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ORIGINAL PAPER

EFFECT OF BASIC CATION SATURATION RATIOS ON THE Mg, K AND Ca CONTENT OF ANNUAL RYEGRASS (*LOLIUM MULTIFLORUM L.*)*

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ABSTRACT

A pot experiment was carried out in a greenhouse to determine the optimal percentage of exchangeable Ca, Mg, and K in the CEC for improving the yield and favourable mineral composition of annual ryegrass plants. The experiment comprised 13 fertilization treatments with various basic cation saturation ratios in soil. Correlation and regression analyses revealed that the K content of ryegrass was influenced mainly by the percentage of K in the soil's exchange complex, but was far less affected by the percentage of saturation with Ca and Mg. Higher saturation of the CEC with Mg and Ca had a negligent effect on limiting the "luxury" uptake of K by grasses. The Mg content of plants grown for green forage was significantly more influenced by the Mg : K ratio in soil than by saturation levels of Mg, which suggests that K has a strong antagonistic effect on the Mg uptake. An increase in the percentage of saturation with Ca led to a progressive increase in the Ca content of ryegrass. An increase in the percentage of saturation with Mg or K had the opposite effect. The K : (Ca+Mg) ratio in ryegrass was most highly correlated with the percentage of the CEC occupied by K. When the percentage of the CEC occupied by K exceeded 5%, the K : (Ca+Mg) ratio of the first cut was higher than 2.0, which points to undesirable proportions of those cations in ryegrass forage. To maximize the yield of annual ryegrass with optimal mineral composition, the soil exchange complex should be occupied by 50-60% Ca, 8-12% Mg and 4-5% K, and the Mg : K ratio in soil should be maintained at 2-3 : 1.

Keywords: exchangeable cation percentage, magnesium, potassium, calcium, ryegrass.

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INTRODUCTION

The uptake and concentrations of K, Mg and Ca in plants are influenced by many factors. The key determinant is the content of available cations in soil, which is modified by the soil's cation exchange capacity (CEC). The release of K^+ , Mg^{2+} and Ca^{2+} from the exchange complex into the soil solution and their uptake by plants are largely influenced by the percentage of those cations in the CEC (BLUME et al. 2010). Plant content of K, Mg and Ca is also significantly affected by the proportions of exchangeable cations in soil. Those ratios reflect the antagonistic and synergistic effects of ions, which influence the uptake of minerals by plant roots. The above determinants of the Mg^{2+} , Ca^{2+} and K^+ uptake by plants have been included in the basic cation saturation ratio (BCSR) concept, which defines both the ratios of all basic cations in soil and their percentage saturation of the CEC, thus providing information about the concentrations of available K, Mg and Ca in soils with a particular CEC (ZALEWSKA 2005a,b, 2008).

Numerous authors have demonstrated that the percentage saturation of the CEC with Ca, Mg and K, and the mutual ratios of those cations in soil also exert a significant influence on the cation uptake and cation levels in plant tissues (ECKERT, McLEAN 1981, McLEAN et al. 1983, ZALEWSKA 2005a, 2008). Changes in K, Mg and Ca concentrations are particularly profound in the vegetative parts of plants. Magnesium deficiencies in soil, crop plants, animal and human diets pose a serious problem (FICCO et al. 2009, GUO et al. 2016). In recent decades, long-term application of unbalanced NPK fertilizers and the absence of Mg fertilization have led to a decrease in the Mg content of plants. Light and acidified soils are particularly deficient in bioavailable Mg. This adverse phenomenon is often exacerbated by high rates of K fertilization (GRZEBISZ 2011, GRANSEE, FÜHRS 2013). Potassium is a strong antagonist of Mg, and Mg deficiency has even been reported in soils with a high content of available Mg when base saturation levels of K are high, above 5% (ZALEWSKA 2008).

To increase the yield of crops with a balanced mineral composition, the base saturation level of K should not exceed 5%, the percentage of the CEC occupied by Mg should be around twice as high (8-12%) and the soil's exchangeable Ca concentration should be around 60-65% (ZALEWSKA 2003, 2008). This is a very important consideration in the process of formulating fertilizer recommendations for grasslands, which are generally characterized by excessive accumulation of K and very low levels of Mg in the first cut. The above can contribute to the risk of grass tetany in ruminants fed diets with an unbalanced mineral content.

The objective of this study was to evaluate the influence of various saturation levels of Ca, Mg and K on their concentrations in annual ryegrass, and to determine the optimal basic cation saturation ratios for improving the yield and ensuring a favourable mineral composition of ryegrass plants.

MATERIAL AND METHODS

A pot experiment was performed in the greenhouse of the University of Warmia and Mazury in Olsztyn, Poland (2007). Thirteen fertilization treatments with various basic cation saturation ratios in soil were analyzed. The experiment consisted of three parts. In part A, the ratio of Ca to the other cations was increased, in part B, the ratio of Mg to the other cations was increased, whereas in part C, the K : Ca and K : Mg ratios were increased (Table 1).

Pots were filled with 6.0 kg of air-dry soil with the textural composition of loamy sand which contained 81.3% of sand (particle size: 2.0-0.05 mm), 16.9% of silt (particle size: 0.05-0.002 mm) and 1.7% of clay (particle size: <0.002 mm) according to the USDA textural soil classification. The remaining physical and chemical properties of soil used in the experiment are presented in Table 2. The experimental plant was annual ryegrass (*Lolium multiflorum* L. cv. *Kroto*), harvested four times at the early heading stage.

Table 1

Soil cation ratios, cation saturation of CEC and other chemical properties of soil after incubation with fertilizer

Cation ratios in soil (mmol _c)				Cation saturation of CEC (%)				Hh (mmol H ⁺ kg ⁻¹ soil)	pH _{KCl}	Exchangeable cations (mg kg ⁻¹ soil)			Dose (mg kg ⁻¹ soil)		
Ca	Mg	K	H	Ca	Mg	K	H			Ca	Mg	K	Ca	Mg	K
Part A															
19.7	1.0	0.49	6.7	70.7	3.6	1.8	24.0	34.1	5.8	2026	62	98	1476	11	12
15.2	1.0	0.51	5.7	68.0	4.5	2.3	25.2	35.6	5.7	1954	79	129	1439	28	43
10.7	1.0	0.52	4.3	64.9	6.1	3.2	25.9	35.8	5.6	1820	111	176	1270	59	90
7.0*	1.0	0.50	3.4	58.8	8.4	4.2	28.6	39.8	5.5	1637	153	246	1087	102	160
2.8	1.0	0.52	2.5	41.3	14.7	7.6	36.3	49.0	5.2	1124	272	438	574	221	352
Part B															
6.6	0.5	0.50	3.1	61.4	4.8	4.6	29.2	40.2	5.5	1733	81	260	1184	29	174
7.0	1.0	0.50	3.4	58.8	8.4	4.2	28.6	39.8	5.5	1637	153	246	1087	102	160
6.4	1.4	0.50	3.4	54.6	12.3	4.3	28.7	38.2	5.5	1553	217	231	1003	166	145
6.4	2.6	0.50	3.8	48.1	19.6	3.7	28.6	39.0	5.5	1343	375	203	793	324	117
6.4	5.7	0.50	4.7	37.1	32.7	2.9	27.3	36.0	5.6	1020	618	152	470	567	67
Part C															
6.6	1.0	0.26	3.2	59.8	9.0	2.3	28.9	38.4	5.6	1683	157	125	1133	105	39
7.0	1.0	0.50	3.4	58.8	8.4	4.2	28.6	39.8	5.5	1637	153	246	1087	102	160
6.8	1.0	0.75	3.5	56.6	8.3	6.2	29.0	40.2	5.5	1593	148	360	1043	97	274
6.7	1.0	0.95	3.5	54.9	8.2	7.8	29.1	40.8	5.5	1553	145	465	1003	93	379
6.4	1.0	1.41	4.1	49.8	7.7	10.9	31.6	44.4	5.3	1475	137	665	925	86	579

* This treatment belongs to parts A, B and C.

Physico-chemical properties of soil used in the experiment

CEC (mmol _c kg ⁻¹ soil)	Exchangeable cations (mg kg ⁻¹ soil)			Cation saturation of CEC (%)				Hh (mmol H ⁺ kg ⁻¹ soil)	pH _{KCl}	C _{org} (g kg ⁻¹ soil)
	Ca	Mg	K	Ca	Mg	K	H			
114.4	550	52	86	24.0	3.7	1.9	70.5	80.6	4.2	26.2

In order to obtain different levels of Ca, Mg and K saturation in experimental treatments (with four replications per treatment), adequate amounts of the above cations were applied to the soil prior to sowing (Table 1). Calcium and magnesium were applied as oxides and potassium as KCl and K₂SO₄ in two equal parts. In addition, 0.51 g of N and 0.57 g of P per pot (in the form of (NH₄)₂HPO₄) were applied before sowing in equal doses in all the treatments. During the growing season, ammonium nitrate was added in the amount of 0.5 g N pot⁻¹ per regrowth. After three weeks of soil incubation with fertilizers, annual ryegrass seeds were sown. After germination, 20 plants were left per pot. Soil moisture was maintained at 70% of maximum water-holding capacity during the experiment.

Simultaneously, another experiment was carried out, in which soil samples containing Ca, Mg and K in the amounts identical to those used in the experiment with ryegrass (expressed per kg of soil) were incubated for 3 weeks. The analysis of soil samples after incubation provided the basis for determining the initial cation saturation of soil exchange complex. Table 1 presents the doses of Ca, Mg and K used in the experiment, the concentrations of exchangeable cations determined after soil incubation with fertilizers, and the per cent saturation of the CEC with Ca, Mg and K in each fertilization treatment.

Plant samples were dried, ground and mineralized (separately from each pot) in concentrated H₂SO₄ with the addition of 30% H₂O₂. Soil samples were air-dried, passed through a 2-mm sieve and analyzed for exchangeable K, Ca and Mg after extraction with 1M NH₄OAc at pH = 7.00 (VAN REEUWIJK 2002). The content of K and Ca was determined by flame emission spectrometry, and the Mg content was determined by atomic absorption spectrometry in both mineralized plant samples and soil samples.

The textural composition of soil was determined by laser diffraction with the use of a Mastersizer 2000 particle size analyzer. Organic C content was determined by the Tiurin's method, soil hydrolytic acidity (Hh) – by the Kappen's method, and soil pH in 1 M KCl (1 : 2.5 soil : solution ratio) – by the potentiometric method. The CEC (cation exchange capacity) was estimated by summation of exchangeable bases (Ca, Mg, K) and soil hydrolytic acidity (Hh):

The 'effective CEC' was calculated as:

$$\text{CEC} = \text{Exch. (Ca + Mg + K + Hh)} [\text{cmol}_c \text{ kg}^{-1} \text{ air-dry soil}].$$

The exchangeable cation percentage was calculated as:

$$\text{exchangeable cation percentage} = \frac{\text{exchangeable cation}}{\text{CEC}} \cdot 100\%.$$

The cation ratios in both plants and soils were calculated on the mmoles of charge basis, mmol_c (VAN REEUWIJK 2002).

The relationships between selected parameters were determined by correlation and regression analyses using Statistica v. 7.0 program.

The effect of basic cation saturation ratios in soil on yield of annual ryegrass are presented in another article, which will be published in the next issue of the Journal of Elementology.

RESULTS AND DISCUSSION

The percentage saturation of the CEC with Ca, Mg and K exerted a significant influence on the cation uptake and mineral composition of annual ryegrass. Considerable differences in K, Mg and Ca concentrations were also observed between four cuts (Table 3). The first cut was characterized by the least desirable mineral composition due to the highest average content of K (37.9 g K kg⁻¹ DM) and the lowest concentrations of Mg (3.2 g Mg kg⁻¹ DM) and Ca (7.0 g Ca kg⁻¹ DM). Levels of K in grass decreased in successive cuts in the corresponding treatments, whereas Mg concentrations increased. The highest average content of Ca was noted in the second cut. Despite differences in the content of the analyzed elements in four successive cuts, the correlations between Ca, Mg and K levels and the K:(Ca+Mg) ratio in plants vs. the analyzed soil properties were similar in all cuts. For this reason, regression curves for the first cut and the weighted averages of four cuts were plotted in the study. The coefficients of determination for the analyzed correlations were given for all cuts (Table 4).

In this experiment, the K content of the first cut was very high in the range of 17.4- 69.4 g K kg⁻¹ DM. In most treatments, the K concentration exceeded 20 g kg⁻¹ DM, which indicates that excessive accumulation of K is very difficult to control in the first cut by increasing saturation levels of Mg or Ca. The above findings were confirmed by correlation and regression analyses (Table 4, Figure 1), which revealed that the K content of ryegrass was determined mainly by the percentage of the CEC occupied by K ($R^2 = 0.998$ for the weighted averages of four cuts) and, to a far lesser and non-significant extent, by saturation levels of Ca and Mg. The regression curve (Figure 1a) indicates that an increase in saturation levels of K led to a proportional rise in the K content of plants. This corresponds well with the results of other studies, where a significant rise in the K content with an increase in the percentage of K saturation has been observed (WEST, REYNOLDS

Table 3

Effect of cation saturation of the CEC on the mineral composition of annual ryegrass

Cation saturation of CEC (%)				Concentration (g kg ⁻¹ DM)												K/(Ca + Mg) (mmol) cut					
				I cut			II cut			III cut			IV cut								
Ca	Mg	K	H	K	Mg	Ca	K	Mg	Ca	K	Mg	Ca	K	Mg	Ca	Mg	Ca	I	II	III	IV
Part A																					
70.7	3.6	1.8	24.0	17.4	3.3	9.8	9.9	4.4	13.1	7.3	4.5	10.3	8.9	4.8	10.4	4.8	10.4	0.59	0.25	0.21	0.25
68.0	4.5	2.3	25.2	22.6	3.3	9.5	10.1	4.2	12.3	7.9	4.5	10.3	9.0	4.9	10.1	4.9	10.1	0.78	0.27	0.23	0.25
64.9	6.1	3.2	25.9	29.2	3.3	8.2	10.6	4.4	11.2	9.0	4.6	9.5	9.8	5.0	9.4	5.0	9.4	1.10	0.29	0.27	0.28
58.8*	8.4	4.2	28.6	38.7	2.9	7.0	12.7	4.1	9.6	10.0	4.2	8.7	10.4	4.9	8.9	4.9	8.9	1.68	0.40	0.33	0.31
41.3	14.7	7.6	36.3	56.2	2.8	5.3	26.4	4.2	7.6	16.0	4.3	6.8	13.9	5.1	7.1	5.1	7.1	2.90	0.93	0.59	0.46
Part B																					
61.4	4.8	4.6	29.2	40.0	2.6	7.0	15.0	3.9	9.9	10.4	4.1	9.2	10.8	4.6	9.2	4.6	9.2	1.82	0.47	0.33	0.33
58.8	8.4	4.2	28.6	38.7	2.9	7.0	12.7	4.1	9.6	10.0	4.2	8.7	10.4	4.9	8.9	4.9	8.9	1.68	0.40	0.33	0.31
54.6	12.3	4.3	28.7	35.9	3.4	6.6	12.7	4.7	9.4	10.1	4.7	8.6	10.5	5.3	8.6	5.3	8.6	1.51	0.38	0.32	0.31
48.1	19.6	3.7	28.6	30.1	4.1	5.8	12.7	5.8	9.4	9.7	5.4	8.5	10.2	5.9	8.2	5.9	8.2	1.23	0.34	0.29	0.29
37.1	32.7	2.9	27.3	23.0	5.0	5.6	11.0	6.5	9.5	8.9	5.9	8.2	9.5	6.4	8.4	6.4	8.4	0.85	0.28	0.25	0.26
Part C																					
59.8	9.0	2.3	28.9	20.8	4.1	6.7	9.7	5.8	11.1	8.6	5.4	9.9	9.0	5.5	9.5	5.5	9.5	0.79	0.24	0.23	0.25
58.8	8.4	4.2	28.6	38.7	2.9	7.0	12.7	4.1	9.6	10.0	4.2	8.7	10.4	4.9	8.9	4.9	8.9	1.68	0.40	0.33	0.31
56.6	8.3	6.2	29.0	50.9	2.6	6.5	20.0	4.2	9.7	13.5	4.2	8.6	12.1	4.7	8.7	4.7	8.7	2.42	0.62	0.45	0.38
54.9	8.2	7.8	29.1	58.3	2.4	6.3	27.5	3.7	8.5	15.2	3.9	8.2	14.6	4.5	8.4	4.5	8.4	2.91	0.97	0.53	0.47
49.8	7.7	10.9	31.6	69.4	2.2	6.1	44.9	3.0	7.9	28.4	3.5	7.1	20.4	4.2	7.1	4.2	7.1	3.66	1.79	1.13	0.75

* This treatment belongs to parts A, B and C.

Table 4

Values of determination coefficients between soil chemical properties and the K, Mg and Ca content of ryegrass and cation uptake by total yield

Plant (y)	Soil chemical properties (x)						
	cation saturation of CEC			cation ratios in soil			
	Ca	Mg	K	Ca/K	Mg/K	Ca/Mg	(Ca+Mg)/K
I cut							
g K kg ⁻¹ DM	ns	ns	0.991***	0.861***	ns	ns	0.971***
g Mg kg ⁻¹ DM	ns	0.506**	0.482**	ns	0.947***	ns	0.592*
g Ca kg ⁻¹ DM	0.964***	0.676**	0.450*	0.756***	ns	0.863***	0.564**
K/(Ca+Mg)	ns	ns	0.991***	0.874***	ns	ns	0.978***
II cut							
g K kg ⁻¹ DM	ns	ns	0.997***	0.897***	0.634*	ns	0.953***
g Mg kg ⁻¹ DM	ns	0.537**	0.413*	ns	0.940***	0.481**	0.506*
g Ca kg ⁻¹ DM	0.852***	0.452*	0.780***	0.930***	ns	0.616**	0.859***
K/(Ca+Mg)	ns	ns	0.998***	0.878***	0.648***	ns	0.940***
III cut							
g K kg ⁻¹ DM	ns	ns	0.986***	0.861***	0.606**	ns	0.913***
g Mg kg ⁻¹ DM	ns	0.493**	0.477**	ns	0.939***	ns	0.580*
g Ca kg ⁻¹ DM	0.780***	ns	0.679***	0.901***	ns	0.540**	0.710***
K/(Ca+Mg)	ns	ns	0.986***	0.857***	0.615**	ns	0.911***
IV cut							
g K kg ⁻¹ DM	ns	ns	0.997***	0.886***	0.638**	ns	0.948***
g Mg kg ⁻¹ DM	ns	0.708***	ns	ns	0.970***	0.547*	ns
g Ca kg ⁻¹ DM	0.810***	0.487*	0.665***	0.795***	ns	0.602**	0.707***
K/(Ca+Mg)	ns	ns	0.996***	0.872***	0.657***	ns	0.939***
Weighted averages of four cuts							
g K kg ⁻¹ DM	ns	ns	0.998***	0.887***	0.610*	ns	0.984***
g Mg kg ⁻¹ DM	ns	0.564**	0.433*	ns	0.964***	ns	0.527*
g Ca kg ⁻¹ DM	0.916***	0.551**	0.669**	0.881***	ns	0.716***	0.755***
K/(Ca+Mg)	ns	ns	0.995***	0.890***	0.415*	ns	0.989***
Total uptake							
K uptake	ns	ns	0.997***	0.925***	0.596*	ns	0.990***
Mg uptake	ns	0.719***	ns	ns	0.923***	0.534*	ns
Ca uptake	0.884***	0.438**	0.361*	0.594**	ns	0.655***	0.424*

*, **, *** significant at: $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively; ns – non-significant correlation

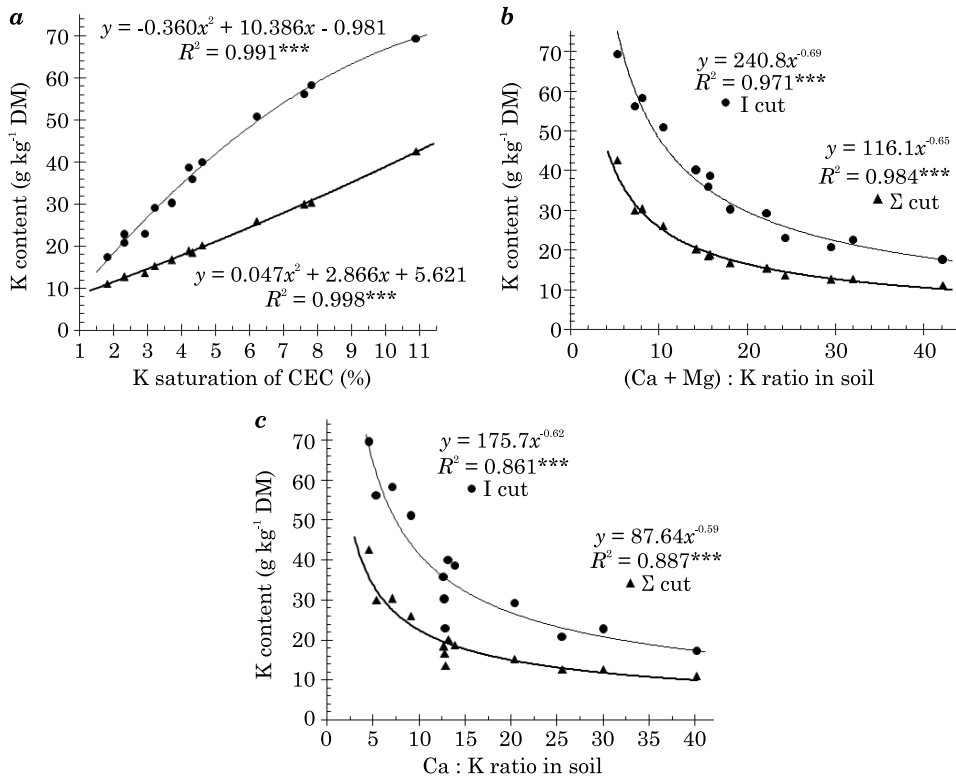


Fig. 1. Potassium content of annual ryegrass as affected by K saturation of CEC (a), (Ca+Mg):K ratio in soil (mmol) (b) and Ca:K ratio in soil (c): ● I cut, ▲ Σ cut (weighted averages of four cuts); *, ** and *** indicate a significant correlation at: $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively (refers to all figures)

1984, NARWAL et al. 1985, ZALEWSKA 2005a,b, 2008). Excessive accumulation of K is particularly often noted in the vegetative organs of young plants. The extent of this process is best illustrated by the fact that an increase in the base saturation level of K from 4% to 11% increased the K concentration from 39 g to 69 g K kg^{-1} DM in the first cut of ryegrass, and from 27 g to 72 g K kg^{-1} DM in the green matter of sunflowers (ZALEWSKA 2008).

An increase in the percentage saturation of the CEC with Mg and Ca had a negligent effect on limiting the "luxury uptake" of K by ryegrass plants. In previous studies by ZALEWSKA (2003, 2005b, 2008) and in the work of other authors (MORTVEDT, KHASAWNEH 1986, DENG et al. 2006), K also effectively competed with Mg and Ca in the uptake process. The strong antagonistic effect of K on Ca and Mg can probably be attributed to the fact that K can be taken up both passively and actively, whereas Ca and Mg are taken up only passively (WHITE 1993, MARSCHNER 2012). It should be noted, however, that an increase in the percentage of saturation with Mg and Ca has a generally minor inhibitory effect on excessive accumulation of K in plants

(in particular in soils abundant in K), but it can contribute to an increase in Mg and Ca concentrations in plant tissues (ZALEWSKA 2005*a,b*, 2008, SWIFT et al. 2007). The above leads to a desirable decrease in the K : (Ca+Mg) ratio, which is a vital parameter in animal feeds. Strong correlations were also observed between the K content of ryegrass vs. the (Ca+Mg) : K ratio in soil ($R^2 = 0.98$ for four cuts) and the Ca : K ratio in soil ($R^2 = 0.89$ for four cuts). Excessive accumulation of K was clearly reduced (from 70 g to 20 g K kg⁻¹ DM in the first cut) when the above ratios increased from around 5 to 25 (Figure 1*b,c*).

The Mg content of the first ryegrass cut ranged from 2.2 g Mg kg⁻¹ DM (treatment with the highest saturation level of K) to 5.0 g Mg kg⁻¹ DM (treatment with the highest saturation level of Mg). The values of determination coefficients (Table 4) suggest that the Mg content of plants was most highly influenced by the Mg : K ratio in soil ($R^2 = 0.96$ for four cuts). The regression curve (Figure 2*a*) indicates that an increase in the Mg : K ratio led to a desirable increase in the Mg content of ryegrass. Similar results were noted with an increase in the percentage of the CEC occupied by Mg (Figure 2*b*), but the observed correlation was much weaker ($R^2 = 0.56$ for four cuts). The Mg concentration in plants did not change considerably in response to an increase in the percentage of saturation with Mg in the range of 5% to 10%, and it increased significantly only with a further increase in the saturation level of Mg. An increase in the saturation percentage of K led to a gradual drop in the Mg concentration in ryegrass (Figure 2*c*). The results of previous studies (ZALEWSKA 2005*a,b*, 2008) also revealed that the Mg content of plants was more influenced by the Mg : K ratio in soil than by the percentage saturation of the CEC with Mg. An increase in the base saturation level of K from 2.3% to 10.9% reduced Mg concentrations from 4.1 g to 2.2 g Mg kg⁻¹ DM in the first cut of ryegrass and from 11.1 g to 3.6 g Mg kg⁻¹ DM in sunflower (ZALEWSKA 2008) despite high Mg levels in soil in the analyzed treatments (137-157 mg exchangeable Mg kg⁻¹ soil). The above indicates that K has a strong antagonistic effect on the uptake of Mg, which has been broadly described in the literature (TÜMA et al. 2004, ZALEWSKA 2003, 2005*a*, 2008, GRANSEE, FÜHRS 2013, GUO et al. 2016). The results of this study revealed that high doses of K fertilization can significantly reduce the Mg uptake by plants, even in soils that are abundant in available Mg.

A significant correlation was also noted between Mg levels in grass and the (Ca+Mg) : K ratio in soil. The parabolic shape of the corresponding curve (Figure 2*d*) indicates that plants were most abundant in Mg when the (Ca+Mg) : K ratio in soil was 25-30 : 1. When the value of the (Ca+Mg) : K ratio in soil decreased below 25, the antagonistic effect of K on the Mg uptake was manifested.

An increase in the percentage saturation of the CEC with Ca did not induce significant changes in the Mg content of ryegrass. This corresponds well with the findings of previous experiment performed on other plant spe-

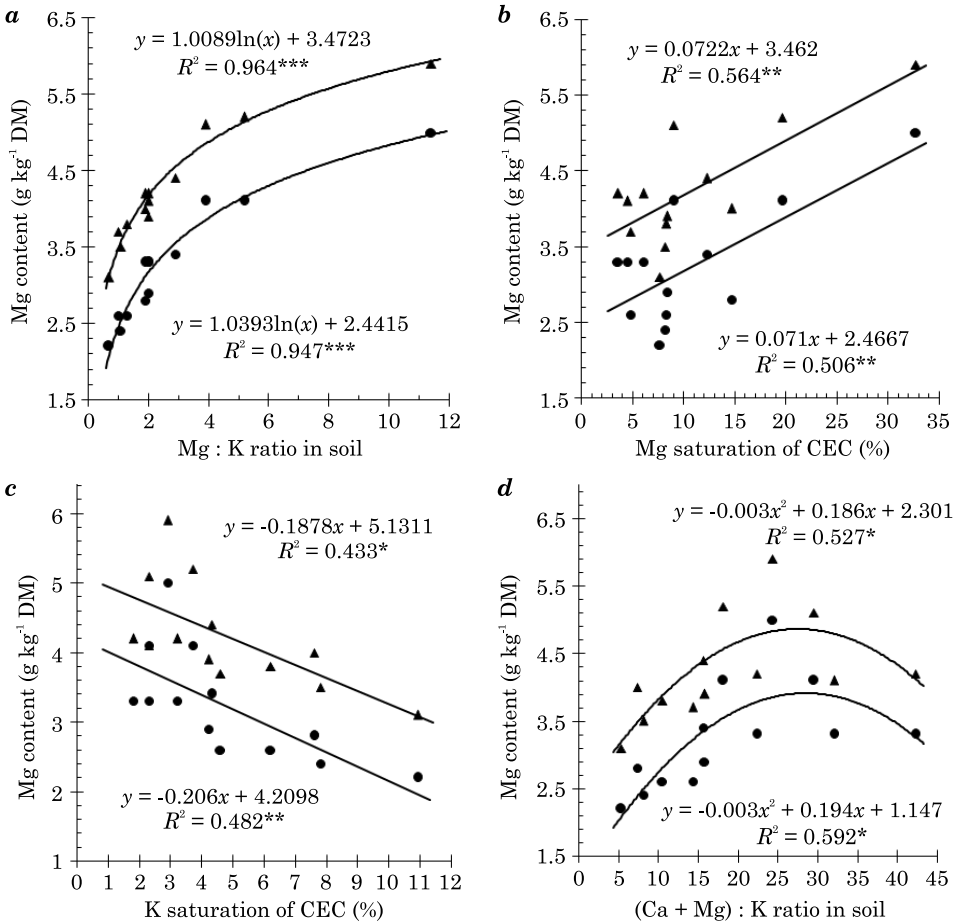


Fig. 2. Magnesium content of annual ryegrass as affected by the Mg:K ratio in soil (mmol) (a), Mg saturation of CEC (b), K saturation of CEC (c) and (Ca + Mg):K ratio in soil (mmol) (d); ● I cut, ▲ Σ cut (weighted averages of four cuts)

cies (ZALEWSKA 2003, 2005a, 2008). Different results were noted in an experiment involving spring oilseed rape, where Ca was a stronger antagonist of Mg than K, whereas K had a negligible effect on Mg accumulation (PANAK, ZALEWSKA 1988). Calcium uptake was significantly higher in spring oilseed rape than in ryegrass and sunflower (ZALEWSKA 2008), whereas ryegrass and sunflower harvested in the plant growing phase accumulated more K than oilseed rape. The differences in various species' ability to accumulate cations could also influence ion competition. The above could be attributed to genetic differences between plant species. In selected plants, higher Ca uptake could result from differences in Ca²⁺ permeability of plasma membranes. Moreover, the antagonistic effect of K on Mg and Ca uptake is particularly manifested during the vegetative growth when K is most readily accumulated. According

to FAGERIA (1983, 2009) and MARSCHNER (2012), Ca can exert both antagonistic and synergistic effects on the uptake of Mg and K, depending on exchangeable Ca concentrations in soil.

Studies investigating the relationships between Ca, Mg and K cations during their uptake often deliver different and seemingly contradictory results. NARWAL et al. (1985) and DENG et al. (2006) reported both antagonistic and synergistic effects of Mg fertilization on K accumulation in plants, as well as positive and negative effects of K on Mg concentration. The mutual relationships between cations were influenced by the levels of both K and Mg in soil. In previous studies by ZALEWSKA (2003, 2005a, 2008), K generally effectively competed with Mg and Ca in the uptake process.

The mechanisms responsible for the uptake and transport of Mg, K and Ca cations, and the antagonism and synergy of ions have not yet been fully explained. Researchers have identified ion uptake mechanisms which partially explain the strong limiting effect of K on Mg uptake (in particular in soils abundant in K) and the absence of the antagonistic effect of Mg on K uptake. Most scientists believe that competition between ions during uptake by the root system should be attributed to the absence of specific uptake mechanisms for different ions (SHAUL 2002, GARDNER 2003, SHABALA, HARIADI 2005, DENG et al. 2006, MARSCHNER 2012). The antagonism of ions usually results from non-specific replacement of ions, which suggests that cations compete for negative charges in a cell. HORIE et al. (2011) demonstrated the presence of ion transporters that can carry K as well as Ca and Mg. However, in soil with high K levels, the transport of Ca and Mg may be difficult because these transporters are characterized by certain selectivity for K. Furthermore, some Mg transporters may also carry K^+ . As a result, in soils abundant in highly available K, non-specific Mg transporters are blocked, which reduces the uptake of Mg. However, high concentrations of Mg^{2+} in the soil solution do not inhibit the uptake of K, even in soils with low levels of K, because specific K transporters of high-affinity transport systems (HATS) are not blocked by Mg and facilitate the transport of K. It should be noted that ion antagonism may also be revealed when ions are transported from roots to aerial parts of plants. Other authors observed that K did not lower the Mg content of roots, whereas the translocation of Mg from roots to stems was significantly impaired by a high concentration of K in the nutrient solution (OHNO, GRUNES 1985, GRANSEE, FÜHRS 2013).

The Ca content of ryegrass was influenced mostly by the percentage of the CEC occupied by this element ($R^2 = 0.92$ for four cuts) – Table 4. An increase in the percentage of saturation with Ca from 41% to 71% caused a gradual increase in the Ca content of annual ryegrass from 6.6 g to 10.8 g Ca kg^{-1} DM (weighted averages of four cuts) – Figure 3a. An identical correlation was reported in a study on sunflower and spring oilseed rape (PANAK, ZALEWSKA 1988, 2008). An increase in base saturation levels of Mg and K or a decrease in Ca : Mg and Ca : K ratios in soil induced an opposite effect (Figure 3). It should be noted, however, that variations in the percen-

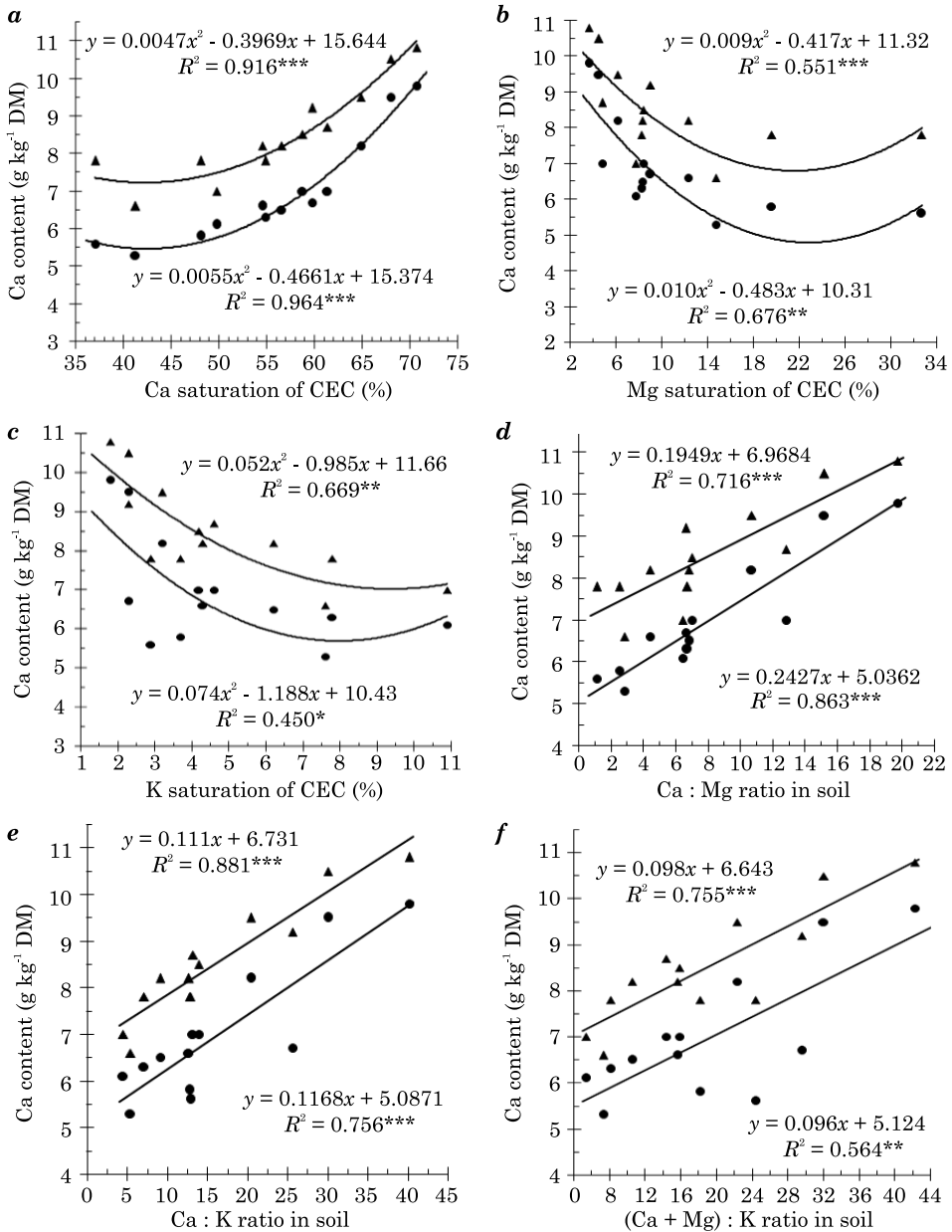


Fig. 3. Calcium content of annual ryegrass as affected by Ca saturation of the CEC (a), Mg saturation of CEC (b), K saturation of CEC (c), Ca : Mg ratio in soil (mmol_c) (d), Ca : K ratio in soil (mmol_c) (e) and (Ca+Mg) : K ratio in soil (mmol_c) (f); ● I cut , ▲ Σ cut (weighted averages of four cuts)

tage of the CEC occupied by cations were less likely to influence Ca concentrations than K levels in plants. The above can probably be attributed to the fact that base saturation levels of Ca (in particular in soils with balanced pH) are significantly higher than the percentage of saturation with K and Mg, which can considerably reduce other cations' antagonistic effects on the Ca uptake. In the soil solution, the Ca concentration is also generally higher than the K and Mg content.

The first ryegrass cut was characterized by the highest average content of K and the lowest concentrations of Ca and Mg in comparison with the remaining cuts, which increased the average value of the K : (Ca+Mg) ratio in the first cut relative to the remaining cuts (Table 3). Correlation and regression analyses revealed that the K : (Ca+Mg) ratio was most highly correlated with the base saturation level of K ($R^2 = 0.99$) – Table 4, Figure 4. When the

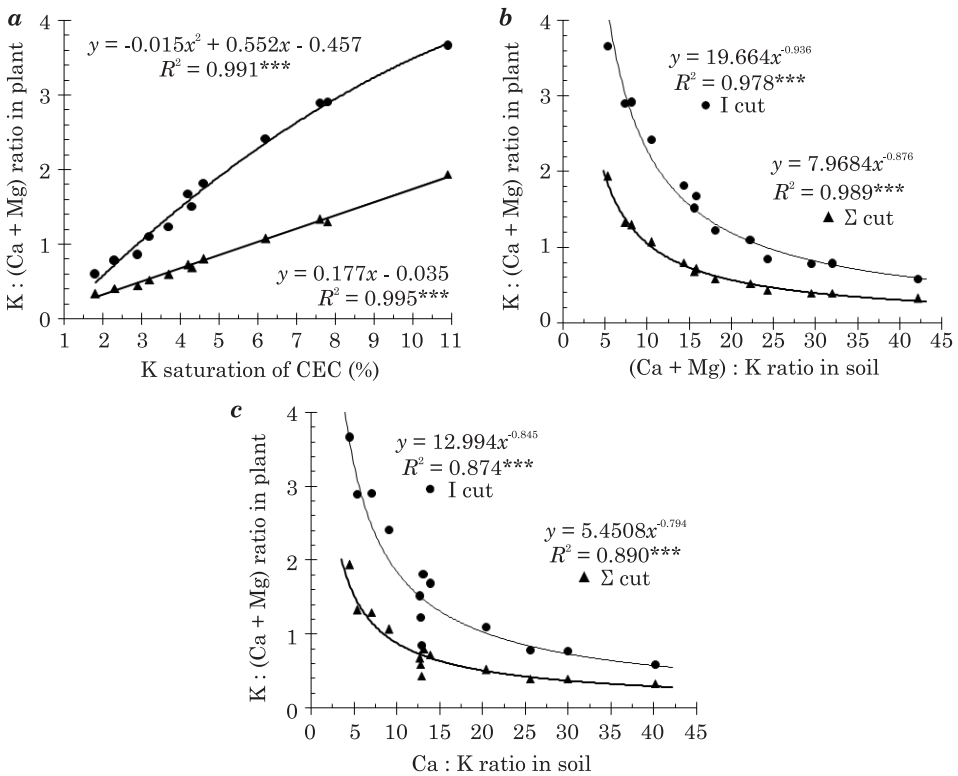


Fig. 4. The K : (Ca+Mg) ratio in annual ryegrass as affected by K saturation of the CEC (a), (Ca+Mg) : K ratio in soil (b) and Ca : K ratio in soil (c); ratios expressed in mmol_i;

● I cut , ▲ Σ cut (weighted averages of four cuts)

percentage of the CEC occupied by K exceeded 5%, the K : (Ca+Mg) ratio in the first cut was higher than 2.0 (Figure 4a), which suggests that the produced forage had an unbalanced mineral composition. In successive cuts, the K : (Ca+Mg) ratio was lower than 2 in all fertilization treatments.

The K : (Ca+Mg) ratio was also highly correlated with the (Ca+Mg) : K ratio in soil ($R^2 = 0.99$) and with the Ca : K ratio ($R^2 = 0.89$). An increase in the above ratios in the soil led to a desirable decline in the K : (Ca+Mg) ratio in plant tissues (Figure 4b,c).

The total K uptake by four cuts of ryegrass was most significantly influenced by the percentage of the CEC occupied by this element and it increased proportionally to the rise in the base saturation level of K (Table 4, Figure 5a). The (Ca+Mg) : K ratio and the Ca : K ratio in soil were also highly correlated with K uptake (Table 4, Figure 5b). The Mg uptake of ryegrass

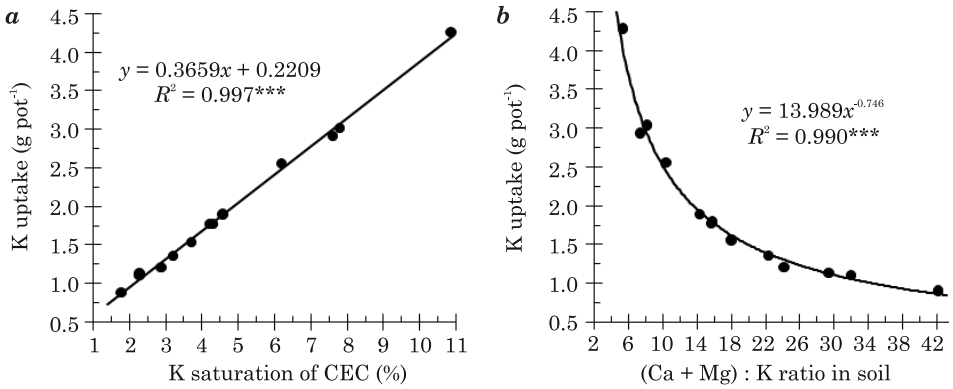


Fig. 5. Potassium uptake by total yield of annual ryegrass as affected by the K saturation of the CEC (a) and (Ca+Mg) : K ratio in soil (mmol) (b)

grass was positively correlated with the soil's Mg : K ratio ($R^2 = 0.92$), and its correlation with the saturation level of Mg ($R^2 = 0.72$) was somewhat weaker, but statistically significant (Table 4, Figure 6). The results of this study suggest that the saturation level of K significantly influences the Mg

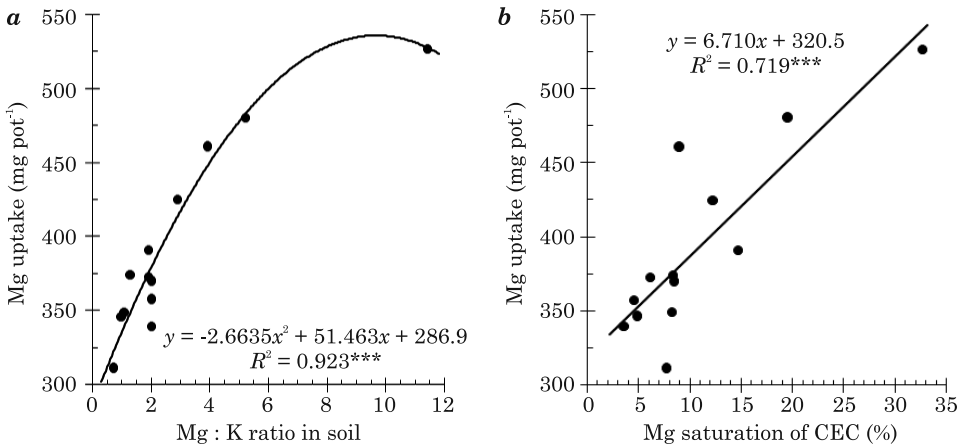


Fig. 6. Magnesium uptake by total yield of annual ryegrass as affected by the Mg : K ratio in soil (mmol) (a) and Mg saturation of the CEC (b)

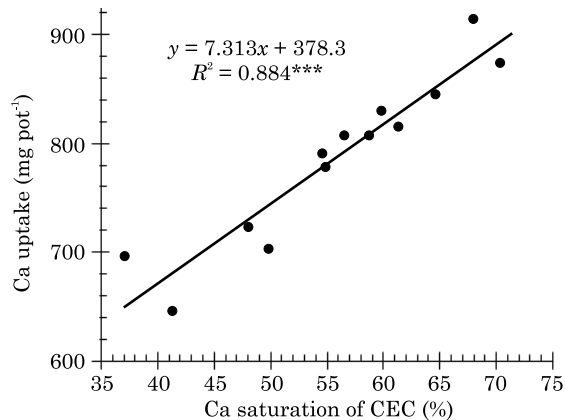


Fig. 7. Calcium uptake by total yield of annual ryegrass as affected by Ca saturation of CEC

uptake by plants, therefore, the soil's Mg : K ratio is a more important determinant of Mg availability for plants than the content of available Mg. Calcium uptake increased with a rise in the saturation level of this element (Figure 7). An analysis of correlations between cation ratios in soil and Ca uptake by plants revealed a significant positive correlation with the Ca : Mg and the Ca : K ratios in soil (Table 4).

CONCLUSIONS

To maximize the yield of annual ryegrass with optimal mineral composition, the soil exchange complex should be occupied by 50-60% Ca, 8-12% Mg and 4-5% K, and the Mg : K ratio in soil should be maintained at 2-3 : 1. When the saturation level of K exceeds 5%, ryegrass yield continues to increase, but plants could accumulate excessive quantities of K, which leads to an adverse decrease in their Mg and Ca content. The K content of ryegrass is determined mainly by the saturation levels of K. An increase in the percentage saturation of the CEC with Mg and Ca had a negligible effect on limiting the "luxury" uptake of K by grasses. The Mg content of ryegrass is considerably more influenced by the Mg : K ratio in soil than by the base saturation levels of Mg, which suggests that K strongly inhibits the Mg uptake by plants. The results of this study indicate that K can significantly reduce the Mg uptake, even in soils abundant in available Mg. For this reason, the exchangeable Mg : K ratio in soil and the percentage saturation of the CEC with those cations should be included in Mg fertilization recommendations.

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