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Elemental Uptake in Relation to Root Characteristics of Tall Fescue[#]

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ABSTRACT

HiMag, an accession of tall fescue (*Festuca arundinacea* Schreb.), was selected for high magnesium (Mg) concentration in leaves to reduce grass tetany risk to ruminants. However, the mechanism for enhanced Mg uptake in HiMag leaves has not been determined. The objective was to investigate if increased Mg uptake in HiMag could be explained by differences in elemental distribution among plant parts, root

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characteristics, or organic acid concentrations compared to its parental cultivars, "Kentucky 31" (KY31) and "Missouri 96" (MO96). The study was conducted on a surface-irrigated calcareous Portneuf silt loam (coarse-silty, mixed, mesic, Durinodic Xeric Haplocalcid). Vegetation and soil cores of 7.6-cm diameter were sampled to a 45-cm soil depth in 15-cm increments. Mass and ash were determined for leaves, crowns, and roots. Leaf area, root length, root area, root length density, elemental concentration, and uptake [potassium (K), calcium (Ca), Mg, sodium (Na), and phosphorus (P)], and malate and citrate concentrations also were determined. Leaf Mg concentration was higher in HiMag than parental cultivars. HiMag generally did not differ in crown and root elemental concentrations from its parents. Risk of causing grass tetany, indicated by leaf K/(Ca + Mg), was lower in HiMag than KY31 and MO96 in both 1994 ($P = 0.03$) and 1995 ($P = 0.01$). Root length, area, and mass were not related to cation concentrations in the three tall fescue accessions, suggesting that HiMag may have an active uptake or transport mechanism for Mg.

Key Words: Herbage; *Festuca arundinacea*; HiMag; Root length; Root area; Magnesium; Calcium; Potassium; Phosphorus; Malate; Citrate.

INTRODUCTION

Cool-season grasses provide an important forage resource throughout temperate regions of the world. However, elemental imbalances in herbage may lead to hypomagnesemia (commonly known as grass tetany), a metabolic disorder in ruminant animals identified by low blood serum Mg, which causes animal production and death losses.[1] These losses are estimated at $400 million annually in the United States,[2] and 40% of these losses are believed to occur on the 12–14 Mha of tall fescue (*Festuca arundinacea* Schreb.).[3] To help alleviate these losses, Sleper et al.,[4] and Mayland and Sleper[5] selected a tall fescue accession, HiMag, for reduced K/(Ca + Mg) and high Mg and Ca levels in herbage of the second generation from parental cultivars, "Kentucky 31" (KY31)[6] and "Missouri 96" (MO96).[7] The ratio of K/(Ca+Mg) is an index used to predict grass tetany incidence, that increases exponentially when K/(Ca + Mg), calculated in moles of charge, exceeds 2.2.[8]

Despite the promise of forage cultivars with reduced tetany risk, little is known about the mechanisms for absorption and partitioning of Mg, Ca, and K in cool-season grasses. HiMag provided about 20% more leaf

Mg than its parents, KY31 and MO96, on both acidic Typic Hapludults in Georgia[9] and a calcareous Durinodic Xeric Haplocalcid soil in Idaho.[5] The mechanism of increased Mg uptake in HiMag is not known. It was hypothesized that high leaf Mg concentrations were due to differences in root characteristics, ability to absorb greater amounts of Mg into the roots, or a difference in elemental transport. In addition, because organic acids exuded from roots may influence the rhizoshpere to affect ion solubility and uptake by plants,[10] it was hypothesized that malate and citrate concentrations in HiMag may be higher than KY31 and MO96. The objective of this study was to determine if enhanced Mg uptake in HiMag is associated with differences in elemental distribution among plant parts, root characteristics, or root tissue malate and citrate concentrations.

MATERIALS AND METHODS

Three tall fescue accessions: HiMag, KY31, and MO96 were sown (4.7 kg seed ha^{-1}) on 20 Sept. 1991 in six 7.6-m long rows spaced at 0.56 m in a randomized complete block design.[11] Accessions were free of a fungal endophyte [(*Neotyphodium coenophialum* Morgan-Jones and Gams) Glen, Bacon and Hanlin comb. nov.] that reduces cattle performance. The soil was a surface-irrigated Portneuf silt loam (coarse-silty, mixed, mesic, Durinodic Xeric Haplocalcid) near Kimberly, ID, USA (42°30′N and 114°8′W, elevation 1200 m). This calcareous soil has an average pH of 7.7 which may allow soil P to be fixed as $Ca_3(PO_4)_2$. However, soil test P levels were adequate (Table 1). In October and again on 1 April of each year, plants were flail-mowed to a height of 8 cm, fertilized with 56 kg N ha^{-1} as broadcast urea or ammonium nitrate, and then irrigated using furrows spaced 1.1 m apart.

Plant Sample Collection and Processing

Concentrations of Ca, Mg, and K were evaluated in roots, crowns, and leaves of HiMag, MO96, and KY31 during 1994 and 1995. Malate and citrate concentrations in root tissue were analyzed in 1994 samples. Leaves within a 7.6-cm diameter ring centered on the row were clipped to a 7.6-cm stubble height from two rows at randomly selected points along the 6.7-m long row. Leaf fresh weight was recorded, and leaf area was determined on a 10-g (1994) or 5-g (1995) subsample. After clipping leaves, a 7.6-cm diameter core was extracted from the soil on 20 April

Table 1. Means ($n = 6$) of saturation water content, bicarbonate-extracted total P, electrical conductivity (EC), cation conc., and cation mol_c ratios in saturated paste extracts of Portneuf silt loam sampled at three depth increments at Kimberly, Idaho. Saturated paste pH was 7.7 for all depths. The K/(Ca + Mg) and K/Mg ratios do not have units and are based on the conc. in $mmol_c\ kg^{-1}$ soil.

Soil depth (cm)	Saturation water content ($kg\ kg^{-1}$)	$NaHCO_3$ extractable P ($mg\ kg^{-1}$)	Saturated paste extract						
			EC ($dS\ m^{-1}$)	K	Ca	Mg	Na	K/(Ca + Mg)	K/Mg
				($mmol\ L^{-1}$)					
0–15	0.361 a	27.8	1.30	0.53 a	4.13	1.68	2.27 a	0.046 a	0.158 a
15–30	0.351 a	22.6	1.55	0.34 b	4.17	1.82	3.02 b	0.033 b	0.110 b
30–45	0.327 b	8.0	1.50	0.17 c	3.70	2.02	4.29 c	0.016 c	0.047 c
Mean	0.346	19.5	1.45	0.35	4.00	1.84	3.19	0.032	0.105
LSD (0.05)	0.016	—	NS	0.11	NS	NS	0.66	0.012	0.039

Within a column, means followed by a common letter or blank are not significantly different at $P = 0.05$ as determined by protected LSD.

1994 and 24 April 1995. A second soil core was extracted 20 cm perpendicular to the row. Cores were sectioned into crown (row center only), 0–15 (R1), 15–30 (R2), and 30–45 cm (R3) depths. Crowns and soil cores were covered by plastic, stored at 3°C, and washed within 3 d. Core sections were placed on 1-mm nylon mesh screen, and soil was washed from the root sections. Cleaned roots and crowns were rinsed with distilled water, blotted, weighed, and placed into plastic bags. Root image analysis was performed on one half of the R1 section in 1994 and one quarter of the R1 section in 1995. One half of the R2 and R3 sections was image analyzed in both years after refrigeration at 3°C. Roots for chemical analyses, leaves, and crowns were frozen, freeze dried, weighed, and ground in a Wiley mill to pass a 1-mm stainless steel screen.

Root Length and Area

Roots used for length and area determination were soaked for 1 h in a 150 mL solution of 135 μg methylene blue L^{-1} at 21°C, rinsed with 100 mL deionized water, cut into 1-cm lengths, and arranged to minimize intersections and overlapping in a glass tray with about 1-mm water depth. Root length and area were determined using an AgVision video camera and digitizing board.[a] AgVision (Decagon Devices, P.O. Box 835, Pullman, WA) software uses a modification[12] of the line-intercept procedure developed by Tennant.[13] Root length density was calculated by dividing root length by core section volume. Root length ratio was calculated by dividing large root length by small root length. Root area ratio was calculated as the large root area divided by the small root area. Large and small root lengths were also expressed as cm g^{-1} root dry matter (DM).

The methylene blue staining procedure allowed imaging of all but the finest roots (estimated as <0.05 mm diameter). The precision of length and area determination was high with only a 3.8% error for known lengths and diameters of wire and black vinyl tubing repositioned with slight overlap 10 times. However, detection of fine roots depends on light intensity, camera height, and aperture setting. Thus, relative lengths and areas have high precision, but absolute values are less accurate.

[a]Mention of a trade does not imply an endorsement or recommendation by the University of Idaho or USDA over similar companies or products not mentioned.

Chemical Analyses

A 0.5-g subsample for each plant part was ashed in an oven at 482°C for 10 h. Ash was dissolved with 10 mL 1 M HNO_3, diluted to 50 mL with deionized distilled water, and filtered through Whatman No. 50 filter paper. An aliquot was diluted with $1\,g\,La\,L^{-1}$ deionized distilled water and analyzed for Mg, Na, and Ca by atomic absorption spectroscopy and for K by flame emission (Perkin Elmer atomic absorption model 5000, Norwalk, CT). The LaCl is used in the dilution to reduce chemical interference by P on Ca determination.[14] Another aliquot was diluted with water, and P was determined colorimetrically using the vanadomolybdate procedure.[15] Unstained roots in the R1 section of three replications in 1994 were analyzed for malate and citrate by high pressure liquid chromatography using an organic acid column.[16]

Twenty soil cores (2.5-cm diameter) corresponding to R1, R2, and R3 were composited by depth for each replication on 25 March 1994. Soil pH was determined on the saturated soil paste, and electrical conductivity (EC) was determined on the saturated soil paste extract.[17] Calcium and Mg cations in the extract were analyzed by atomic absorption in a $10\,g\,La\,L^{-1}$ matrix, and Na and K were analyzed by flame emission spectroscopy.[17]

Statistical Analyses

Each of the three accessions was replicated six times in a randomized complete block. Physical measurements and chemical data were analyzed with plant part as the sub-plot and year as the sub-sub-plot and analyzed as a split-plot in time model.[18] Data were analyzed by least squares to fit general linear models (SAS Institute Inc., SAS Campus Drive, Cary, NC). Experimental units were accessions (main plots) obtained by reducing row data to plot means within replications and years. Plant samples were partitioned into roots (three soil depths), crowns, and leaves. Significance of accessions was tested by the replication × accession interaction, and significance of plant parts was tested by the replication × plant part interaction. Preplanned contrasts between HiMag vs. KY31 and MO96 were conducted. Physical and chemical variables were subjected to correlation analysis. Soil properties were subjected to protected LSD mean separation at three soil-depth increments. All variables were normally distributed.

RESULTS

Saturated soil paste extracts contained 1.8 mmol Mg^{2+} L^{-1} and 4.0 mmol Ca^{2+} L^{-1} and did not differ with depth (Table 1). The K concentration decreased with depth, while Na concentration increased with depth. Soil solution K concentration in the 30–45 cm depth was about 32% of the 0–15 cm depth. Thus, roots growing at the lower soil depth had considerably more favorable K/(Ca + Mg) and K/Mg ratios in the soil solution than at shallower depths. A lower K/(Ca + Mg) ratio in soil solution should allow for a lower grass tetany risk in the plant tissue.

In the overall analysis of the data, plant parts differed significantly for ash, all elemental concentrations, and cation mol_c ratios. The year × part interaction was significant for ash, elemental concentrations (except for Ca and P), and cation mol_c ratios. As a result, separate ANOVAs were conducted for each plant part in each year including leaves, crowns, and roots (R1, R2, and R3 depths in the center core and side core). For roots, accessions did not vary for any chemical or physical characteristic in the center or side cores, thus only center core data are presented. However, differences in both chemical and physical root characteristics were observed across root depths. Root depth and the year × depth interaction were significant for length, area of large and small roots, and total root mass. The year × accession interaction was not significant for elemental concentrations, but was significant for all physical root characteristics except total root mass. The significant year × accession interaction may have been caused by a differential response of accessions to yearly differences in air and soil temperatures. Average maximum air temperature was 17.8 during 6–20 April 1994 compared to 12.8°C during 10–24 April 1995. Average maximum 10-cm soil temperature was 13.8°C during 6–20 April 1994 compared to 10.9°C during 10–24 April 1995.

Leaves and Crowns

HiMag contained more Mg ($P = 0.08$), more Ca ($P = 0.08$), and a lower K/(Ca + Mg) ($P = 0.03$) in leaves than the parental cultivars in 1994 (Table 2). In 1995 HiMag contained less K, more Mg and P, and lower K/(Ca + Mg) and K/Mg ratios than parental cultivars. Coefficients of variation (CV) were low for leaf concentrations of K, Ca, and Mg, ranging from 5 to 11% for both years. Leaf mass was about fourfold greater in 1994 than 1995. The lower leaf masses in 1995 were associated with physiologically younger leaves because the average minimum air

Table 2. Mean ($n = 6$) mass, elemental concentration, and cation mol_c ratios for leaves; CV and contrast (HiMag vs. KY31 plus MO96) probabilities of three tall fescue accessions in a 7.6-cm diameter core for 1994 and 1995. Concentrations are expressed on a tissue dry matter basis.

		Concentration					Ratio[a]	
		K	Ca	Mg	Na	P		
	Mass (g)	($g\ kg^{-1}$)					K/(Ca + Mg)	K/Mg
1994								
HiMag	3.17	29.1	5.74	3.12	1.44	2.74	1.39	2.94
KY31	2.87	29.7	5.31	2.87	1.60	2.89	1.53	3.26
MO96	3.81	30.7	5.19	2.74	1.44	2.82	1.63	3.50
CV (%)	11	5	9	11	28	5	10	11
Contrast[b]	NS	NS	0.08	0.08	NS	NS	0.03	0.03
1995								
HiMag	0.77	21.5	5.50	2.92	0.97	3.14	1.07	2.29
KY31	0.87	24.0	4.87	2.40	0.86	3.09	1.40	3.15
MO96	0.86	23.4	5.18	2.52	1.22	2.65	1.29	2.92
CV (%)	24	6	8	10	25	10	9	11
Contrast[b]	NS	0.01	0.04	0.01	NS	0.10	0.01	0.01

[a]Ratios are unit-less but are calculated on a mol_c basis.
[b]Indicates the P level that means of HiMag vs. its parents, KY31 and MO96, are different by single df t test, NS = not significant.

temperature in the 14 d prior to sampling was 2.2°C in 1994 compared to −1.5°C in 1995. Leaf area within the 7.6-cm diameter core averaged 12.5 (1994) and 3.0 $cm^2\ core^{-1}$ (1995). Leaf ash averaged 119 (1994) and 103 $g\ kg^{-1}$ dry matter (1995). Leaf K and Mg concentrations also were greater in 1994 than 1995 for all accessions. The K/(Ca + Mg) and K/Mg ratios were also higher in 1994 than 1995, but still were well below the threshold value of 2.2 that indicates a high incidence of grass tetany.[8]

In 1994, crown ash varied among accessions, but no other elemental concentrations varied for crowns in 1994 or 1995. HiMag crowns contained less ash than parental cultivars in 1994, but not in 1995. Crown mass for all accessions was higher in 1994 than in 1995 (Table 3).

Root Mass and Elemental Concentrations

Root mass varied both among depths and between years, and the year by depth interaction was significant. The chemical analyses for roots

Table 3. Means ($n=6$) and root mean square errors (RMSE) for mass, ash, elemental concentrations, and cation mol_c ratios for crowns and root sections of tall fescue in a 7.6-cm diameter core in 0- to 15-cm (R1), 15- to 30-cm (R2), and 30- to 45-cm (R3) depths. Concentrations are expressed on a tissue dry matter basis.

		Concentration						Ratio[a]	
		Ash	K	Ca	Mg	Na	P	K/(Ca + Mg)	K/Mg
	Mass (g)	($g\ kg^{-1}$)							
1994 means									
Crown	9.36	103.0	9.03	5.96	1.94	1.15	1.42	0.51	1.46
R1	1.86	66.5	3.66	5.67	0.89	0.92	0.97	0.28	1.30
R2	0.40	71.4	2.73	6.13	0.81	1.23	0.95	0.20	1.06
R3	0.30	66.3	2.01	7.77	0.85	1.30	0.77	0.12	0.78
1994 RMSE									
Crown	2.06	7.8	1.02	0.43	0.22	0.31	0.15	0.06	0.13
R1	0.27	7.7	1.09	1.92	0.21	0.25	0.17	0.07	0.27
R2	0.06	10.9	0.51	1.85	0.14	0.29	0.14	0.04	0.18
R3	0.10	12.3	0.46	2.49	0.21	0.30	0.14	0.03	0.14
1995 means									
Crown	5.35	81.5	9.75	5.00	1.54	0.58	1.84	0.67	1.97
R1	2.13	76.3	5.98	5.27	1.04	0.76	1.13	0.46	1.84
R2	0.45	90.0	5.60	6.16	1.24	1.81	1.28	0.36	1.42
R3	0.29	83.0	3.15	9.23	1.45	1.94	1.00	0.16	0.73
1995 RMSE									
Crown	1.43	14.6	2.23	1.07	0.19	0.12	0.27	0.18	0.39
R1	0.48	10.5	1.48	0.90	0.13	0.15	0.21	0.15	0.52
R2	0.32	17.5	1.10	1.31	0.18	0.40	0.25	0.08	0.26
R3	0.09	20.2	1.20	2.61	0.28	0.67	0.21	0.08	0.29

[a]Ratios are unit less but are calculated on a mol_c basis.

conducted in 1994 were done with stained roots, whereas the 1995 roots were not stained. A methods evaluation using paired samples found that 76, 65, 55, and 77% of the K, Ca, Mg, and Na conc. in the roots, respectively, were present in stained compared to unstained roots (data not shown). Dry-ashing of the stained roots resulted in almost complete solubilization whereas digestion with nitric and perchloric acids was not complete. This suggests that the methylene blue stain may have chelated the cations that were adsorbed on the external root surface. The stain solution leached 2.04, 0.78, and 0.27 $g\ kg^{-1}$ root of K, Ca, and Mg, respectively, whereas the rinse solution contained no significant cation conc.

Accessions did not vary in the R1 or R2 depth increments for elemental concentrations, cation ratios, or elemental uptake (analysis not shown) in either 1994 or 1995. For the R3 root increment in 1994, the K/Mg ratio for HiMag was 0.60 (contrast $P = 0.01$) compared to 0.94 for KY31 and 0.81 for MO96. In 1995 accessions did not vary for any elemental characteristics in the R3 root increment.

Root Length and Area

Root length, area, and root length density in R1 (Table 4) were generally 2–3 times the values for R2 and R3. Length per kg root in R1 was less than R2 and R3. For R1 roots in 1994, HiMag had greater root length of large (>1 mm diameter) roots per unit weight (9,290 m kg^{-1}) than KY31 (7,710 m kg^{-1}) or MO96 (7,260 m kg^{-1}), but accessions did not differ for this characteristic in 1995. The small (<1 mm diameter) roots for R1 were not statistically different among accessions in either year, and the R2 root characteristics did not differ between HiMag and its parents in 1994 or 1995 for either large or small roots. Accessions generally did not vary for root length or area for either large or small roots in the R3 depth increment in 1994 or 1995, except that HiMag had greater length of small roots per unit weight (143,600 m kg^{-1}) than KY31 (119,100 m kg^{-1}) or MO96 (121,600 m kg^{-1}) in 1995.

Relationships Between Chemical and Physical Characteristics

Leaf Mg conc. was not significantly correlated to any physical measurement in HiMag, KY31, or MO96. However, leaf Mg and Ca were positively correlated in all three accessions (Table 5). Leaf Mg also was positively related to leaf K in KY31 and MO96 but not in HiMag. Leaf K conc. was negatively correlated with length of small roots and area for the R1 depth increment. This is probably because less soil K was taken up by fewer roots at the R1 depth increment, relative to the R2 or R3 depth increments where the soil K was lower (Table 1).

Root Mg conc. in the R1 depth increment was not highly correlated with R1 physical characteristics ($r < 0.54$) in the three accessions. Root Mg in R1 was strongly correlated with root Ca in R1 ($P \leq 0.05$, df = 23) for HiMag, KY31, and MO96. Root Mg conc. in the R2 depth increment was positively correlated to R2 small root lengths and root K. Root Mg conc. was related to large root length with an r value of 0.71 for HiMag. Root Mg was related to root Ca in R3 for all accessions.

Table 4. Means ($n = 6$) and square root of the mean square errors (RMSE) for root length, area, root length density, and root length per unit of mass for large (>1 mm diameter) and small (≤1 mm diameter) roots of three tall fescue accessions in 0- to 15-cm (R1), 15- to 30-cm (R2), and 30- to 45-cm (R3) depths of a 7.6-cm diameter core.

	Root length		Root area		Root length density		Length kg^{-1} root	
	Large ($cm\ core^{-1}$)	Small ($cm^2\ core^{-1}$)	Large ($cm^2\ core^{-1}$)	Small ($cm^2\ core^{-1}$)	Large ($m\ m^{-3}$)	Small ($m\ m^{-3}$)	Large ($m\ kg^{-1}$)	Small ($m\ kg^{-1}$)
1994 means								
R1	1,470	8,590	74	321	19,800	115,500	8,090	47,600
R2	440	3,630	18	140	5,920	50,200	11,000	94,700
R3	483	3,020	19	106	6,490	40,700	17,400	107,900
1994 RMSE								
R1	382	1,570	25	71	5,130	21,180	1,200	7,170
R2	120	934	6.3	39	1,620	12,560	2,260	18,730
R3	146	703	6.8	28	1,970	9,460	8,140	36,610
1995 means								
R1	2,110	14,000	108	545	28,400	188,000	9,990	67,900
R2	481	4,930	22	203	6,480	66,300	8,940	93,100
R3	461	3,550	19	139	6,180	47,800	15,900	128,100
1995 RMSE								
R1	453	1,190	24	66	6,090	16,020	2,110	15,690
R2	146	827	8.9	40	1,960	11,130	5,890	68,930
R3	150	974	5.6	43	2,010	13,130	3,730	18,280

Table 5. Selected Pearson correlation coefficients (r) between various chemical and physical characteristics of three tall fescue accessions. Values of r are significant at $P = 0.05$ (df = 23) if $r > 0.40$.

	Accession		
Relationship	HiMag	KY31	MO96
Leaf Mg to Ca	0.77**	0.65**	0.80**
Leaf Mg to K	0.20	0.70**	0.55**
Leaf K to R1 small root[a] length	−0.69**	−0.42[d]	−0.48[d]
Leaf K to R1 small root area	−0.70**	−0.33	−0.45**
R1 Mg to R1 physical characteristics[b]	<0.40	<0.30	<0.54
R1 Mg to R1 Ca	0.89**	0.70**	0.93**
R2 Mg to R2 small root length	0.71**	0.20	0.54**
R2 Mg to R2 K	0.90**	0.75**	0.62**
R3 Mg to R3 large root[c] length	0.71**	0.12**	0.35**
R3 Mg to R3 Ca	0.79**	0.83**	0.59**

[a]Small roots are defined as <1 mm diameter.
[b]Root length, area, and root length density; and root mass.
[c]Large roots are defined as >1 mm diameter.
*, **, indicate significant F-test at $P < 0.05$ and 0.01, respectively.

The Mg^{2+} and Ca^{2+} ions are supplied to the roots by mass flow, whereas PO_4^{3-} and K^+ are supplied by diffusion.[19] If it is assumed that 300 kg water was transpired kg^{-1} plant dry matter and whole plant Mg conc. of HiMag was 1.84 g kg^{-1}, then Mg conc. needed in the soil solution (X) can be calculated as[19]:

$$X = (1.84\,\text{mg Mg/g DM}) \times (\text{g DM}/300\,\text{g water}) \times (1000\,\text{g/L})$$
$$= 66.1\,\text{mg Mg L}^{-1}$$

which is equivalent to 2.8 mmol Mg^{2+} L^{-1}. As a result, the average soil solution conc. of 1.8 mmol L^{-1} (Table 1) would provide less Mg by mass flow than required by the plant, suggesting some other process is involved, i.e., an active uptake mechanism for Mg in tall fescue.

Citrate and Malate Concentrations in Roots

No significant differences for R1 roots were observed for root tissue citrate concentrations of 0.66 (HiMag), 0.62 (KY31), and 0.47 mM

(MO96). There were no differences in malate concentrations of 1.51 (HiMag), 1.80 (KY31), and 1.39 mM (MO96).

DISCUSSION

Leaf Mg concentration was higher in HiMag than parental cultivars, although this difference was not highly significant ($P = 0.08$) in 1994. Similarly, HiMag had higher concentrations of leaf Mg compared to KY31 and MO96 on an acidic Cecil soil[9] and on the same soil as this study.[5] Leaf Mg concentrations of HiMag, KY31, and MO96 were greater than 2 g kg^{-1}, which is considered a low grass tetany risk.[9]

Roots in the three depth increments evaluated in our study did not consistently vary for Mg concentration, uptake, or K/Mg and K/(Ca + Mg) ratios for any of the three tall fescue accessions. Crowns had relatively small concentrations of K, Ca, and Mg. In 1995, 80% of K, 64% of Ca, 75% of Mg, 56% of Na, and 77% of P were partitioned in aboveground portions of plants. Leaf Mg concentration for HiMag was about twice that in crowns and roots, whereas leaf Mg in KY31 and MO96 was about 1.5 times greater than the concentrations in crowns and roots. Sleper et al.[4] reported that high Mg and Ca concentrations in leaves were highly heritable. Because leaf Mg concentration was greater in HiMag than MO96 or KY31 and root concentrations were generally not different, HiMag apparently absorbs and translocates more Mg from roots to leaves.

The question remains whether Mg is taken up actively. Both Ca and Mg concentrations in leaves were greater in HiMag than its parental cultivars, while K concentrations were about the same. Thus, one could hypothesize that HiMag has some characteristic that enhances transport of Ca and Mg from roots to leaves. Hannaway et al.[20] reported K had a greater depressive effect on Mg translocation to the shoot than Mg uptake by roots in tall fescue.

Saturated paste extractable K in the 30–45 cm depth was about 30% of that in the 0–15 cm depth in Portneuf soil (Table 1). Magnesium uptake in plants depends on concentrations and activity of Mg in soil solution and ability of soil to replenish Mg in the soil solution.[19] Availability of Mg is affected by the proportion of Mg relative to soluble and exchangeable amounts of K, Ca, Na, aluminum (Al), and manganese (Mn).[19] Although root distributions were not different between accessions, if a plant was able to extract more soil solution from the 30–45 cm depth, this should be advantageous because the K/Mg ratio would be lower because of K dilution, and more Mg would be available to the plant relative to K. Although HiMag also contained more Ca and Mg in leaves from plants grown on acid soils,[9] soluble cation concentrations in the soil were not reported.

Soil test P was adequate in our study and apparently was not related to leaf Mg concentration. Reinbott and Blevins[21] reported that applying P fertilizers to KY31 growing in soil with low P increased Ca and Mg concentrations in leaf tissue. However, when soil test P levels were adequate, Wilkinson and Mayland[9] found no evidence in support of the relationship of P fertilization to leaf Mg in tall fescue even when increased leaf P concentration resulted from P applications.

Root length, root surface area, and root length density did not vary consistently for accession in the three depth increments examined in our study (Table 4). Values for root length density in our study were generally similar to those (45,000 mm^{-3}) for KY31 reported by Beyrouty et al.[22] in Arkansas. Mycorrhizal associations through extension of their hyphae can increase effective root surface area.[19] Hyphae may have affected P and Mg absorption in our study because mass flow did not supply enough Mg to the root surface to account for the amounts in shoots. Even if hyphae aided in the absorption of Mg into the root, mycorrhizal associations do not explain the transport of more Mg to the leaves of HiMag.

It was also hypothesized that HiMag might absorb more Mg^{2+} and Ca^{2+} because of enhanced organic acid production, which could balance the electrical charge. Charge balance theory suggests that electrical neutrality must be maintained. Thus, for every cation absorbed either an anion must be adsorbed or created organically in the root. Malate exchange, influx and efflux, occurred in root cells of carrot (*Daucus carota* L.) and barley (*Hordeum vulgare* L.).[23] No evidence was found of enhanced citrate or malate in root tissues of the accessions, but organic acid exudates from roots into the soil were not measured.

Most of the root characteristics examined in our study did not vary among the three tall fescue accessions, and none of these characteristics were consistently related to elemental concentrations within the accessions. As a result, none of these characteristics appeared to explain the high leaf Mg concentrations for HiMag found in this study or other studies.[5,9] The process responsible for increased transport of Mg from roots to leaves of HiMag may be carrier-mediated transport because it can occur against an electrochemical or concentration gradient. Even though our study did not conclusively identify the factor(s) responsible for the high leaf Mg concentrations in HiMag, these results indicated that the root characteristics measured were not responsible for the higher concentrations in HiMag.

CONCLUSIONS

HiMag exhibits higher leaf Mg concentrations than its parental cultivars; however, the mechanism for increased Mg concentrations is unknown. It was hypothesized that these high leaf Mg concentrations were due to differences in root characteristics, ability to absorb greater amounts of Mg into the roots, or a difference in the ability to transport the elements. However, none of the root characteristics examined in our study were consistently related to elemental concentrations in roots or leaves. Although HiMag had higher leaf concentrations of Mg than its parental cultivars, root and crown Mg concentrations did not differ among the three tall fescue accessions. This suggests that HiMag translocates more Mg from roots to leaves than its parents, and that HiMag has more active transport of Mg. An experiment that measures energy flow in respiration would probably be necessary to address the active uptake hypothesis.

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