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Root traits, nutrient uptake, multi-location grain yield and benefit–cost ratio of two lentil (*Lens culinaris*, Medikus.) varieties

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Abstract

Lentil is a protein-rich pulse, grown mainly in developing countries as a rain-fed crop in nutrient-poor soils. Hence, the importance of root traits for efficient capture of soil nutrients and water can be crucial to its economical yield. Little is known about the lentil root system and even less about its relationship to grain yield. We compared the root system of two Bangladeshi lentil varieties, Barimasur-3 (BM-3) and Barimasur-4 (BM-4), in a pot experiment and related it to their multi-location grain yield in the fields. BM-4 maintained faster root development both at an early growth stage (20 days after sowing) and at flowering (60 days) compared to BM-3. The roots of BM-4 penetrated the 25 cm depth of the soil profile after 19 ± 1 days and while those of BM-3 took 24 ± 2 days to reach the same depth. The roots of BM-4 were covered with denser (26 ± 3 mm^{-1}) and longer (0.48 ± 0.11) root hairs than BM-3 (density 17 ± 2 mm^{-1}, length 0.32 ± 0.09 mm). The differential presence of root hairs increased the effective length of root system of BM-4 by 12 times and that of BM-3 by five times. The lentil varieties did not differ in their ability to induce pH change and acid phosphatase activity in rhizosphere. In the pot experiment, the uptake of macro-nutrients (K, P, Ca, and Mg) as well as micro-nutrients (Fe, Mn, Zn, Cu, B and Mo) by BM-4 was significantly higher, compared to BM-3. The varieties produced the same amount of shoot biomass. At five of six agro-ecological distinct field locations in Bangladesh, BM-4 gave significantly higher (10–20%) grain yield than BM-3. Linked with the higher grain yield, the benefit-cost ratio (BCR) of BM-4 was 3.14 and that of BM-3 were 2.62, indicating that BM-4 provided better return per unit investment, compared to BM-3, supported by the better root morphology and higher nutrient uptake. This may be one of the reasons supporting the popularity and preferred adoption of BM-4 among the Bangladeshi farmers, who grow lentil mainly on nutrient-poor soils. The results indicate the benefits of selection and breeding for superior root traits for better agro-economics.

Introduction

Lentil (*Lens culinaris* L.) is an annual diploid ($2n = 14$), protein-rich staple pulse grown in many developing countries including the Indian subcontinent, West Asia, North Africa, Sudan, Yemen, Ethiopia, Eritrea and South America; where it complements the cereal-rich diet of the general population, particularly the vegetarians and low-income groups. Approximately half of the world's area cultivated to this crop is estimated to lie in South Asia (Erskine and Saxena, 1993).

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In Bangladesh lentils cover about 33% of the total area under pulses and they are, from the consumer's point of view, the most preferred pulse, popularly known as *masur dhal*. Lentil seed is a source of high-quality protein for human and its straw and milling wastes are high value animal feed (Kurdali et al., 1997).

Lentil is often grown on nutrient-poor soils with no or little fertilizer applications and is largely a rain-fed crop, often subjected to intermittent drought during the growth period and/or terminal drought in the reproductive phase. As receding soil moisture is better conserved in deeper soil layers, lentil varieties developing larger and deeper root system are advantageous for sustaining yield in nutrient-poor soils of dry areas.

Superior morphological (root length, root hairs) and physiological (exudation of protons and enzymes) root traits facilitate efficient use of existing and added nutrients and water resources in soils and may confer better return of the fertilizers and irrigation inputs. However, root traits of lentil have rarely been investigated (Sarker et al., 2003) and any linkage of root traits to the economic performance of lentil varieties is largely unknown. The knowledge on the genetic diversity in root traits is desirable, as it will enhance targeted breeding of improved varieties, able to resist nutrient and water stresses in the fields of resource-poor growers, ensuring them better harvests and improved livelihoods.

This paper reports the link of various morphological (root length, root hairs), and physiological (rhizosphere pH and exo-cellular phosphatase enzymes) with grain yield and benefit-cost ratio (BCR) of two lentil varieties.

Materials and methods

The various root traits of the two lentil varieties, Barimasur-3 (BM-3) and Barimasur-4 (BM-4), were studied, because they are high yielding, but often contrast in grain yield and popularity and adoption among farmers in Bangladesh. Both varieties are small seeded (*microsperma*) and considered to be tolerant/resistance to Rust and *Stemphylium* Blight diseases. The seeds of BM-4 are light pink in color, which accords them slightly higher market price. BM-3 was developed through a national hybridization program from a cross between BLL 79666 (Indian) and local landrace from Pabna Bangladesh (Sarker et al., 1999a). BM-4 was developed from the cross between ILL 5888 (improved landrace) and ILL5782 (ICARDA breeding line) at ICARDA-Syria specifically for Bangladesh (Sarker et al., 1999b).

Soil properties

The available data on the properties of soil used in the pot experiment are given below, Soil pH 7.7 (0.01 M $CaCl_2$); organic matter 0.55%; total N 0.029%; major cations extracted with ammonium acetate and measured with flame photometer (Doll and Lucas, 1973) (meq/100 mL), Ca 12.0; Mg 2.5; K 0.25 and other nutrients (μg/g) P 10.3 (Olsen-P, Olsen et al., 1954); S 20 (Tabatabai, 1982); B 0.59 (hot water extract, Bingham (1982); Cu 6.3; Fe 11; Mn 6; Zn 1.7 (extracted with DTPA and measured with atomic absorption spectroscopy, Lindsay and Norvell, 1978).

Determination of root growth and length

The root growth and length of the two varieties was studied in a pot experiment at Pulses Research Center, Ishurdi, Bangladesh. Pots were made by cutting two liter transparent plastic bottles (Figure 1a). These were filled with 2.2 kg of soil by shaking to achieve soil bulk density of 1.4 g $cm^{-3.}$ The soil columns of all the pots were 25 cm high. The pots were placed in the open, sides of pots wrapped in black polythene to prevent exposure of roots to light and maintained at 20% soil moisture by weighing and adding water. Six seeds per pot were planted at 1-cm depth. After germination, three uniform, healthy seedlings were evenly left in each pot by removing extra seedlings along with the roots. There were four replicates. The date of germination (3–4 days after sowing in both cases) and the date when roots reached the bottom of the pot was recorded to calculate the root penetration time in the soil profile. No major differential disease occurrence was observed in the pot experiment.

At 20 and 60 days after sowing, shoots were cut and stored in paper bags for drying. The roots were washed out of soil and cleaned of debris and examined for any differences in nodulation. About 1 g of root sample was spread

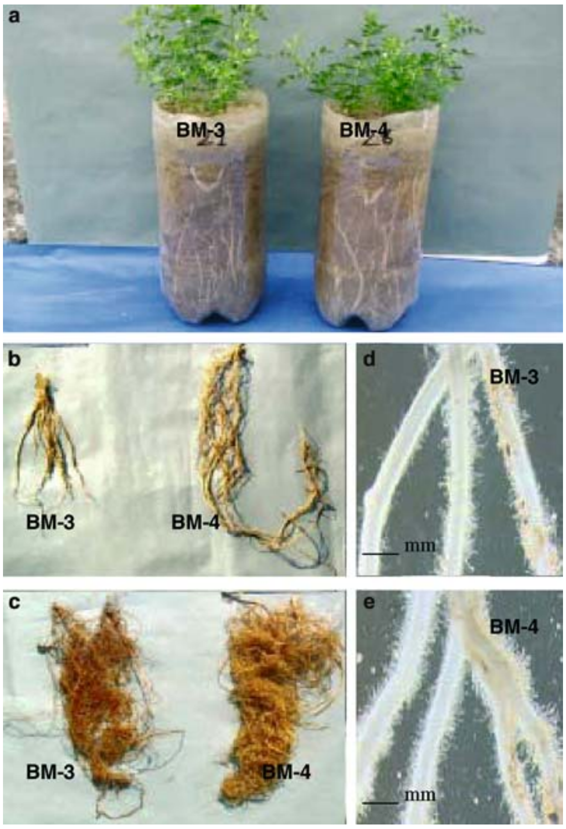

Figure 1. Roots and shoot of two lentil varieties, Barimasur-3 (BM-3) and Barimasur-4 (BM-4). Pots with visible roots and shoot growth of BM-3 and BM-4 at 60 days after sowing (a). Root system of BM-3 and BM-4 at 20 days after sowing (b) and at 60 days after sowing (c). Root hairs of BM-3 (d) and of BM-4 (e).

between polythene transparencies and scanned using ScanJet IIcx. The total length of the root system was measured using *Dt-Scan software* (Delta-T Devices, Cambridge, England) as described in Gahoonia et al. (1999).

Plant analyses

Digestion of plant material

Shoots of the pot experiment at flowering stage (60 DAS) was dried at 60 °C until constant weight was recorded. The whole plant material of each pot was ground using a Ultra Centrifugal Mill (Retsch ZM 100). The plant material (0.25 g) was digested in an open vessel system using 70 mL HD polyethylene vials (Capitol Vial Corp, Fulton Ville, NY, USA) and a graphite-heating block (Mod Block, CPI International, Amsterdam, Holland). The plant material was digested at 95 °C using a slight modification of the EPA (Environmental Protection Agency, USA) Method 3050B, as described below. Five milliliter of 35% HNO_3 (Instra analyzed, Baker, Deventer, Holland) was added to the samples and the samples were boiled for approximately 15 min. After cooling, 2.5 mL 70% HNO_3 was added and the samples were reheated. Twenty-five minutes later samples was cooled and 1.5 mL H_2O_2 (Extra pure, Riedel-de-Haën, Seelze, Germany) was applied. When the peroxide reaction ceased, 1 mL of H_2O_2 was added and samples were reheated for approximately 40 min. During the digestion, vials were covered by watch glasses. Samples were cooled overnight and diluted to 50 mL with ultra pure water. For each digestion five blank samples were included. Furthermore samples of a certified reference material-CRM (Apple leaf, standard reference material 1515; National Institute of Standards and Technology, Gaithersburg, MD, USA) were digested to estimate the accuracy and precision of the analysis. Finally, an in-house barley reference material was included in order to keep a check of element concentrations in each individual run on the ICP-MS. Samples were diluted to the same acid concentration (1.75% HNO_3) as standards and quantification was done by external calibration (P/N 4400 ICP-MS, Multi-elemental calibration standard, CPI-International, Amsterdam, Holland). Dilutions were performed in a class 100 laminar flow bench (KR-170s Bio-wizard, Kojair Tech Oy, Vilppula, Finland).

ICP-MS and IR-MS

A total of 12 elements (K, P, Ca, Mg, S, Fe, Zn, Mn, Cu, B, Mo, Co) were analyzed by ICP-MS (Agilent 7500c, Agilent Technologies, Manchester, England). Nitrogen (N) was not analyzed, because lentil, a legume, can fix and make use of atmospheric N_2 and the uptake of N is less dependent on size of the root system.

Determination of root hairs

The soil was filled in 10 cm long test tubes (diameter 3 cm, soil bulk density 1.4 g cm^{-3} and 20% soil moisture, four replicates). One pre-germinated seed was planted in each tube. After 20 days, the tubes, after cutting the shoot, were immersed in water overnight in a dark room to prevent mucilage formation. All roots were removed carefully using a kitchen sieve and transferred into an Ultrasound water bath (Branson 5200, 120W, 47 kHz). The ultrasound treatment for about 5–10 min removed remaining soil particles without damaging the root hairs. The root hairs were quantified using Quantimet 500_{+} Image Processing and Analysis System (Leica) at 10× magnification (Gahoonia and Nielsen, 1997).

Determination of rhizosphere pH

The roots of 10-days-old seedlings of the two lentil varieties were embedded in agar containing pH indicator dye *Bromocresol purple* and adjusted to pH 6 (Marschner and Romheld, 1983). The root-induced pH change, revealed by color change, was recorded after one hour following the agar embedding.

Rhizosphere phosphatase activity

The ability of the lentil varieties to release acid phosphatase (Aptase) in the rhizosphere was determined by the method described in Dinkelaker and Marschner (1992), based on enzymatic hydrolysis of 1-naphtylphosphate (substrate) by root released Aptase, yielding 1-naphtol, which forms a red complex with Fast Red TR (dye). The intact roots of 10-days-old seedlings were sandwiched between two ashless filter papers, soaked in a mixture of the dye and the substrate. If the roots release variable phosphatase enzymes, their activity is visible as brownish red color of variale intensity near the roots, because root released phosphatase produces a brownish red complex with the dye Fast Red TR after ca. 60 min.

Field experiments

Field plot trials were conducted in six districts (Faridpur, Rajshahi, Meherpur, Jhanaidah, Jessore and Kushtia) of Bangladesh, as lentils are extensively cultivated in these regions. The experiments were laid out during same season in RCB design, where each location had three replications. Plot size was 5 × 5 m. All experiments were sown in the first week of November and harvested in first week of March. All plots at all locations were treated similarly. At harvest grain yield was recorded. Chemical sprayings controlled minor occurrence of diseases of the two varieties at all locations.

Benefit–cost ratio (BCR)

Benefit–cost ratio (BCR = gross return per ha/total variable costs per ha, Table 2) of a variety indicates the amount of money earned by investing a given unit amount of the money. To avoid confusions, BCR in this paper should be understood as it is defined here. Gross return was calculated as the current market value of grains, straw and other milling by-products harvested per ha. Total variable cost accounts for those costs which were purchased or hired (seeds, soil preparation and chemical spraying). No fertilizers were applied in the experiments. As it was necessary to treat both the varieties equal at all field locations, the total variable costs were also equal (Table 2). Due to the attractive seed color of BM-4, its market price is slightly better (20 Takka kg^{-1}) compared to BM-3 (19 Takka kg^{-1}) and the higher value of by-products of BM-4 is mainly due to its higher milling waste which followed its higher grain yield (Table 2). As the production of straw did not differ between the varieties and it was valued equal.

Statistical analyses were performed with Statistical Analysis System (SAS) Institute, (1989) and Microsoft Excel software as found appropriate. Statistical significance of the differences between the treatments was analyzed by analysis of variance (ANOVA).

Results

Root traits, shoot biomass and nutrient uptake

The two lentil varieties Barimasur-3 (BM-3) and Barimasur-4 (BM-4) differed markedly in root length (RL) at early (20 days after sowing, Figure 1b) as well as at later (60 days after sowing, Figure 1c) reproductive stages. At the early growth stage, RL of lentil variety BM-4 (RL = 4.8 ± 0.15 m per plant) was three times larger than that of BM-3 (Figure 2). At 60 days after sowing, when the both varieties were flowering, the RL of BM-4 was 24 ± 1 m plant^{-1} as

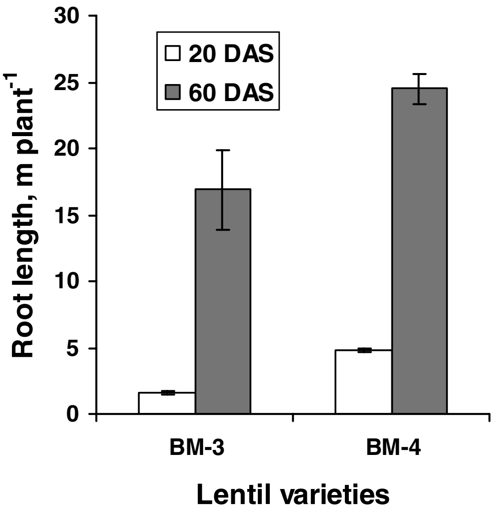

Figure 2. Root lengths of two lentil varieties Barimasur-‘3 (BM-3) and Barimasur-4 (BM-4), 20 days (20 DAS) and 60 days (60 DAS) after sowing. Bars are standard error of means ($n = 4$).

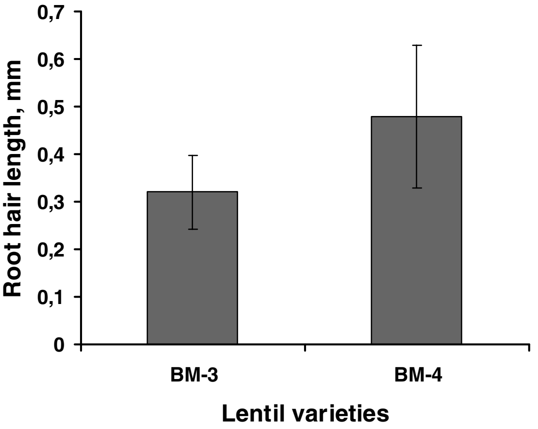

Figure 3. Average root hair lengths of Barimasur-3 (BM-3) and Barimasur-4 (BM-4), 20 days after sowing. Bars are standard error of means ($n = 60$).

Table 1. Shoot dry weight (DM) and the nutrients uptake of two lentil varieties Barimasur-3 (BM-3) and Barimasur-4 (BM-4) in the pot experiment. (Mean ± standard error of means $n = 4$)

DM and nutrients uptake	Variety	
	BM-3	BM-4
DM (g plant^{-1})	1.16 ± 0.05	1.12 ± 0.03
Macro-nutrients(g kg^{-1} DM)		
K	20.43 ± 0.75	28.12 ± 1.03
P	3.62 ± 0.05	3.95 ± 0.06
Ca	16.44 ± 0.04	20.14 ± 0.57
Mg	2.52 ± 0.06	3.06 ± 0.10
S	3.04 ± 0.11	3.05 ± 0.20
Micro-nutrients(mg kg^{-1} DM)		
Fe	376.2 ± 5.0	400.3 ± 7.0
Mn	49.1 ± 0.21	57.4 ± 1.76
Zn	25.7 ± 1.75	35.18 ± 1.46
Cu	15.6 ± 0.47	20.2 ± 1.52
B	14.7 ± 0.07	16.0 ± 0.72
Mo	1.12 ± 0.02	1.96 ± 0.04
Co	0.26 ± 0.03	0.26 ± 0.02

compared to 17 ± 2 m plant^{-1} for BM-3 (Figure 2). The roots of BM-4 penetrated the 25 cm depth of the soil profile in 19 ± 1 and that of BM-3 in 24 ± 2 days. The differences between RL at both the growth stages and root penetration of the two varieties were significant ($P < 0.05$).

The roots of BM-3 (Figure 1d) were covered with less root hair than BM-4 (Figure 1e). The average root hair length (RHL) of BM-4 was 0.48 ± 0.11 mm and that of BM-3 was 0.32 ± 0.09 mm (Figure 3). The average root hair density (RHD, number mm^{-1} root) of BM-4 was 26 ± 3 mm^{-1} and that of BM-3 was 17 ± 2 mm^{-1}. The differences in RHD between BM-4 and BM-3 were significant ($P < 0.05$), but not in RHL. By using average values of RHL and RHD of the two varieties it was calculated that the differential presence of root hairs increased the effective RL of BM-4 by 12 times and that of BM-3 by five times. The two lentil varieties did not differ in their ability to induce change in rhizosphere pH and rhizosphere Aptase activity (data not shown).

The shoot biomass (DM) of the two varieties did not differ ($P < 0.05$) in the pot experiment (Table 1). The uptake of macro-nutrients (K, P, Ca, Mg) as well as micro-nutrients (Fe, Mn, Zn, Cu, B, Mo) by BM-4 was higher compared to BM-3 and the differences were significant ($P <$ 0.05), except in case of S and Co uptake (Table 1).

Field experiments and benefit-cost ratio (BCR)

From the results of field experiments, it appears that BM-4 possesses the ability to translate the advantage of capturing extra nutrients to produce extra grain yield. At five field locations in Bangladesh, BM-4 produced significantly ($P < 0.05$) higher grain yield than BM-3 and at

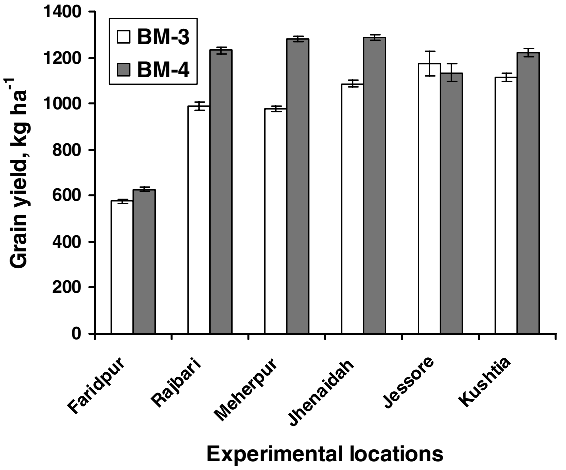

Figure 4. Grain yield of two lentil varieties Barimasur-3 (BM-3) and Barimasur-4 (BM-4) at six locations in Bangladesh. Bars are standard error of means ($n = 3$).

Table 2. Average grain yield of six locations, gross return, total variable cost and benefit cost ratio (BCR) of two lentil varieties Barimasur-3 (BM-3) and Barimasur-4 (BM-4). All money values are given in Bangladesh Takka (Tk)

Items	Lentil varieties	
	BM-3	BM-4
Average grain yield (kg ha^{-1})[a]	986	1130
Value of grain yield (Tk ha^{-1})[b]	18734	22600
Value of by product (Tk ha^{-1})[c]	655	698
Gross return (Tk ha^{-1})	19389	23298
Total variable cost (Tk ha^{-1})	7409	7409
Cash cost basis		
BCR	2.62	3.14

[a] Average of six locations.

[b] BM-3 = 19 Tk kg^{-1}; BM-4 = 20 Tk kg^{-1} (due to better seed color).

[c] Higher value of BM-4 due to higher milling waste which followed its higher grain yield. The value of straw was equal.

one location (Jessore) its yield did not differ significantly (large variation between the replicates) from that of BM-3 (Figure 4). The grain yields of both the varieties differed with location, ranging from 575 ± 8 to 1176 ± 54 kg ha^{-1} in case of BM-3 and ranging from 628 ± 11 to 1287 ± 11 kg ha^{-1} in case of BM-4, showing that the overall performance of BM-4 was better than BM-3. Linked with the higher grain yield and the associated higher amount of milling by-product, the BCR of BM-4 was 3.14 and that of BM-3 were 2.62 (Table 2), indicating that BM-4 provided better return per unit investment compared to BM-3. This, at least partially, seems to support the popularity and preferred adoption of BM-4 among the Bangladeshi farmers, who often cannot afford to apply fertilizers to their nutrients-poor soils.

Discussion

The simple and cost-effective technique applied to rank the root systems of the two varieties allowed visual assessment of the growth and penetration of roots in soil, before actually washing them out and measuring their length using image analysis. This systematic approach reduced the likelihood of the major errors, usually associated with root measurements, as indicated by the agreement between the visual observations (Figure 1) and quantitative measurements (Figure 2). Limiting the investigation only to the two contrasting varieties offered the advantage that major morphological and physiological root traits, known to influence the capture of nutrients and soil moisture, could be studied in detail for examining their linkage to grain yield in multi-location field experiments. The study suggested a strong link between morphological root traits, nutrients uptake, grain yield and BCR as the indicators of economic output of the two lentil varieties. The much lower yields of both the varieties at the Faridpur location (Figure 4) was due to heavy rain at the flowering stage, which affected the crop performance. Even then BM-4 was superior than BM-3.

The results of this study suggest that the variation in root morphology of the two varieties is pronounced, without the variation in the ability to induce chemical (rhizosphere pH) and biochemical (Aptase) change in the rhizosphere environment through root exudation. Root induced rhizosphere pH is known to influence availability of soil inorganic phosphorus (Gahoonia and Nielsen, 1992) and micro-nutrients to plants (Marschner and Römheld, 1996). The role of Aptase for catalyzing the conversion of soil organic phosphorus into plant available inorganic phosphorus is also reported (Asmar et al., 1995). The lack of variation in the rhizosphere pH and Aptase among the two varieties, two nutrient mobilizing processes, suggested that root morphology traits, enhancing the exploration of soil for nutrients (Table 1) and water, might be a criterion worth giving more attention for the selection of nutrient efficient and drought tolerant varieties for nutrient limiting and dry soils. This finding is supported by the results of other recent studies where genetic diversity was found in root size of lentil (Sarker et al., 2003) and root hair formation of soybean (Wang et al., 2004), common bean (Yan and Lynch, 1998) and cowpea (Krasilnikoff et al., 2003).

The roots of both varieties were covered with root hairs, but the disparity in the presence of root hairs on the roots extended the effective root length of BM-4 by 12 times as compared that of BM-3 by five times. This enormous extension of the effective root length by root hairs conferred extra advantage for BM-4 to absorb most of the nutrients from the soil (Table 1), also reported in other studies (Bates and Lynch, 2000; Gahoonia and Nielsen 1998; Hofer, 1996). The root hair production on the roots is enhanced as a response to limitation of water and phosphorus (Bates and Lynch, 1996; Gahoonia et al., 1999). Additionally root hair formation is a photosynthetic carbon saving strategy for extending the root surface area i.e., three times by investing only 2% of the root weight (Clarkson, 1996; Röhm and Werner, 1987).

Bangladeshi soils are generally low in both macro- and micro-nutrients (Yusuf Ali et al., 2002). In pot experiment, BM-4 absorbed significantly higher amount of nutrients (Table 1) and such ability of BM-4 may have supported to produce higher grain yields in multi-location field trials (Figure 4). Lentil is rain-fed winter crop and winter is dry in Bangladesh. Therefore, in addition to higher absorption of soil nutrients, better capture of soil moisture might have played a role in better performance of BM-4, which was not investigated in the present study. Due to very small diameter (5–10 μm), root hairs are able to penetrate and grow into tiny soil pores to extract water, not directly accessible to roots as such. Hence, varieties with abundant root hairs on their roots can be expected to be superior in using soil water more efficiently, when soil moisture is receding. This together with faster growth of roots into the deeper soil layers may be expected to provide extra advantages for BM-4 in capturing soil nutrients and very likely also soil moisture.

Root hair trait followed monogenic Mendel's law of inheritance as it was indicated by 3:1 segregation ratio of F_2 generation, when a bald root barley, *brb* mutant and its wild type was crossed (Gahoonia et al., 2001), suggesting that the trait may be easy to handle in breeding. Comparable to the variation in root hair trait of lentil varieties reported here, a wide genetic variation in root hair formation of other grain legumes like common bean (Yan and Lynch, 1998), soybean (Wang et al., 2004) and cowpea (Krasilnikoff et al., 2003) has been reported. QTL mapping of root hair trait is progressing (Yan et al., 2004).

In the pot experiment, no inoculation was applied and both the varieties formed nodules, but they did not show differences in nodulation at the time of flowering (60 days after sowing), when the roots were washed out and examined visually for the presence of nodules. In the field experiments, no inoculation was applied and the nodulation ability of the varieties was not determined and the link of potential nitrogen fixation ability to the differential grain yield could not be determined. Other studies (Shah et al., 2000) suggest that inoculation has significant benefits for nodulation, biomass, grain yield, nitrogen and phosphorus uptake, irrespective of the levels of nitrogen and phosphorus in soil.

The higher potential return of investment in the cultivation of lentil variety BM-4, as indicated by the higher BCR values (Table 2) which was related to its better root system and better nutrients uptake might be one of the reasons supporting its higher yield and popularity among the local farmers. However, it must be kept in mind that a number other factors, like the cooking quality, seed size and color, the availability of seeds and resistance to diseases may also affect the popularity and adoption of the varieties. The results of this study indicate the economical utility of exploring the genetic diversity in root traits of lentil genotypes/landraces. The superior root traits can then be incorporated in disease resistant and other superior agronomic backgrounds for breeding of high and stable yielding varieties. Hamdi (1992) reported high broad-sense heritability (65-85%) of root morphological traits in lentil, signifying the feasibility of using them successfully in the breeding programs.

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