04 bc	0.84 ab
Peela Raya	17.39 b	5.43 de	55 b-e	67 abc	0.25 abc	0.11	1.08 bc	0.89 ab
Rain Bow	18.04 ab	7.26 bc	48 cde	60 bcd	0.24 abc	0.15	1.23 bc	0.63 bc
Gold Rush	15.60 cd	9.29 a	67 a	77 a	0.30 a	0.15	0.61 de	0.28 c
Toria	11.80 e	4.94 e	58 abc	58 bcd	0.13 cd	0.10	0.41 e	0.34 c
Toria Selection	14.26 d	6.07 cde	62 ab	62 bcd	0.17 bcd	0.08	1.10 bc	0.44 c
Sultan Raya	11.71 e	6.97 cd	47 de	65 bc	0.18 bcd	0.14	0.94 cd	0.39 c
Mean[2]	**15.25 A**	**6.74 B**	**56 B**	**63 A**	**0.22 A**	**0.12 B**	**1.06 A**	**0.57 B**
F- values for analysis of variance								
P-level (P)	2169.115***		1333.333***		331.482***		10.110***	
Cultivar (C)	379.972***		318.519***		2.676NS		21.551***	
P X C	211.639***		261.031***		1.031NS		5.689**	

[1] Individaul treatment means in the Means in the same column with different letter(s) differ significantly according to Duncan's multiple Range test (P = 0.05): ** Significant at P = 0.01: * Significant at P = 0.001: [NS] Non-significant.**
[2] Avergae of all treatments (Treatment means)

Figure 6. Symptoms of P-deficiency in B.S.A. cultivar at low (20 µM) P supply in growth medium.

shoot of tested Brassica cultivars. Brown Raya had maximum shoot P content while minimum was observed in B.S.A. and Gold Rush averaged over both P levels. Plants exposed to P-deficiency stress retained more P in their roots than shoots (Adu-Gyamfi *et al*., 1990) similarly to Gill and Ahmad (2003) and Snapp and Lynch (1996) who reported that efficient cultivars retained a relatively larger amount of stressed element in their roots, in a bid to develop a more efficient root system. In this experiment, the Brassica cultivars growing under control conditions retained 8.3 % of total acquired P in their roots compared to cultivars growing under P-deficiency stress, which retained 33.9% of total P in their roots. These results suggested smooth translocation of P to aerial plant parts under conditions of adequate P supply compared to P-deficient conditions. Phosphorus uptake in shoot had a highly significant ($p<0.01$) positive correlation with RDM and SDM (Table 3), suggesting that the genotypes with higher RDM accumulated higher amounts of P in their shoots similar to Machado and Furlani (2004), who reported a positive correlation between SDM, RDM and P uptake.

A two-fold decrease in RSR of Brassica cultivars was observed when P concentration in the nutrient solution was increased from 20 to 200 µM (Table 2). Higher RSR is often reported for P-deficient plants when compared with P sufficient plants. This is attributed to higher export rates of photosynthates to the roots and utilization of photoassimilates in the roots (Chamk *et al*., 1994; Blair and Wilson, 1990). Preferential root growth helps the stressed plants to acquire more P from the environment in response to P stress conditions. RSR had a highly significant ($p<0.01$) positive correlation with RDM at deficient P level (Table 3).

Zinc and calcium concentration in shoot

Zinc concentration in shoots of Brassica cultivars at both P levels with analysis of variance is presented in Table 2. Statistical analysis revealed highly significant ($P<0.01$) variation of individual cultivars and P levels and also the combined effects for cultivar and P levels. Brassica cultivars varied significantly in zinc concentration at both P levels. Averaged across P levels, zinc concentration in shoots of genotypes ranged from 54 to 72 µg g^{-1}. Negative correlation between SDM and Zn concentration revealed that Zn played no role in SDM production under low and high P-supply (Table 1). The magnitude of relationship, however, was meager in both cases and statistically meaningless at both P-levels. Zn concentration increased at about 1.13-fold, with increasing P level from 20 to 200 µM in the growth medium. This is in agree-

Table 3. Correlation Matrix of different parameters of Brassica cultivars studied at deficient (20 µM) and adequate (200 µM) P levels.

	P- Level	SDM	RDM	TDM	P Conc.	PUE	P Uptake	RSR	Ca
RDM	Low P	0.757**							
	High P	0.835**							
TDM	Low P	0.991**	0.837**						
	High P	0.998**	0.866**						
P-Conc.	Low P	0.055^{NS}	0.034^{NS}	0.053^{NS}					
	High P	-0.183^{NS}	-0.213^{NS}	-0.186^{NS}					
PUE	Low P	0.982**	0.748**	0.974**	-0.105^{NS}				
	High P	0.976**	0.830**	0.975**	-0.366**				
P-uptake	Low P	0.985**	0.739**	0.975**	0.199^{NS}	0.935**			
	High P	0.979**	0.830**	0.975**	0.002^{NS}	0.911**			
RSR	Low P	-0.017^{NS}	0.467**	0.005^{NS}	-0.061^{NS}	-0.112^{NS}	-0.103^{NS}		
	High P	-0.207^{NS}	0.313*	-0.155^{NS}	-0.037^{NS}	-0.197^{NS}	-0.208^{NS}		
Ca	Low P	0.544**	0.689**	0.525**	0.052^{NS}	0.529**	0.538**	0.375*	
	High P	-0.059^{NS}	0.015^{NS}	-0.045^{NS}	0.196^{NS}	-0.093^{NS}	-0.018^{NS}	0.239^{NS}	
Zn	Low P	-0.252^{NS}	-0.30*	-0.027*	0.070^{NS}	-0.265*	-0.243^{NS}	-0.142^{NS}	-0.179^{NS}
	High P	-0.055^{NS}	0.161^{NS}	0.066^{NS}	0.172^{NS}	0.012^{NS}	0.087^{NS}	0.152^{NS}	0.184^{NS}

SDM: shoot dry matter, RDM: Root dry matter, TDM: Total dry matter, PUE: Phosphorus utilization efficiency, RSR: Root: Shoot ratio.
**** = Highly significant, * = Significant, ^{NS} = Non-significant**

ment with the results reported by Shamsa *et al.* (2005) who reported that P addition decreased shoot Zn concentration in maize and sunflower; however, it increased Zn concentration in Brassica over control. This may be attributed to an increase in P-supply reducing the molar ratio (MR) of Zn to P in maize and sunflower, while increasing it in the case of Brassica, evidencing that P-Zn interaction is highly species dependent and P-induced reduction in shoot Zn concentration varied among species and cultivars due to differences in P and Zn use efficiencies. At low P-level, the impact of Zn on SDM production was negative and nominal among tested Brassica cultivars (Figure 7), however; significant negative correlation between PUE and Zn concentration (Table 3) showed that cultivars exhibiting more PUE accumulated marginally low Zn concentration in their shoot.

Various Brassica cultivars and rate of P supply had a significant ($p<0.01$) direct and interactive effect on Ca concentration in Brassica shoot. Calcium concentration in shoot of Brassica cultivars decreased 2.25 times with increasing P from 20 to 200 µM in the growth medium (Table 2) . This may be attributed to growth dilution effect, which is clear from the difference in SDM production (Figure 1) at both P levels, evidencing that when the rate of plant growth exceeds the rate of uptake of a particular nutrient, the concentration of that nutrient in tissue decreases or is 'diluted' in the

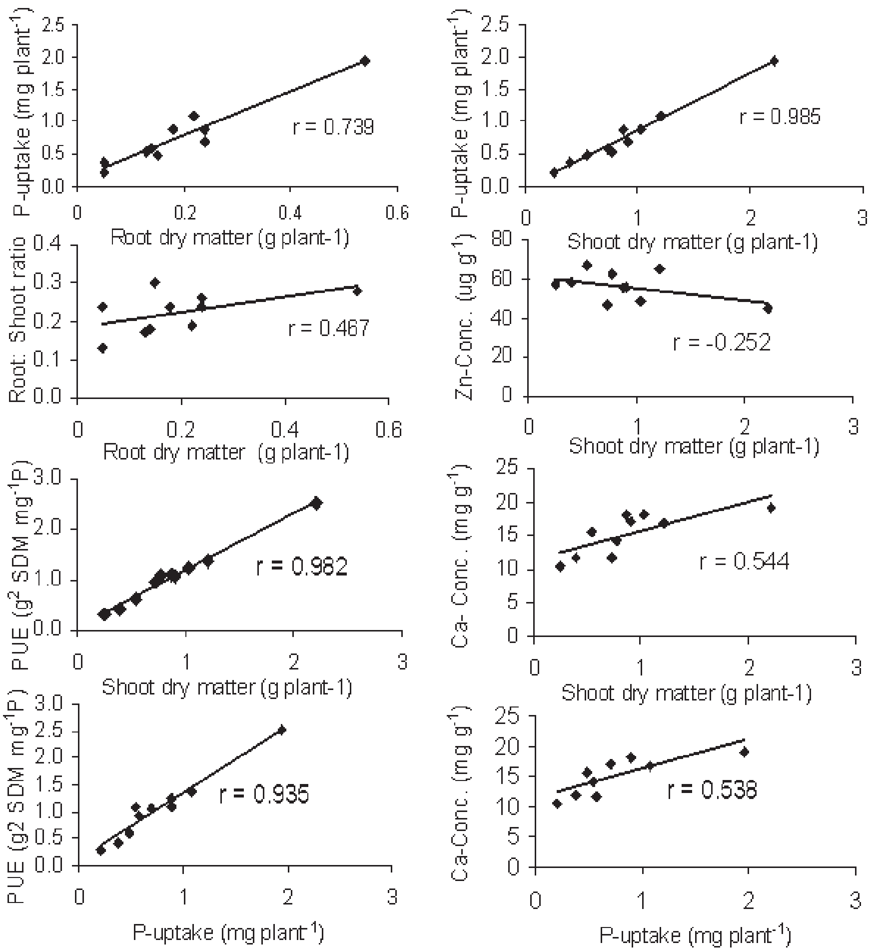

Figure 7. Relationship between various growth parameters and root and shoot dry matter production of ten Brassica cultivars under P-stress conditions in solution culture.

plant tissue. Some cultivars such as Brown Raya that had taken up higher Ca in their shoots also showed higher shoot P-uptake and were able to produce more shoot dry matter at stress P-level.

Higher uptake of Ca by plants reduces its activity in the system and, hence, the plant availability of Ca-bound P is increased. Shoot dry matter and shoot P-uptake correlated significantly with calcium concentration in shoot of Brassica cultivars at stress P level (Figure 7), implying that cultivars had taken up higher Ca and P-content in their shoots, which leads them to produce more biomass at stress P-level. This can also lead to the assumption that higher P-acquisition of efficient cultivars was because of their high Ca-uptake and cultivars that are efficient accumulators of Ca are desirable as they can acquire higher amounts of P from otherwise P-deficient soils.

Phosphorus utilization efficiency (PUE)

Cultivars and level of P had a significant ($p<0.01$) effect on PUE in Brassica genotypes (Table 2). About a 2-fold decrease in PUE was observed with increasing P from 20 to 200 µM in the growth medium, implying that less dry matter was produced for each additional unit of P absorbed. The highest and lowest PUE's were observed in Brown Raya and B.S.A. averaged over both treatments, respectively. These findings agree well with the results presented by Eliot and Lauchli (1985), Fageria *et al*. (1988) and Gill *et al*. (2002), who reported significant differences in PUE of various crops. Cultivars can be categorized into four groups in terms of responsiveness and efficiency on the basis of the relationship between SDM and PUE (Figure 4). Nutrient-use efficiency is generally considered to result from either a better ability in uptake of nutrients or better efficiency in using nutrients already available in the tissue (Blume, 1988). P utilization efficiency exhibited a significant ($p<0.01$) and positive relationship with shoot P uptake, SDM and RDM at both P levels (Table 3). Relationship between various growth parameters and shoot and root dry matter production of six Brassica cultivars exposed to low P-supply in solution is presented graphically in Figure 7, evidencing that PUE and P-uptake are important growth parameters in selection of cultivars and providing a basis for P-deficiency tolerance in Brassica. A very strong positive correlation between PUE and total P-uptake is specifically important as it indicates lack of interaction between these two traits and thus efficient utilization of P taken up by the plant for production of SDM.

Conclusions

Considerable variability was observed in shoot dry matter (SDM), root dry matter (RDM), shoot P content and PUE among the tested Brassica cultivars at both P levels in nutrient solution. Cultivars which were efficient in P utilization such as Brown Raya, were also efficient accumulators of biomass at both P levels. Brown Raya was an efficient cultivar in SDM production at stress P level while B.S.A. and Toria were inefficient in terms of SDM production. SDM and RDM of all Brassica cultivars were correlated significantly with their shoot P content, P utilization efficiency and calcium concentration in shoot. Higher shoot dry matter of the cultivars was related to their better P-acquisition ability, which in turn was related to higher Ca uptake. However, validation of these results is warranted under field conditions.
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