

Total root length was significantly longer in emmer 1 (614.20 mm, $P < 0.001$) when compared to all other genotypes (Figure 01C). The average length of lateral roots was not significantly different between genotypes. Emmer 2 produced root systems with maximum width of 143.74 mm ($P < 0.001$) (Figure 01D) and width to depth ratio (1.06, $P < 0.001$). Root systems of einkorn genotypes were narrow and shallower than all other genotypes. It was observed that bread wheat cv. JB Diego had a deep root system (Figure 01E) recording the maximum root depth of 201.56 mm ($P < 0.001$). Average width to depth ratio for emmer, bread wheat, einkorn and spelt was 0.97, 0.63, 0.48 and 0.42, respectively. The convex hull of the root system was significantly different between genotypes; highest in Xi 19 and lowest in einkorn 3 (Figure 01F). Tip angle of the seminal roots was significantly different among genotypes in the range of 16.73° to 35.78° (Figure 01G). Emmer 2 recorded the widest tip angle of seminal roots while narrow angles of seminal roots were observed in all spelt genotypes. Average emergence angle of the seminal root was 21.6° to 35.1° between genotypes ($P < 0.01$) (Figure 01H). Einkorn 1 showed the widest emergence angles at 14 DAT while spelt Oberkulmer had the narrowest emergence angle which was 61% narrower than einkorn 1. Nevertheless, the average emergence angle of einkorn was not significantly different from emmer species. Also, the emergence angle of emmer was not significantly different from bread wheat while spelt had the narrowest emergence angle at 14 DAT. Figure 02 and 3 show root system architecture (RSA) of 10 genotypes at 14 DAT.

There was a positive correlation between the tip angle of the seminal roots and the maximum width of the root system ($r = 0.84$; $P < 0.001$). Also, the ratio between width to depth was strongly correlated with the tip angle of the seminal roots ($r = 0.92$, $P < 0.001$). A strong relationship was observed between the average length of seminal root and the maximum depth of the root system ($r = 0.85$; $P < 0.01$).

At every sampling date, genotypes differed in the number of tillers per plant ($P < 0.001$) in Experiment 2. Spelt SB had the most tillers while einkorn 2 produced the least. When averaged across species, emmer and spelt showed vigorous tiller production at 41 DAT (Table 01). Green area was the highest in spelt at most of the sampling points followed by emmer, then bread wheat and least in einkorn ($P < 0.001$) (Table 01). Spelt and emmer produced the most shoot biomass when compared to bread wheat and einkorn ($P < 0.001$) (Table 02).

Chlorophyll concentration index of the leaf (as SPAD value) was very high in bread wheat cv. Xi 19 throughout the experiment, despite the fact that all genotypes were supplied with the same amount of nutrients (data not shown). The spelt and emmer genotypes had low SPAD values representing less N in their leaves but had higher N uptake than cv. Xi 19. It may therefore, be presumed that the genotypes utilise N differently. While the spelt and emmer used it to produce more shoot biomass with the lower leaf N concentration, modern bread wheat seemed to produce less shoot biomass but with a higher leaf N concentration.

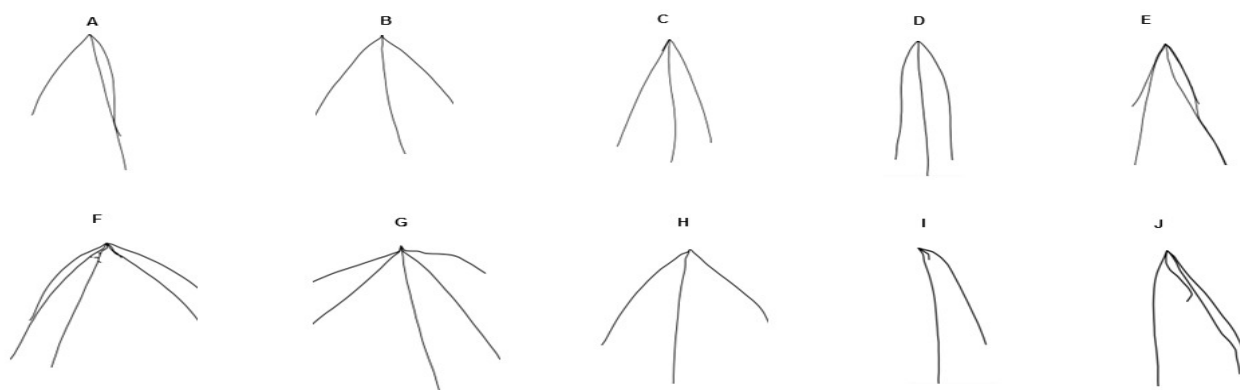


Figure 02: Representative root system architectural images of bread wheat (A) JB Diego (B) Xi 19 (C) Spelt Tauro (D) Spelt SB (E) Spelt Oberkulmer (F) Emmer 1 (G) Emmer 2 (H) Einkorn 1 (I) Einkorn 2 and (J) Einkorn 3 at 14 DAT in experiment 1

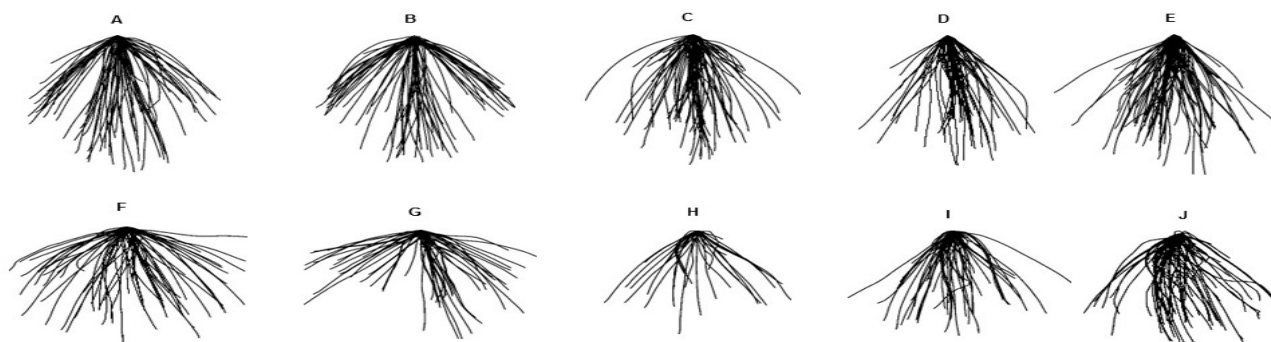


Figure 03: Root system architecture of bread wheat (A) JB Diego (B) Xi 19 (C) Spelt Tauro (D) Spelt SB (E) Spelt Oberkulmer (F) Emmer 1 (G) Emmer 2 (H) Einkorn 1 (I) Einkorn 2 and (J) Einkorn 3 at 14 DAT in experiment 1. These images are produced by overlaying all RSA images of the replicates of 10 genotypes using *RootNav* software (n = 10 to 25)

Table 01: Number of tillers per plant, green area ($\text{cm}^2 \text{plant}^{-1}$) and biomass production (g plant^{-1}) of the plant at 14, 23, 32 and 41 days after transplanting (DAT) in Experiment 2

GT	Number of tillers (plant^{-1})				Green area ($\text{cm}^2 \text{plant}^{-1}$)			
	14 DAT	23 DAT	32 DAT	41 DAT	14 DAT	23 DAT	32 DAT	41 DAT
JB Diego	9	23	31	59	151.57	365.37	471.59	1070.83
Xi 19	6	13	26	56	174.33	478.75	590.32	1252.82
Spelt Tauro	7	19	22	35	247.85	646.67	647.62	740.53
Spelt SB	8	26	88	87	242.59	694.02	1117.31	2277.46
Spelt Oberkulmer	10	27	55	79	230.87	693.54	832.45	1922.62
Emmer 1	7	13	30	72	201.81	570.47	959.94	1427.81
Emmer 2	6	16	27	67	228.68	647.91	925.90	1408.47
Einkorn 1	7	14	22	36	88.86	196.96	200.52	453.73
Einkorn 2	5	9	16	26	35.85	54.21	91.82	159.61
Einkorn 3	7	7	17	37	88.41	146.69	230.75	359.47
SED ($df=18$)	0.71	2.71	5.66	8.70	33.722	59.504	67.001	269.707
P value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 02: Shoot biomass production (g plant^{-1}) and nitrogen uptake (gN shoot^{-1}) of the plant at 14, 23, 32 and 41 days after transplanting (DAT) in Experiment 2.

GT	Shoot biomass (g plant^{-1})				N_{off} (gN shoot^{-1})			
	14 DAT	23 DAT	32 DAT	41 DAT	14 DAT	23 DAT	32 DAT	41 DAT
JB Diego	0.79	2.35	3.56	8.61	0.04	0.09	0.14	0.36
Xi 19	0.87	2.94	5.69	13.53	0.04	0.12	0.22	0.54
Spelt Tauro	1.19	3.78	6.11	6.01	0.06	0.14	0.19	0.20

GT	Shoot biomass (g plant ⁻¹)				N _{off} (gN shoot ⁻¹)			
	14 DAT	23 DAT	32 DAT	41 DAT	14 DAT	23 DAT	32 DAT	41 DAT
Spelt Oberkulmer	1.10	3.71	6.63	16.16	0.06	0.15	0.23	0.63
Emmer 1	0.95	3.10	7.26	13.03	0.05	0.12	0.26	0.47
Emmer 2	1.08	3.81	7.45	15.77	0.05	0.14	0.28	0.54
Einkorn 1	0.50	1.27	1.90	4.60	0.02	0.04	0.06	0.09
Einkorn 2	0.20	0.40	0.83	1.41	0.01	0.01	0.02	0.04
Einkorn 3	0.49	1.29	2.38	3.58	0.02	0.04	0.07	0.10
SED (<i>df</i> =18)	0.13	0.29	0.61	2.72	0.01	0.01	0.03	0.11
P value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

The highest shoot N% was recorded in bread wheat cv. JB Diego; 5.06 and 4.14 at 23 and 41 DAT, respectively ($P < 0.001$). Einkorn 2 recorded the lowest shoot N% during the experiment. Table 2 shows shoot N uptake of the ten genotypes throughout the experimental period. The ranking of the genotypes for N uptake at 41 DAT was spelt cv. SB > spelt cv. Oberkulmer > bread wheat cv. Xi 19 and emmer 2 > emmer 1 > bread wheat cv. JB Diego > spelt cv. Tauro >> einkorn 3 > einkorn 1 > einkorn 2.

The highest total root length was recorded in spelt cv. SB and Oberkulmer than other genotypes throughout the experiment 2 ($P < 0.001$) (Figure 04A). All einkorn genotypes showed very weak root growth and produced fewer roots than the other genotypes. The total root length of emmer and bread wheat was in between spelt and einkorn. The highest root biomass (Figure 04B) of the genotypes was recorded in spelt cv. SB at 32 and 41 DAT (87% and 81% higher than the lowest value produced by einkorn 2, respectively). The ranking of the genotypes for

root biomass production at 41 DAT was spelt cv. SB > spelt cv. Oberkulmer > bread wheat cv. Xi 19 > emmer 2 > bread wheat cv. JB Diego > spelt cv. Tauro > emmer 1 > einkorn 1 > einkorn 3 > einkorn 2.

Similar to the results of total root length, the highest root volume (Figure 05) was observed in spelt genotypes and the lowest values in einkorn. Average root diameter was high in emmer genotypes and lower in einkorn, suggesting that emmer has thicker roots than all other genotypes. Specific root length (SRL) was high in einkorn 2 and low in emmer genotypes. SRL of all genotypes decreased over time, indicating younger plants had thinner roots.

Root length was recorded in different diameter (mm) classes where lower diameters represent more lateral roots and the higher diameter classes represent more seminal and nodal roots. Length of very fine roots (LVFR; < 0.5 mm diameter) represented 78% to 85% of the total root length at 41 DAT, depending on the species.

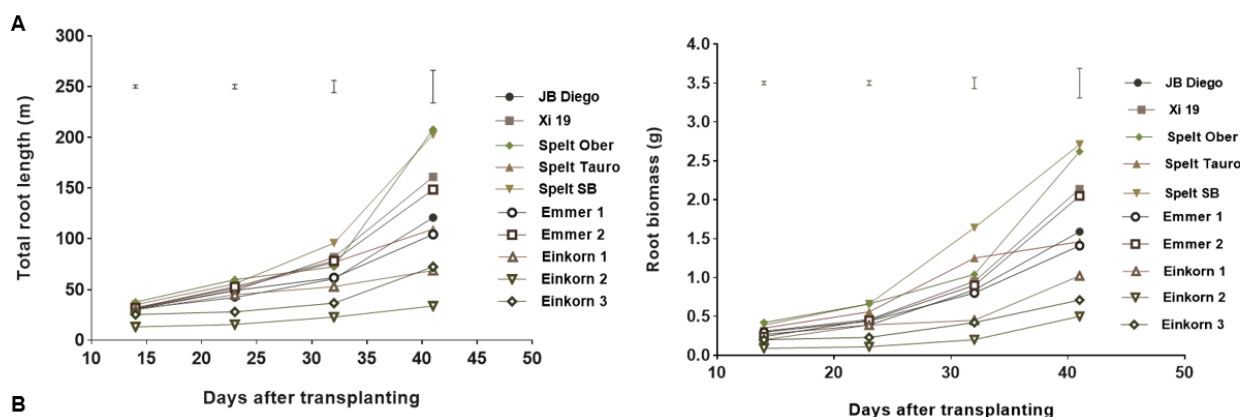


Figure 04: (A) Total root length (B) root biomass of the genotypes at 14 DAT in Experiment 2. Error bars represent the SED of the genotypes at $P < 0.001$ ($df=18$).

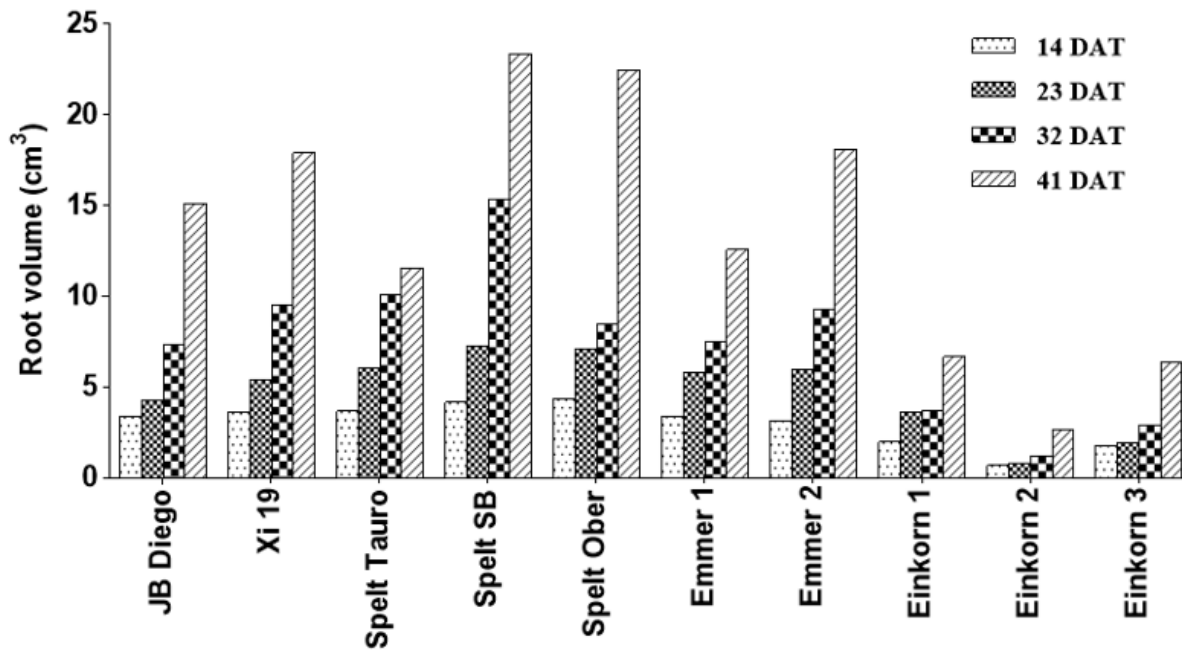


Figure 05: Root volume of the genotypes at 14, 23, 32 and 41DAT in Experiment 2. SED for GT at 14, 23, 32 and 41 DAT was 0.49, 0.56, 1.69 and 3.68, respectively ($df=18$).

Spelt genotypes had the highest root elongation rate (RER) and einkorn the lowest. RER of spelt was higher than bread wheat by 23%, while emmer and einkorn genotypes had lower RER than bread wheat by 11% and 142%, respectively. Nitrogen uptake efficiency of roots ($NUpE_R$) was significantly different among genotypes throughout the experiment and mean across all sampling dates, the highest value was recorded in emmer and lowest in einkorn ($P < 0.001$) (Table 03). The average $NUpE_R$ of emmer at 41 DAT was 25%, 35% and 166% higher than bread wheat, spelt and einkorn, correspondingly. The highest specific absorption rate of roots ($S_{AB}R_N$) was recorded in emmer 1 both for root biomass and total root length but there is no significant difference between Spelt cv. SB and emmer 1 ($P < 0.001$) (Table 03).

The green area of the plant at all sampling dates had a positive and strong relationship with respective shoot N uptake ($r = 0.97$, $P < 0.001$). A similar relationship was observed between shoot biomass and N uptake of the shoot ($r = 0.96$, $P < 0.001$). Nitrogen uptake efficiency of roots ($NUpE_R$) explained green area (50% to 66%) and shoot biomass production (53% to 74%) in all genotypes throughout the experiment. The number of tillers explained 70% of the variation

in total root length ($P < 0.001$) and observed variation of green area production per plant is associated with tiller production ($r = 0.90$, $P < 0.001$) and therefore, total root length of the plant had a strong relationship with green area production ($r = 0.87$, $P < 0.001$) or number of leaves/ number of tillers per plant at 41 DAT.

Total root length and root length density explained 90% of N uptake of the shoot at 41 DAT. The relationship between root volume and N uptake of the shoot was strong ($r = 0.94$, $P < 0.001$). Root biomass explained 93% of N uptake of the shoot ($P < 0.001$). A close relationship was found between N uptake and length of very fine roots, and more than 88% of the variation in N uptake was explained by this diameter class ($P < 0.001$).

In experiment 3, above-ground biomass (AGB) and grain yield were significantly different between genotypes ($P < 0.001$) and N level ($P < 0.01$) at maturity. Emmer 2 had the highest AGB at both N levels and einkorn the lowest. The most grain yield was observed in bread wheat cv. JB Diego for LN and HN conditions (Table 04).

Plants treated with HN had greater N% in the straw, chaff and grain than LN plants ($P < 0.05$). Genotypes differed significantly ($P < 0.001$) although there was no significant interaction

between genotype and N level. Spelt cv. Oberkulmer recorded the lowest straw N% at 0.42 and 0.86 for LN and HN treatments, respectively, while einkorn 3 recorded the highest values for both N levels (Table 05). Chaff N% varied between 0.33 to 1.04 for LN and 0.88 to 1.59

for HN plants. Highest grain N% was recorded in einkorn 2 in both LN (3.45) and HN (3.99). Bread wheat cv. JB Diego recorded the lowest N% of the grain of 1.40 and 2.19 for LN and HN, respectively.

Table 03: Root N uptake efficiency (%) at 14, 23, 32 and 41 days after transplanting (DAT) and the specific absorption rate of N based on root biomass (mg g⁻¹ root day⁻¹) and root length (mg m⁻¹ root day⁻¹) of the plants during 14 DAT to 41 DAT in Experiment 2

GT	Root N uptake efficiency (%)				Specific absorption rate	
	14 DAT	23 DAT	32 DAT	41 DAT	mg g ⁻¹	mg m ⁻¹
					root day ⁻¹	root day ⁻¹
JB Diego	15.33	22.27	16.59	22.17	15.58	0.18
Xi 19	14.34	26.40	23.09	24.87	18.88	0.23
Spelt Tauro	16.56	26.14	15.30	15.26	7.43	0.09
Spelt SB	14.04	23.18	19.34	25.94	19.37	0.24
Spelt Oberkulmer	13.17	22.29	22.89	23.99	16.94	0.21
Emmer 1	15.65	27.41	32.94	33.54	22.05	0.27
Emmer 2	21.58	32.43	30.87	25.37	20.25	0.23
Einkorn 1	11.83	10.60	13.29	8.81	5.38	0.05
Einkorn 2	9.06	10.47	11.65	9.60	5.32	0.05
Einkorn 3	12.35	17.91	16.87	14.79	7.27	0.06
SED (df = 18)	1.83	3.09	2.35	3.46	2.72	0.04
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 04: Above-ground biomass (g plant⁻¹) and grain yield (g plant⁻¹) of the plant at maturity in Experiment 3 at LN (an equivalent rate of 50 kg N ha⁻¹) and HN (an equivalent rate of 200 kg N ha⁻¹)

GT	Above-ground biomass (g plant ⁻¹)		Grain yield (g plant ⁻¹)	
	LN	HN	LN	HN
JB Diego	36.03	50.98	12.47	20.59
Xi 19	32.27	50.91	11.71	18.89
Spelt Tauro	30.37	44.83	8.94	12.60
Spelt SB	32.53	60.42	8.26	16.03
Spelt Oberkulmer	33.57	49.43	5.42	12.35
Emmer 1	37.75	56.40	8.28	14.04
Emmer 2	41.99	61.81	10.10	13.26
Einkorn 1	17.55	39.38	3.36	5.55
Einkorn 2	12.56	28.63	1.46	3.27
Einkorn 3	18.34	25.44	2.18	3.24
SED ; GT (df)	3.541 (36)***		1.957 (36)***	
N (df)	0.835 (2)**		0.326 (2)**	
GT x N (df)	4.823 (37.6) ^{NS}		2.646 (36.9) ^{NS}	

*** Significant at $P < 0.001$, **significant at $P < 0.01$, *significant at $P < 0.05$, NS - Not significant

Table 05: Straw N%, chaff N% and grain N% of the genotypes at maturity in Experiment 3 at LN (an equivalent rate of 50 kg N ha⁻¹) and HN (an equivalent rate of 200 kg N ha⁻¹)

GT	Straw N%		Chaff N%		Grain N%	
	LN	HN	LN	HN	LN	HN
JB Diego	0.52	1.33	0.59	1.50	1.40	2.19
Xi 19	0.47	1.21	0.42	1.22	1.42	2.28
Spelt Tauro	0.63	1.14	0.44	0.88	2.34	3.20
Spelt SB	0.70	0.89	0.68	1.59	2.20	3.27
Spelt Ober	0.42	0.86	1.04	1.35	3.08	3.62
Emmer 1	0.53	1.11	0.33	1.02	2.42	3.26
Emmer 2	0.53	0.86	0.40	1.23	2.27	3.43
Einkorn 1	0.91	1.43	0.69	1.39	2.86	3.67
Einkorn 2	0.76	1.32	0.72	1.40	3.17	3.89
Einkorn 3	0.95	2.13	0.95	1.44	3.45	3.99
SED ; GT (<i>df</i>)	0.190 (36)**		0.135(36)***		0.176(36)***	
N (<i>df</i>)	0.81 (2)*		0.104 (2)*		0.098 (2)*	
GT x N (<i>df</i>)	0.268 (36.9) ^{NS}		0.201(21.6) ^{NS}		0.256 (32.1) ^{NS}	

*** Significant at $P < 0.001$, **significant at $P < 0.01$, *significant at $P < 0.05$, NS - Not significant

NUpE of the genotypes was between 0.20 to 0.54 for LN and 0.16 to 0.34 for HN plants. The highest NUpE was recorded in emmer species followed by spelt, bread wheat and then einkorn ($P < 0.001$) (Figure 06) and always higher at LN. However, no interaction was observed between genotype and N level.

DISCUSSION

The development of root systems which promote N uptake is important (Delmer, 2005; Foulkes *et al.*, 2009; Gaju *et al.*, 2011) considering the significant impact of artificial N fertiliser on cost of production and its detrimental effects on the environment (Conley *et al.*, 2009; Vitousek *et al.*, 2009; Dourado-Neto *et al.*, 2010).

In Experiment 1 the ancient wheat genotypes, together with bread wheat, exhibited substantial variation in the number of seminal roots which ranged from 3.76 to 5.27, compared to Gregory *et al.* (1978) who reported that, on average, the winter wheat grown in temperate weather conditions produced six seminal roots. The

greatest number of seminal roots was recorded in emmer 2, suggesting that emmer has the potential to develop a strong root system at the early stages of crop growth. The total root length of the seedling was also high in emmer when compared to all other genotypes. Therefore, it can be proposed that, mature emmer will develop a horizontally grown root system enabling it to uptake more fertiliser N from the top layers of the soil before it is transferred to deeper layers of the soil horizon.

The seminal root tip angle of emmer 2 was wider than the other ancient wheat genotypes suggesting the development of a wider root system. Supporting the above suggestion, emmer 2 recorded the maximum width of the root system within 14 DAT. Spelt and bread wheat genotypes had a narrow tip angle of seminal roots and deeper root systems when compared to emmer and einkorn. The current results showed some consistency with previous investigations by Nakomoto and Oyangi (1994) who, based on the variation of the angular spread of seminal roots of Japanese wheat germplasm, found that genotypes with narrower angles of seminal

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