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REGULAR ARTICLE

Mg and K effects on cation uptake and dry matter accumulation in tall fescue (*Festuca arundinacea*)

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Abstract HiMag tall fescue (*Lolium arundinaceum* (Schreb.) S.J. Darbyshire = *Festuca arundinacea* Schreb) was selected for high Mg concentration in the herbage to reduce grass tetany risk to ruminants; however, the mechanism of increased Mg uptake into shoots is unknown. The objective was to determine cation concentrations of roots, crowns, and leaves in plants of *cv.* HiMag and its parents, *cv.* Kentucky 31 and *cv.* Missouri 96, grown in nutrient solution for 42 days, and determine if cation ratios in roots, crowns, and leaves are different, indicating a difference due to translocation. Treatments were "basal" (1.5 *mM* K and 0.5 *mM* Mg), "K" (3.2 *mM* K), "Mg" (1 *mM* Mg), and "K+Mg" (3.2 *mM* K and 1 *mM* Mg). For HiMag, Mg was lower in roots (Trial 2 only), not different in crowns, and greater in leaves than Kentucky 31 and Missouri 96. Doubling the K and Mg of the nutrient solution from basal levels resulted in a 44% reduction of root Mg in Kentucky 31 and Missouri 96, compared to a 17% reduction in root Mg for HiMag. The K inflow rate in HiMag for the basal treatment was lower than that in Kentucky 31 and Missouri 96. These results provide evidence for a process that limits K uptake and an active Mg translocation mechanism in tall fescue. HiMag was apparently selected for traits that promote translocation of Mg from roots to shoots.

Keywords Ca · *Festuca arundinacea* · HiMag · Mg · P · Roots

Abbreviations

CV	coefficient of variation
DM	dry matter
MSE	mean square error
RO	reverse osmosis
SD	standard deviation

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Introduction

A selection program in Missouri using clones of *cv.* Kentucky 31 (KY31) (Alderson and Sharp 1995) and *cv.* Missouri 96 (MO96) produced a tall fescue cul-

tivar called *cv.* HiMag (Mayland and Sleper 1993). HiMag had 20% higher Mg and Ca in forage, and a lower K/(Mg+Ca) ratio than populations of its parent cultivars. HiMag could reduce the risk of grass tetany from tall fescue by 80%; annual losses from grass tetany are estimated to be $50 million in the USA (Mayland and Sleper 1993).

Mass flow and diffusion theory predicts that Mg and Ca are provided to the rhizosphere in excess of plant needs (Barber 1984). However, solution-cultured plants of wheat (*Triticum aestivum* L.) had much higher shoot Ca and Mg concentrations than soil-grown plants (Miyasaka and Grunes 1992). This occurred even though cation concentrations in soil solution were similar to those in nutrient solution. They hypothesized that cation concentrations in the rhizosphere were lower than in bulk soil solution due to depletion of anions near the root surface with a concomitant decrease in cations to maintain charge balance.

Nutrient solution culture minimizes the effect of edaphic factors on cation uptake, and theoretically minimizes the depletion zone around roots. Thus, if HiMag contains higher Mg and Ca concentration in shoots than its parental cultivars when grown in nutrient solution, it is not due to greater soil exploration. However, experiments with nutrient solution culture do not rule out the presence of more active uptake mechanisms.

We 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. The objectives of our study were to: (1) determine cation concentrations of roots, crowns, and leaves in HiMag, KY31, and MO96 plants grown in nutrient solution for 42 days; and (2) analyze cultivar and tissue differences for mass balances and ratios to provide a better understanding of cation uptake mechanisms and rates in tall fescue.

Materials and methods

Experimental design

Two trials were conducted in separate growth chambers with similar conditions, except that Trial 2 had a 7 °C higher temperature than Trial 1. The 12 treatment combinations (three cultivars × two K levels × two Mg levels) were arranged in a randomized complete block with four replications. The four nutrient treatments comprised a "basal" treatment with adequate levels of nutrients, "K" treatment with twice the basal K concentration, "Mg" treatment with twice the basal Mg concentration, and "K+Mg" treatment with twice the basal K and Mg concentrations. Plants were partitioned into parts (roots, crowns, and leaves).

Plant establishment and maintenance

Tall fescue cultivars tested were *cv.* HiMag and its parents, *cv.* Kentucky 31 and *cv.* Missouri 96. Seeds free from the fungal endophyte [*Neotyphodium coenophialum* (Morgan-Jones & Gams) Glen, Bacon & Hanlin] were germinated on blotter paper wetted with reverse osmosis (RO) water, and placed in covered plastic tubs. On Days 11 and 12, four seedlings per pot were transplanted into 4-L pots containing one of four starter nutrient solution treatments (Table 1). Individual plants were placed in split-foam stoppers

Table 1 Initial and refill nutrient solution concentrations for the basal, K, Mg, and K+Mg treatments

	Initial solution treatment				Refill solution treatment			
	Basal	K	Mg	K+Mg	Basal	K	Mg	K+Mg
Compound	mmol L^{-1}							
$MgSO_4$	0.50	0.50	1.00	1.00	0.50	0.50	1.00	1.00
K_2SO_4	0.00	0.85	0.00	0.85	0.00	2.35	0.00	2.35
Ratio	mol_c mol_c^{-1}							
K/Mg	1.50	3.20	0.75	1.60	4.50	9.20	2.25	4.60
K/(Ca+Mg)	0.50	1.07	0.37	0.80	1.50	3.07	1.12	2.30

The following concentrations of salts were common to all treatments: Initial solution/Refill solution (units, mM) $Ca(NO_3)_2+4H_2O$ 1/1, KH_2PO_4 0.5/0.5, $Na_2SiO_3+9H_2O$ 0.1/0.1, KNO_3 1/4; (units μM) $Fe(Cl)_3+6H_2O$ 10/2.5, $Fe(NO_3)_3+9H_2O$ 25/5, HEDTA 25/5, $MnCl_2+4H_2O$ 3/6, $ZnSO_4+7H_2O$ 4/2, H_3BO_3 2/1, $Na_2MoO_4+2H_2O$ 0.1/0.03.

supported by a Styrofoam lid. Solutions were aerated with compressed air in the pot center.

Nutrient solution was prepared using reverse osmosis (RO) water and analytical grade chemicals (Table 1). Nutrient solutions were buffered with 0.1 mM 2(*N*-morpholino)ethane-sulfonic acid (MES) (Bugbee and Salisbury 1985). Although 5 mM MES buffers pH more effectively than 1 mM MES L^{-1}, it may cause decreased shoot Mg and Zn concentration with increasing solution Ca (Miyasaka et al. 1988). The initial pH was not adjusted to 5.8, as recommended by Bugbee (1995), because addition of Na^+ or Cl^- ions would confound the nutrient treatments. Solution pH was determined twice each week, and 1 to 2 mL of 1 M HNO_3 was added to maintain nutrient solutions at pH<6. A pH range of 5.5–5.8 is considered optimum for nutrient uptake (Bugbee 1995). Silicon was also provided in nutrient solutions at 0.1 M to simulate soil solution chemistry (Epstein 1994).

Plants were provided with initial nutrient solutions of 0.5 or 1 mM for Mg and 1.5 or 3.2 m*M* for K. The K concentrations in refill solution were 4.5 and 9.2 *mM* (Table 1). Starter nutrient solutions were used to initially fill the pots, and subsequent additions were made with refill solutions (Table 1), which were calculated to provide nutrient quantities predicted to be taken up by the plant (Bugbee 1995). This method simulates field conditions where nutrient concentrations change gradually rather than suddenly, for example, when depleted solutions are renewed.

Electrical conductivity (EC) is directly related to solution salt concentration and can be used to monitor relative strength of the solution (Bugbee 1995). Changes in the concentrations of salts in the pots were measured as solution EC three to five times per week. This enabled us to calculate the quantity of nutrient solution required to replace the nutrients taken up by the plants. The target EC levels for the different treatments were to maintain EC levels of 0.50 dS m^{-1} for the basal treatment, 0.60 dS m^{-1} for the K treatment, 0.58 dS m^{-1} for the Mg treatment, and 0.60 dS m^{-1} for the K+Mg treatment. We maintained the volume of solution in each pot between 3.5 – 4 L, and the desired concentration by regularly adding a combination of water and nutrient solution. Refill solution was added in equal volumes to the appropriate treatment of each pot. After 28 days of growth, 100 mL of refill solution usually was added per day, and RO water was added once or twice a week to equalize volume in pots.

The 4-L pots were placed in four blocks in each of two growth chambers with a 16-h photo period. Lights were a mixture of fluorescent and incandescent, which produced an intensity at plant canopy level of 137 W m^{-2} in Trial 1 and 107 W m^{-2} in Trial 2. Mean night air temperature was 11 °C, and mean day air temperature was 18 °C for Trial 1. For Trial 2, mean night and day temperatures were 19 and 25 °C, respectively. Mean night and day relative humidities during the 7-day period at the end of each trial were 82 and 71% in Trial 1 and 89 and 63% in Trial 2, respectively.

Pots were removed from growth chambers once a week, and weights of solution and plants were recorded. Water use was calculated from the amount of water and solution added to the pot to replace the volume used. Evaporation was measured as the net weight loss in pots without plants (blanks). Transpiration was calculated as the difference between water use in pots with plants and evaporation. At 14-day intervals, 20 mL of solution from each pot was taken for chemical analysis. Pots were re-randomized within a block when replaced in the growth chamber.

Forage harvest and measurements

Plants were harvested 42 days after transplanting. Leaves were clipped at the junction of the first leaf blade and stem, counted and weighed separately by plant, composited by pot, rinsed with RO water, and freeze-dried; then dry matter was determined. Roots were clipped from each crown, stems were counted, and crowns were weighed for each plant, then composited by pot, rinsed in 200 mL of RO water, and freeze-dried. Root fresh weight was obtained for each plant separately; roots of each plant were immersed in 200 mL RO water for 10 s, allowed to drip, immersed again for 10 s, and allowed to drip into a beaker. Roots of each plant were divided into four vertical subsamples; one fourth of the roots were composited for four plants, blotted dry, weighed, placed into a plastic bag, and stored in a refrigerator until root length and area were determined. The remaining roots were composited by pot, freeze-dried, weighed, dry matter was determined, and they were stored for cation analysis. Samples of all dried fractions were ground to pass a 1-mm screen in a

Wiley[1] shear-mill. A 100-mL sample of root and crown rinse solutions was collected from each pot for one block, stored in plastic bottles, refrigerated, and analyzed to determine cations leached from plant material.

Root length and surface area

Roots used for length and surface area determination were soaked for 1 h in a 150-mL solution of 135 μg methylene blue L^{-1}, rinsed with 100 mL deionized water, cut into 3-cm lengths, and arranged to minimize intersections and overlapping in a glass tray with 1 mm standing water. Root length and surface area were determined using an AgVision™ video camera and digitizing board.[1] AgVision (1991) software uses an automated modification (Harris and Campbell 1989) of the line-intercept procedures developed by Tennant (1975).

Large roots were defined as >1 mm diameter and small roots as <1 mm diameter. Root length ratio was calculated by dividing large root length by small root length. Root area ratio was calculated by dividing large root area by small root area. Root length density was calculated by dividing root length by weight (m kg^{-1} root DM).

Chemical analyses

A 0.5-g ground 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. Plant and nutrient solution samples were analyzed for Mg, Na, Ca, Cu, Fe, Mn, and Zn by atomic absorption spectroscopy and for K by flame emission spectroscopy (Perkin Elmer atomic absorption model 5000, Norwalk, CT). The LaCl dilution (1 g La L^{-1} deionized distilled water) is used to reduce chemical interference by P on Ca determination (Perkin-Elmer Corp 1982). Another aliquot was diluted with water, and P was determined colorimetrically using the vanadomolybdate procedure (Kitson and Mellon 1944).

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

Cation uptake rates

Mean rate of Mg, Ca, and K uptake per g of fresh root, I for "inflow", was calculated after Williams (1948) as modified by Huang and Grunes (1992) for use with fresh root weight instead of root length:

$$I = \frac{(U_2 - U_1)}{(t_2 - t_1)} \times \frac{\ln(W_2 - W_1)}{W_2 - W_1}$$

where U is the individual cation uptake through the root and into the total plant (the sum of the products of concentration×mass of roots, crowns, and leaves) in moles, ln is the natural logarithm function, W is root fresh weight in g, and subscripts 1 and 2 refer to measurements made at the beginning (t_1) and end (t_2) of the experimental period. The beginning values for t_1 are assumed to be 0 although the seed would have contained minor amounts of cations used in initial growth.

Leaf uptake coefficients are calculated as mol nutrient kg^{-1} dried plant leaves divided by the mol nutrient kg^{-1} growth solution; assuming 1 L of growth solution=1 kg and using mean cation concentration in solution for the trial. Translocation of a nutrient was quantified by dividing the amount of a nutrient present in shoots by total amount of nutrient present in roots and shoots.

Statistical analyses

Data were analyzed by the method of least squares to fit general linear models (SAS Institute Inc. 1990). Results were considered significant if P values were <0.05, unless indicated otherwise. Experimental units were the individual pots, which contained four plants of a single cultivar. The significance of the cultivar main effect was tested by the cultivar×rep (nested within trial) interaction, and the plant part main effect was tested by the part×rep (nested within trial) interaction.

Preplanned contrasts between HiMag and its parents, MO96 and KY31, and protected LSD mean separation were conducted. Other treatment contrasts included K vs. basal, Mg vs. basal, and K+Mg vs. basal. Because plant parts are not random, they were analyzed as an approximation to repeated measures with a conventional split–plot model.

Results

Root physical variables

The methylene blue stain procedure allowed imaging of all but the finest of roots, <0.25 mm. Precision of length and area determination was high, as indicated by a 3.8% error for known lengths and diameters of wire and black vinyl tubing repositioned with slight overlap for 10 times. Kokko et al. (1993) also concluded that digital grey-scale image analysis of stained root samples was precise and repeatable, and that root surface area may be better than linear root length because surface area values integrate continuously changing root diameters.

Root physical characteristics did not vary among cultivars or treatments in Trial 1. Therefore, root length, root area, and root length density were not measured in Trial 2. These physical factors should not affect cation uptake in this experiment because nutrient solution medium minimized the effect of physical limitations compared to roots in soil. Furthermore, treatment with high levels of K, Mg, and K+Mg did not affect root length, area, mass, or root length kg^{-1} DM. Total root length averaged 555 m, and total root surface area averaged 4,083 cm^2 for four plants in each pot (Table 2). Average root mass was 2.73±0.62 g per pot for Trial 1 and 2.20± 0.51 g per pot for Trial 2. Root length density was 7,878±384 m kg^{-1} root dry matter.

Nutrient concentrations in plant parts

Part and trial×part were significant for most elements (data not shown). This is probably explained by temperature differences between growth chambers (trials).

Root elemental concentrations

For roots, cultivars varied significantly only for Mg in Trial 1, whereas root mass, Ca, and Mn concentrations varied in Trial 2 (analysis not shown). The treatment effect was significant for all elemental concentrations except P, Cu, Mn, and Fe in Trial 1 and P, Cu, and Mn in Trial 2. A significant cultivar× treatment interaction for Ca concentration occurred in Trial 2.

Root K concentrations did not differ for cultivar in Trial 1 (Table 3), but HiMag had less K than KY31 and MO96 (P=0.01) in Trial 2 (Table 4). HiMag roots contained 49.1 g K kg^{-1} across treatments in Trial 1 (Table 3). However, in Trial 2 with higher temperatures, HiMag roots contained 39.7 compared to 44.8 and 45.1 g K kg^{-1} for KY31 and MO96, respectively (Table 4). The K and K+Mg treatments produced elevated K but reduced Ca concentration in roots compared to the basal treatment, and the contrasts were highly significant in both trials (data not shown).

Root Mg in all cultivars was reduced by the K and K+Mg treatments by about half compared to the basal treatment (data not shown). Root Mg concentration in HiMag was lower than KY31 and MO96 in Trial 1 but not significantly in Trial 2. The K and K+Mg treatments also greatly reduced root Na.

Concentrations of P did not vary among cultivars or treatments in either trial. HiMag had more (P= 0.001) root DM mass than KY31 and MO96 in Trial 2 but not in Trial 1. The K+Mg treatment produced more root mass than the basal treatment (P=0.01) in Trial 2. The K/Mg ratio in roots did not vary among cultivars in either trial. Treatments varied significantly for K/Mg and K/(Ca+Mg) ratios in both trials. The K and K+Mg treatments produced ratios about twice

Table 2 Means, standard errors of sample means (SE), and coefficient of variation (CV) of HiMag, KY31, and MO96 tall fescue accessions for root physical characteristics of four tall fescue plants per pot grown in four nutrient solution treatments at 55 days after germination (42 days after transplanting for Trial 1)

Statistic	Root length		Root area		Mean root radius (cm)	Root DM mass (g)	Length ratio	Area ratio	Root length density (m kg^{-1})
	Large (cm)	Small (cm)	Large (cm^2)	Small (cm^2)					
Mean	5,814	49,655	479	3,604	0.092	2.47	0.117	0.133	7,876
SE	227	2,477	22	190	0.003	0.065	0.092	0.116	384
CV, %	24	26	30	31	20	26	32	44	33

Analysis of variance indicated no significant differences among accessions or treatments. Large indicates roots >1 mm diameter, and small indicates roots <1 mm diameter. Root mass is on a dry matter (DM) basis. Ratios are the proportion of large root length or area to small root length or area.

Table 3 Dry matter yield (mass), elemental concentration means (n=16), and cation mol_c ratio means for roots, crowns, and leaves of four plants per pot of HiMag, KY31, and MO96 tall fescue across four nutrient solution treatments in Trial 1

Part and cultivar	Mass (g pot $^{-1}$)	Concentration				Ratio[a]	
		K (g kg^{-1})	Ca (g kg^{-1})	Mg (g kg^{-1})	Na (g kg^{-1})	K/Mg (mol_c mol_c^{-1})	K/(Ca+Mg) (mol_c mol_c^{-1})
Roots							
HiMag	2.53	49.1	1.31	1.52	1.45	11.7	7.10
KY31	2.72	46.9	1.30	1.78	1.69	11.3	6.86
MO96	2.95	45.5	1.30	2.00	1.86	9.7	6.10
LSD	NS	NS	NS	0.33	NS	NS	0.95
Crowns							
HiMag	2.59	42.5	3.02	3.47	0.465	3.88	2.53
KY31	2.33	43.7	3.11	3.61	0.352	3.84	2.51
MO96	2.17	40.3	2.83	3.34	0.323	3.79	2.52
LSD	NS	NS	NS	NS	NS	NS	NS
Leaves							
HiMag	4.66	49.8	7.59	5.28	0.248	2.97	1.59
KY31	5.56	50.1	7.15	5.04	0.243	3.19	1.70
MO96	5.53	49.0	6.64	4.87	0.232	3.17	1.75
LSD	0.76	NS	0.79	NS	NS	NS	NS

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

NS indicates ANOVA main effect not significant (P<0.05).

Plants were grown for 42 days in basal (1.5 mM K and 0.5 mM Mg), K (3.2 mM K), Mg (2 mM Mg), and K+Mg nutrient solution treatments.

Table 4 Dry matter yield (mass), elemental concentration means (n=16), and cation mol_c ratio means for roots, crowns, and leaves of four plants per pot of HiMag, KY31, and MO96 tall fescue across four nutrient solution treatments in Trial 2

Part and cultivar	Mass (g pot^{-1})	Concentration				Ratio[a]	
		K (g kg^{-1})	Ca (g kg^{-1})	Mg (g kg^{-1})	Na (g kg^{-1})	K/Mg (mol_c mol_c^{-1})	K/(Ca+Mg) (mol_c mol_c^{-1})
Roots							
HiMag	2.45	39.7	1.70	1.14	2.67	14.7	6.57
KY31	2.07	44.8	1.58	1.41	1.32	15.4	7.25
MO96	2.08	45.1	1.50	1.28	1.74	14.4	7.31
LSD	0.26	4.5	0.11	NS	NS	NS	NS
Crowns							
HiMag	2.21	43.9	3.71	4.58	0.380	3.05	2.04
KY31	1.92	45.9	3.48	4.43	0.391	3.29	2.21
MO96	1.85	46.5	3.43	4.56	0.408	3.22	2.21
LSD	0.29	NS	NS	NS	NS	NS	NS
Leaves							
HiMag	5.49	50.1	7.27	6.44	0.233	2.48	1.47
KY31	5.37	55.4	6.4	5.15	0.247	3.41	1.93
MO96	4.83	54.0	6.76	5.68	0.276	3.02	1.74
LSD	NS	2.75	NS	0.37	0.039	0.26	0.18

Plants were grown for 42 days in basal (1.5 mM K and 0.5 mM Mg), K (3.2 mM K), Mg (2 mM Mg), and K+Mg nutrient solution treatments.

NS indicates ANOVA main effect not significant (P<0.05).

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

those of basal, and the Mg treatment reduced the ratios compared to the basal treatment.

Plants in the K and K+Mg treatments exhibited reduced root Zn concentration in Trial 2 (data not shown).

Crown elemental concentrations

For crowns, cultivars varied significantly only for crown mass in Trial 2. Treatments varied significantly for Ca, Mg, K/Mg ratio, and K/(Ca+Mg) ratio in Trial 1, and for all characteristics except P in Trial 2 (data not shown). The cultivar×treatment interaction was not significant for any characteristic in either Trial 1 or 2.

Means for crown elemental concentration are given in Tables 3 and 4. HiMag had the highest crown Mn concentration in Trial 1 (data not shown) and highest mass in Trial 2. Across cultivars, Ca in crowns was reduced from 3.68 (SE=0.15) for the basal treatment to 3.20 (SE=0.26), 2.06 (SE=0.08), and 3.01 (SE=0.10) for K, Mg, and K+Mg treatments, respectively. The Mg treatment increased crown Mg concentration and reduced the K/Mg ratio in crowns (data not shown). The K treatment increased the K/(Ca+Mg) ratio.

Leaf elemental concentrations

For leaves (analysis not shown), cultivars differed significantly only for mass and Mn in Trial 1, but in Trial 2 cultivars differed for K, Mg, K/Mg and K/(Ca+Mg) ratios. Treatment differences were significant for Ca, Mg, K/Mg ratio, and K/(Ca+Mg) ratio in both trials, and additionally for K, Na, and Zn in Trial 2. None of the interactions were significant.

Mean elemental concentrations for leaves are given in Tables 3 and 4. HiMag had less K and more Mg than KY31 and MO96 in Trial 2, but not in Trial 1. The K/Mg and K/(Ca+Mg) ratios in leaves were lower for HiMag compared to KY31 and MO96 in Trial 2, and this was consistent across treatments. The K and K+Mg treatments increased leaf K concentration in Trial 2. The Mg treatment increased leaf Mg, and the K treatment generally increased K/Mg and K/(Ca+Mg) ratios in both trials. The K+Mg treatment reduced leaf Ca in both trials and leaf Na in Trial 2, but increased leaf Mg compared to the basal treatment.

Changes in nutrient solution characteristics

Figure 1 presents K, Ca, and Mg concentration in pot solutions by treatment through time for Trial 2, which was similar to Trial 1. Nutrient solution K concentration in basal and Mg treatments were maintained about 60 mg L^{-1} until Day 28, when K uptake exceeded the amount provided by the refill solution. By Day 42, solution K concentration dropped to about 5 mg L^{-1} in both trials. Thus, we achieved our goal of providing the amount of K necessary for plant growth (basal), but not an excess. Solution K concentration was maintained at about 120 mg L^{-1} in the K and K+Mg treatments. Solution Ca concentration was maintained between 35 to 45 mg L^{-1} in all treatments, except the starter solution for the K+Mg treatment was at 22 mg L^{-1} in Trial 1 because apparently only half of the $CaNO_3$ was added to the batch. This level was provided to all treatment combinations and blocks in Trial 1, but apparently had little effect on Ca concentration because the trial effect was not significant. Refill solution increased Ca to about 30 mg L^{-1} by the end of the trial in the K+Mg treatment. The Mg concentration in basal and K treatments declined from an initial value of about 12 mg L^{-1} after Day 28 to about 5 mg L^{-1} at Day 42 (Fig. 1).

The electrical conductivity (EC) of nutrient solution treatments was maintained at levels greater than 0.50, 0.60, 0.70, and 0.70 dS m^{-1} for basal, Mg, K, and K+Mg treatments, respectively, in both trials until Day 30 when basal and Mg treatment solution EC began to decline below 0.40 dS m^{-1}.

The pH values of nutrient solutions were constant at about 5.3 until Day 14, increased to a pH of 7 by Day 28, and then varied daily as 1 mL of 1 *M* HNO_3 was added in increments to maintain pH<7.

Biomass accumulation and transpiration rates

Plant biomass (fresh basis) increased at 2 g day^{-1} until Day 28 when growth increased exponentially from 15 to 17 g day^{-1}. Treatments were not significantly different for biomass accumulation rate in Trial 1; however, in Trial 2 the K+Mg treatment had a lower (P=0.01) biomass accumulation rate than the basal treatment.

Transpiration rate slowly increased to about 40 g day^{-1} by Day 35, and by Day 42 transpiration

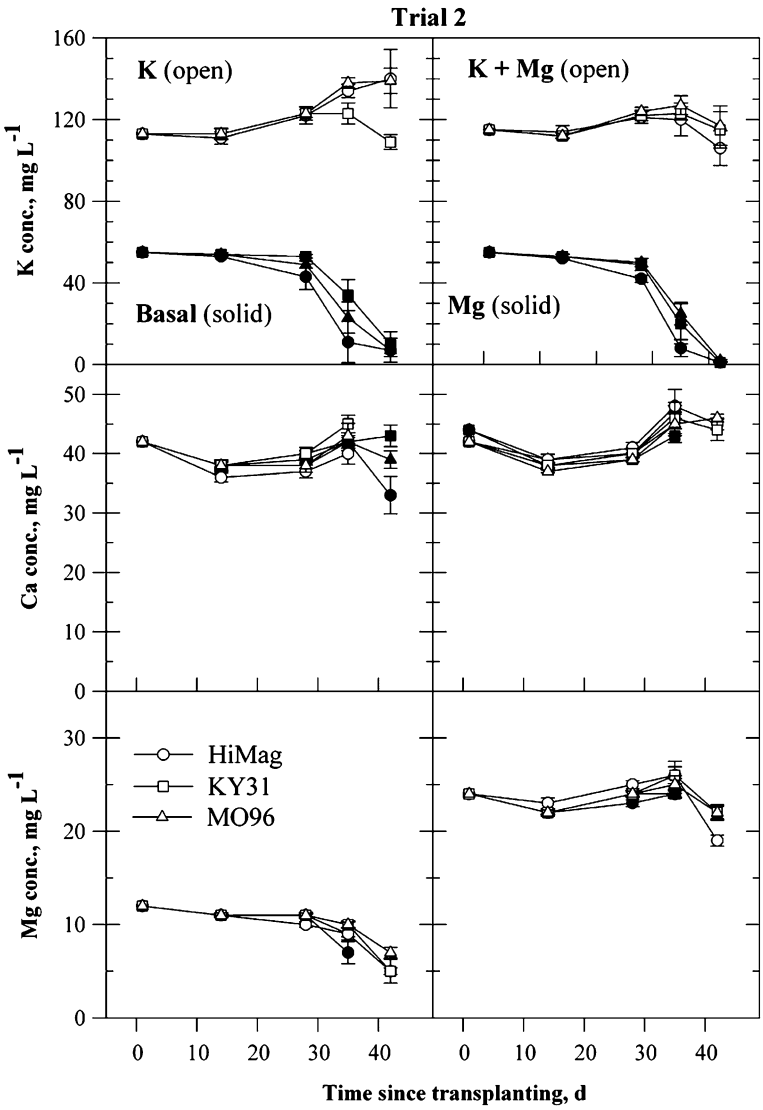

Fig. 1 Means and standard errors of K, Ca, and Mg concentrations of nutrient solutions in pots as a function of time since transplanting in Trial 2. Treatments were basal (1.5 mM K and 0.5 mM Mg) as *solid symbols in left column*, K (3.2 mM K) as *open symbols in left column*, Mg (1 mM Mg) as *solid symbols in right column*, and K+Mg (3.2 K and 1 mM Mg) as *open symbols in the right column*. A pot contained four plants of one of three tall fescue cultivars: HiMag, KY31, and MO96

increased to >150 g day^{-1} in Trial 1. Transpiration rate increased to about 40 g day^{-1} by Day 28 in Trial 2. After that, transpiration rate rapidly rose to about 200 g day^{-1} in Trial 2. The night/day temperatures in Trial 2 were 7–8 °C greater than those in Trial 1; thus, transpiration rates were higher in Trial 2.

Cation inflow rates and leaf uptake coefficients

HiMag had lower K inflow rates (I_K) than KY31 and MO96 in both trials (Table 5). Cultivars did not vary significantly for I_{Ca} (analysis not shown). The I_{Mg} was lower for HiMag in Trial 1, but not different than KY31 and MO96 in Trial 2. Contrast probabilities indicated I_K was not affected by treatment, but I_{Ca} was reduced by the K and Mg treatments. The K+Mg treatment reduced I_{Ca} by about 50% in Trial 1 but not as much in Trial 2. The K treatment reduced I_{Mg} compared to basal, and the Mg treatment increased I_{Mg} compared to the basal treatment. The K+Mg treatment was not different from the basal treatment for I_{Mg}.

Cultivars did not vary for leaf uptake coefficients for K and Ca, except HiMag had higher coefficients for Mg in Trial 2. The K and K+Mg treatments reduced leaf uptake coefficients for K by more than 50%, the K+Mg treatment lowered leaf uptake

Table 5 Means and contrast probabilities of cation inflow rates (I) per kg root in four tall fescue plants per pot on a fresh weight basis

Treatment	Mean inflow rates								
	I_K			I_{Ca}			I_{Mg}		
	HiMag (nmol kg^{-1} s^{-1})	KY31 (nmol kg^{-1} s^{-1})	MO96 (nmol kg^{-1} s^{-1})	HiMag (nmol kg^{-1} s^{-1})	KY31 (nmol kg^{-1} s^{-1})	MO96 (nmol kg^{-1} s^{-1})	HiMag (nmol kg^{-1} s^{-1})	KY31 (nmol kg^{-1} s^{-1})	MO96 (nmol kg^{-1} s^{-1})
Trial 1									
Basal	238	298	261	29	36	34	30	38	36
K	244	253	263	27	24	23	27	25	28
Mg	237	239	252	25	26	24	37	42	42
K+Mg	237	280	270	16	19	16	31	35	33
Trial 2									
Basal	236	323	286	32	32	35	40	40	44
K	273	325	307	29	28	27	36	34	34
Mg	254	291	239	30	28	23	56	49	43
K+Mg	274	322	311	22	27	22	41	42	40
Trial 1	Contrast probabilities ($P>F$)								
HiMag vs. others		0.017			NS			0.030	
K vs. basal		NS			0.001			0.001	
Mg vs. basal		0.093			0.001			0.017	
K+Mg vs. basal		NS			0.001			NS	
Trial 2									
HiMag vs. others		0.001			NS			NS	
K vs. basal		NS			0.073			0.004	
Mg vs. basal		NS			0.027			0.001	
dK+Mg vs. basal		NS			0.001			NS	

Plants were grown for 42 days in basal (1.5 mM K and 0.5 mM Mg), K (3.2 mM K), Mg (2 mM Mg), and K+Mg nutrient solution treatments.

NS indicates ANOVA main effect not significant ($P<0.05$).

coefficients for Ca and Mg compared to the basal treatment (Table 6).

Whole plant elemental uptake

Cultivars differed significantly only for the ratio of leaf K uptake to total plant K uptake across treatments in Trial 1. HiMag trended toward significantly (P= 0.09) higher total plant uptake of Mg in Trial 1.

For Trial 2, cultivars differed for leaf Mg uptake, crown Mg uptake, root Ca uptake, total plant uptake of Mg, and the ratio of leaf to total plant uptake for K and Mg. Leaf Mg uptake was 35.0 mg (SE=2.25) for HiMag and 27.7 mg (SE=1.8) for both KY31 and MO96. Crown Mg uptake was 9.94 mg (SE=0.60) for HiMag and 8.43 (SE=0.48) for both KY31 and MO96. Root Ca uptake was 4.19 mg (SE=0.40) for HiMag and 3.18 mg (SE=0.18) for both KY31 and MO96. Total plant Mg uptake was 47.7 mg (SE= 3.14) for HiMag and 39.0 mg (SE=2.65) for both KY31 and MO96. Leaf Mg composed 73% of total plant uptake for HiMag compared to 71% for both KY31 and MO96.

Discussion

Cultivar effects

Root physical characteristics examined in Trial 1 did not vary among three tall fescue cultivars. In Trial 1 of our study, HiMag did not have significantly more Mg in leaves than KY31 and MO96, but in Trial 2 HiMag had 9% more Mg in leaves than its parental cultivars. Leaf dry matter production was lower for HiMag in Trial 1, but higher in Trial 2 compared to KY31 and MO96. The slower growth rate of HiMag in Trial 1 compared to Trial 2 may explain the lack of significantly greater Mg concentration in leaves compared to KY31 and MO96. HiMag had 11%

Table 6 Means and contrast probabilities of leaf uptake coefficients (LU) for four tall fescue plants per pot on a dry matter basis

Treatment	Mean leaf uptake coefficients								
	LU_K			LU_{Ca}			LU_{Mg}		
	HiMag	KY31	MO96	HiMag	KY31	MO96	HiMag	KY31	MO96
Trial 1									
Basal	982	1136	968	185	190	198	464	489	479
K	380	388	394	194	172	147	507	452	498
Mg	964	1036	1043	162	160	143	243	254	239
K+Mg	366	387	364	170	172	140	244	238	210
Trial 2									
Basal	1642	1493	1532	173	152	178	699	482	628
K	434	487	442	186	139	150	615	469	466
Mg	1815	1720	1566	152	136	136	335	255	274
K+Mg	450	453	462	115	124	109	252	220	228
Trial 1	Contrast probabilities ($P>F$)								
HiMag vs. others		NS			NS			NS	
K vs. basal		0.001			NS			NS	
Mg vs. basal		NS			0.004			0.001	
K+Mg vs. basal		0.001			0.011			0.001	
Trial 2									
HiMag vs. others		NS			NS			0.001	
K vs. basal		0.001			NS			0.005	
Mg vs. basal		0.031			NS			0.001	
K+Mg vs. basal		0.001			0.001			0.001	

Leaf uptake coefficients are calculated as mol of nutrient kg^{-1} dried plant leaves divided by mol of nutrient kg^{-1} growth solution; assuming 1 L of growth solution=1 kg. Plants were grown for 42 days in basal (1.5 mM K and 0.5 Mg), K (3.2 mM K), Mg (2 mM Mg), and K+Mg nutrient solution treatments.

NS indicates ANOVA main effect not significant ($P<0.05$).

more leaf Mg than KY31 and MO96 in a companion field study (Shewmaker et al. 2004). In other studies, HiMag provided about 20% more leaf Mg than its parents, KY31 and MO96, on both acidic Typic Hapludults in Georgia (Wilkinson and Mayland 1997) and a calcareous Durinodic Xeric Haplocalcid soil in Idaho (Mayland and Sleper 1993). Different ecotypes of tall fescue in Japan produced different K, Ca, and Mg transport efficiencies (Rahman and Saiga 2005).

Risk of causing grass tetany, indicated by leaf K/(Ca+Mg), was lower in HiMag than in KY31 and MO96 in Trial 2 (Table 4). Shewmaker et al. (2004) also reported lower K/(Ca+Mg) for HiMag than KY31 and MO96 in a field study.

Treatment effects and Mg uptake mechanisms

Doubling K in nutrient solution decreased root Mg concentration and increased the root K/Mg ratio compared to the basal nutrient treatment, but had no significant effect on crown or leaf Mg. Doubling Mg in solution increased the Mg concentration in roots, crowns, and leaves. Clearly the leaf K concentration is not directly proportional to K concentration in nutrient solution. Although doubling K in solution reduced Mg in roots, all three tall fescue cultivars were able to translocate Mg to leaves. These results provide evidence supporting an active uptake mechanism for Mg in tall fescue and possibly a mechanism that limits K uptake at high K levels in solution around roots. Lazaroff and Pitman (1966) also found that barley (*Hordeum vulgare* L.) shoot uptake of Ca and Mg was little affected by Na and K concentration in shoots.

The increased leaf Mg concentration with increased Mg in nutrient solution in our study is supported by the results of Hannaway et al. (1982). They reported that increased solution concentration of Mg in sand raised shoot Mg concentration in 'Kenhy' tall fescue. In contrast to our study, they found that increasing solution K reduced shoot Mg, and in one case the interaction of solution K and Mg was significant. Ohno and Grunes (1985) reported that increasing K supply depressed Mg shoot concentration, but not root Mg concentration in wheat. They concluded that an antagonistic interaction between K and Mg occurred during root to shoot translocation. Huang et al. (1990) reported that Mg supply did not affect K concentration in 'Centurk' winter wheat (*Triticum aestivum* L.) grown in nutrient solution, and that increasing Mg in solution from 0.4 to 4 mmol L^{-1} increased Mg and decreased Ca concentration in roots and shoots. Huang et al. (1990) found that ratios of Mg accumulated in shoots compared to Mg in whole plants were negatively correlated with root K concentrations, and concluded that increasing root K concentration slowed the rate of net Mg translocation from roots to shoots. In most of these other studies, nutrient solutions were completely replaced about once a week. This replacement may have maintained K levels at unrealistically high levels. Similar to our study, Rossi et al. (1988) found that K concentration in soil solution was decreased at Day 30 compared to Day 20 or Day 10 in wheat.

The K×Mg interaction apparently depends on the magnitudes of concentrations in solution. For example, Mg uptake in rice (*Oryza sativa* L.) increased with increasing K up to 0.5 m*M*, but at higher K levels Mg uptake rate decreased (Fageria 1983). Fageria also reported that Mg content in roots and shoots decreased at high K levels, which may be due to competition for metabolically produced binding compounds. In our study, if Mg replaced K in a 1:1 ratio, doubling Mg should have decreased K by half, yet Mg level had no effect on root, crown, or leaf K concentration.

Leaf Mg concentrations in this study ranged from 4.87 to 6.44 g kg^{-1} compared to 2.40–3.12 g kg^{-1} in a companion field study (Shewmaker et al. 2004). However, plants in the field study were several years old, the leaves were more mature, and the root temperatures colder.

Temperature effects

The temperature differences between Trials 1 and 2 affected transpiration rates, and possibly cation uptake and translocation. Miyasaka and Grunes (1990a, b) reported that shoot and root concentration of K, Ca, and Mg were reduced in winter wheat grown at 8 °C compared to 16 °C root temperature. In contrast, Leggett et al. (1977) reported that cation accumulation in Kenhy tall fescue shoots did not respond to changes in root-zone temperature. They concluded that neither the root-zone temperature nor dry matter production rate limited cation accumulation in tall fescue. A plant's nutrient status, growth rate, translocation rate, transpiration rate, and root respiration rate

are factors that may interact with temperature (Barber 1984). The specific mechanisms responsible for the different cation uptakes observed in our study are unknown.

Changes in pH

The pH in nutrient solutions was not affected by cultivars or treatments but pH increased as plant biomass increased in our study (data not shown). Bugbee (1995) warned of the difficulty of maintaining pH<6 in solutions that contain rapidly growing plants because of efflux of HCO_3^- from roots. A decrease in root zone pH may be caused by: (1) H^+ efflux from excess cation compared to anion absorption, (2) release and hydrolysis of CO_2, (3) excretion of H^+ from carboxyl groups of polygalacturonic acid residues of pectic acid, and (4) excretion of protons from microorganisms associated with roots (Wilkinson 1970). Mugwira and Patel (1977) suggested that the relationship between anion–cation uptake and pH was evidence that pH changes in solution induced by triticale (x *Triticosecale* Witt Mack), wheat, and rye (*Secale cereale* L.) were caused by ion uptake imbalances and excretion of HCO_3^- by roots.

Because pH in the nutrient solution changed, there must have been a cation:anion uptake imbalance in our study, however, we did not determine the cause of the pH change. HiMag does not appear to affect pH differently than KY31 or MO96 (data not shown).

Cation inflow rates and leaf uptake coefficients

Cation inflow rates in our study ranged from 240 to 320 nmol kg^{-1} s^{-1} for K and 25 to 56 nmol kg^{-1} s^{-1} for Mg. Huang and Grunes (1992) reported net Mg uptake by wheat plants from Days 30 to 40 varied from 330 to 970 and from 440 to 1,390 nmol kg^{-1} s^{-1}, depending on root temperature, when 0.4 and 4 mmol Mg L^{-1} were supplied. Maas and Ogata (1971) reported Mg absorption rates in corn (*Zea mays* L.) roots in the range of 560 to 830 nmol kg^{-1} s^{-1}. These higher Mg inflow rates in wheat and corn may be due to their higher transpiration rates.

Leaf uptake coefficients indicate ability or efficiency of the plant to absorb a nutrient from solution in relation to the environment around the root system and transport the nutrient to the leaf. In our study, doubling the K in nutrient solution greatly reduced K uptake efficiency. Similarly, doubling Mg in solution decreased Mg uptake efficiency. This is evidence against passive uptake for both K and Mg.

Cation uptake and translocation to leaves

In Trial 2, HiMag had higher Mg uptake and transport to leaves, but the effect was not significant for Trial 1.

Conclusions

Root length, area, and radius did not vary consistently among the three tall fescue cultivars nor in nutrient treatments containing twice the K and Mg concentrations. HiMag was not more efficient at Mg uptake into the whole plant, but apparently translocated more Mg from roots to leaves than KY31 or MO96. Doubling the K in nutrient solution decreased Mg concentration and increased K/Mg ratio in roots, but did not significantly affect Mg concentration in crowns or leaves. Doubling the Mg in solution increased Mg concentration in roots, crowns, and leaves. This may be evidence for some process that limits K uptake and possibly an active Mg translocation mechanism for Mg in all three tall fescue cultivars.

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