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Variation in potassium and calcium uptake with time and root depth

1 CEU IN NUTRIENT MANAGEMENT

Plant roots take up water and mineral nutrients essential for growth, but some localization of nutrient uptake is seen within the root system (Marschner 1995). For example, movement of calcium (Ca) across the root radius is strictly apoplastic, and this element cannot cross the Casparian strip formed in the endodermis immediately behind the root apex (Gregory 1988). Therefore, Ca uptake is mostly limited to the distal 1–2 cm behind the tip (Russell 1977). In contrast, uptake of potassium (K) occurs across root cell membranes, so uptake of this element occurs for a greater proximal distance along the root than for Ca.

The timing of nutrient uptake can vary with different plant species. In forage blends, some grasses will take up K and phosphorus (P) earlier in the growing season than will the other grasses in the mixture, thus avoiding competition (Veresouglou and Fitter 1984). Separation of root activity in time for different plant species improves resource utilization and can promote biodiversity.

Fertilizer applications are commonly used to optimize nutrient supplies in commercial crop production. Effectiveness of fertilizer application can be improved by placing it to coincide with crop demand and with root activity in time and space (Randall and Hoeft 1988). Understanding the mechanisms of root growth and nutrient uptake can help formulate nutrient management practices to improve nutrient use efficiency.

The Ca and K distributed through the soil profile serve as a source of nutrient uptake by plants. The presence of relatively high concentrations of these nutrients through the soil profile makes it difficult to determine the precise position from which the nutrients are accessed by the root system. Plants take up rubidium (Rb) and strontium (Sr) in the same manner as K and Ca, respectively, yet both Rb and Sr are normally at low concentration in the environment, and so the appearance of these tracer elements in the plant tissues following their addition to the environs of roots indicates the roots were active in the region where the tracer elements were present (Krstich 1987; Kodur et al. 2011).

Uptake of nutrients by the roots of row crops is not affected solely by depth of nutrient placement, but also by the lateral separation of fertilizer placement from the seed row.

An additional confounding effect may be the activity of arbuscular mycorrhizal (AM) fungi. The roots of many plants including maize (Zea mays L.) are normally colonized with AM fungi in the field (McGonigle and Miller 1993). The AM fungi take sugar from the plant, and in return these fungi assist with nutrient uptake by plants, most commonly P (Smith and Read 2008), but also K (George et al. 1992). In keeping with mycorrhizal stimulation of K uptake, AM plants can show greater Rb-tracer enrichment than non-mycorrhizal species (Hawkes and Casper 2002).

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Root tracers were used here in a field experiment to investigate mineral nutrient uptake of maize roots in relation to depth in soil and through time. In order to determine the impact of depth without any effect of time of root interception of tracer from lateral root spread, an aqueous blend of rubidium chloride (RbCl) and $SrCl_2$ solution was distributed evenly across the plot and within the depth interval of study in the field, rather than as a point source. In this way, activity of roots in relation to depth could be investigated at various times, in the absence of confounding effects of lateral separation. Rb was used to investigate K uptake with regard to fertilizer band placement, and Sr was used to investigate Ca uptake. Although Ca uptake was predicted from published laboratory data to be restricted to root tips, such an effect had to our knowledge not been hitherto investigated in the field. The influence of mycorrhizae on rare-element tracer uptake was simultaneously evaluated by use of a soil pasteurization treatment to eliminate mycorrhizal fungi, compared with a control not pasteurized.

MATERIALS AND METHODS

The experiment was conducted at the Phillips Experimental Farm (lat. 99.98W, long. 50.08N), near the Brandon Research Station of Agriculture and Agri-Food Canada in Brandon, Manitoba, Canada. The soil at the site is an Orthic Black Chernozem of pH 7.4, with 30 g organic-C kg^{-1}, 30% clay, 39% silt, 31% sand, cation exchange capacity of 35 cmol kg^{-1}, and conductivity of 310 mS kg^{-1} (Grant et al. 2013). The area used had been sown to flax in the previous year of the study, and so it was expected to have abundant mycorrhizal inoculum. Each of four replicates consisted of two main plots, with each of the eight main plots being a single open-bottom wood-board structure dug into the ground and enclosing four 30-cm by 30-cm cells arranged in a square. The field experiment thereby had 32 micro-plots, each of 30 cm by 30 cm. The upper edge of each wood-board structure was inserted flush to the soil surface, with subsequent soil replacement. Two treatment factors applied were (1) soil pasteurization and (2) amendment with a mixture of aqueous chlorides of Rb and Sr. There were two levels to the soil pasteurization treatment: not pasteurized, and pasteurized. There were four levels to the soil amendment treatment factor: control with no amendment, and the addition of 0.62 mmol kg^{-1} dry soil of both Sr and Rb to depth intervals of 0–5 cm, 5–10 cm, or 10–15 cm. The experiment had four blocked replicates in a split-plot design with pasteurization as the main plot factor and amendment as the split-plot factor: 4 replicates × 2 pasteurization treatments × 4 Rb-Sr treatments = 32 micro-plots.

A root sample for mycorrhizal assessment in the form of a 3.5-cm-diameter by 15-cm-deep core was taken directly over the base of the shoot that had been removed at 25 days after planting (DAP).

Dried shoots were ground to pass a 2-mm screen, and 0.05-g subsamples were digested by heating to reflux in 7 mL of a mixture of 10 parts concentrated nitric acid and one part concentrated sulfuric acid. The Rb and Sr concentrations were determined for diluted digests using inductively coupled plasma optical emission spectrometry (ICP-OES).

Movement of Rb and Sr in soil was checked by determination at final harvest of the ammonium-acetate extractable (Simard 1993) soil concentration of Rb and Sr by depth for soil not pasteurized but amended in the 0- to 5-cm depth fraction. Simultaneously, Ca, magnesium (Mg), and K were determined for the same extracts using ICP-OES as above to provide a contrast to the tracer elements, the macronutrient elements being expected to not change in response to amendment.

RESULTS

Amendment of Rb and Sr successfully elevated extractable soil concentrations of Rb and Sr without changing levels of Ca, Mg, and K, as seen for the 0- to 5-cm depth interval (Table 1). There was no downward movement of the rare-element tracers within the soil profile over the course of the experiment, with no elevation of tracer levels outside of the applied depth (Table 1). Root length density over the 15-cm depth interval at 25 DAP was not affected by any treatment, with overall mean ± SD of 2.0 ± 0.6 cm cm^{-3} for n = 32. Mycorrhizal development was extensive in plants in the not pasteurized treatment at 25 DAP, with close to half of the root length colonized with arbuscules (Table 2). Colonization was building within plants of the pasteurized treatment at 25 DAP, with close to 10% of root length colonized by arbuscules (Table 2). Shoot P concentration and shoot dry mass were stimulated for plants in the pasteurized soil during the early growth period, but shoot P concentration was greater significantly for plants in the not pasteurized treatment compared with the pasteurized treatment at the final harvest (Table 3).

Shoot Rb concentration was not affected by soil pasteurization at any harvest, and shoot Sr concentration was not affected by soil pasteurization at six of the seven harvests (Table 4). However, placement of Rb and Sr had a major impact on shoot recovery of these elements in almost all cases, with no interaction occurring between pasteurization and placement (Table 4). The significant value for effect of pasteurization on shoot Sr concentration at the sixth harvest corresponded to 0.012 mg g^{-1} shoot Sr concentration for plants in the not pasteurized soil compared with 0.026 mg g^{-1} shoot Sr concentration for plants in the pasteurized soil. This result offers no correspondence to other harvests and appeared anomalous.

DISCUSSION

Maximum shoot concentration of Sr at 16 DAP with placement at 0–5 cm depth and maximum shoot concentration of Rb at 25 DAP with placement at 5–10 cm depth most likely reflect earlier and more shallow tracer interception by distal parts of the root system active for Sr uptake, and subsequent, deeper tracer interception by more proximal sections of the root system active for Rb uptake. Accumulation for K and there by Rb will be related to the quantity of absorbing surface of the root and the concentration of nutrient present at the root surface, with the rate of uptake for a given root cylinder limited by diffusion through soil to that root (Drew et al. 1969; Barber 1995). In contrast, mass flow of water delivers Ca to the root tips as needed for uptake (Barber 1995 root contacting the nutrient for both Sr (Moyen and Roblin 2010) and Rb (Kodur et al. 2011).

Changes with time for the distribution of maize root with depth can be expected to have proceeded during the experiment in accordance

with previous studies. Whereas most studies quantify roots of maize with depth across coarse intervals of 10 cm (Gao et al. 2010) or 20 cm (Tardieu 1988), Taboada and Alvarez (2008) recorded maize roots at anthesis using the profile wall method with root abundance scores averaged across multiple plots at each of three sites as 4.2, 3.4, and 2.7, for respective depths of 0–5 cm, 5–10 cm, and 10–15 cm. Thus, even at close to maximum root production, earlier development of root length in the upper profile is still manifest in terms of decreasing quantity of root with increasing depth as designated with the intervals here studied. The establishment and persistence of differences in root quantity with depth supports the interpretation relating function to depth as made here for uptake of Sr and Rb. The root length density of 2.0 cm cm^{-3} scored here for 0–15 cm depth below the shoot base at 25 DAP corresponds well to published values of 1.8 cm cm^{-3} for maize at 52 DAP within the row (Gao et al. 2010) and 2.0 cm cm^{-3} for maize at 97 DAP within the row (McGonigle and Miller 1993).

Greatest total shoot accumulation at final harvest from the 5- to 15-cm placement for Rb (data not shown) and 5- to 10-cm placement for Sr (data not shown) indicate that root uptake of both K and Ca may be reduced from 0 to 5 cm compared with greater depths, and therefore that soil testing and fertilizer placement should focus more on the 5- to 15-cm depth interval than the surface soil for plant acquisition of K and Ca. Improved yield response to deeper placement of K banded fertilizer has been reported for maize (Mallarino and Murrell 1998). Periodic drying at the soil surface during the growing season is to be expected in a normal year, and so deployment of roots for uptake of nutrients at least 5 cm below the surface avoids such risk.

Higher shoot P concentration in plants of the pasteurized soil treatment at early harvests was likely caused by release of nutrients caused by soil heating during the pasteurization process. Soil pasteurization was previously shown to raise sharply extractible levels of soil ammonium and nitrate, but not available soil P (McGonigle and Miller 1996). Stimulation of shoot P concentration seen here likely occurred in tandem with an elevation of shoot N concentration following release of available soil mineral N in response to soil heating, although soil N and shoot N were not monitored. Shoot dry mass was stimulated in the plants in the pasteurized treatment at 35 DAP, in keeping with an explanation of nutrient release associated with pasteurization.

Roots in the pasteurized treatment had reduced development of mycorrhizae but colonization was not prevented, which can be attributed to some combination of uneven heating of soil in the pasteurization unit and recolonization by AM fungi from the surrounding environment after placement in the field. The functional capacity of the mycorrhizal system in the pasteurized treatment seems to have been at least partially compromised by reduction of arbuscular colonization from 49 to 10% of root length, because a significant increase in shoot P concentration in the not pasteurized treatment, relative to the pasteurized treatment, at the final harvest. Delayed development of mycorrhizal colonization of plants in the pasteurized treatment (Table 2) likely caused the significantly greater shoot P concentration of plants in the not pasteurized treatment at the final harvest (Table 3). The lack of any impact of soil pasteurization on Sr at most harvests was expected, given that mycorrhizae do not modify uptake of Ca. The lack of any impact of pasteurization on Rb uptake suggests that mycorrhizae did not influence plant acquisition of K, in contrast to previous data for K (George et al. 1992) and Rb (Hawkes and Casper 2002). The high initial concentration of available K (Table 1) and the reasonably high clay content of 30% for the soil probably ensured K was well supplied to these young maize plants.

From the present study, a recommendation emerges for future work with Sr and Rb tracers to study root activity. Depth placement of Rb and Sr tracers in the range 5 to 15 cm should be selected in preference to a more shallow amendment when maize plants of 3–7 wk or more in age are to be sampled in research. These results for maize should be extended to other species for use in research with caution, because early work established differences among plant species in spatial patterns of nutrient uptake (Soper and Kalra 1969).

To conclude, the agronomic implications of the study are developed thus. Sr and Rb tracers to mimic uptake of Ca and K, respectively, showed that movement of Ca into plant roots can be expected in the first 2 or 3 wk of growth from the top 5 cm of soil, whereas K uptake is expected in the weeks to follow and at greater depth. However, Ca uptake from greater depth later exceeds that acquired earlier, so that the greatest uptake of both Ca and K is expected for the 5-to-15 cm depth over 3–7 wk for maize. Recommendations for agriculture that emerge, therefore, are that banded K fertilizer is expected to be most effective for early season uptake when placed between 5 and 15-cm depth, and assessment of soil Ca for maize early season uptake should focus on the 5- to-15cm depth interval.

TABLE 1

Ammonium-acetate extractable soil concentrations with depth at final harvest for the not pasteurized treatment for K, Ca, Mg, Rb, and Sr. Amendment was made before planting with 0.62 mmol Rb kg–1 and 0.62 mmol Sr kg^{-1} throughout the 0- to-5cm depth interval

Treatment	Depth (cm)	K	Ca	Mg	Rb	Sr
	(mg kg^{-1})					
Control	0–5	290*g*	4850*f*	882*e*	10.2*c*	6.9*a*
	5–10	295*g*	5120*f*	837*e*	7.3*c*	6.9*a*
	10–15	287*g*	6570*f*	1092*e*	8.0*c*	8.5*a*
Amended	0–5	459*g*	6380*f*	934*e*	16.3*d*	46.8*b*
	5–10	310*g*	5000*f*	815*e*	8.5*c*	7.4*a*
	10–15	346*g*	6670*f*	1045*e*	9.8*c*	8.9*a*

a–f Means in any column followed by different letters are different significantly at $P = 0.05$; $n = 4$.

TABLE 2

Percentage of root length colonized by mycorrhizal structures at 25 d after planting in the not pasteurized treatment and the pasteurized treatment

Mycorrhizal structure	Not pasteurized	Pasteurized	Probability[z]
	(%)		
Arbuscules	48.8	9.8	<0.001
Vesicles	2.7	0.4	<0.001
Hyphae	81.8	50.1	<0.001

[z]Probabilities are given for comparison of means of the two treatments for data given the angular transformation; $n = 16$.

TABLE 3

Shoot concentrations of P and shoot dry mass for plants grown in the not pasteurized treatment and the pasteurized treatment at each of the seven harvests

Harvest	Not pasteurized	Pasteurized	P^z	Not pasteurized	Pasteurized	P
	(mg P g^{-1})			Shoot dry mass (g)		
1	6.51	6.80	0.59	0.031	0.034	0.48
2	2.94	3.50	0.04	0.11	0.13	0.18
3	1.86	2.21	0.10	0.28	0.36	0.06
4	1.75	2.08	0.20	0.40	0.45	0.49
5	1.76	2.15	0.08	0.73	1.36	0.006
6	2.47	2.36	0.84	1.49	0.92	0.12
7	2.74	2.19	0.015	5.90	4.30	0.24

[z]Probabilities are for comparisons of means at a harvest in the preceding two columns; $n = 16$.

TABLE 4

Probabilities from split-plot analyses of variance at the seven harvests for shoot Rb concentration and shoot Sr concentration. The main-plot factor was pasteurization, with soil either not pasteurized or pasteurized. The split plot factor was placement, with the rare element tracers either none or placed at 0–5 cm, 5–10 cm, or 10–15 cm

Factor	Trace element	Harvest						
		1	2	3	4	5	6	7
		Probability of a greater value of F						
Pasteurization	Rb	0.22	0.10	0.58	0.31	0.11	0.13	0.68
	Sr	0.28	0.36	0.52	0.59	0.99	0.02	0.96
Placement	Rb	0.13	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Sr	0.015	0.046	<0.001	0.002	0.002	0.40	0.09
Pasteurization x Placement	Rb	0.91	0.93	0.55	0.65	0.91	0.33	0.06
	Sr	0.43	0.21	0.06	0.74	0.11	0.24	0.76