Root Hairs and Root Lengths in Nine Warm-season Turfgrass Genotypes

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Abstract. Root hairs contributed variously to total root length, ranging from a low of 1% for 'Emerald' zoysiagrass (*Zoysia japonica* Steud. x *Z. tenuifolia* Willd. ex Trin.) and 5% for 'Georgia Common' centipedegrass [*Eremochloa ophiuroides* (Munro.) Hack], to a high of 95% and 89% for 'Texturf 10' and 'FB 119' bermudagrasses [*Cynodon dactylon* (L.) Pers.], respectively. Genotypes ranking highest for root lengths with root hairs also ranked highest for root lengths without root hairs and for number of main roots per plant. In terms of root lengths with root hairs, first-order lateral roots contributed more to total root length than root lengths of either main roots or second-order lateral roots for all nine genotypes. Number and length of root hairs arising from either main or lateral roots were not significantly affected by their relative distance from the cap of the main root. 'Texturf 10' and 'FB 119' bermudagrasses ranked highest for root and root-hair extent.

Root hairs are cylindrical elongations from root epidermal cells. Their life span, length, and number per cell may vary with location of the root epidermal cell and plant species (Clarke et al., 1979; Clarkson, 1985; Cormack, 1949, 1962; Farr, 1928; Leavitt, 1904; Robards, 1983; Snow, 1905). Root hairs usually are assumed to be short-lived (Tanaka and Woods, 1972). However, root hairs of some species may become suberized or lignified and persist for months or even years, although they may not remain alive (Hayward and Long, 1942; McDougall, 1921).

Root hairs increase root length and absorbing surface, thus they may be an important site for water and mineral absorption. They have been reported to contribute substantially to root length among various plant species (Dittmer, 1937, 1938, 1949), increasing the absorbing surface by a factor of 5 to 18 (Dittmer, 1937). Root hairs have been shown to absorb water (Hayward et al., 1942; Rosene, 1943), a phenomenon involving metabolism (Cailloux, 1972). Root hairs facilitate ion uptake, especially when the process is limited by diffusion of ions from the medium to the root surface. Lauchli (1967) reported that root hairs of corn (*Zea mays* L.) unequivocally accumulated ions. Drew and Nye (1969) reported that the presence of root hairs of Italian ryegrass (*Lolium multiflorum* Lam.) increased K uptake by 77% compared with roots without root hairs. Itoh and Barber (1983a) reported that root hairs contributed to P uptake in several plant species, including Russian thistle (*Salsola kali* L.), tomato (*Lycopersicon esculentum* Mill.), and lettuce (*Lactuca sativa* L.), but not wheat (*Triticum aestivum* L.), carrot (*Daucus carota* L.), or onion (*Allium cepa* L.). Length of root hairs, root-hair density, and root-hair radius influenced predicted P uptake, with root-hair length being the most significant factor (Itoh and Barber, 1983b). Caradus (1981) grew white clover (*Trifolium repens* L. 'Tamar') on low-P soil and reported that plant selections with longer root hairs had higher plant dry weight and P content than plant selections with shorter root hairs. He also reported that root-hair length did not affect plant dry weight or P content if roots were mycorrhizal.

There is important emphasis in the development of turfgrasses with greater drought resistance and/or with the ability to main-

tain acceptable turf quality under low water inputs. Water absorption is an important aspect of the tissue dehydration-avoidance component of drought resistance. Thus, characterizations of root and root-hair extent among the major warm-season turfgrasses may help explain their relative differences in tissue dehydration avoidance and drought resistance. Approaches to root characterizations include describing root mass per soil volume; depth of root extensions; total root length per plant, with or without root hairs; and root length per soil volume. The objective of this study was to determine the contributions of root hairs to root length among nine warm-season turfgrass genotypes, grown under glasshouse conditions, in a sand medium, and maintained under nonlimiting soil moisture.

Materials and Methods

The nine warm-season turfgrass genotypes characterized in this study were: bahiagrasses (*Paspalum notatum* Flüggé 'Argentine' and 'Pensacola'); bermudagrasses [*Cynodon dactylon* (L.) Pers. 'FB 119' and 'Texturf 10' and *C. dactylon* x *C. transvaalensis* Davy and reciprocal 'Tifgreen' and 'Tifway']; centipedegrass 'Georgia Common' and zoysiagrasses (*Zoysia japonica* Steud. 'Meyer' and *Z. japonica* x *Z. tenuifolia* Willd. ex Trin. 'Emerald'). Four uniform, prerooted (for 3 weeks) sprigs of each genotype were individually transplanted to polyethylene tubes (50-mm diameter x 1200 mm long), filled with a medium-textured, washed sand. Number and length of shoots per prerooted sprig and number and length of main roots (Fig. 1A) per prerooted sprig were uniform among the four replicates of each genotype but were variable across the nine genotypes, due to their different -growth habits. The bottom end of each tube was heat-sealed and perforated for drainage, while the upper end was stretched over a plastic ring that also had a 50-mm diameter. The polyethylene tube was suspended inside a polyvinyl chloride (PVC) cylinder (50 mm diameter x 1200 mm long) by placing the plastic ring on the upper end of the PVC cylinder. The PVC cylinder was coated with silver paint to prevent light from reaching the roots. Grasses were grown in a glasshouse where maxima and minima did not exceed 35 and 24C, respectively, and were maintained under nonlimiting soil moisture conditions by daily irrigations with an automatic drip irrigation system. Grasses were fertilized twice each week with a granular fertilizer (19N-3.5P-8.3K, plus micronutrients) at 751 g N/m² per month, and not mowed. Previous studies (Green

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Fig. 1. (A) One main root with lateral roots that has been sectioned for lateral-root and root-hair analyses. (B) Main-root intervals and sections for one main root.

et al., 1989) indicated this irrigation/fertilization regime was required to ensure adequate growth.

The root system of each turf was prepared for root measurements and subsampling 131 days after transplanting; exceptions were 'Texturf 10' and 'FB 119' bermudagrasses, which were measured and subsampled 89 days after transplanting because visual inspection showed their main roots had approached the bottom of the polyethylene tube. The polyethylene tube was laid on a plastic sheet, cut longitudinally, and removed from the intact sand core. The sand was gently washed from the root system with water by a hand-held hose with nozzle. Microscopic determinations showed that this procedure caused negligible damage to "root hairs. The number of main roots per plant was counted and their lengths measured.

The three longest main roots from each plant (subsamples) were collected for subsequent lateral-root and root-hair analyses. Sampling the three main roots consisted of excising 25-mm sections at 152-mm intervals along the entire root length, beginning 5 mm proximal to the root cap (Fig. 1A). The maximum number of main-root sections per main root was eight ('FB 119' and 'Texturf 10' bermudagrasses) and the minimum was one ('Emerald' zoysiagrass). Each main-root section included intact first- and second-order lateral (first and second lateral) roots. Third-order lateral roots were infrequent and short (<3.0 mm), so they were not included in this study. Main-root sections were placed immediately in individual vials containing a paraformaldehyde solution (40 g-liter⁻¹), fixed for 24 h, and then dehydrated in the same vials by sequential submersions for 1 h each in 25%, 50%, and 70% (v/v) ethanol solutions. Main-

root sections were stored in a 70% (v/v) ethanol solution under refrigeration (5C) for subsequent lateral-root and root-hair analyses.

Lateral-root analyses were conducted with a binocular microscope (B&L Stereozoom Seven; Bausch and Lomb, Rochester, N.Y.) and consisted of counting each first lateral root arising from each 25-mm main-root section along with counting each second lateral root arising from each first lateral root. Average lengths of first and second lateral roots of each main-root section were estimated from a subsample, the lengths of five first and five second lateral roots; exceptions were 'Meyer' zoysiagrass and 'Pensacola' bahiagrass, which had less than five second lateral roots. The basis for lateral-root selection was a subsample that contained relatively short, medium, and long lateral roots. Lateral-root length was determined by 1) direct measurement with a calliper when the root was straight, 2) gentle straightening with tweezers, causing negligible stretching, followed by measurement with a calliper, or 3) measurement of adjacent straight segments, one at a time, with a calliper.

Root-hair analyses were conducted at x 100 to 400 with an Olympus CH microscope (Olympus, Lake Success, N.Y.). An eyepiece micrometer disk allowed for accurate (0.01 mm) determinations of root-hair length and a consistent length (1.0 mm) of main or lateral roots for determinations of root-hair density. Root-hair analyses of main roots consisted of selecting a 10-mm subsection of each 25-mm main-root section and making five (1-mm-long) individual observations that did not overlap. Root-hair density was determined in each 1-mm root segment by counting root hairs in two 90° arcs (each arc = one-fourth of the area) on opposite sides of the root. The procedure involved observations at consecutive focal depths to cover the 1-mm segment; care was taken to make counts within a consistent area of root surface. Root-hair tips were counted when density was relatively high while root-hair bases were counted when density was relatively low. Root-hair density data were converted to a 360° basis. Average root-hair length for each 1-mm observation was estimated from a subsample, the length of five root hairs. The basis for root-hair selection was a subsample that contained relatively short, medium, and long root hairs. Root-hair analyses of first and second lateral roots consisted of selecting five first and five second lateral roots arising from the 10-mm subsection of main root. One 1-mm long observation was made from each lateral root for number of root hairs and their average length. As with main roots, a five root-hair subsample was used to estimate the average root-hair length for each 1-mm observation.

Analysis of variance (ANOVA) was made by a general linear model (GLM) procedure for number of main roots per plant and mean length of main roots per plant using a completely randomized design (CRD) with genotypes as the treatment effect. ANOVA by a GLM procedure was made on the means of the three main-root subsamples for number of first and second lateral roots arising from 25-mm main-root sections and average length of first and second lateral roots using a split-plot extension of a CRD where polyethylene tubes nested in genotypes were main plots, split by depth (relative distance from the main-root cap). This same statistical design also was used on the means of five microscopic observations and three main-root subsamples for number of root hairs and their average length arising from 1 mm of main root, first lateral root, and second lateral root. ANOVA by a GLM procedure for all lateral-root and root-hair measurements also was made treating depth as a linear or quadratic effect. Generally, models with a linear depth effect

best fit the data. Therefore, data presented in Tables 2 and 3 were extracted from this type of statistical analysis.

Main-root length per plant, without root hairs, was calculated by the sum of individual main-root lengths measured at harvest. Main-root length per plant, without root hairs, was divided into a maximum of eight intervals by dividing each main root into intervals (Fig. 1B) and subsequently calculating the sum length of all main roots within each interval. The first interval for each main root was between the two 25-mm main-root sections nearest the main-root cap (only the first main-root section was included in the first main-root interval). The eighth interval was between the eighth 25-mm main-root section and the crown (the eighth main-root section was 'included in the eighth main-root interval').

Main-root, first lateral-root, and second lateral-root lengths, with and without root hairs, within each main-root interval for each plant were calculated by using the subsample means of lateral-root and root-hair measurements with the corresponding main-root intervals. Thus, the lateral-root and root-hair means from the first main-root section were multiplied by the sum length of all main roots within the first main-root interval. Main-root, first lateral-root, and second lateral-root lengths per plant, with and without root hairs, were calculated by summing over main-root intervals. Total root lengths, with and without root hairs, were calculated by summing over the three root components. Root-hair contributions (%) to root length for the three root components and total root length were calculated by the following equation [(root length with root hairs – root length without root hairs) ÷ root length with root hairs] × 100. ANOVA, by a GLM procedure, was made for root length, with and without root hairs, and root-hair contributions to root length using a CRD design with genotypes as the treatment effect. The percentages in Table 1 were not transformed for two reasons.

First, a test on the residual values from each ANOVA involving percentages showed only modest departures from normal distribution; thus, percentage values not having a normal distribution should be a minor concern. Second, ANOVA on arcsin-transformed percentages showed that in all cases the genotype effect was highly significant and the order of rankings of the genotypes was basically the same as the rankings that appear in Table 1.

Results and Discussion

Root-hair contributions to root length were significantly affected by genotypes for main roots, first lateral roots, second lateral roots, and total root length (Table 1). Root-hair contributions to total root length ranged from a low of 1% and 5% for 'Emerald' zoysiagrass and 'Georgia Common' centipedegrass, respectively, to a high of 95% and 89% for 'Texturf 10' and 'FB 119' bermudagrasses, respectively. There was a trend for the bermudagrass genotypes to have the highest root-hair contribution to total root length. Also, there was a trend for the two *C. dactylon* bermudagrass genotypes ('Texturf 10' and 'FB 119') to have higher root-hair contributions to total root length than the two hybrid bermudagrass genotypes ('Tifway' and 'Tifgreen').

Root lengths, with or without root hairs, were significantly affected by genotypes for main roots, first lateral roots, second lateral roots, and total root length; an exception was length of second lateral roots with root hairs (Table 1). Total root length with root hairs was highest for 'Texturf 10' and 'FB 119' bermudagrasses, 1480 and 958 m, respectively, and lowest for 'Pensacola' bahiagrass and 'Georgia Common' centipedegrass, 4.8 and 6.2 m, respectively. In terms of root lengths with root hairs, root lengths of first lateral roots contributed more to total root length than root lengths of either main roots or second

Table 1. Root-hair contributions to root length and root lengths for nine warm-season turfgrass genotypes.

Species and genotype	Main roots			First-order lateral roots			Second-order lateral roots			Total root length		
	Root length/plant (m)		Root-hair contribution ^a (%)	Root length/plant (m)		Root-hair contribution (%)	Root length/plant (m)		Root-hair contribution (%)	Root length/plant (m)		Root-hair contribution (%)
	Without hairs	With hairs		Without hairs	With hairs		Without hairs	With hairs		Without hairs	With hairs	
Bermudagrass Texturf 10	11.3	661	98	66.5	723	78	8.7	95.8	90	86.5	1480	95
Bermudagrass FB 119	7.2	202	96	71.4	648	86	17.7	108	82	96.3	958	89
Bahiagrass Argentine	4.6	6.8	32	17.2	65.1	58	1.7	6.3	46	23.6	78.3	57
Zoysiagrass Meyer	1.7	1.7	1	4.0	24.3	44	0.1	0.1	7	5.8	26.1	42
Bermudagrass Tifway	0.7	4.4	77	2.4	13.3	72	0.5	1.4	43	3.5	19.1	73
Bermudagrass Tifgreen	1.2	2.2	33	3.2	10.3	46	0.4	0.7	32	4.7	13.0	64
Zoysiagrass Emerald	0.8	0.8	5	4.8	4.8	0	2.7	2.7	0	8.2	8.3	1
Centipedegrass Georgia Common	1.4	1.6	10	3.3	3.4	3	1.2	1.2	0	5.9	6.2	5
Bahiagrass Pensacola	0.7	1.6	29	2.0	3.2	19	0.0	0.0	10	2.6	4.8	34
LSD <i>P</i> = 0.05	2.3	284	44	45.5	513	56	9.2	NS	47	54.4	839	46

^aRoot-hair contributions to root length were calculated by the following equation: [(root length with root hairs – root length without root hairs) ÷ root length with root hairs] × 100.

^bNonsignificant genotype effect.

Table 2. Selected sources of variation extracted from statistical analyses of main-root, first- and second-order lateral root, and root-hair measurements for nine warm-season turfgrass genotypes.

Dependent variable	Source of variation					
	Genotype (df = 8)		Linear depth ^a (df = 1)		Genotype × linear depth (df = 8)	
	Mean square	F	Mean square	F	Mean square	F
Main roots ^y						
No.	180.27	15.52***	---	---	---	---
Mean length	454.47	50.80***	---	---	---	---
Root hairs on main roots ^x						
No.	1080.50	1.18	26.30	0.05	48.69	0.09
Mean length	0.10	4.29**	<0.01	0.01	0.01	0.18
First-order lateral roots ^x						
No.	329.57	2.95*	1005.38	13.44***	292.38	3.91***
Mean length	8.10	0.28	36.25	1.08	14.73	0.44
Root hairs on first-order lateral roots ^x						
No.	497.80	6.15***	248.67	0.97	422.64	1.65
Mean length	0.04	6.65***	<0.01	0.59	0.01	1.13
Second-order lateral roots ^x						
No.	587.23	0.96	1100.55	1.56	1474.85	2.09*
Mean length	1.77	1.81	2.18	3.73	2.26	3.87***
Root hairs on second-order lateral roots ^x						
No.	128.29	1.40	78.20	0.72	154.52	1.43
Mean length	0.01	8.95***	<0.01	0.04	<0.01	0.52

^aDepth = relative distance from the main-root cap.

^yANOVA was a completely randomized design (CRD) with genotypes as the treatment effect.

ANOVA was a split-plot extension of a CRD with plants (genotypes) = main plots, split by depth.

*, **, *** Significant at $P = 0.05$, 0.01 , and 0.001 , respectively.

Table 3. Root and root-air measurements averaged over all depths for nine warm-season turfgrass genotypes.

Species and genotype	Main roots				First-order lateral roots				Second-order lateral roots			
	Roots ^z		Root hairs		Roots		Root hairs		Roots		Root hairs	
	No./plant	Mean length/plant (mm)	No./mm root	Mean length (mm)	No./25 mm main root	Mean length (mm)	No./mm root	Mean length (mm)	No./25 mm main root	Mean length (mm)	No./mm root	Mean length (mm)
Bermudagrass Texturf 10	30	380	128	0.35	19	7	44	0.21	20	0.9	36	0.16
Bermudagrass FB 119	20	360	86	0.34	23	13	32	0.19	40	1.7	26	0.13
Bahiagrass Argentine	22	209	12	0.02	16	5	40	0.02	13	0.5	14	0.02
Zoysiagrass Meyer	19	94	2	0.01	28	3	16	0.04	5	0.2	6	0.02
Bermudagrass Tifway	5	127	118	0.07	20	5	28	0.06	28	0.6	22	0.03
Bermudagrass Tifgreen	15	77	10	0.02	20	5	14	0.03	12	0.3	10	0.02
Zoysiagrass Emerald	11	69	6	0.04	36	2	1	0.01	19	1.1	1	0.01
Centipedegrass												
Georgia Common	22	63	6	0.01	12	2	2	0.01	8	0.7	1	0.01
Bahiagrass Pensacola	7	86	18	0.03	19	3	12	0.01	1	1.0	4	0.01
LSD $P = 0.05$	6	55	NS ^y	0.18	12	NS	10	0.09	NS	NS	NS	0.06

^zMeans are not an average over depths.

^{NS}Nonsignificant genotype effect.

lateral roots for all nine genotypes. The two *C. dactylon* bermudagrasses had significantly higher total root lengths, with or without root hairs, than the two hybrid bermudagrasses. Unpublished data from a preliminary root-hair characterization study (Green et al., 1989) showed that, in terms of the estimated cumulative length of all root hairs arising from the average, longest main root, 'Tifway' ranked lower than either 'Tifgreen', 'Texturf 10', or 'FB 119' at 6.70, 93.76, 88.58, and 75.50 m, respectively. The methodology of the preliminary study was the same as the present study except that plants were harvested following 77 days of growth. In terms of the bermudagrasses, the basic difference between the two studies was the relative root and root-hair extent of 'Tifgreen' bermudagrass.

Casnoff and Beard (1985) characterized root extent among the major warm-season turfgrasses in terms of root mass, longest root extensions, and number of roots intersecting a plane at given depths. Individual sprigs were grown for 130 days in PVC cylinders measuring 100 mm diameter × 2100 mm long and filled with a washed, medium-textured sand. They reported that 'FB 119' bermudagrass ranked highest for root extent, 'Tifgreen' and 'Tifway' bermudagrasses, 'Emerald' zoysiagrass, and 'Adalayd' seashore paspalum (*Paspalum vaginatum* Sw.) ranked intermediate, while 'Argentine' bahiagrass, 'Georgia Common' centipedegrass, 'Meyer' zoysiagrass, and 'Texoka' buffalograss [*Buchloë dactyloides* (Nutt.) Engelm] ranked lowest. They reported, overall, that bermudagrasses exhibited superior rooting

capabilities in terms of depth of root extensions and total root weight.

Selected sources of variation from ANOVA for measurements of main roots, first and second lateral roots, and root hairs are shown in Table 2. Results from root-hair measurements were more understandable than results from root measurements because, for the majority of the latter measurements, the genotype effect was not significant and the genotype $\times$ linear depth interaction was significant. In contrast, the genotype effect was significant for the majority of root-hair measurements and neither the linear depth effect nor the genotype $\times$ linear depth interaction was significant. These findings are important because they suggest that root-hair extent on main or lateral roots was affected by genotype but not by the relative distance (depth) from the main-root cap. Some caution should be exercised when assessing these findings, because only three genotypes had plants that were subsampled to at least four depths, which meant ANOVA was made with considerable missing data. The linear depth $\times$ genotype interaction was never significant for root-hair measurements, which indicated ANOVA assumptions concerning missing data were sufficient.

The four genotypes that ranked highest for number of main roots per plant (Table 3) also were among the five genotypes that ranked highest for total root length with root hairs (Table 1). 'Texturf 10' and 'FB 119' bermudagrasses ranked highest for mean main-root length per plant, and there was a trend for these genotypes to be high for number of root hairs arising from main or lateral roots. 'Texturf 10' and 'FB 119' also had the longest root hairs arising from either main or lateral roots (Table 3).

Root hairs contributed substantially to root lengths. Consequently, calculations of root lengths would be underestimated if root hairs were not included. Exceptions were 'Georgia Common' centipedegrass and 'Emerald' zoysiagrass in which root-hair contributions to root length were small. Genotypes highest for root lengths without root hairs also were highest for root lengths with root hairs (Table 1). In terms of elucidating mechanisms of drought resistance among the warm-season turfgrasses, root-hair contributions to root length maybe important in species that rely substantially on tissue dehydration avoidance by enhanced rooting and water absorption. Differences in tissue dehydration avoidance and drought resistance among the bermudagrasses may be partially attributed to differences in root and root-hair extent, because enhanced rooting and water absorption have been reported to be important in the tissue dehydration avoidance and drought resistance of bermudagrasses (Kim, 1987).

In summary, root hairs significantly contributed to root lengths among the warm-season turfgrasses ranging from 1% and 5% for 'Emerald' zoysiagrass and 'Georgia Common' centipedegrass, respectively, to 95% and 89% for 'Texturf 10' and 'FB 119' bermudagrasses, respectively. Previous research with vital stains suggests that the majority of root hairs were alive (Oprisko et al., 1990). Genotypes highest for root lengths with root hairs were highest for root lengths without root hairs. Genotypes highest for root lengths with root hairs also were highest for number of main roots per plant. In terms of root lengths with root hairs, first lateral roots contributed more to total root length than root lengths of either main roots or second lateral roots for all nine genotypes. Number and length of root hairs arising from either main roots or first and second lateral roots were not significantly

affected by their relative distance from the main-root cap. 'Texturf 10' and 'FB 119' bermudagrasses had the highest root and root-hair extent.

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