Morphology of lateral roots of twelve rice cultivars of Bangladesh: dimension increase and diameter reduction in progressive root branching at the vegetative stage

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Abstract: Understanding morphology of lateral roots in rice is important in modeling different agricultural management system. The objective of the study was to explore the morphology of lateral roots of lowland transplanted-aman rice cultivars to mechanistically model length, surface area and volume of an individual root. Seedlings of twelve selected rice cultivars at 30 days of age were transplanted and a series of measurements was carried out on 14, 20, 33 and 60 days after transplantation (DAT). Lateral roots and root hairs were studied under a light microscope. Individual main axes produced up to second-order laterals. Mean main axis diameter and length of twelve cultivars measured 0.94 mm and 20.4 cm respectively at 60 days after transplantation. Diameter reduced at the first-order and second-order laterals up to 4.56 and 21.4 times respectively compared to main axis on 60 DAT. Root hair diameter measured 4.0 µm. An individual root on 60 DAT estimated 911 m in the length, 1714 cm^2 in the surface area and in the 467 mm^3 volume. Root hairs had the highest contribution towards total length and surface area of an individual root whereas main axis and first order laterals mostly contributed root volume.

Keywords: lateral roots, main axis, rice (*Oryza sativa* L.), root hairs

Introduction

Root system, the hidden part of plants, uptakes essential nutrients and water from soil required for the growth and development and thus contributes to around half of the total dry matter of the plants tissues while shoot system contribute the rest mainly as carbon (Thornly 1972). The growth and development of the root system of a plant is a dynamic process. The developmental morphology, architecture, molecular and genetic reasons therein have been studied quite extensively during the last 30 years. Earlier, morphological and anatomical development of rice root system was extensively reviewed by Morita and Nemoto (1995). Ryser (2006) wrote an interesting commentary on 'mystery' of root length. A recent review described the growth, development and genetic reasons of root morphology and function of crop plants (Hodge et al. 2009). An excellent study on root system architecture and its molecular and genetic background also greatly contributed to the relevant literature recently (Rebouillat et al. 2009). Nibau et al. (2008) and Osmont et al. (2007) explained the physiological background of root branching. Root axes of rice plants serve functions of anchorage and typically establish overall root system architecture (e.g., Henry et al. 2011). The lateral roots are the functionally active part of the root system actively involved in nutrient acquisition and water uptake. The size, type and distribution of lateral roots eventually decide ultimate length and surface area of an individual root and finally of a whole tiller. Understanding morphology of the lateral roots is therefore important to develop rice cultivars with an efficient root system.

With the generation of knowledge on segmental architecture of grasses and cereals (Nemoto et al. 1995, Robin et al. 2010, Robin 2011), the focus on studying root morphology and architecture has intensified at the phytomer level. Majority of the earlier reports focused on total root length, root dry weight, mean root diameter, root thickness, ratio of deep rooting and root-shoot ratio etc. of the whole root system of a plant or plant population (e.g., Kato et al. 2006, Thanh et al. 1999, Uga et al. 2009). A few studies reported the morphology of root hairs (Ma et al. 2006, Peterson and Farquhar 1996, Yoshida and Hasegawa 1982). Developmental morphology of the individual roots with special reference to different lateral root branches was not studied in detail as far as the literature explored, probably due to lack of the most appropriate tools and methods. With a view to understand morphology of lateral roots and to model the length, surface area and volume of an individual rice root mechanistically, the present study attempted to measure individual lateral roots and root hairs under a light microscope.

Materials and Methods

The experiment was conducted at the field laboratory of the Department of Genetics and Plant Breeding, Bangladesh Agricultural University. The experimental location is under the agro-ecological zone namely '*Old Bramhaputra Floodplain (AEZ 9)*'. This agro-ecological zone is characterized by the dark grey floodplain soils with mainly silt loams and silty clays, medium to strongly acidic top-soil pH 4.2 to 5.3, top-soil organic matter percentage 1.3- 3.9, average annual rainfall 1547 to 3934 mm and average annual temperature 24.8 to 26.5, varying between sub-regions (Brammer et al. 1988). Seeds for the selected twelve rice cultivars; *BR11*, *BRRI dhan29*, *BRRI dhan39*, *BRRI dhan40*, *BRRI dhan46*, *BRRI dhan51*, *BRRI dhan52*, *Nizershail*, *Pajam*, *Kalijira*, *BINA dhan7* and *BINA dhan8* were sown at the prepared seedbeds in aman (generally rainfed, monsoon) season of 2012. A description of the cultivars is given in Table 1.

Seedlings at their 30 days of age were collected from the seedbed and transplanted in the main field following a completely randomized design with five replications; one individual plot of 10 m^2 in size represented a replication. A row to row spacing of 20 cm and plant to plant spacing of 15 cm were maintained at the transplantation. Plots were fertilized with a basal dose of N, P, K and S at the rate of 30, 10, 30 and 4 kg ha^{-1}, respectively (Ali et al. 2009, BARC, 2005). Urea was top dressed at 40 days after transplantation (DAT) at the rate of 30 N kg ha^{-1} (BARC, 2005). Irrigation was given as and when required. At least 2–3 cm standing water was maintained above the soil surface until the final day of sample collection with irrigation water unless plots received sufficient precipitation. Five individual plants for each variety were collected randomly, one plant from each plot, with a great care so that

Table 1. Description of the rice cultivars used for studying the root traits

Variety	Year of release	Source of breeding material	Target season	Plant height	Growth duration	Grain quality	Yield (t ha^{-1})	Special characteristics
BR11	1980	BRRI	Aman	115	145	Coarse	6.5	High yielding
BRRI dhan29	1994	BRRI	Boro	95	95	Medium	7.5	High yielding
BRRI dhan39	1999	BRRI	Aman	122	106	Fine	4.5	Fine grain quality
BRRI dhan40	2003	BRRI	Aman	145	110	Coarse	4.5	Salt tolerant
BRRI dhan46	2007	BRRI	Aman	105	124	Medium	4.7	Late variety
BRRI dhan51	2010	BRRI	Aman	90	142	Medium	4.5	Submergence tolerant
BRRI dhan52	2010	IRRI/ BRRI	Aman	116	145	Coarse	5.0	Submergence Tolerant
[1]Nizershail	1974	Indigenous variety	Aman	150-156	156	Medium	*3.9 (15.7 g $hill^{-1}$)	Locally popular for grain quality
[1]Pajam	2009	Indigenous variety	Aman	148-151	127	Fine	*3.1 (12.4 g $hill^{-1}$)	Locally popular for grain quality
[1]Kalijira	1976	Indigenous variety	Aman	127-130	139	Medium	*2.2 (8.59 g $hill^{-1}$)	Aromatic
[2]BINA dhan7	2007	Vietnam	Aman	95-100	110-125	Long, medium	4.5-5.5	Short duration in aman
[2]BINA dhan8	2010	IRRI/Indian var. Pokkali	Aman Aus	90-95	120-125 100-106	Medium coarse	4.5-5.0	Salt tolerant

Source:
BRRI (Bangladesh Rice Research Institute) (2011)
[1]Rice descriptor, Bangladesh Rice Research Institute Gene Bank, Genetic Resources and Seed Division, BRRI, Gazipur
[2]BINA (Bangladesh Institute of Nuclear Agriculture) (2012a; b)
*Yield in t ha^{-1} when calculated from g $hill^{-1}$ was considered 20 cm × 20 cm spacing. Aman & Aus season are rainfed (with supplementary irrigation) and Boro season in irrigated.

loss of any order of lateral roots remain as minimum as possible. A core sampler of 15 cm diameter and 30 cm depth made out of a PVC pipe was used to collect individual plants from the field. At least a 7 cm soil around the root zone of an individual plant was taken out during sample collection. Individual plants were washed thoroughly, after collecting from the field, in clean water to remove the soil particles adhered to the root system. Washing was done with a great care to minimize the loss of any individual root or lateral branches. Samples were collected on four different dates after transplantation; 14, 20, 33 and 60 DAT, during the vegetative growth period of the plants.

All measurements were carried out for the nodal roots only. Main axis of nodal roots (MA_o in Fig. 1, adopted from Morita and Abe, 1994), first order laterals and second order laterals were measured. Diameter and length of first- and second-order later roots were recorded only for L-type but density of lateral roots, at their unit axis of origin, was recorded for both L-type and S-type roots (Fig.1). L-type lateral roots are generally long, thick and branched and S-type roots are short, thin and non-branching (Yamauchi et al. 1994). Diameter of the main axis was measured at their middle position at 100x magnification under a light microscope on all four DATs. Length of the main root axes of the five longest individual roots, i.e.; the comparatively older five roots that formed after transplanting, from the five sample plants were recorded on 20, 33 and 60 DAT using a 30 cm ruler. Number of first-order laterals, both L-type and S-type, accommodated per mm main axis was also recorded at 100x magnification for all five samples at the 33 DAT. L-type first-order laterals formed on a randomly selected comparatively mature nodal root (i.e., a root emerged from a basal phytomer) were dissected for all the five sample plants of each variety at the point of their attachment, using a dissecting blade. Five individual slides were prepared for the dissected first-order laterals for each of the sample plant. Acetocarmine solution of 1% was used for staining roots. Length and diameter of the longest first-order lateral from each slide were recorded at the 100x magnification. Number of second-order laterals including both L-type and S-type appeared per mm first-order laterals was also recorded at 100x magnification. Slides prepared to measure the traits of first-order laterals were also used to record data for second-order laterals as the second-order laterals are not visible without magnification. Length and diameter of the longest second-order laterals (L-type) for each slide at 100x, and those of root hairs originated from the axis of second-order laterals, and number of root hairs present per 0.25 mm axes were recorded. Length and diameter of the individual root hairs and density of root hairs (number per unit axis) at their axis of origin were recorded at 400x for both main axis and lateral roots. In case when number of root hairs per 0.25 mm root axis was more than one, length and diameter of the longest root hair was recorded. To record the density of root hairs, root axes and laterals were scanned under microscope from the base to the tip to find out the dense zones with root hairs. Number of root hairs recorded was converted to density of root hairs per mm^2 root surface area.

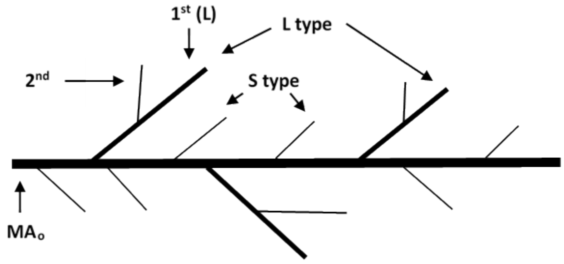

Fig. 1. Schematic of lateral roots of rice. MA_o, main axis of the nodal roots; 1^{st} (L), first-order L-type lateral root; 2^{nd}, second-order lateral root; L type, thick lateral roots and S type; thin lateral root roots (adopted from Morita and Abe, 1994).

The recorded data were analyzed using Minitab 15 statistical software (Minitab Inc. State College, Pennsylvania). One-way analysis of variance was carried out to test the variation among the cultivars for different root traits. Variation between DATs and variety × DAT interaction were tested using GLM command where DATs were tested against variety within DAT using a user defined model.

The maximum possible total length of the first-order laterals present in an individual root was estimated using the following equation: $a \times L_m \times N_p \times L_p$ (where, a is the constant equal to 0.7 indicating that length of the main axis where first-order laterals form, L_m is the length of a main axis, N_p is the number of first-order laterals recorded per unit length of the main axis, L_p is the length of a first-order lateral). As per eye estimation, around 70% length of a root axis accommodated laterals and rest of the region, primarily the root tip region, lacked any lateral branches; that is why a was regarded as 0.7. Maximum possible length of the second-order laterals and root hairs were estimated following similar equation. The total root length of an individual root was calculated by adding up the length of all order of roots. Maximum possible surface area and volume of an individual developed root on 60 DAT were also estimated following the similar steps.

Results

Main axis of nodal roots

Diameter of main axis varied significantly among cultivars at all four DATs (Table 2). Main axis length increased significantly from DAT 14 to DAT 30 with a $p<0.001$. Mean diameter of the main axes of all cultivars measured below 0.94 mm for all DATs (Table 2). Similar to diameter, length of the main axes differed significantly among cultivars (Table 2). Seedlings at the transplantation bore a few older seminal roots, measuring around 2–3 cm in length and blackish in colour. New nodal roots, whitish in appearance, started to initiate within one or two days after transplantation as some of the spare plants were intermittently sampled to monitor root growth visually. Considering the mean age of the main axes on 14 DAT was 12 days, the rate of main axis elongation was 1.23 cm day^{-1}. The highest main axis length was recorded 26 cm for the variety *Kalijira* and the lowest, 16.2 cm, for the *BINA dhan7*, on DAT 60 (Table 2). Mean main axis length measured a progressively higher value from DAT 20 towards DAT 60 with a highly significant variation between DAT ($p<0.001$) and variety × DAT interaction ($p<0.001$).

First-order lateral roots

The density of first-order laterals appeared at the main axis varied significantly between cultivars on DAT 33 (Table 3). The highest density recorded for the *Pajam* and the lowest for the *BRRI dhan29* (Table 3). Diameter of the first-order laterals increased as they became older from DAT 14 to DAT 20 ($p<0.001$, Table 3). The L-type first-order laterals measured a mean diameter of 0.22 and 0.21 mm for all cultivars on DAT 33 and DAT 60, respectively. Compared to the main axes, diameter reduction at the first-order laterals was 4.56 times on DAT 60. Length of the first-order laterals was significantly different between cultivars on each of the following sampling DAT: 20, 33 and 60 DAT and also among four different DATs ($p=0.027$). The length of the first-order laterals was never above 50.4 mm (Table 3). Similar to main axis, the variety *Kalijira* also measured the longest first-order lateral (Table 3).

Second-order lateral roots

Density of second-order laterals appeared at the axis of the first-order laterals increased from DAT 33 to DAT 60 ($p=0.006$, Table 4). The first-order laterals of *BRRI dhan52* were most densely branched compared to any other cultivars (Table 4). Five cultivars out of 12 did not produce any second-order laterals till DAT 14. Mean diameter of the second-order laterals was 0.05 mm or less (Table 4). The length of second-order laterals marginally increased between DAT 20 and DAT 33 ($p=0.08$, Table 4). The mean length of second-order laterals for all cultivars measured below 7.0 mm at any time (Table 4).

Table 2. Diameter and maximum axis length of main axis of nodal roots of 12 rice cultivars on different days after transplantation (DAT). Seedling age was 30 days on the day of transplantation. SE, standard error of mean; *p*, statistical significance.

Variety	Diameter (mm)				Length (cm)		
	DAT 14	DAT 20	DAT 33	DAT 60	DAT 20	DAT 33	DAT 60
BR11	0.64	0.94	0.77	0.81	14.7	10.1	16.6
BRRI dhan29	0.69	0.74	1.00	0.80	14.3	11.1	18.2
BRRI dhan39	0.80	0.88	0.88	0.90	9.7	15.5	18.8
BRRI dhan40	0.63	0.93	0.80	0.81	9.9	15.9	21.9
BRRI dhan46	0.81	1.08	0.87	1.11	12.6	13.4	22.1
BRRI dhan51	1.07	0.83	0.87	0.94	10.8	11.7	18.6
BRRI dhan52	0.65	0.82	0.97	0.99	11.4	13.4	23.5
Nizershail	0.52	1.02	0.90	1.03	13.6	11.5	22.1
Pajam	0.74	0.65	0.66	1.12	12.4	16.9	23.0
Kalijira	0.62	1.09	0.77	0.97	14.5	11.7	26.0
BINA dhan7	0.77	0.76	0.87	0.93	12.1	16.5	16.2
BINA dhan8	0.53	0.90	0.82	0.81	13.3	13.7	17.2
SE (±)	0.058	0.044	0.042	0.041	0.044	0.042	0.041
p value	0.04	<0.001	0.05	0.002	<0.001	<0.001	<0.001

Root hairs

Number of root hairs appeared per mm^2 axes of second-order laterals recorded the highest for *BINA dhan8* followed by *BRRI dhan29* on DAT 33 (Table 5, p=0.05). There was no significant regression between thickness of second order laterals and density of root hairs per unit surface area across 12 rice cultivars indicating that this root trait is variety dependent. Mean root hair diameter measured 3.8, 4.2 and 3.9 µm for all cultivars on DAT 14, 20 and 33. *BINA dhan7* measured the thinnest root hairs of 1.8 µm on DAT 14 and DAT 20 (Table 5). Root hair length significantly varied between cultivars on DAT 14. *BRRI dhan51* measured the longest root hair of 253 µm and *Nizershail* measured the shortest root hair of 28.4 µm (Table 5). Root hair length significantly increased from DAT 14 (75 µm) to DAT 20 (323 µm).

Discussion

It is generally assumed that root axes and root hairs of the grasses and cereals are cylindrical in shape. As a progressive development root cells divide at the root tip, elongate longitudinally and expand in size and thus dynamically increase the root length. Diameter of a root axis or lateral root, therefore, was measured

Table 3. Diameter and length of L-type first order lateral roots of 12 rice cultivars and also density of first order lateral roots (both L-type and S-type) on per mm main axis of nodal roots on different days after transplantation (DAT). Seedling age was 30 days on the day of transplantation. SE, standard error of mean; *p*, statistical significance.

Variety	Diameter (mm)				Length (mm)			Density of first-order lateral roots per mm main axis
	DAT 14	DAT 20	DAT 33	DAT 60	DAT 20	DAT 33	DAT 60	DAT 33
BR11	0.21	0.28	0.22	0.20	28.0	37.6	30.2	2.4
BRRI dhan29	0.07	0.18	0.16	0.21	28.6	23.0	38.8	1.4
BRRI dhan39	0.07	0.16	0.19	0.18	12.2	21.2	26.4	3.2
BRRI dhan40	0.05	0.15	0.34	0.23	27.4	36.6	32.0	3.4
BRRI dhan46	0.16	0.15	0.17	0.19	28.3	18.4	37.0	1.8
BRRI dhan51	0.08	0.22	0.18	0.18	38.2	34.8	23.6	2.6
BRRI dhan52	0.09	0.17	0.31	0.20	17.3	31.2	27.8	2.2
Nizershail	0.08	0.19	0.23	0.20	11.8	28.0	38.2	2.6
Pajam	0.09	0.14	0.22	0.20	16.4	40.8	46.4	3.0
Kalijira	0.08	0.24	0.25	0.23	34.0	38.8	50.4	2.6
BINA dhan7	0.11	0.16	0.24	0.20	32.4	31.4	30.4	2.4
BINA dhan8	0.09	0.22	0.17	0.24	30.8	25.4	36.4	2.8
SE (±)	0.008	0.011	0.011	0.01	2.15	2.47	1.70	0.26
p value	<0.001	<0.001	<0.001	0.14	<0.001	0.001	<0.001	0.048

Table 4. Diameter and length of L-type second order lateral roots and density of second order lateral roots (both L-type & S-type) on per mm first order lateral roots of 12 rice cultivars on different days after transplantation (DAT). Seedling age was 30 days on the day of transplantation. NA, not appeared; SE, standard error of mean; *p*, statistical significance.

Variety	Diameter (mm)				Length (mm)			Density of second order lateral roots on per mm first order lateral roots	
	DAT 14	DAT 20	DAT 33	DAT 60	DAT 20	DAT 33	DAT 60	DAT 33	DAT 60
BR11	0.062	0.052	0.048	0.042	6.50	9.60	4.80	2.20	3.60
BRRI dhan29	0.050	0.052	0.052	0.050	4.64	5.70	4.70	2.60	4.00
BRRI dhan39	NA	0.050	0.044	0.042	1.61	9.30	2.54	3.40	4.80
BRRI dhan40	NA	0.046	0.070	0.041	5.18	5.90	5.86	3.00	3.60
BRRI dhan46	0.038	0.056	0.052	0.033	1.70	4.40	9.20	2.20	3.80
BRRI dhan51	0.031	0.052	0.045	0.044	3.30	9.60	9.60	4.20	3.40
BRRI dhan52	0.040	0.056	0.062	0.046	3.82	2.50	4.86	3.20	5.20
Nizershail	NA	0.070	0.046	0.048	5.70	9.50	6.80	2.80	3.60
Pajam	NA	0.042	0.054	0.046	5.20	6.10	8.60	2.20	4.80
Kalijira	NA	0.064	0.056	0.048	6.80	3.70	9.40	2.80	3.60
BINA dhan7	0.046	0.036	0.050	0.044	3.50	3.50	10.60	1.40	2.80
BINA dhan8	0.044	0.076	0.046	0.044	7.40	4.26	5.10	4.00	2.60
SE (±)	0.003	0.003	0.002	0.002	0.47	0.35	0.46	0.23	0.19
p value	0.001	<0.001	<0.001	0.026	<0.001	<0.001	<0.001	<0.001	<0.001

at the middle position of the axis to get a better reflection of average diameter of an individual axis. Even though data was recorded with a great care and only from the intact roots, it is still possible that some root hairs were washed out during sample preparation and processing. Hence actual density of root hairs per unit surface area of axis might be higher than the recorded one in some cases. In modeling the total length, surface area or volume of the individual roots in future, a few issues needs to be considered: i) as per eye estimation around 30% length of a root axis, closer to the its tip, bears no lateral roots; ii) as lateral root formation in an axis is a dynamic process, length of the laterals increases until they stop cell division and extension at the tip; iii) number of laterals per unit axis might vary depending on the location at the axis of origin, i.e., base, middle and tip.

Main axis elongation rate, cm d^{-1}, of lowland rice cultivars in this study, 1.23 was comparatively slower than *Lolium perenne*, around 2.0 (Robin 2011) and

Table 5. Root hair diameter, root hair length and number of root hairs per mm^2 second-order lateral root axis of 12 rice cultivars on different days after transplantation (DAT). Seedling age was 30 days on the day of transplantation. SE, standard error of mean; *p*, statistical significance.

Variety	Root hair diameter (µm)				Root hair length (µm)				Density of root hairs per mm^2 second-order of lateral axis		
	DAT 14	DAT 20	DAT 33	DAT 60	DAT 14	DAT 20	DAT 33	DAT 60	DAT 20	DAT 33	DAT 60
BR11	4.00	5.20	2.30	3.00	36.3	252	294	196	176	224	196
BRRI dhan29	3.60	5.00	4.00	3.60	39.0	342	192	157	319	467	367
BRRI dhan39	5.25	4.00	2.40	3.80	42.0	137	327	540	357	120	84
BRRI dhan40	4.20	3.80	2.40	3.90	58.0	321	218	387	227	167	187
BRRI dhan46	3.80	3.80	4.30	4.00	32.0	324	240	440	595	129	311
BRRI dhan51	4.75	3.60	5.80	3.80	253	572	191	490	93	414	211
BRRI dhan52	4.80	2.40	2.40	3.60	116	71.0	376	572	395	125	187
Nizershail	5.80	4.60	3.40	4.60	28.4	438	296	256	470	116	153
Pajam	3.20	5.20	4.00	2.80	97.4	296	155	234	425	333	90
Kalijira	5.00	3.20	2.00	4.60	37.5	680	111	246	181	413	258
BINA dhan7	1.80	1.80	2.80	4.60	116	192	294	376	222	190	173
BINA dhan8	4.40	4.20	5.20	5.00	49.4	253	294	440	91	493	300
SE (±)	0.39	0.30	0.35	0.33	25.3	93.6	50.32	124	41	33	22
p value	0.005	<0.001	<0.001	0.118	0.03	0.194	0.470	0.87	0.19	0.05	0.29

Table 6. Total length, surface area and volume of an individual developed root on 33 and 60 days after transplantation estimated from diameter, length and number of lateral roots recorded for different order of roots for 12 rice cultivars and the percentage of each of the traits distributed for the main axis, first-order lateral roots, second-order lateral roots and root hairs.

Cultivars	Total length (m)		Surface area (cm^2)		Volume (mm^3)	
	DAT 33	DAT 60	DAT 33	DAT 60	DAT 33	DAT 60
BR11	335	222	1543	1495	163	224
BRRI dhan29	175	235	461	1558	127	215
BRRI dhan39	350	482	2362	1437	225	301
BRRI dhan40	564	1773	4188	3514	741	477
BRRI dhan46	64	1012	395	2778	122	502
BRRI dhan51	576	745	3050	2635	187	275
BRRI dhan52	134	819	893	2742	464	431
Nizershail	589	1000	1691	4225	233	598
Pajam	471	1095	2593	9673	250	953
Kalijira	94	2075	1245	8949	246	955
BINA dhan7	93	873	673	2511	333	292
BINA dhan8	712	607	1279	1848	156	378
Mean	346	911	1698	1714	271	467
Percentage distributed for						
% main axis	<0.01	<0.01	0.21	0.16	28.1	30.9
% First-order laterals[1,2]	2.2	1.4	8.6	6.9	69.9	66.9
% second-order laterals[2]	27.4	26.7	17.2	18.6	2.01	2.13
% root hairs	70.4	71.9	74.0	74.0	<0.01	0.01

[1] Number of first-order laterals per unit main axis at DAT 60 was considered equal to that of DAT 33.

[2] Densities of first- and second- order lateral roots on per mm axis of origin were recorded for both L-type and S-type.

wheat 1.49 (calculated from Robin et al. 2014). Main root axis elongation is a carbon expensive process. Plants therefore possibly modify root axis elongation depending on nutrient availability under different soil and environmental condition. Kondo et al. (2003) found deep rooting ratio of 4.3 and 14.6 m g^{-1} for the roots between 30-90 cm soil depth under upland field conditions but the present study recorded no main axis length above 26 cm till 60 DAT. This result agrees with the previous reports suggesting that lowland rice cultivars are generally shallow rooting compared to those of upland cultivars (O'Toole and Bland 1987). One the other hand, main axis diameter of rice in this study was quite similar to that of *L. perenne* measured 0.73 mm (Robin 2011) and wheat varieties of Bangladesh measured between 0.6 and 0.7 mm (Robin et al. 2014) at the youngest root bearing phytomer. In some previous studies average root diameter was estimated from total root length and root dry weight. A mean root diameter of 0.2 mm was recorded for the whole root system of the rice plants as reported in IRRI (1978). Problem associated with using mean diameter in estimating root volume and root tissue density is discussed by Ryser (2006) as root volume relates to the square of the diameter, where coarse root branches contribute much more to the volume than they do to the average diameter. Mean main axis diameter in this study was 4.7 times higher compared to mean root diameter of all roots (0.2 mm) meaning that average diameter reduction is also 4.7 folds.

One general feature to note that diameter reduction is associated with dimension increase at the successively developed lateral roots. These characteristic features of the lateral roots facilitate plant roots to increase total length and surface area by progressively reducing volume of the new lateral roots. Diameter reduction is associated with reduction in expenses of carbon for root construction and maintenance. Generally, density of the lateral roots and root hairs was cultivar dependent rather than diameter of their axis of origin. This particular trait is very important from the rice breeding perspective. Plant with thin, dense and long lateral roots can explore more soil particles with the expense of less carbon. Rice breeders should therefore concentrate on selecting for these types of rice genotypes. A strikingly lower measure of L-type first order lateral root length, 1.18-5.04 cm, was recorded in this study compared to a previous study conducted under well-watered, drought and submerged conditions by Bañoc et al. (2000), 6.3-13.8 cm, which might be associated with moderately acidic soil condition.

Estimated total length, surface area and volume for twelve cultivars differed greatly among 12 rice cultivars because of their variation in size and density of lateral roots (Table 6). A lion share of the length and surface area of an individual root is determined by the size and density of second-order laterals and the root hairs, but that of root volume was primarily contributed by main axis and the first-order laterals (Table 6). The data indicates breeding for efficient root type is a prospective research area of the rice breeders which is not much explored to date.

The estimated total length and surface area of an individual root at 60 DAT accounted for around 0.9 km and 0.17 m^2, respectively, which comprise 467 mm^3 root volume (Table 6). It is important to note that root hairs alone contributed more than 70% to total length and 74% of total root surface area (Table 6). Robin (2011) for the WINRHIZO scanned roots of *L. perenne* excluding root hairs accounted for around 20 cm^2 surface area of an individual root. On an average, a main tiller (parent tiller only) of rice plant at 60 DAT accounted for 75 live roots (data not presented) meaning that at individual rice tiller can produce up to 67.5 km root length, 12.8 m^2 root surface area by the expense of 350 cm^3 root volume to explore its rhizosphere (Table 6).

A single root hair is the growing extension of a single epidermal cell (Dolan and Costa 2001, Peterson and Farquhar 1996). Root hairs forming at the different order of root branches measured the diameter of around 4 µm (Table 5) suggesting that this trait is not depended on the diameter of the axis of the origin. Mean density of root hairs for all cultivars per mm axis accounted for 15.7 on DAT 20 (extrapolated from Table 5) in this study which is much different from the *japonica* rice variety Oochikara, recorded 42.1 root hairs per mm for the 22 days old seedlings (Suzuki et al. 2003). This variation might be explained either as ecotype variation (*indica* and *japonica*) or variation in growing condition.

In conclusions, this study described the genotypic variations for diameter and length of main axis, lateral roots and root hairs of 12 wet-land transplanted *aman* rice cultivars of Bangladesh. The twelve rice cultivars differed significantly for different root traits, but the general pattern of diameter reduction is associated with dimension increase by lateral root branching. The most characteristic feature of higher order of lateral roots and root hairs are they increase total length and surface area of roots exponentially with limited expense of root volume. The data obtained in this study can potentially be useful to calculate the root construction cost of an individual nodal root or a lateral root, when the data on the rate of photosynthesis, C utilization pattern during assimilation and % C present in rice root branches are available (Robin, 2011).

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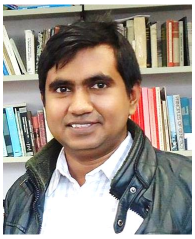

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