CHAPTER 6

Soil-Climate-Plant Relationships in the Etiology of Grass Tetany

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INTRODUCTION

Hypomagnesemia is a metabolic disorder of ruminants not receiving adequate utilizable magnesium, either because of low Mg concentration in the forage or because of complicating factors affecting Mg availability. The disorder is more likely to affect cattle than sheep or goats and generally affects older, lactating animals. Magnesium deficiency may result in decreased milk or beef production (Grunes & Mayland, 1975; Grunes et al., 1970). An intensified hypomagnesemia, known as grass tetany, has caused a large number of cattle deaths in the temperate regions of the United States and other countries, resulting in losses of up to 3% in dairy or beef herds in a bad year (Baker & Gould, 1976; Grunes et al., 1970; Mansfield et al., 1975; Molloy, 1971). In some individual herds in some years losses have been even higher. Reid et al. (1978a) estimated annual losses in the United States at 1 to 2% of mature grazing animals. The severity of the problem is quite sporadic.

Many factors affect Mg uptake by plants and its subsequent availability to animals. It is our objective to discuss the soil, climate, and plant factors that may ultimately affect Mg intake and availability to ruminants.

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SOIL FACTORS

Estimating Soil Magnesium Availability

Some success has been achieved in mapping geographical or soil resource areas that generally have low soil Mg values (Beeson, 1959; Jones, 1972). Stout et al. (1977) mapped out geographical areas in which forage Mg was generally low and grass tetany was frequently a hazard. However, present knowledge does not permit us to consistently predict the grass tetany hazard from soil, climate, and forage quality information. Research efforts in modeling this complex system are needed.

Metson (1974) reported that exchangeable soil Mg should be at least 10% of the cation exchange capacity and that the ratio Mg/K (exchangeable) should be at least 0.5 for good plant growth. He concluded, however, that seasonal variations in temperature and moisture reduce our ability to use these rules of thumb in predicting Mg availability to plants.

Salmon (1964) reported that for a constant level of exchangeable soil potassium, the Mg concentration in grass was doubled only when the exchangeable soil Mg was quadrupled. With increasing exchangeable soil K, Mg concentration in the grass decreased. McNaught et al. (1973b) reported that only 46 to 61% of the variation in forage Mg levels could be accounted for by the logarithmic value of soil solution Mg, and it was generally a less satisfactory indicator of Mg availability than was the Mg activity ratio. They found that a significant portion of the variation in Mg concentration in perennial ryegrass (*Lolium perenne* L.) tissue could be attributed to the soil K concentration. Alston's (1972) review provides the same conclusions.

Metson and Brooks (1975) studied the distribution of exchangeable and "reserve" Mg (a hot acid extraction) in the main soil groups in New Zealand. The same research group (Kidson et al., 1975) studied Mg uptake by white clover (*Trifolium repens* L.) grown in the greenhouse. They found that dry matter Mg concentrations, total dry matter yield, and residual exchangeable soil Mg were all significantly correlated with the initial exchangeable Mg, but not with "reserve" Mg.

Several British papers concerned with soil and fertilizer K and Mg are contained in two technical bulletins (Davies, 1971; Dermott & Eagle, 1967). Some other reviews dealing with soil Mg are by Baker (1972), Beckett (1972), Doll and Lucas (1973), Nelson and Jones (1972), and Reid and Jung (1974). Other papers of interest are those of Baker (1971, 1973), who considered theoretical relationships in an attempt to develop extractants that would indicate the available K and Mg in the soil.

Magnesium Fertilization

In general, Mg fertilization has been most effective in increasing Mg concentrations in plants grown on acid, coarse-textured soil (Birch & Wolton, 1961; Grunes, 1973; Grunes et al., 1970). The example shown in

Table 1 illustrates that forage Mg concentrations were increased when a pH 5.4 loamy sand was fertilized with $MgSO_4$. On moderate- to fine-textured soils, or neutral to alkaline soils, very high Mg fertilizer rates may be required to increase forage Mg concentrations sufficiently to prevent grass tetany. This was illustrated by Mayland and Grunes (1974a) in Nevada, where 600 kg Mg/ha as $MgSO_4 \cdot 7H_2O$ were required to appreciably increase Mg concentrations in crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult] grown on calcareous loam soils (pH 7 to 8, ratio of exchangeable Mg/K >0.8). The Mg fertilization had much less effect on Mg concentrations in the plants the second, third, and fourth years after fertilization than in the first year.

Gross and Jung (1978) measured significant increases in forage Mg levels of fertilized (672 kg Mg/ha as $MgSO_4$) compared to unfertilized grass and legume tissue. Their study was conducted over 14 months in the greenhouse on a Hagerstown silt loam with pH 6.4.

McNaught et al. (1973a), in a 5-year New Zealand experiment on a weakly acid loam of medium Mg status, compared several rates of finely ground dolomite, serpentine, talc-magnesite, and calcined magnesite (MgO) as Mg fertilizer sources. Overall, MgO increased forage Mg concentrations more than did dolomite. The MgO had its maximum effect on forage Mg in the first cutting after application, but dolomite required from about 6 months at the lowest rate to 18 months at the highest rate (440 kg Mg/ha) to achieve maximum effects. Ground serpentine and talc-magnesite had relatively small effects on forage Mg levels.

Hogg and Dorofaeff (1976), in a New Zealand study, found that residual Mg effects were smaller from serpentine than from dolomite treatments. Over the 6-year period, only 29 to 61% of the surface-applied Mg was accounted for in the forage plus the increase in soil-exchangeable Mg in the 0- to 22.5-cm depth. These authors, therefore, suggested high leaching losses of the added fertilizer Mg.

McNaught et al. (1973b), in another extensive New Zealand field study, found MgO gave greater increases than other Mg sources at comparable rates. Finely ground dolomite produced maximum effects between 4 and 9 months after application on pumice-derived soils and between 10 and 14 months on other soils. McIntosh et al. (1973b) reported that forage Mg concentrations were increased most by fertilizing with

Table 1. Effect of Mg and K fertilization on the mean January-February N and mineral composition of rye (*Secale cereale* L.) forage grown on a pH 5.4 loamy sand at Tifton, Ga. (adapted from Lowrey & Grunes, 1968)†

Fertilizer treatment	N	Mg	Ca	K	K/(Ca+Mg)
	%				
NP	4.5	0.16	0.45	3.9	2.8
NPK	4.5	0.13	0.39	4.5	3.8
NPKMg	4.3	0.18	0.33	4.6	3.7

† Fertilizer rates (kg/ha) were 140 N as NH_4NO_3, 25 P as superphosphate, 121 K as KCl, and 72 Mg as $MgSO_4$.

$MgSO_4$, less by calcined-magnesite, less yet by magnesium ammonium phosphate, and least by magnesian limestone. They found that the Mg concentration in the grass-clover forage mixture increased with increase in the rate of applied Mg.

Many different Mg sources are available. Metson (1974) grouped the available Mg sources into two categories based on their solubilities.

Slightly soluble forms		
Dolomite	$MgCO_3 \cdot CaCO_3$	10% Mg
Dolomite (selectively calcined)	$MgO \cdot CaCO_3$	16% Mg
Dolomite (hydrated)	$MgO \cdot Ca(OH)_2$	17% Mg
Magnesite	$MgCO_3$	26% Mg
Brucite	$Mg(OH)_2$	36% Mg
Magnesium oxide (calcined magnesite)	MgO	56% Mg
Very soluble forms		
Kieserite	$MgSO_4 \cdot H_2O$	16% Mg
Epsom salts	$MgSO_4 \cdot 7H_2O$	9% Mg
Kainite	$MgSO_4 \cdot KCl \cdot 3H_2O$	7% Mg
Langbeinite	$2MgSO_4 \cdot K_2SO_4$	11% Mg
Soluble forms not considered by Metson (1974)		
Bischifite	$MgCl_2 \cdot 6H_2O$	12% Mg

Soil Calcium and pH

Calcium may be expected to interfere with Mg uptake in a way similar to K, since Mg, Ca, and K would be competing ions in cation exchange reactions (Metson, 1974). Horvath and Todd (1968) recommended that the ratio Ca/Mg (exchangeable) not exceed 5, if Mg deficiencies in plants were to be avoided.

Fine and Shannon (1976) measured the growth and mineral composition of sudangrass [*Sorghum sudanese* (Piper) Stapf] grown on a slightly calcareous Haverson soil in the greenhouse. Magnesium and K were added to soils initially containing as much as 30, 1.4, and 4.6 meq/100 g extractable Ca, Mg, and K, respectively. The Mg concentration of plants grown on untreated soil ranged from 0.13 to 0.20%. Soil K additions increased Ca and Mg values, whereas Mg additions depressed Ca and K values. These researchers suggested a Ca/Mg/K ratio of 10:1:1 for increasing forage Mg.

Christenson et al. (1973) reported that soil pH seemed to affect Mg uptake by oats (*Avena sativa* L. 'Garry') more than did the soil Ca level. Metson (1974) concluded that the probability of Mg deficiency at relatively low exchangeable Mg values is higher at high pH (>7.0) and at high base saturation (>90%) than at a lower pH or lower base saturation. He further concluded that exchangeable Ca/Mg ratios were rather unreliable indexes of soil Mg availability.

Morgan and Jackson (1976) evaluated the effect of Ca on Mg uptake by using double-labelling (^{45}Ca or ^{28}Mg) procedures with 30-day-old intact ryegrass plants grown in nutrient solutions. The presence of solution

Ca suppressed Mg accumulation in roots and Mg translocation to shoots, apparently by blocking or altering the cell wall sites where Mg is absorbed.

Aluminum

Exchangeable or soluble Al may be involved in the etiology of grass tetany by reducing Mg uptake by plants relative to uptake of other minerals, or by interfering with Mg absorption in the animal. The latter will be discussed in a later section.

Soil Al concentrations may range from 2 to 7% (Brady, 1974). Most of the soil-derived Al is either amorphous or an integral part of the crystalline structure of the soil particle and would not be expected to become available as Al^{+++} except under conditions of high strong acidity or strong base attack.

Plants grown on highly acid soils, like some mine spoils or soils fertilized with acid-forming N sources (NH_4-N), may have high concentrations of Fe and Al in their tops. At pH 3.5, Al and Fe concentrations may be in the hundreds or thousands parts per million, depending on species and cultivar. Foy and co-workers (1974) found that Al-tolerant wheat (*Triticum aestivum* L.) contained up to 140 ppm Al in tops, whereas Al-sensitive wheat cultivars contained up to 220 ppm Al in tops when grown in soils having pH 4.4 and 3.5 meq Al/100 g (KCl extractable). Liming reduced Al uptake and concentrations in tops.

Clark (1977) found concentrations of 0.35, 0.22, 0.18, 0.21, and 0.15% Mg in Al-tolerant B57 corn, but only 0.25, 0.14, 0.11, 0.08, and 0.06% Mg in the Al-intolerant Oh40B line when grown for 17 days in full-strength nutrient solution containing 0, 2.5, 5, 10, or 20 mg Al/liter, respectively, as Al $K(SO_4)_2$. Even though Al inhibited the uptake of all elements, Mg concentration decreased more than that of others as solution Al increased. The selection of Al-tolerant forages may coincide with the selection of Mg-efficient forages.

Similar findings are reported by C. D. Foy (USDA-SEA-AR, Plant Stress Laboratory, personal communication). Large decreases in wheat tissue Mg occurred when Al was added to the nutrient solution (Fig. 1) even though pH was daily adjusted to pH 4.5. The Mg concentration was reduced more dramatically in the Al-intolerant 'Sonora' than in the Al-tolerant BH 1146 cultivar. Tissue K levels were not different between the 0 and 3 ppm Al treatments, whereas the Ca levels in the 3 ppm Al treatment were about 65% those in the control. Since solution Al suppressed Mg more than K and Ca levels, K/(Ca + Mg) levels tended to increase with increases in solution Al. The Al-tolerant wheat (BH 1146) and corn (*Zea mays* L.) (B57) had lower K/(Ca + Mg) values than did their Al-intolerant counterparts (Sonora and Oh40B).

Fleming et al. (1974) found that lovegrass [*Eragrostis curvula* (Schrad.) Nees.] was quite tolerant of solution Al concentrations up to 4 ppm Al. Furthermore, forage mineral concentrations were not greatly

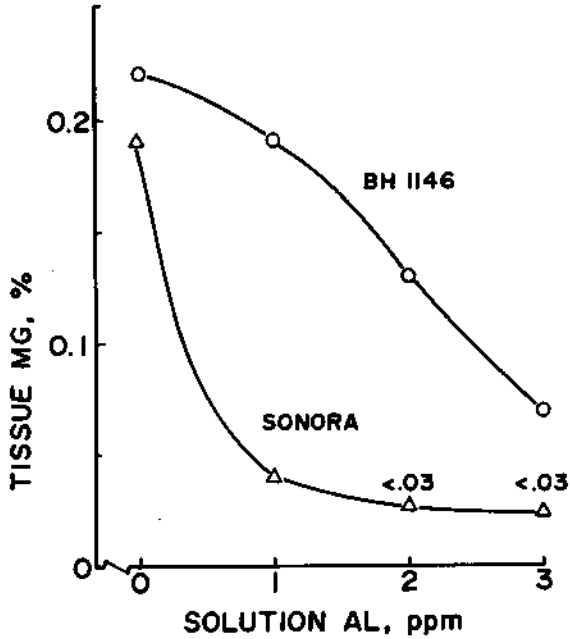

Fig. 1. Tissue Mg concentrations in an Al-tolerant (BH-1146) and an Al-intolerant (Sonora) wheat (*Triticum aestivum* L.) cultivar grown in nutrient culture containing various Al levels. Solution pH was adjusted daily to 4.5 (C. D. Foy, USDA-SEA-AR, Plant Stress Laboratory, Beltsville, Md., personal communication).

different when grown with 0 or 4 ppm Al in the nutrient solution (initial pH 4.6). Tall fescue (*Festuca arundinacea* Schreb.) grown in the 4 ppm Al solution contained about 40% as much Ca, 25% as much Mg, and 130% as much K as when grown with 0 ppm Al. The lovegrass would be a more desirable species than tall fescue for acid soils because of its greater dry matter production and its more desirable mineral composition with respect to animal health.

Liming

Long-term effects of liming practices may be related to the incidence of grass tetany through effects of liming sources, application rates, and subsequent soil pH. A high Ca limestone is often preferred because of its greater solubility as compared with dolomite (Gross, 1973). The continued use of calcitic limestone will provide added Ca, but not Mg, eventually resulting in little plant-available soil Mg and also a large Ca/Mg ratio that reduces the plant's ability to absorb Mg.

Amos et al. (1975) showed that on fine-textured soils dolomitic limestone increased Mg concentrations more than did calcitic limestone. Data

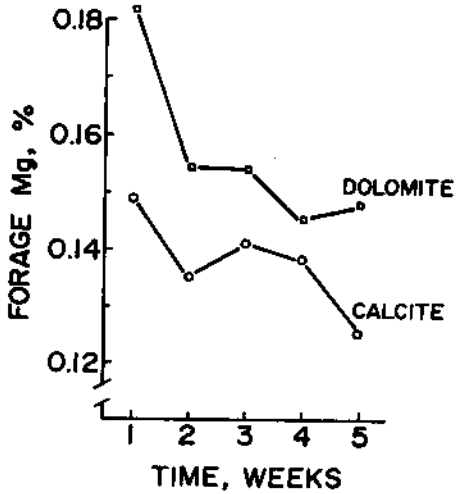

Fig. 2. Four-year mean forage Mg concentrations (5-week period beginning in late April) of orchardgrass (*Dactylis glomerata* L.) grown on two silt loam soils in West Virginia initially topdressed with either dolomite or calcite (adapted from Amos et al., 1975).

from their liming experiment with orchardgrass (*Dactylis glomerata* L.) are shown in Fig. 2. If dolomite is top dressed, however, its beneficial effect on forage Mg concentrations may not be observed for several years. Mixing dolomite into the root zone has sharply increased its effectiveness in increasing forage Mg levels (Reid & Jung, 1974). The application of dolomitic limestone to increase soil pH up to the 6.5 to 7.0 range will increase forage tissue Mg levels, but higher application rates that increase soil pH above 7.0 may result in depressed tissue Mg levels (Price & Moschler, 1970).

Soil Potassium Competition

High soil K levels or high K fertilizer rates increase forage K levels and, in some cases, decrease forage Mg (Fleming & Murphy, 1968). This antagonistic relationship between K and Mg is generally more pronounced at lower soil pH (Batey, 1967). Claassen and Barber (1977) found that the Mg influx into roots of young corn plants in nutrient culture solutions was much greater on the K-absent side than on the K-present side of a split root system.

Although the tolerance range is wide in the exchangeable soil K/Mg ratio, a value of 0.5 to 1 or less is advised (Horvath & Todd, 1968). Baker (1972) emphasized the need for maintaining an adequate soil $\sqrt{Mg}/K$ ratio to assure adequate Mg uptake by plants. The antagonism between K and Mg uptake is greater in grasses than in associated clovers (McNaught et al., 1973a). High Mg fertilizer rates will generally increase forage Mg,

but will not affect K concentrations (Dermott & Eagle, 1967). This one-way antagonism between K and Mg is discussed in the review by Metson (1974) and is shown in Table 1, where K fertilizer additions decrease forage Mg concentrations, but the Mg fertilizer application does not change forage K levels.

Exceptions to this one-way antagonism may occur, at least under greenhouse conditions. Roberts and Weaver (1974) grew sudangrass in a slightly calcareous Shano silt loam fertilized with several rates of K and Mg. Plant tissue Mg decreased following K application and increased with each increment of Mg. The Mg application lowered plant tissue K levels.

Nitrogen Fertilization

Nitrogen fertilizer is generally applied to increase dry matter forage yields. This fertilization may also increase forage Mg concentrations (Noller & Rhykerd, 1974), but here the N source plays a very important role. Grunes (1973) reviewed earlier work indicating that NH_4-N resulted in lower Mg concentrations in plants than did NO_3-N, unless nitrification could occur in the soil. In the absence of nitrification, soil NH_4-N accumulation may adversely affect Mg availability to the plant. Some of these effects have been reviewed by Grunes et al. (1970) and Molloy (1971).

Claassen and Wilcox (1974) showed that Mg concentrations were much lower in 33-day-old corn ('Bravo') plants when fertilized with

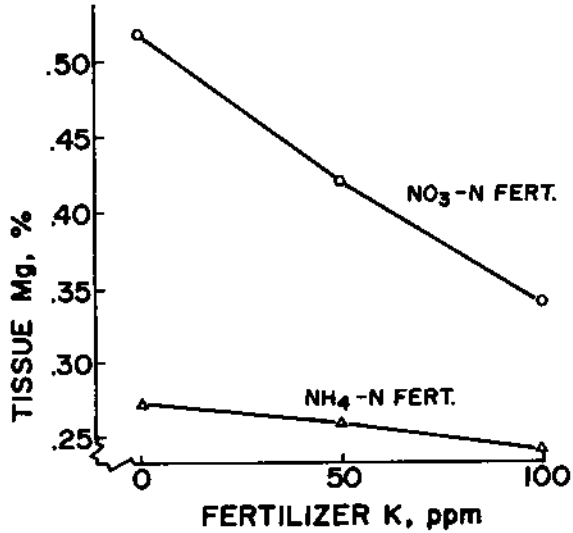

Fig. 3. Effect of N source and K rate on corn (*Zea mays* L. 'Bravo') tissue Mg levels: 100 ppm N added as $NaNO_3$ or $(NH_4)_2SO_4$, and K as KCl. Data are means of responses measured on a sand and a silt loam with pH = 6.3 and 6.8, K = 148 and 66 kg/ha, Ca = 650 and 3,600 kg/ha, and Mg = 67 and 800 kg/ha, respectively (adapted from Claassen & Wilcox, 1974).

Table 2. Effect of N form and K rate on growth and composition of 33-day old corn (*Zea mays* L.) plants on two soil types (adapted from Claassen & Wilcox, 1974)

Treatment			Composition			
Nitrogen form	K rate	Dry weight	N	K	Ca	Mg
	ppm	g	%			
		Princeton Sand				
NO_3	0	2.01	2.85	3.79	0.86	0.32
	50	2.24	2.69	4.51	0.79	0.27
	100	2.20	2.40	4.99	0.71	0.24
NH_4	0	1.00	2.91	2.98	0.67	0.20
	50	1.30	2.65	3.43	0.63	0.19
	100	1.89	2.80	3.66	0.69	0.18
L.S.D. $P=0.05$		0.574	NS	0.589	0.115	0.033
		Fincastle Silt Loam				
NO_3	0	2.38	2.38	1.83	0.78	0.71
	50	2.63	2.54	2.62	0.66	0.57
	100	3.28	2.49	3.48	0.62	0.44
NH_4	0	1.74	2.55	1.95	0.50	0.33
	50	2.60	2.32	2.54	0.45	0.33
	100	3.85	2.20	3.13	0.47	0.30
L.S.D. $P=0.05$		0.763	NS	0.682	0.123	0.070

$(NH_4)_2SO_4$ than in plants fertilized with $NaNO_3$ (Fig. 3). The difference in forage Mg concentrations between the two N sources diminished at higher soil K levels. The effect of the N source was greater on the high Mg silt loam than on the low Mg sand (Table 2). The effects of N source and KCl on Ca concentrations in the corn plants were generally similar to the effects on Mg concentrations, although the magnitudes of these effects were much less. The antagonism of both NH_4-N and K to Mg absorption is nicely shown by the data of MacLeod and Carson (1966) as adapted in Fig. 4.

The effect of the N source should be very real under field conditions where NH_4-N fertilizer is applied during late fall or very early spring to soils low in NO_3-N and soil temperatures have not warmed to allow for nitrification. Wilcox and Hoff (1974) hypothesized that a principal cause of grass tetany could be high NH_4-N concentrations in the soil during early spring. They suggested that winter leaching of NO_3-N and lack of nitrification of added NH_4-N would result in a predominance of NH_4-N in the soil solution. This NH_4-N could decrease forage Mg concentrations and have indirect effects that might reduce Mg availability to ruminants.

Cox and Reisenauer (1977) measured the effect of NH_4-N and Mg concentrations in the rooting media on Mg absorption rate by 'INIA' wheat in solution culture containing 200 μM NO_3-N. They found that Mg absorption rates decreased with increasing root-media NH_4-N concentrations (Fig. 5). The Mg absorption rate increased at higher root-media Mg concentrations. Thus, a very definite antagonism exists between NH_4-N and Mg absorption.

That this antagonism is truly a N source phenomenon is further illustrated in Fig. 6. Here, Cox and Reisenauer (1973) measured Mg concen-

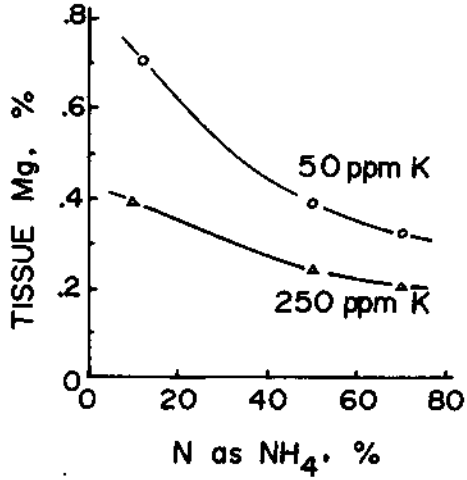

Fig. 4. Effect of N source at two K rates on the mean-tissue Mg concentration for three grasses in early vegetative stage [bromegrass (*Bromus inermis* L.), orchardgrass (*Dactylis glomerata* L.), and timothy (*Phleum pratense* 'Climax')] grown in a greenhouse sand culture: 250 ppm NO_3^- + NH_4^+ − N in all pots (adapted from MacLeod & Carson, 1966).

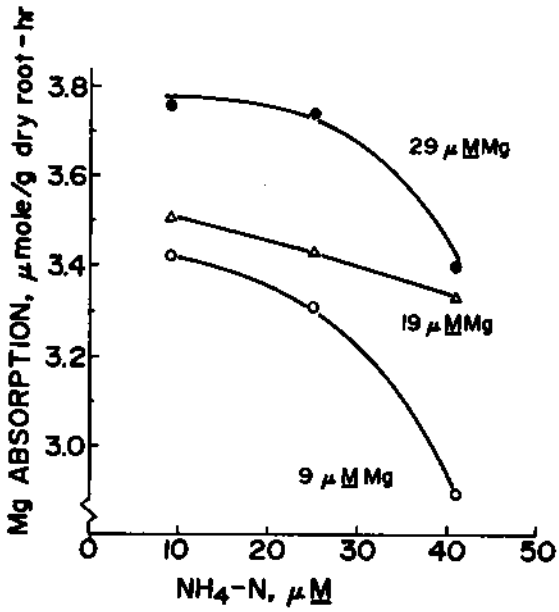

Fig. 5. Effect of NH_4-N and Mg concentration in the root medium on Mg adsorption rate by wheat (*Triticum aestivum* L. 'INIA'). All solutions contained 200 μM NO_3-N (adapted from Cox & Reisenauer, 1977).

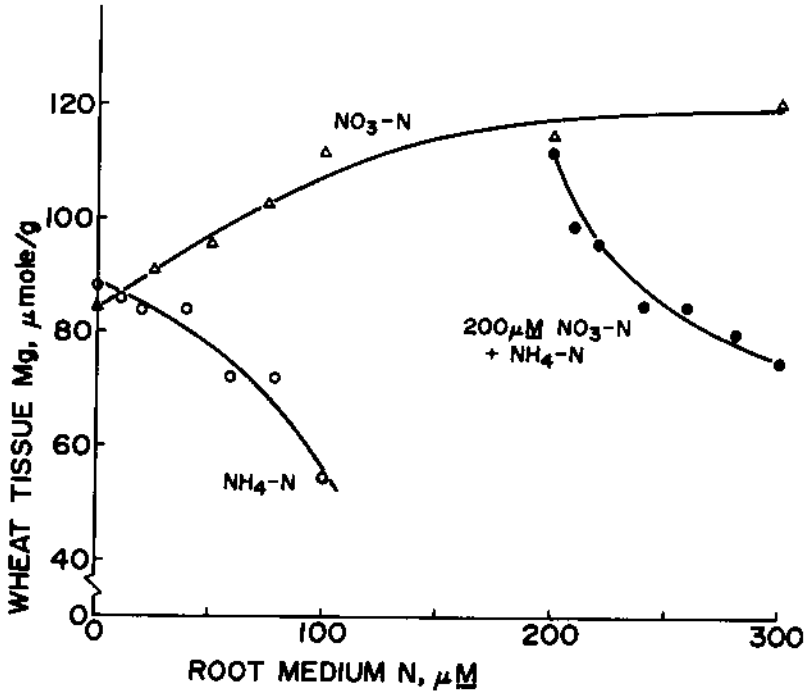

Fig. 6. Effect of N source and concentration on Mg concentration in wheat (*Triticum aestivum* L. 'INIA') tissue (adapted from Cox & Reisenauer, 1973).

trations in wheat tissue grown in rooting medium with various N rates and sources. Wheat tissue Mg concentration increased as root media NO_3-N increased even up to 300 μM concentration. However, wheat tissue Mg concentrations decreased with increasing concentrations of NH_4-N. This direct antagonism by NH_4-N is also evidenced in the presence of 200 μM NO_3-N (Fig. 6).

Nielsen and Cunningham (1964) found that Mg concentrations, like those of Ca, in Italian ryegrass (*Lolium multiflorum* Lam.) S22 were larger when the grass had been fertilized with NO_3-N than when fertilized with NH_4-N. Forage Mg concentrations tended to increase with root zone temperature over the 11 to 28°C range when the NO_3-N was used, but little change was noted when the NH_4-N was used.

Mayland and Grunes (1974a) found that fertilizing a semiarid calcareous soil with 150 kg N/ha as NH_4NO_3 increased Mg concentrations in crested wheatgrass as much as did 200 kg Mg/ha added as $MgSO_4 \cdot 7H_2O$. Forage Ca and K were also increased by NH_4NO_3 fertilization (Mayland et al., 1975b). However, in a field experiment with cool season bromegrass (*Bromus inermis* Leyss.) in North Dakota, NH_4NO_3 fertilization markedly increased K concentrations in the plants, but had little consistent effect on Mg or Ca concentrations (Follett et al., 1975).

Barta et al. (1973) reported that in Ohio the average N, K, and Mg concentrations of three grasses were respectively increased from 2.25 to 3.54%, 2.07 to 2.60%, and 0.15 to 0.19% when 112 kg N/ha were applied. Reid et al. (1974) in West Virginia also found that N fertilization (NH_4NO_3) significantly increased forage N and Mg concentrations, but there were no significant effects on the K and Ca levels. These results suggest that N probably increases the ability of the plant's root system to take up Mg, and in some cases other cations, from the soil and thus increase the concentration in the plant. Barta (1973) found that 112 kg N/ha as NH_4NO_3 increased forage K from 2.33% in the control to 2.66% in the N-fertilized orchardgrass and bromegrass. Information was not provided on forage Ca and Mg concentrations. Apparently additional research is needed on N sources, soil Mg, and K levels, and plant species effects on the comparative concentrations of Mg and K in plants in relation to the grass tetany problem.

Wilkinson et al. (1972) indicated that fertilization of tall fescue (*Festuca arundinacea* Schreb. 'Kentucky-31') with NH_4NO_3 resulted in a loss of acid-extractable Mg from the top 15 cm of soil. The amount lost was much more than could be accounted for by forage Mg removal. They reviewed other research indicating that N fertilization increased leaching of both Mg and Ca in the soil. Leaching losses of Mg do occur, but appear more variable (Metson, 1974) than plant uptake. Factors contributing to this variability include soil texture, extent of drainage, amount of Mg present, and quantity and quality of irrigation water or rainfall.

As indicated earlier, Cox and Reisenauer (1977) grew wheat in dilute nutrient solutions in a greenhouse with three NH_4 levels and four levels of either K, Ca, Mg, manganese, or zinc. Ammonium-N reduced plant uptake of divalent cations more than the uptake of monovalent cations. Among the divalent cations, the magnitude of the NH_4-N effect varied in the order: Zn > Mn ≥ Mg > Ca. The reduced influx of multivalent cations when NH_4-N is added is postulated to result from the NH_4^+-induced reduction in slowly diffusible organic anion concentrations within the root. This results in a smaller chelate sink, increased internal cation activity, and reduced net influx of metal cations. In another nutrient solution experiment (Cox & Reisenauer, 1973), wheat growth was 100, 92, and 154% of that of the control for NO_3^-, NH_4-N, and NH_4 + NO_3-N sources, respectively. Wheat grown with NO_3-N took up more Ca, Mg, and K than did wheat grown on the NH_4-N source. Since rooting medium pH was controlled, the differential growth and yield response of the NO_3 compared with the NH_4 + NO_3-N sources is suggested to result from "the reduced energy requirement for utilization of ammonium, as compared to nitrate in protein synthesis."

CLIMATE FACTORS

Grass tetany generally occurs during cool weather, and more frequently in spring than in autumn (Kemp & 't Hart, 1957). The incidence of grass tetany has also been higher in years with a sudden, quick growth

of grass in the spring than in years with slower growth. Tetany occurs more frequently when moisture is adequate for growth.

Aside from the soil-plant aspects, it has been noted by Sykes et al. (1969) that exposing sheep to temperatures of 8°C compared to 30°C resulted in a 12% reduction in blood plasma Mg levels but no change in Ca, Na, or K levels. Exposure to acute cold (−20°C and 4 mph wind) caused further reductions in blood plasma Mg and also reductions in Ca levels.

't Hart (1960) summarized the influence of meteorological conditions in relation to grass tetany. He stated that 95% of the tetany cases in the Netherlands occurred when the temperature was between 8 and 14°C. Grass tetany occurred only when soil moisture was ample and less frequently on very dry or very wet pastures. Grass tetany incidence also increased after a sudden rise in temperature and was higher in years when a flush of forage growth occurred.

Temperature Influences

Grunes (1967) and Grunes et al. (1968) presented data indicating that Mg and Ca concentrations in perennial ryegrass (Fig. 7) and 'Nordan' crested wheatgrass (Table 3) were higher when the grasses were grown at warm temperatures than when grown at cool temperatures. The ratios of K/(Ca+Mg) were lower at the higher temperatures, which may be one reason why cattle grazing grass or small grains forages grown for extended time at warmer temperatures do not develop grass tetany.

Sabbe et al. (1972) studied the K, Mg, and Ca accumulation in tall fescue grown on four soils (one receiving different Mg fertilizer rates) and

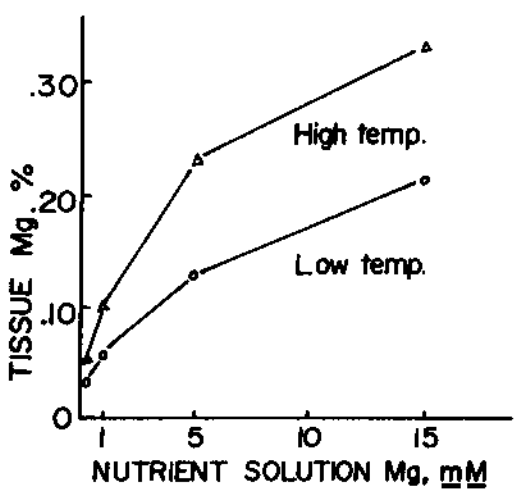

Fig. 7. Tissue Mg levels in perennial ryegrass (*Lolium perenne* L.) grown at 20°C day, 14°C night (low temp.), or 26°C day, 23°C night (high temp.) in sand culture containing 4 m*M* K and 4 Mg levels (adapted from Grunes et al., 1968).

Table 3. Tissue dry matter yield and mineral levels of Nordan crested wheatgrass [*Agropyron desertorum* (Fisch.) Schult] grown at 10 or 20°C in sand culture containing two Mg levels (from Grunes, 1967)

Temperature	Nutrient solution Mg	Yield	Mg	Ca	K	K/(Ca+Mg)
°C	m*M*	g	%			Eq. basis
10	0.03	4.2	0.04	0.42	3.0	3.2
10	4.00	8.6	0.21	0.24	3.3	2.9
20	0.03	5.1	0.07	0.65	4.4	2.9
20	4.00	7.2	0.52	0.50	4.8	1.8

at three successive 2-week temperature regimes (day/night temperatures of 13/7, 18/13, and 24/18°C). They found that the forage Mg levels decreased with each successive increase in temperature regardless of soil type or Mg fertilizer treatment. These temperature effects contrast with those of Grunes et al. (1968), but may have resulted from increased dry matter production (data not given) and increased K uptake at the successively higher temperature regimes. The K levels of the third-harvest material were twice those of the first-harvest material (8.6 vs. 4.5% K).

Leggett et al. (1977) measured a nearly 50% reduction in tall fescue dry matter production when grown at a 28°C air temperature in a hydroponic solution, but when root temperature was maintained at about 12 compared to 25°C. Plant tissue contained >4.6, >0.42, and >0.38% of K, Ca, and Mg, respectively. Tissue mineral concentrations were not different between root temperature treatments, possibly as a result of the high solution concentrations: 3.7, 3.7, and 2 m*M* of K, Ca, and Mg, respectively. Thus, high nutrient concentrations may dampen the temperature effects observed at low concentrations, but more work is needed to verify this.

Stuart et al. (1973) measured the change in crested wheatgrass mineral composition grown on a semiarid Nevada rangeland. When the air temperature increased, blade length and K concentrations increased markedly, the Mg concentration remained essentially unchanged, and the Ca concentration decreased. Therefore the K/(Ca+Mg) values increased markedly when the temperature increased. This may partially explain the high incidence of tetany which occurs immediately after temperature increases and small grain and grass forage begins rapid growth.

The chemical composition of diammonium phosphate-fertilized crested wheatgrass was significantly changed when the temperature and light intensity of the environmental chamber were increased (Stuart et al., 1973). Forage K and *trans*-aconitic acid concentrations increased, while Ca concentrations decreased markedly and Mg concentrations decreased slightly. As a result, the K/(Ca+Mg) values also increased markedly.

The mineral composition of crested wheatgrass (Mayland et al., 1975b) and 'Lincoln' cool-season bromegrass (Follett et al., 1975) adjusted in four to five days as air temperature was increased and grasses began rapid growth. The K concentration increased appreciably, while at the

same time Ca concentrations decreased markedly and the Mg concentrations decreased slightly. Thus, the K/(Ca+Mg) values increased appreciably.

't Hart and Kemp (summarized by Kemp & 't Hart, 1957 and by Wind, 1958) found a significant correlation between the occurrence of grass tetany in the Netherlands and the mean 24-hour air temperature. Grass tetany occurred only in spring and autumn as long as the daily air temperature, averaged over five days, was below approximately 14°C. They reported a five-day time lag between changes in temperature and changes in the frequency of grass tetany cases. The four- to five-day lag is also supported by the studies of Brougham and Glenday (1969), who reported marked differences in seasonal growth rates. These were attributed to seasonal changes in temperature, light, and rainfall such that a four-day time lag for some weather factors was significantly correlated with plant growth rate.

Some forages, like tall fescue, continue growth into the summer (Hannaway & Reynolds, 1976; Wilkinson et al., 1972, 1971). In these forages, the Mg concentration, and sometimes the Ca, are higher during the summer without a corresponding increase in K concentration. Values of K/(Ca+Mg) are not as high as they are earlier in the growing season. Wilkinson et al., 1972, 1971) reported that the most critical time for grass tetany in north Georgia is in February and March. Mayland et al. (1974) noted that, in Utah, Nevada, and Idaho, tetany usually occurred in April or May at a time when both forage yield and dry matter content were low. Concentrations of Mg and Ca were low while K, N, and the K/(Ca+Mg) values were high.

Light Intensity Effects

Mayland and Grunes (1974b) indicated that reduced solar radiation may be a factor in the grass tetany etiology. The incidence of grass tetany in cattle in Idaho, Nevada, and Utah was greater when daily radiation levels were low during April. Daily radiation levels averaged 18.3 MJm^{-2} day^{-1}, 22.8 MJm^{-2} day^{-1}, and 23.1 MJm^{-2} day^{-1} during April 1967, 1968, and 1969, respectively. The incidence of grass tetany for those respective years was severe, light, and near zero in the three-state area. They concluded that in this semiarid region the low mean radiation levels were associated with cloudy conditions leading to greater precipitation and more rapid growth of forage.

Mayland and Grunes (1974b) also studied the effect of shading on the chemical composition of Nordan crested wheatgrass and basin wildrye (*Elymus cinereus* Scribn. & Merr.) (Table 4). While shaded forage had higher Mg and Ca concentrations, it also contained higher concentrations of K, total N, organic acids, and higher fatty acids. Shading also reduced the concentration of total water-soluble carbohydrates. For one grass species, the percentage dry matter was also lower. The overall shading effect would likely reduce forage Mg availability.

Table 4. Effect of shading on mean chemical composition of Nordan crested wheatgrass [*Agropyron desertorum* (Fisch.) Schult] and basin wildrye (*Elymus cinereus* Scribn. and Merr.) grass (from Mayland & Grunes, 1974b)†

Component	Nordan crested wheatgrass		Basin wildrye grass	
	R_{100}	R_{25}	R_{100}	R_{25}
K (%)	1.9	2.3*	3.0	3.5*
Mg (%)	0.12	0.15*	0.11	0.18**
Ca (%)	0.42	0.62*	0.29	0.46**
K/(Ca+Mg) (meq basis)	1.6	1.4**	3.3	2.4**
Total N (%)	4.0	5.1**	3.9	5.1**
TWSC (%)	20.0	15.0	15.0	11.0
N:TWSC	0.21	0.36**	0.29	0.53*
C-A (meq/kg)	550.0	660.0*	570.0	640.0*
Aconitic acid (meq/kg)	270.0	320.0	420.0	490.0**
Higher fatty acids (meq/kg)	96.0	130.0*	95.0	110.0*
Dry matter (%)	34.5	33.1	29.5	23.7**
Height (cm)	28.0	15.0**	21.0	18.0*

† R_{100} and R_{25} are full sunlight and 25% full sunlight, respectively. TWSC = total water soluble carbohydrates. Paired *t*-test at $P \leq 0.05$ (*) and $P \leq 0.01$ (**) compares effect of shade with that of full sunlight.

Hight et al. (1968) reported that shading (22% of full sunlight) perennial ryegrass for 2 to 3 days prior to ingestion by sheep significantly reduced dry matter intake and soluble carbohydrate concentrations and increased the proportion of cellulose and lignin in the shaded material, thereby reducing forage digestibility.

Seasonal Changes

Forage mineral concentrations may be related to stage of growth, which is seasonally dependent. Murray et al. (1978) found that the K and K/(Ca + Mg) values in seven semiarid grasses grown on calcareous soils decreased with increasing plant maturity. The Ca and Mg values also decreased in the early maturing species, but not in the later maturing species.

Contrasting results may be obtained under pasture conditions where soil moisture, temperature, and fertility allow vegetative growth throughout summer and fall. Fleming and Murphy (1968) evaluated the mineral concentration of perennial ryegrass (*Lolium perenne* 'Glasnevin'), timothy (*Phleum pratense*) S48, and tall fescue (*Festuca elatior* Kentucky-31) when grown on a moderately well-drained acid brown loam soil in Ireland. They found little change in Mg concentrations of plant tops as maturity progressed during the season. The Mg concentration of regrowth vegetative tissue, when clipped at biweekly intervals, increased in the April through the September cuttings and thereafter declined. Monthly applications of 36 kg N/ha and plentiful soil moisture allowed good growth and the fertilizer N may have enhanced Mg uptake in the regrowth.

Jones (1963) studied the Mg concentration of a clover-grass mixture grown at Aberystwyth (in Wales of England) on a pH 5.5 freely drained loam. The forage was clipped at intervals allowing a 10-cm growth during the March to October growing season. The Mg concentrations in the regrowth of S22 Italian ryegrass (*Lolium multiflorum* Lam.) and S36 cocksfoot (*Dactylis glomerata* L.) were lowest in the spring and increased to maximum values by autumn. Reid et al. (1970) reported a linear decrease in the Mg and Ca concentrations in the first growth of legumes and especially grasses as plants matured. The regrowth of grasses following clipping contained higher levels of Mg and Ca than did earlier growth. Under these and earlier described conditions, it appears that the early spring growth might contain greater Mg concentrations than the more mature stages of the same plant. On the other hand, clipping and grazing forces the plant into a vegetative growth form with its accompanying higher Mg demand and uptake at a time when soil temperatures are increasing and soil Mg and Ca can move more rapidly into the plant.

Seasonal changes in forage Mg levels may be far greater than changes induced by fertilizer application (McNaught et al., 1968). While seasonal differences in K levels were much smaller than changes in Mg values, it does appear that the maximum or minimum K levels were usually out of phase with Mg levels for times ranging from a few weeks to several months. Thus, the seasonal changes in forage Mg levels may be associated with factors other than just K, and the Mg levels likely are more strongly affected by climatic changes, including seasonal changes in the levels and forms of N taken up by the forage species.

When soil temperatures are above about 7°C, NH_4-N from mineralization of organic N sources is rapidly converted to NO_3-N and taken up in that form by grasses (Frederick, 1956). At lower temperatures, the process tends to stop at the NH_4-N stage and N may be absorbed in that form. Results under simulated spring soil temperature conditions indicate that low temperatures probably restrict the nitrifying bacteria more than the ammonifying bacteria, with a subsequent buildup of NH_4 (Campbell et al., 1971). A temporary accumulation of NH_4 is also observed under simulated autumn conditions. More nitrification—oxidation of NH_4 to NO_3—occurs under autumn- than spring-simulated conditions, indicating that the freezing pretreatment is at least partially responsible for subsequent destruction of nitrifiers by fluctuating low, but not freezing, temperatures.

It is well established that NH_4-N depresses Mg absorption, whereas NO_3-N aids the Mg uptake by plants. Calcium is affected similarly. Minimum Mg and Ca levels can, therefore, be expected in late winter and early spring, and perhaps again for a short period in the autumn when air temperatures may be conducive to forage growth but low temperatures have minimized nitrification.

Apparently, low temperature increases the animal's Mg requirement (Sykes et al., 1969). Also, adverse weather may reduce grazing time and forage intake. The combination of lower intake and higher maintenance requirements contributes to an increased grass tetany hazard.

Soil Oxygen Influences

Elkins et al. (1977) and Elkins and Hoveland (1977) have studied the effect of various soil-air O_2 levels on Ca, Mg, and K concentrations in various forages. Increasing soil O_2 levels from 2 to 21% had little effect on Ca and Mg concentrations in rye (*Secale cereale* L.), but increased K concentration from 2 up to 5% (Fig. 8), resulting in K/(Ca+Mg) values that exceeded 4 (Elkins & Hoveland, 1977). The Ca, Mg, and K concentrations in perennial ryegrass forage were increased as soil oxygen levels were increased from a level of 2 up to 21%. The K/(Ca+Mg) values were not changed over this soil oxygen range. These authors therefore concluded that perennial ryegrass forage grown on poorly drained soil would probably be more tetanigenic than that on well-drained soil. However, rye forage would be more tetanigenic when grown on well-drained soil.

Elkins et al. (1977) reported that at low soil O_2 levels forage Mg concentrations in ryegrass and tall fescue were potentially tetanigenic. The low Mg concentration (<0.2%) of tall fescue forage was closely related to poor soil drainage under pasture conditions. They screened 216 tall fescue genotypes at both low (2%) and high (21%) soil O_2 levels for their ability to accumulate Mg. They reported the Mg concentration in three of these genotypes (Table 5). Genotype #96 was from Kentucky-31, and genotypes #21 and #81 were two Auburn selections from a Moroccan tall fescue introduction, PI-231560. Genotypes #96 and #21 could produce forage high in Mg concentration under low soil O_2 levels. The low Mg forage concentration in genotype #81 under the low soil O_2 regime would be considered tetanigenic.

Soil Water Effects on Mineral Uptake

Elkins et al. (1977) further tested the effect of low soil O_2 on Mg accumulation in tall fescue by sampling forage from replicated caged plots in pasture areas that were well or poorly drained. Mg concentration in forage from the well-drained soil was significantly higher ($P < 0.05$) than that from the poorly drained soil. The authors noted that O_2 levels were lower in the poorly drained soil than in the other, but did not specify the soil Mg status of the two sites. Karlen et al. (1977)[1] also reported that Mg and Ca concentrations in wheat tissue were decreased and K concentrations increased when soil was maintained at 125% of field capacity, as compared to 60%. They concluded that the differential change in tissue cation composition under wet soil conditions could be explained by the dilution and valency aspects of the Donnan equilibrium theory (Marshall, 1964, 1977).

[1] Karlen, D. L., R. Ellis, Jr., D. A. Whitney, and D. L. Grunes. 1977. Influence of soil moisture on cation uptake by wheat with respect to grass tetany. Agron. Abstr. Am. Soc. Agron., Madison, Wis. p. 160.

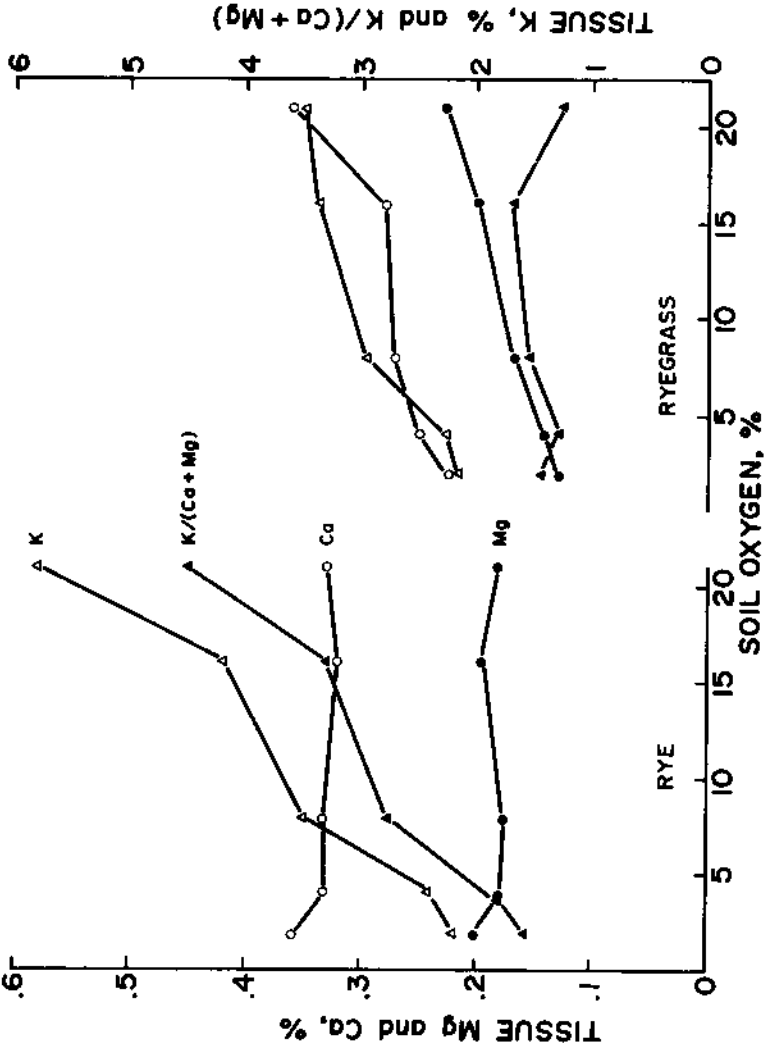

Fig. 8. Tissue K, Ca, Mg, and K/(Ca+Mg) equivalent ratio for rye (*Secale cereale* L.) and ryegrass (*Lolium multiflorum* Lam.) grown at 22°C day and 12°C night temperatures as affected by soil oxygen level (adapted from Elkins & Hoveland, 1977).

Table 5. Magnesium concentration in three tall fescue genotypes (*Festuca arundinacea* Schreb.) at low and high soil oxygen levels (from Elkins et al., 1977)†

Tall fescue genotype	Forage Mg at soil O_2 levels of: 21%	2%
	%	
96	0.58_b	0.27_a
21	0.43_a	0.28_b
81	0.33_a	0.16_a

† Within column values not labeled with the same letter differ at the $P \leq 0.05$ (Duncan's MRT).

Oliver and Barber (1966) evaluated the mechanisms governing the supply of Ca, Mg, and K to soybean [*Glycine max* (L.) Merr.] roots. They found that root interception accounted for 12 to 14% of total Mg uptake, while mass flow supplied the remainder except at the low transpiration rate where some diffusion apparently occurred. At the medium and high transpiration rates, Mg apparently accumulated about the root as a result of mass flow. Root interception of Ca represented 14 to 19% of the uptake, while the remaining uptake was supplied by mass flow. The results for K are different from those for Mg and Ca in that 87 to 96% of the K reached the root by diffusion.

Brewster and Tinker (1970) reported that apparent mass flow of Ca and Mg is eightfold and twofold, respectively, of the inflow into leek (*Allium porrum* L. 'Musselburgh') roots and that depletion around the roots seems unlikely. Diffusion accounted for most of the K supply to the plant and apparent mass flow supplied only a small portion.

In a field study with bromegrass, Follett et al. (1977) found that much more Mg and Ca would be expected to move to plant roots by mass flow than was found in the tops. For plots not fertilized with N, P, or K, much of the K in the plant tops could be accounted for by mass flow. However, when the yields were appreciably increased by fertilization with N, P, and K, movement of K by mass flow was not sufficient to account for the K in the plant tops. Under these conditions, diffusion evidently was the primary mechanism moving K from the soil to the plant roots.

Since appreciably more Mg and Ca is supplied by mass flow than is taken up by the plant roots, it would not be expected that increasing the supply of soil water would appreciably increase the uptake of Mg and Ca by the plants. However, diffusion of K would be expected to be increased, since the mean path length for diffusion of K from the soil to plant roots would decrease as the amount of water in the soil increased. Therefore, unless the soil aeration was decreased to a critical level, one would expect appreciably greater uptake of K when moisture is adequate than when the soil is more dry.

PLANT FACTORS AFFECTING Mg AVAILABILITY TO ANIMALS

Forage Nitrogen

Kemp (1960) studied the response of serum Mg in lactating cows to changes in dietary forage composition resulting from K and N fertilization. High K application rates led to increased forage K concentration and reduced N, Mg, and Ca concentrations. The Mg reductions averaged 15 to 20% of the Mg in untreated forage. A high N application rate increased N, sodium, Ca, and Mg concentrations in the forage. High K and N application rates, whether applications were separate or combined, caused the blood serum Mg levels to fall. Significant negative correlations were found between the serum Mg and forage N concentrations, and between the serum Mg and forage K concentrations. This relationship ultimately led to the development of the curve shown in Fig. 9 and to the Dutch nomogram discussed later in this chapter.

Daniel et al. (1969) studied the mineral balance of lactating goats fed orchardgrass hay grown at low (56 kg N/ha) and high N (504 kg N/ha) fertilization with NH_4NO_3. The high N fertilization significantly increased apparent (feed minus feces) Ca availability, but apparent Mg availability was 34% on the low N treatment, 31% on the moderate N, and 12% on the high N fertilizer treatment. The high N rates depressed

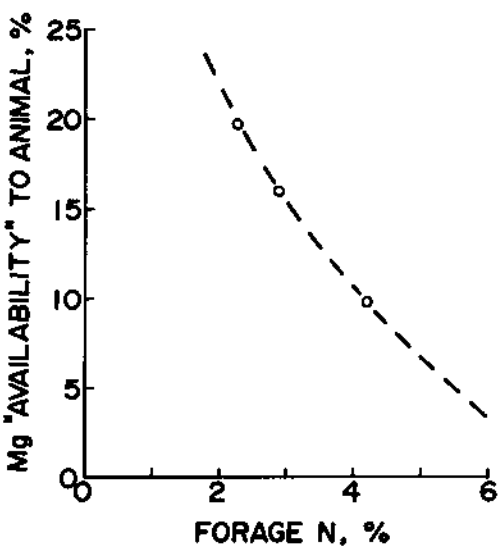

Fig. 9. Relationship between total forage N and Mg "availability" to cattle (from Kemp et al., 1961 and Metson et al., 1966).

apparent absorption and retention of Mg by the goats (Reid et al., 1974). Rook and Campling (1962), using metabolism trials, studied the Mg availability from fresh and cured grass, alfalfa (*Medicago sativa* L.), straw, and concentrates. Availability of Mg was highest from the concentrates and lowest, only 5%, from early cuttings of fresh grass.

Stillings et al. (1964) studied the Mg utilization by ruminants consuming low and high N-containing forages. They found that the apparent Mg availability from forage having 2.1 to 2.6% N ranged from 18 to 24%, while forage having 3.7 to 4.4% N had 11 to 16% apparent available Mg. Rosero et al. (1975) grew orchardgrass and a fescue-rye hybrid at 0 or 84 kg N/ha rates and then fed these at two maturity stages (April 23 and June 4 harvests) to sheep. Nitrogen fertilization lowered the Mg intake, percent Mg absorption ($P < 0.10$), and Mg balance ($P < 0.01$) in lambs. Animal retention of Mg was significantly less ($P < 0.01$) for the early harvested than for the late-harvested forage. There was no significant difference in the Mg balance between animals fed the two forages. The evidence presents a strong case for reduced Mg availability in the early vegetative growth stage compared to more mature grass.

The fact that immature forage diets are accompanied by low Mg availability may not be a direct result of the forage N level. L'Estrange et al. (1967) did not find differences in serum Mg or Ca when sheep were fed forages of various maturities and N levels. The crossover experimental design, using only two wethers, may have precluded an adequate evaluation of N fertilization effects on forage Mg availability.

Fontenot (1972) indicated that high dietary N did not affect Mg absorption or blood plasma Mg in wether lambs even though urinary Mg excretion was higher, and Mg retention was lower ($P < 0.01$) for the animals consuming the high N rations (Moore et al., 1972). He suggested that the detrimental effect of N fertilization on Mg absorption by ruminants may be because the N increases the K concentrations in plants. An increased K level could decrease the efficiency of Mg absorption by the animals.

Fontenot et al. (1973) summarized the interrelationships of K, Mg, and N in ruminants as follows: feeding N at high levels does not appear to influence Mg absorption, regardless of the N form. There have been small increases in urinary Mg excretion when high levels of dietary N were used, but they do not seem to be large enough to be important in the etiology of hypomagnesemic tetany. Application of high N fertilizer rates appears to lower Mg utilization in ruminants consuming the forage. It is suggested that this effect is due to some alteration in the plant other than the increase in N content, perhaps an increase in K content. High levels of dietary N, in addition to high levels of dietary K, do not appear to adversely affect Mg utilization more than high K levels alone.

Forage Carbohydrates

Miller (1939) observed that reducing sugars as well as total carbohydrates in wheat forage were very low during November through March in Kansas. That the forage K ranged from 3.6 to 5% and total N ranged

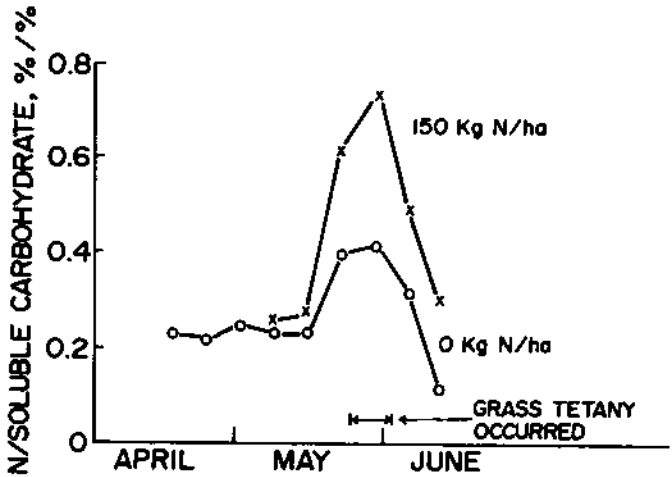

Fig. 10. Influence of N fertilization on the ratio of N/total water-soluble carbohydrates in crested wheatgrass [*Agropyron desertorum* (Fisch.) Schult] grown in Nevada (adapted from Mayland & Grunes, 1975 and Mayland et al., 1975b).

from 4 to 5%, of which one-third was nonprotein N, leads us to suspect this forage had a very high tetany hazard. Several years later, McMillan and Langham (1942), in studying phosphorus nutrition of animals grazing winter wheat pasture, incidentally observed that the serum Mg of steers receiving a readily fermentable energy supplement was slightly greater than that for those not receiving energy supplements. Metson et al. (1966) considered a number of factors associated with grass tetany, including a low energy-high protein (high N) diet. Mayland et al. (1974) later indicated that a rapid increase in the ratio of N/total water soluble carbohydrates (N/TWSC) was a good indicator of the likelihood of grass tetany in cattle grazing crested wheatgrass in Nevada. Mayland et al. (1975b), Mayland and Grunes (1975) (Fig. 10), and Follett et al. (1975) showed that N fertilization increased the N/TWSC ratio of the forage.

House and Mayland (1976) found that apparent Mg availability to sheep was increased by supplementing a low Mg diet with sucrose. Madsen et al. (1976) reported that glucose supplemented to hay-fed sheep increased apparent Mg absorption ($P < 0.01$) as shown in Fig. 11. Glucose added to a vegetative grass diet did not change Mg absorption, but plasma Mg concentrations were higher ($P < 0.05$) than for unsupplemented sheep. They observed that varying dietary glucose levels in the sheep diets did not influence ($P < 0.05$) apparent absorption of Ca, K, or P.

Okolo et al. (1976) found energy and Mg supplementation beneficial in reducing the tetany hazard. They assigned 48 spring-calving beef cows to a tall fescue pasture in Kentucky and followed blood serum Mg levels at biweekly intervals during January through May. The control group of 18 cows was assigned to a pasture receiving 67, 25, and 140 kg/ha of N, P, and K, respectively, the previous fall, plus another 134 kg K/ha in April

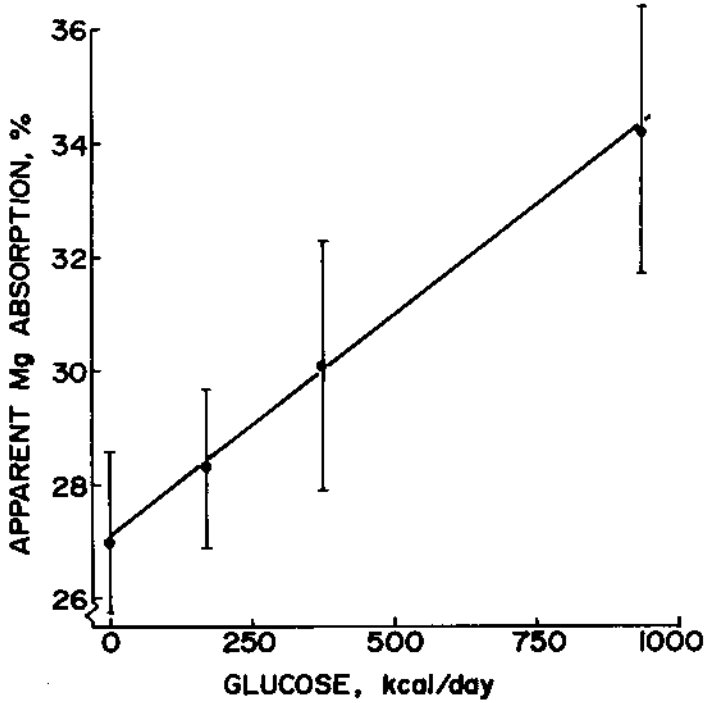

Fig. 11. Apparent magnesium absorption in red clover (*Trifolium pratense* L.)/orchardgrass (*Dactylis glomerata* L.) hay-fed sheep in relation to supplemental glucose levels. Basal diet contained 11.3% crude protein, 0.26% Mg, 0.81% Ca, 1.7% K, and 7.6% total nonstructural carbohydrates (from Madsen et al., 1976).

(Okolo, 1977). Groups 2 (15 cows) and 3 (15 cows) were assigned to pastures receiving only 134 kg K/ha in April. Group 2 received some supplemental fescue hay and MgO *ad libitum* in a salt mixture. Group 3 (15 cows) was fed as Group 2, but also received an energy source of 3.6 kg corn silage per cow-day. Eight, one, and zero incidences of grass tetany occurred during this period and mean serum Mg levels were 1.24, 2.00, and 2.48 mg Mg/100 ml for Groups 1, 2, and 3, respectively.

The apparent beneficial effects of energy supplementation on increasing Mg availability should be explored further, especially since forages have low soluble carbohydrate levels coincident with the occurrence of grass tetany (Mayland et al., 1974).

Robertson and Hawke (1965) examined the effect of dietary carbohydrates on NH_4-N levels in the rumen of pasture-fed cows and in rumen liquors incubated with ryegrass extracts. They suggested that one of the factors limiting forage N utilization is likely the amount of soluble sugars and other readily hydrolizable carbohydrates available in the forage, especially when N concentrations are high. House and Mayland (1976) observed that ruminal NH_4-N levels increased ($P < 0.05$) as dietary su-

crose intake decreased. Madsen et al. (1976) reported that glucose supplementation did reduce urinary N excretion. Reduced Mg absorption has been associated with high dietary N (Fig. 9) and elevated rumen NH_4-N levels (Head & Rook, 1957; Stillings et al., 1964). Christian and Williams' (1960) data did not support these findings. They nearly doubled ruminal ammonium levels by dosing wethers on fresh grass with 28 g ammonium acetate twice daily. Serum Mg levels, which were 2.7 mg/100 ml in control animals, were not lowered by the treatment. Perhaps the effect of NH_4-N (direct or indirect) on the etiology of grass tetany is important at low but not high dietary Mg availability levels.

Wilcox and Hoff (1974) hypothesized that the high forage ratio of N/TWSC when ingested by the animal created a high concentration of free ammonia in the rumen and an increased pH and depletion of the remaining carbohydrates, thereby further reducing the availability of the already low Mg and Ca.

Higher Fatty Acids

Deuel (1955), in reviewing the biochemistry, digestion, absorption, transport, and storage of lipids in monogastric animals, reported that marked excretions of Ca + Mg can be expected when feeding such higher fatty acids (HFA) as oleate, palmitate, and stearate, and that the Ca + Mg loss will be proportional to the amount of fat fed. Plant materials ingested by grazing cattle may contain significant amounts of HFA. An estimated 300 to 400 g of these dietary fatty acids may enter the bovine rumen each day, but they are not absorbed in significant amounts from the rumen (Garton, 1969). Instead, the unsaturated fatty acids are hydrogenated and the esterified fatty acids liberated by hydrolysis before passing with the rest of the digesta into the intestine. The uncomplexed HFA may be absorbed in the small intestine. Cows consuming 9 kg dry matter that contains 120 to 160 mmoles HFA/kg and 0.2% Mg would be ingesting about 1.0 to 1.4 moles of HFA and 0.8 mole Mg. These amounts of HFA could be sufficient to complex a significant proportion of dietary Mg.

Kemp et al. (1966) reviewed the medical literature indicating that Mg may form water-insoluble soaps with HFA. When the fat content in animal rations was increased, the fecal soap content increased and, in some cases, blood serum Mg decreased. They assumed that a decrease in total HFA in the ration might explain an increase in the "availability" of forage Mg in maturing grass. They observed a significant ($P < 0.05$) negative relationship between forage Mg availability to lactating cows and the HFA level in the ration. They also reported a significant relationship between crude protein and total HFA in a variety of fresh grass and hay materials.

Molloy et al. (1973) reviewed the earlier literature in which the presence of Ca and Mg soaps in cattle feces was established. These reviews generally postulated that the forage HFA reduced Mg availability to the ruminant animal through the formation of water-insoluble soaps in the rumen. Magnesium excretion in the feces would consequently be expected

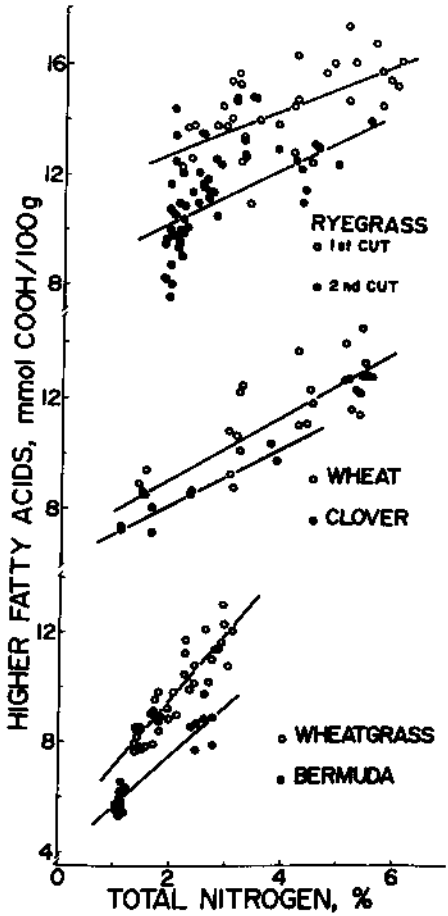

Fig. 12. Regression of total HFA concentration on total N concentration in five forage species. 'Nordan' crested wheatgrass [*Agropyron desertorum* (Fisch.) Schult], 'common' perennial ryegrass (*Lolium perenne* L.), 'Wanser' hard red winter wheat (*Triticum aestivum* L.), 'common' bermudagrass (*Cynodon dactylon* L.), and 'ladino' clover (*Trifolium repens* L.) (from Mayland et al., 1976b).

to increase in proportion to the forage HFA content. Researchers interested in determining HFA on plant tissue should refer to Molloy et al. (1974) for precautions on sample preparation.

A close relationship was subsequently established between HFA levels in several forage species and their respective N (Fig. 12) or crude protein concentration (Molloy et al., 1973; Mayland et al., 1976b). Barta (1975) found that the HFA concentrations in orchardgrass and bromegrass increased 25 and 46%, respectively, when fertilized with 112 kg N/ha. Fertilizing these plots near Wooster, Ohio with high K rates did not

change the HFA concentrations. In a solution culture study, Barta (1975) found that the N source (NO_3-N vs. NH_4-N) did not differentially influence HFA concentrations in perennial ryegrass. Mayland et al. (1976b) reported that HFA concentrations were positively and linearly related to forage N levels, but regression coefficients were not the same for all the species tested. The individual fatty acid concentrations were determined by gas-liquid chromatography and total HFA concentrations were determined by titration. The individual fatty acids expressed as percent of total HFA and averaged over all grasses were: 2% myristic, 13% palmitic, 1% palmitoleic, 1% stearic plus oleic, 11% linoleic, and 67% linolenic. As expected, the total HFA concentrations were positively correlated with chlorophyll $a+b$ concentrations, since the HFA in green plants is largely associated with the chloroplast membrane.

In tests with a small number of dairy cows, Wind et al. (1966) found that increasing the ration fat content increased fecal soap concentrations, sometimes with a concomitant decrease in blood-serum Mg. Wilson et al. (1969) measured blood-plasma Mg concentrations in dairy cows grazing high FHA perennial ryegrass (18 moles COOH/100 g DM). Cows supplemented with 50 to 70% additional HFA as peanut (*Arachis hypogaea* L.) oil suffered significant depressions in blood plasma Mg, as compared with non-HFA supplemented cows (Fig. 13). They concluded that the forma-

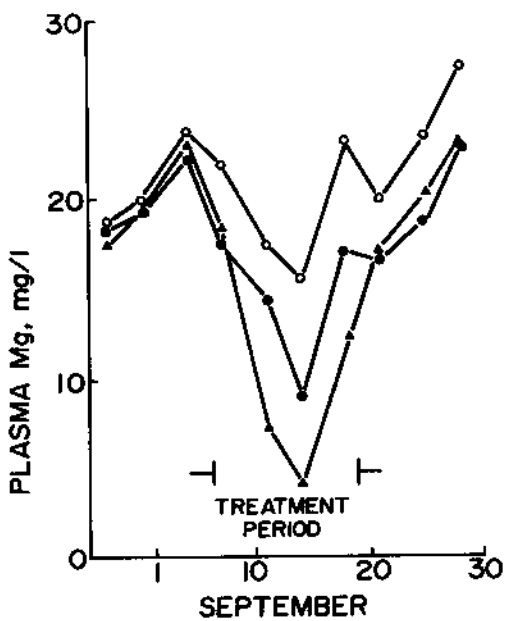

Fig. 13. Mean plasma Mg concentration of mature lactating cows grazing a tetanigenic perennial ryegrass (*Lolium perenne* L.) forage (treatment period only) and supplemented with .454 kg (1 lb) starch (○), or 220 ml peanut (*Arachis hypogaea* L.) oil (△) fed twice daily, or no supplement (●) (from Wilson et al., 1969).

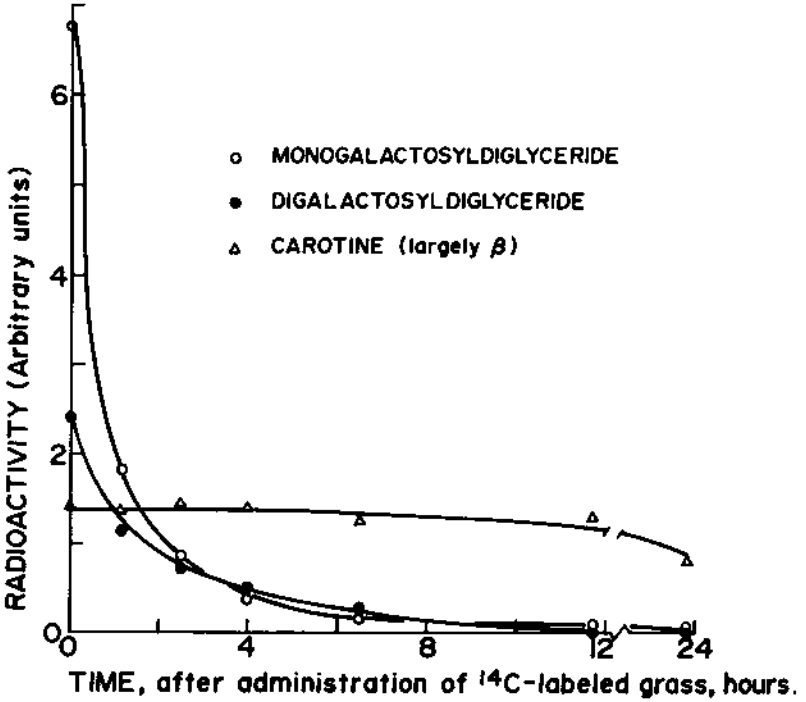

Fig. 14. Decomposition of ^{14}C-labelled perennial ryegrass (*Lolium perenne* L.) galactolipids and carotene in the sheep rumen (from Dawson & Hemington, 1974).

tion of Mg soaps reduced forage Mg availability. The oil supplement lowered plasma Mg concentration more in mature than in young animals. A starch supplement, which served as an energy source, produced plasma Mg levels higher than those in the control (ryegrass only) animals (Fig. 13).

The higher fatty acids in pasture forages are found in the leaf lipid material primarily associated with membrane structures, such as those in the chloroplast lamellae, mitochondria, endoplasmic reticulum, and plasma membranes, although waxes are present as constituents of the leaf cuticle. In terms of mass, the main lipids of photosynthetic plants are those present in chloroplasts, i.e., monogalactosyldiglycerides, digalactosyldiglycerides, and chlorophyll pigments (Dawson & Hemington, 1974). The tissue HFA are readily autoxidized in harvested and cured feeds. Thus, HFA are most numerous and most important in the etiology of tetany when ruminants graze very immature grass.

Following ingestion, the forage lipids are rapidly hydrolyzed by the lipase enzyme in the rumen system, with the consequent liberation of free fatty acids (Fig. 14). Carotene pigments are resistant to decomposition during prolonged incubation with rumen contents and, therefore, serve as an excellent reference for measuring the lipid hydrolysis, as shown in Fig.

14 (Dawson & Hemington, 1974). Chlorophyll molecules within the chloroplasts are readily exposed for subsequent release of the chelated Mg.

Organic Acids

Burau and Stout (1965) and Stout et al. (1967) identified a number of grasses that accumulated large concentrations of *trans*-aconitate. This acid inhibits the tricarboxylic acid cycle. High concentrations were found in early season forage grasses and, since these concentrations coincided with the occurrence of grass tetany, they hypothesized that perhaps *trans*-aconitate might be partially responsible for nutritional disorders, including grass tetany. Based on these reports, considerable research was conducted on the relationship of organic acids, especially aconitic acid, to Mg availability to livestock.

METABOLISM AND CONCENTRATION IN FORAGES

In plant metabolism, organic acids help maintain ionic balance and assist in cation absorption and translocation into the upper plant parts. The translocation of a NO_3 salt to the shoot and subsequent NO_3 metabolism is the only process capable of supplying the shoot with significant amounts of carboxylate. Absorbed bicarbonate is a good carboxylate source in the roots, but transpiration rates are too slow in the tops relative to growth, and carboxylate concentrations may fall to approximately half of their normal value (Dijkshoorn et al., 1968). With an NH_4-N source, forage organic N is as high as with NO_3^- since NH_4^+ is also readily absorbed and metabolized by new growth. When the number of absorbed equivalents of cations, including NH_4^+, and of anions is considered, it seems that substantially more cations than anions are absorbed from the supply of salts. This excess is balanced with bicarbonate. The NH_4^+, balanced by HCO_3^-, is metabolized to organic N with no residual equivalents. More commonly, HCO_3^- is absorbed in excess of NH_4^+ and this excess is in balance with the cations. This is the only source of carboxylates in plants supplied with NH_4-N. Their rate of formation is slow in this instance and the carboxylate is low (Table 6). With NO_3 the N is absorbed, transferred to the leaves, and metabolized to support growth and foliage. The NO_3^- thus increases the carboxylate concentration (Dijkshoorn et al., 1968; Kirkby, 1969).

Blevins et al. (1974) noted that both excess cation absorption and the reduction of NO_3^- resulted in increased organic acid concentration, and that the NO_3^- reduction stimulated malic acid synthesis. The data shown in Table 6 illustrate the reduced accumulation of organic acids in rye grown with NH_4-N as compared with NO_3-N (Kirkby, 1969). The NO_3-N source, when compared to the NH_4-N source, favored an increase in the malic acid fraction at the expense of the citric acid concentration. In a dilute nutrient culture study, Kirkby (1968) found that, even though pH was carefully maintained, the inclusion of the NH_4-N source depressed

Table 6. Effect of N source on the organic acid anion and mineral cation concentrations in rye (*Secale cereale* L.) tissue grown in nutrient solution containing 5 meq/liter Ca and N, 2.0 meq/liter Mg (adapted from Kirkby, 1969)

	Ionic concentration					
	Organic acid anion (fresh wt. basis)†					
N source	Fumaric	Succinic	Aconitic	Malic	Citric	Total in tissue
	% of total					meq/kg
NO_3	2	3	55	26	15	78
NH_4	2	3	55	21	19	40
	Mineral cation (dry wt. basis)					
	Ca	Mg	K	Na	Total	
	meq/100 g					
NO_3	50	18	86	1	155	
NH_4	31	14	80	1	126	

† Malonic and oxalic acids were not detected in rye.

growth and decreased the concentration of forage Ca, Mg, and K and the organic acid anions in particular.

Fertilizing tall fescue with 150 kg N/ha as NH_4NO_3 increased the organic acid concentration from 149 up to 238 meq/kg and the proportion of malic from 14 up to 50% of the total when compared with the unfertilized (Teel, 1966). Follett et al. (1977) found that N fertilization, regardless of N source, generally increased ($P < 0.05$) organic acid levels in bromegrass. Fertilization with KCl significantly decreased ($P < 0.05$) organic acid concentration, probably because of the increased chlorine levels in the forage.

Barta (1973) reported that application of KCl significantly reduced malic, quinic, and shikimic acid levels in both bromegrass and orchardgrass, and *trans*-aconitic acid levels in bromegrass (Table 7). No effect of K was measured on citric acid concentrations. A significant increase in forage N and K was measured in both forages fertilized with N and K, respectively. Nevertheless, the total organic acid concentrations were decreased by N and K fertilization in both species, with the exception of an increase in the N-fertilized bromegrass.

Prior et al. (1973) grew Nordan [*Agropyron desertorum* (Fisch.) Schult] and 'Fairway' (*A. cristatum* L.) crested wheatgrass in the greenhouse in a mixture of 50% silt loam soil and 50% coarse sand. One treatment consisted of 112 kg N/ha as NH_4NO_3 and the second treatment was KNO_3 at 312 kg K/ha and 112 kg N/ha. The addition of KNO_3 markedly increased the concentration of total organic acids in both plant species (Table 8). The organic acid concentrations were similar for both species, regardless of fertilizer level. Fertilization with K did not change the relative distribution of organic acids in either plant species. The primary difference was that *trans*-aconitic acid was much higher in Nordan and malic acid was much higher in Fairway. It is not known whether this difference would affect the incidence of grass tetany in cattle grazing these

Table 7. Effect of N and K fertilization on the organic acid distribution in orchardgrass (*Dactylis glomerata* L.) and bromegrass (*Bromus inermis* L.). Field plots were fertilized with 0 or 112 N/ha as NH_4NO_3, and 0 or 403 kg K/ha as KCL (adapted from Barta, 1973)

Treatment	Organic acids (dry matter basis)					
	Malic	*T*-aconitic	Citric	Shikimic	Quinic	Total concentration in plants
	% of total					%
			Orchardgrass			
Control	41	3	15	12	29	2.41
N	46	4	24	7	18	2.14
K	34	5	25	9	26	1.48
NK	47	4	31	4	13	1.88
			Bromegrass			
Control	10	58	7	7	18	2.52
N	20	56	9	3	11	3.18
K	9	57	8	7	19	2.16
NK	18	58	12	3	10	2.36

Table 8. Effect of K added as KCl on the organic acid concentrations in two crested wheatgrass species grown in a mixture of 50% silt loam soil and 50% coarse sand in the greenhouse (adapted from Prior et al., 1973)

Fertilizer K	Organic acid						
	Fumaric†	Formic	Acetic	Aconitic	Malic	Citric	Total
	% of total						meq/kg
			Agropyron desertorum				
0	T†	1	4	23	67	5	417
312	T	1	2	28	61	8	734
			Agropyron cristatum				
0	T	1	5	5	83	7	440
312	T	1	3	5	80	10	763

† T = trace.

two species, but it does illustrate the genetic variation in organic acids in different species of crested wheatgrass.

Banwart and Pierre (1975) noted that the increase in total organic acids normally associated with an increase in N fertilization rate was much less where large amounts of K fertilizer were applied, and was counteracted when moderate amounts of NO_3-N accumulated in the plant. The apparent discrepancies in K and N effects on total organic acid concentrations noted between data in Tables 7 and 8 may be explained by the findings of Dijkshoorn et al. (1968) that in low N, low K plants increased NO_3^- uptake stimulated organic acid synthesis, whereas increased Cl (as KCl) uptake reduced it.

Mayland et al. (1975b) found that N fertilization of crested wheatgrass in northern Nevada increased aconitic acid and titratable ash alkalinity. Total organic acids in forage may be measured directly or determined by indirect methods, such as calculation of cation minus anion concentrations (deWit et al., 1963) or as titratable ash alkalinity from which the concentration of NO_3-N is subtracted (van Tuil et al., 1964). Dijkshoorn (1973) provides an easily read summary on the accumulation mechanisms and plant composition of organic acids.

ORGANIC ACID EFFECTS ON DIETARY Mg AVAILABILITY

Garner et al. (1974) reported that dry matter intake by sheep was slightly depressed by a ration containing a 4% organic acid mixture. Apparent Mg absorption was similar for both the organic acid and the basal ration; however, Mg balance averaged over the three collection periods was lower for the organic acid than for the basal ration (−2 vs. +11 mg Mg/day). Dietary organic acids consistently depressed plasma Mg but had no effect on plasma Ca levels. Burt and Thomas (1961) measured significant decreases in blood Mg levels in heifers receiving diets containing 1% citric acid. Camp et al. (1968) found that oral doses of potassium *trans*-aconitate depressed blood serum Mg levels in sheep, but *trans*-aconitic acid did not.

Bohman et al. (1969), after the report of high *trans*-aconitic acid levels in spring forage (Burau & Stout, 1965), treated cattle with two organic acids. A tetany resembling "field grass tetany" was induced in cattle by orally administering KCl plus either citric or *trans*-aconitic acid. The KCl or either of the two organic acids when administered alone did not produce the tetany. Wright (1971) discussed the findings of Bohman et al. (1969) and indicated that, if citric acid was absorbed into the animal's circulatory system, the organic acid could complex the Mg, thereby decreasing its availability. Scotto et al. (1971) did find that oral administration of both KCl and citric acid increased blood citrate levels in cattle. For a given citric acid dose, blood citrate levels at one-half hour were increased proportionately to the increase in KCl levels.

Other researchers have repeated this work by daily feeding *trans*-aconitic or citric acid, or by infusing each of these acids into the rumen or blood stream (Kennedy, 1968; Lomba et al., 1969a, b; Wright & Wolff, 1969). These researchers have concluded that *trans*-aconitic acid is not a major factor in determining the blood serum Mg concentration. Furthermore, since the acids were rapidly metabolized in the rumen, they did not appear to have a toxic effect in vivo.

The Mg kinetics of sheep fed different levels of K and citric acid were studied by House and Van Campen (1971). They reported that plasma Mg concentrations, Mg retention, and exchangeable Mg pool size were unaffected by the treatments. Feeding the 4% K ration to the yearling wethers elevated total fecal and ^{28}Mg (injected intravenously) output and markedly depressed absorption, urinary excretion, and endogenous fecal excretion of Mg. The 3% citric acid in the diet had no measurable effect on Mg metabolism. House and Bird (1975) also found that high dietary K levels depressed Mg availability to ruminants. Research by other animal

scientists on the effect of dietary K on Mg availability to animals was reviewed by Fontenot (1972).

Fertilization with K will generally increase K and organic acid concentrations in the forage. The increased K concentration has a major effect, then, on reducing Mg absorption by the animal, but the role of organic acids is not yet clear. If organic acids are important in complexing Mg, they would most likely be so shortly after animals start grazing a forage high in organic acids and before rumen microflora populations are built up that could metabolically degrade the organic acids. Wright (1971) also indicated that the presence of high K levels decreased the rate of citric acid utilization by rumen microorganisms.

Cell Wall and Other Cell Constituents

Molloy and Richards (1971a, b) examined the complexing of Ca and Mg by organic constituents of Yorkshire Fog (*Holcus lanatus* L.). Pectin, lignin, and the organic acids complexed a large proportion of the Ca in a nonionic form, but only lignin and the organic acids complexed significant amounts of Mg. The hemicelluloses and cellulose have little ability to complex either Ca or Mg. Citric and *trans*-aconitic acids were the most active in complexing the divalent cations. In a qualitative ranking, exchangeable Mg was complexed in the following order: citric $\gg$ oxalic $>$ aconitic $=$ malonic $=$ malic $\gg$ lignin. For most of the fractions examined, pH affected the extent of complexing, since the percentages of bound Ca and Mg were larger at the weakly alkaline pH (cf. ileal region) than at the slightly acidic pH (cf. duodenal region). They surmised that the organic acid survival in the rumen and subsequent passage into the small intestine was very doubtful because of the rapid utilization by rumen microorganisms and the rapid absorption of at least some of the acids through the rumen epithelium. They further noted that lignified plant tissues are degraded slowly in the rumen. While Mg binding by lignin is small, it would nevertheless be of interest, especially in the occurrence of grass tetany.

Care et al. (1966) also studied factors affecting Mg availability in relation to the occurrence of hypomagnesemia. Intraruminal administration of ^{28}Mg showed that its absorption was depressed by the presence of spring grass, relative to hay, supplying the same daily amount of Mg. They suggested that the relatively poor absorption of Mg was not due to the presence of a bound form in the grass, but rather that some chelation occurred within the small intestine that inhibited Ca and Mg absorption.

Miscellaneous Complexing Factors

HISTAMINE

Fowler (1963) reported blood serum histamine levels from animals experiencing grass tetany were either abnormally high or abnormally low. Antihistaminics were used for a short time in conjunction with Mg-

Ca therapy. This led to a series of investigations of histamine in the etiology of grass tetany. (Histamine accentuates the neuromuscular excitability induced by K.) O'Sullivan (1968) reported that herbage histamine levels rose 4 to 7 days after the start of a dry period, especially if temperatures were low during that period. He reported 3 to 20 μg histamine/g dry matter in grass when tetany occurred. Suggestions were advanced to show how climate and pasture histamine content might contribute to the occurrence of grass tetany. More recent studies have discounted the involvement of histamine in the etiology of grass tetany.

Neumark and Tadmor (1968) found that when histamine was infused with either formic or acetic acid into the sheep omasum, the animals stopped feeding and rumen motility was reduced. The separate infusion of the organic acids and histamine had no effect on food intake. Henry et al. (1977) made intraruminal infusions of histamine, ammonia, histamine plus ammonia, or dionized water into 16 rumen fistulated lambs. Their results indicated that high levels of ammonia might be responsible for depressing serum Mg levels, thereby leading to tetany, but that histamine had no effect. They further concluded that "it is possible that high levels of NPN increased the incidence of hypomagnesemia possibly through a change in ionic balance, i.e., monovalent vs. divalent cations which could alter membrane potentials and consequently change nervous excitability." They also noted that Mg deficiency did not cause an endogenous histamine release.

ALUMINUM

High Al concentrations (500 to 1,000 ppm) found in a few forage samples of winter-grazed cereals and grass grown on soil containing free lime were suggested as a causative agent of grass tetany (Dennis, 1971). These calcareous conditions do not favor soil Al solubility and uptake by plants. Mayland et al. (1974) reported 10 to 15 ppm Al in crested wheatgrass forage grown on similar soil conditions in northern Nevada coincident to the occurrence of tetany in 1967 and attributed these Al values to soil contamination.

Grazing animals do ingest Al that may be endogenous or exogenous to the forage, as well as the Al that is associated with soil that might be directly consumed by the animal (Mayland et al., 1975a). This soil Al is generally considered quite insoluble except under strongly acid conditions. However, very little is actually known about the solubility of Al

Table 9. Blood serum Mg in sheep after 56 days on diet containing two levels each of Al as $AlCl_3$ and P as *mono*sodium phosphate (from Valdivia, 1977)[a]

	Serum Mg at P intakes of:	
Al	0.15%	0.29%
ppm	mg %	
0	2.60	2.23
2,000	1.75	1.83

from soils or forages when ingested by ruminants. Valdivia (1977)[2] found no change in serum Mg concentrations of steers fed diets containing as high as 1,200 ppm Al as the readily soluble $AlCl_3$. However, in a second study, sheep fed up to 2,000 ppm Al as $AlCl_3$ did exhibit a significantly ($P < 0.1$) depressed serum Mg (Table 9).

SODIUM VS. POTASSIUM

Two factors have been implicated in the etiology of hypomagnesemia: (i) the lower Na levels observed in grass compared with legumes, and (ii) the lower blood plasma Na levels measured in animals with grass tetany. Powley et al. (1977) tested the hypothesis that higher dietary Na levels would have a sparing effect on grass tetany. Sheep were fed perennial ryegrass containing 0.73% Na and 1.55% K or 0.15% Na and 3.12% K produced by fertilizing with different Na and K rates. The forages were fed to sheep in a crossover experiment using ^{28}Mg isotope dilution techniques. True Mg availability was greater in the Na-fertilized grass than in the K-fertilized grass. Daily endogenous fecal Mg excretion was not affected by altering K and Na levels. True Mg availability may have increased more as a result of decreased dietary K rather than the small increase in dietary Na levels. Since K, but not Na, is required for forage growth, it does not seem plausible to do much agronomic research on this aspect of the problem, except perhaps on the comparative use of $NaNO_3$ vs. KNO_3-N sources.

PHOSPHORUS

Simesen (1959) suggested that the ammonia liberated during the rumination of tetanigenic grass could contribute to Mg precipitation in the intestinal tract as the magnesium ammonium phosphate complex. Neither he nor Storry (1961) could find the complex in the ruminant intestine. Data from Linke (1965) suggest a moderately low solubility for $MgNH_4PO_4 \cdot 6H_2O$. The solubilities at 25°C are 13.6, 18.8, 26.4, 296, 499, 22, and 32 mg Mg/liter in pure water, 0.1 and 0.5 *N* KCl, 0.1 and 0.5 *N* $CaCl_2$, and 0.1 and 0.5 *N* NaCl solutions, respectively.

Smith (1969) and Smith and McAllan (1966) discussed aspects of mineral absorption in the small and large intestine of the ruminant. They noted that evidence exists for the passive Mg transport across the small intestine wall; that the absorption depends on the availability, concentration, and time of passage (transit time); and that some materials are present in the digesta that are able to bind Mg at the intestinal pH. They also reported on the precipitation of $(Ca-Mg)NH_4PO_4$. Smith and McAllan (1966) found that 34 to 74% of the Mg fed to ruminating calves was in a nonultrafilterable portion. The binding was attributable to at least two processes: one depended on the presence of phosphate; the other did not.

[2] Valdivia, Ricardo. 1977. Effect of dietary aluminum on phosphorus utilization by ruminants. Ph.D. Diss., Univ. Fla., Gainesville.

Magnesium Distribution in Forage Tissue

Todd (1962) found that 50% of the Mg in a low Mg spring forage was water soluble. The proportion of the water-soluble Mg increased to approximately 70 to 80% as forage matured. He also found that the acetone-soluble Mg (chlorophyll-Mg) decreased from about 12% in vegetative material to 5% at the ripe seed stage. Nitrogen, P, and K fertilizer combinations had no effect on the Mg distribution in the three fractions. Insoluble Mg, measured as the difference between total Mg and the sum of the water-soluble and acetone-soluble fractions, decreased as forage matured.

Grace and Davies (1975) briefly defined a fractionation scheme to determine the Mg distribution in fresh perennial ryegrass (*Lolium perenne* L. 'Grassland Ruanui') and in the digesta as it passed through the sheep. The forage Mg was distributed as follows: 5, 55, 20, 5, and 15% in ethanol-precipitated protein, water soluble, solvent soluble, alkali soluble, and alkali insoluble, respectively. More of the Mg was found with the water-soluble faction in the acidic digesta from the duodenum (pH 2.5) as compared with digesta from other regions (pH 5.5 to 8.0).

McIntosh et al. (1973a) examined the effects of fertilizer N, K, and Mg on the Mg distribution in perennial ryegrass S.24 when grown in potted soil. They found a good correlation between the water-soluble Mg and total Mg fractions; both increased with maturity and correlated linearly with exchangeable soil Mg. Increasing the N fertilizer rate increased total and water-soluble Mg fractions, but only at low K fertilizer levels.

van't Klooster (1967) reported that nearly all the Ca, Mg, and P in the nonultrafilterable fraction of cow feces were present as insoluble compounds. About 25 to 30% of the fecal Ca and Mg was adsorbed to fibrous particles.

CHLOROPHYLL MAGNESIUM

Nason and McElroy (1963) reported that Mg occurred in three fractions: in free or soluble salt in the cellular sap; in a combined form in protoplasm; or in the chlorophyll molecule, which consists of 2.7% Mg (on mass basis). Forage containing 0.7 to 1.3% chlorophyll $a+b$ and 0.2% Mg would have 9 to 18% of the total Mg chelated in the chlorophyll molecules.

Magnesium availability is undoubtedly controlled by a number of factors, including the ease with which chlorophyll Mg is released during the digestion process. Mangan and West (1977) found that the chlorophyll of intact purified chloroplasts was rapidly degraded, with a half-life of 50 to 60 min in sheep rumen. Dawson and Hemington (1974) found that the chlorophyll *a* molecule in ingested perennial ryegrass S.24 released its Mg about three times faster than did the chlorophyll *b* molecule. Thus, factors increasing the chlorophyll *a/b* ratio in plant material would tend to increase Mg availability to the animal.

C_3 VS. C_4 GRASSES

The chlorophyll *a/b* values may relate to the type of C fixation cycle of the forage. In the gramineae, the genera *Agropyron*, *Avena*, *Bromus*, *Dactylis*, *Elymus*, *Festuca*, *Hordeum*, *Lolium*, *Phalaris*, and *Triticum* are C_3 (pentose phosphate cycle and tricarboxylic acid cycle) plants and are generally recognized as posing a grass tetany potential hazard to livestock under some conditions. The C_4 (dicarboxylic acid cycle) gramineae genera include: *Agrostis*, *Andropogon*, *Aristida*, *Bouteloua*, *Calamagrostis*, *Cynodon*, *Digitaria*, *Panicum* (this genus contains 104 C_3 species and 137 C_4 species, Brown, 1977), *Paspalum*, *Sorghum*, *Sporobolus*, and *Zea*. Grass tetany is not known to occur on these grasses except occasionally as winter tetany when cured grass hay contains very low Mg levels.

In general, the chlorophyll *a/b* ratio is approximately 2.8 for C_3 plants and 3.9 in C_4 plants (Black & Mayne, 1970; Mayne et al., 1971). Therefore, chlorophyll *a*, which more readily releases the Mg molecule during the digestion process, makes up 74% of the total chlorophyll in the C_3 plants and 80% in C_4 plants. While the difference between the amount of Mg in chlorophyll *a* of C_3 vs. C_4 in plants is small, representing less than 2% of the total forage Mg, it is interesting to speculate that this might be part of the difference in potential tetany hazard between C_3 and C_4 plants.

Most C_4 plants grow better under warmer conditions and may contain lower N and K levels than C_3 plants. Other differences may exist between C_3 and C_4 plants relating to Mg distribution in the plant and subsequent release during digestion. The C_4 grasses have about half of the chlorophyll in the mesophyll cells and half in parenchyma bundle sheaf cells (Hatch et al., 1971), but chlorophyll *a* composes about 85% of the total chlorophyll in the mesophyll, and only 77% of the chlorophyll in the bundle sheaf cells of *Sorghum bicolor* (L.) Moench. The chlorophyll *a/b* ratio in the bundle sheaf tends to increase with plant maturity, at least in *Zea mays* L. (Hatch et al., 1971). The C_3 type plants have only mesophyll cells.

An offsetting factor concerning the Mg availability may be that parenchyma sheaf cells of C_4 plants are degraded less rapidly by rumen microbial action than are mesophyll cells in coastal bermudagrass (*Cynodon dactylon* L. Pers.), bahiagrass (*Paspalum notatum* Fluegge), and digitgrass (*Digitaria decumbens* Strent.) (Akin & Burdick, 1977). Another factor yet to be considered is the possible increase in the chlorophyll *a/b* ratio as young grass leaves expand and mature. This occurs in the dicotyledon, *Populus deltoides*, in which the ratio increases as the leaves mature (Dickmann, 1971). Such a change would alter the subsequent release rate of chlorophyll Mg during digestion.

Additional information is needed on the chlorophyll *a* and *b* distribution in C_3 vs. C_4 plants, and in very immature vs. older vegetative tissue in relation to the rate of Mg release from the chlorophyll molecules during the rumen digestive process. Other information, including N and K accumulation by C_3 and C_4 plants, might help explain why grass tetany occurs in C_3 but not C_4 plants.

Plant Species: Magnesium Uptake and Availability

Baker and Reid (1977) list the Mg concentration of forage species collected from hill pastures and meadows during two growing seasons in northcentral West Virginia. They show an average of 0.14, 0.25, and 0.49% Mg in grasses, legumes, and weeds, respectively. The Mg concentration in the grasses examined ranged from 0.04 to 0.44%.

Tingle and Elliott (1975) determined the mineral composition of 15 cool-season grass species comprising 63 cultivars growing on a wet gleyed gray wooded soil (pH 5.5 to 5.8) at Prince George, British Columbia. The forages, annually fertilized with 112 kg N/ha and harvested at early heading stage, contained 0.15 to 0.28% Mg, 0.12 to 0.32% Ca, and 1.59 to 2.45% K. Significant ($P < 0.05$) differences in Mg, Ca, and K levels occurred between some species, but not between cultivars within species except for Ca levels in timothy (*Phleum pratense* L.). Larger differences in mineral levels might have occurred during the vegetative stage.

Arroyo-Aguilu and Coward-Lord (1975) reported that the mineral composition of 10 tropical forage grasses in Puerto Rico ranged from 0.15 to 0.46% Mg, 0.11 to 0.43% Ca, and 0.68 to 7.33% K. Forage K levels declined rapidly from 4.99% when grasses were harvested at 30 days to 1.01% when harvested at 180 days. Forage Ca and Mg declined less than K as plants matured. The K/(Ca + Mg) values decreased from 3.0 in early harvested forage to 0.8 in the last harvest. Corresponding N levels were not reported, except that K and N levels were highly correlated ($r^2 = 0.76$). Grass tetany is not known to occur on tropical grasses (assumed to be C_4 type plants) when grazed during the vegetative growth stage. More information is needed to explain the apparent differences in tetany hazard between C_3 and C_4 plants.

Hill and Guss (1976) reported a range in Mg concentrations within genera as follows: corn, 0.15 to 0.40; wheat-hay, 0.11 to 0.40; barley (*Hordeum vulgare* L.) hay, 0.08 to 0.45; orchardgrass hay, 0.14 to 0.19; timothy, 0.09 to 0.11; ryegrass, 0.13 to 0.21; and alfalfa, 0.19 to 0.27%. They concluded that plant breeding had considerable potential for increasing Mg concentrations in a number of forage plants.

Concentrations of Mg certainly differ between grasses grown on the same soil. Fleming (1973) reported a range of 0.16 up to 0.32% Mg in forage from different grass species growing on the same site. Gross (1973) reported that under spring conditions high Mg levels were found in a *Lolium* × *Festuca* synthetic and red top (*Agrostis alba* L.), whereas tall fescue, orchardgrass, Kentucky bluegrass (*Poa pratensis* L.), reed canarygrass (*Phlaris arundinacea* L.), and perennial ryegrass contained intermediate levels of Mg. Timothy and smooth brome contained low concentrations of forage Mg. These same rankings were maintained during the summer growing period, except that tall fescue was placed in the high Mg accumulation ranking. Gross and Jung (1978) studied the Mg uptake by a number of grass and legume species under greenhouse conditions. They found that rankings based on tissue Mg concentrations were similar over a wide temperature range and over different soil Mg levels.

Sleper et al. (1977) stated that the K/(Ca+Mg) ratio was highly heritable and progress in breeding a tall fescue with low hypomagnesemia hazard was possible. They further indicated that if forages were selected for low K/(Ca+Mg) values, Mg levels would increase slower than Ca levels.

Thill and George (1975) also indicate a wide range in concentrations of K and Mg, and K/(Ca+Mg) values for nine grasses grown in a field study in Iowa. Forage species may also respond differently to Mg fertilization. Gross and Jung (1978) reported that the Mg concentration of some grasses grown in a greenhouse study increased only 0.04%, while in other species it increased 0.10% when fertilized with 612 kg Mg/ha as $MgSO_4 \cdot H_2O$.

Selecting plants, or perhaps even breeding plants, to alter some of the organic components involved in the tetany process may also be possible. As indicated earlier, Prior et al. (1973) found that Nordan crested wheatgrass contained a high concentration of *trans*-aconitic acid, while Fairway crested wheatgrass (*Agropyron cristatum* L.) contained a high concentration of malic acid.

Boland et al. (1976) measured significant differences ($P < 0.01$) among tall fescue genotypes in the concentration of malic, citric, α ketoglutaric, succinic, malonic, quinic, shikimic, and the total of nine organic acids. Malic was the most abundant. These researchers concluded that organic acid levels in tall fescue leaves could be altered through plant breeding.

Mayland et al. (1976a) studied the chemical composition of Nordan crested wheatgrass and of 'Thatcher' wheat forage grown in a field experiment in southcentral Idaho. While Mg and total N concentrations were similar for the two forages, the wheat had lower values for Ca and higher values for K, K/(Ca+Mg), organic acids, and higher fatty acids. Using the Dutch nomogram (Committee on Mineral Nutrition, 1973) described later in this chapter, they indicated that much lower values for blood serum Mg would be expected if lactating cows grazed the wheat forage as compared with the wheatgrass. The chemical forage analysis from a greenhouse experiment indicated that the estimated grass tetany hazard was wheat > oats = barley > rye.

Benefits of increased apparent Mg absorption and Mg retention by ruminants may be experienced when Mg fertilization increases forage Mg concentrations. These fertilizer responses are more likely to occur on acid soils than on alkaline soils, and on coarse-textured than fine-textured soils.

The chemical composition of forage is a convenient monitor of treatment effects for solving animal nutritional problems. Ultimately, animal feeding trials must be conducted to evaluate forage quality. This is especially true for Mg, the availability of which may range from 5 to 35% (Committee on Mineral Nutrition, 1973). The fact that high Mg forage may not necessarily result in high blood plasma Mg levels must also be considered (Grace & Wilson, 1972). Cooperative research between animal nutritionists and agronomists will enable us to better understand grass tetany, and to design alternative management practices to reduce the economic losses presently sustained by the stockman.

Table 10. Mean forage Mg concentration and apparent Mg absorption and retention by lambs. Data are means of four harvest dates (from Powell et al., 1978)

Variable	Perennial ryegrass	Smooth brome	Orchard-grass	Tall fescue
Forage Mg concentration, %	0.15	0.10	0.15	0.24
Apparent absorption, %	38.0	35.0	44.0	30.0
Retention, g/day	0.22	0.15	0.29	0.15

Powell et al. (1978) measured wide differences in the Mg concentrations in perennial ryegrass, smooth brome, orchardgrass, and tall fescue (Table 10). Values of apparent Mg absorption and Mg retention by lambs were not ranked in the same order as were forage Mg concentrations. These data strongly emphasize the need for further research on forage Mg availability to animals.

Reid et al. (1978b) studied the effects of 112 kg Mg/ha as kieserite ($MgSO_4 \cdot H_2O$) applied to orchardgrass, Kentucky bluegrass, timothy, brome, tall fescue, and tall oatgrass [*Arrhenatherum elatius* (L.) Presl]. These forages were grown on several soils in Pennsylvania and West Virginia and were harvested at two growth stages to determine the effect of Mg fertilization on dry matter digestibility and Mg availability to the lambs. Magnesium fertilization increased the mean Mg concentration in the grass hays from 0.15 to 0.18%, but had no significant effect on dry matter digestibility of forage fed to lambs. Apparent Mg absorption by the lambs was increased significantly from 24 to 30% and Mg retention was generally increased by Mg fertilization of grasses.

Estimating the Grass Tetany Hazard

Jolley and Leaver (1974) studied the incidence of grass tetany on mixed forage pastures in Victoria and New South Wales, Australia. They found that the proportion of clover in the "prone" pastures was significantly less than that of the pastures having a low incidence. The clover had higher Na, Ca, and Mg, and lower K concentrations than did the grass.

Grass or small grains forages containing less than 0.2% Mg and more than 3% K and 4% N (25% crude protein), on a dry-weight basis, are especially likely to cause grass tetany. Kemp and 't Hart (1957) indicated (Fig. 15) that when the equivalent ratio of K/(Ca + Mg) in forages was less than 2.2, there were very few grass tetany cases in cattle. However, the frequency increased with K/(Ca + Mg) values greater than 2.2.

Many workers have obtained high K/(Ca + Mg) values that coincided with the occurrence of grass tetany on spring or fall grazed pastures (Grunes, 1973). The ratio has utility, particularly in situations where forage Ca concentrations are low. The ratio could be misleading in cases of high Ca concentration. However, the ratio is not in general use in the Netherlands as an indicator of grass tetany.

A nomogram (Fig. 16) prepared by the Committee on Mineral Nutri-

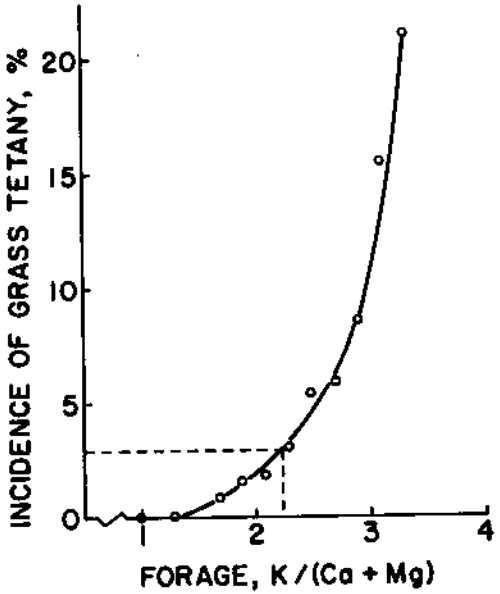

Fig. 15. Relationship between the forage K/(Ca+Mg), calculated on an equivalent basis, and the relative incidence of grass tetany in the Netherlands (adapted from Kemp & 't Hart, 1957).

tion (1973) in the Netherlands provides estimates of blood serum Mg from concentrations of forage Mg, K, and crude protein (N × 6.24). This approach for estimating the grass tetany hazard has advantages over the K/(Ca+Mg) ratio in that forage N effects are considered. While N is not necessarily directly involved in reducing Mg absorption by the animal, N values do correlate well with other factors (e.g., HFA) that may be involved. The nomogram was developed under conditions of moderate to high forage Ca, and this should be considered when it is used for estimating the tetany hazard of forage with low Ca concentrations. The nomogram is useful although actual values for blood serum Mg may be higher for grazing beef cattle than for grazing dairy cattle for which the nomogram was developed in the Netherlands. This occurs because a dairy cow may produce 20 to 55 liters of milk per day containing 2.0 to 2.5 g Mg, whereas the beef cow may produce less than 4 liters of milk per day containing less than 0.4 g Mg.

Follett et al. (1975) and Mayland et al. (1976a) found the nomogram useful in ranking the tetany hazard of U.S. forages, even though blood serum Mg values near and below zero were sometimes calculated. The coefficients used by J. L. Stevens and H. F. Mayland (unpublished data, Kimberly, Idaho) in calculating the estimated blood serum levels are given in Table 11. A basic language program, written for the Hewlett-Packard 9830A, for calculating nomogram values is available from Dr. Mayland's laboratory.

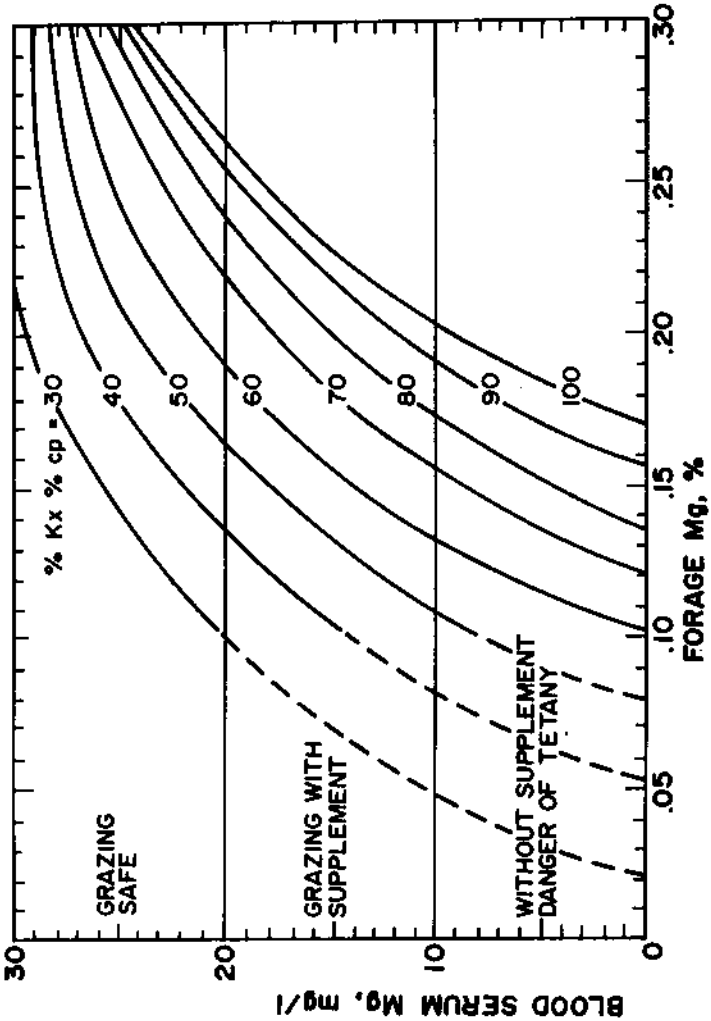

Fig. 16. Relation between blood-serum Mg of producing dairy cows and forage Mg, K, and crude protein (CP = 6.25 N). Isolines are products of percent K and percent crude protein. The figure is taken with permission from the Committee on Mineral Nutrition (1973).

Table 11. Coefficients for calculating blood serum Mg of cattle given forage N, K, and Mg levels. Coefficients are for the equation form: Serum Mg = $a + b_1Mg + b_2Mg^2 + b_3Mg^3$. Calculation must be made for the two nearest K × CP isolines and the serum Mg value obtained by interpolation (unpublished data, J. L. Stevens & H. F. Mayland, Kimberly, Idaho)

(% N) (6.24) (% K)	a	b_1	b_2	b_3
10	18.5	158	−528	386
20	9.9	199	−509	336
30	−6.8	374	−1,159	827
40	−19.1	443	−1,236	847
50	−25.5	432	−1,056	684
60	−45.5	592	−1,477	965
70	−51.1	569	−1,283	800
80	−56.2	572	−1,234	754
90	−75.7	698	−1,489	902
100	−97.1	849	−1,818	1,101

Most incidences of grass tetany occur while ruminants are grazing lush and rapidly growing grass pastures. However, tetany may also occur while animals are grazing field crop aftermaths, such as corn stover, cured grass, or grass-alfalfa hays (H. F. Mayland, unpublished data, Snake River Conservation Research Center, Kimberly, Id.). This is frequently called winter tetany and occurs because of a simple Mg deficiency in the diet. Cows maintained on hays containing less than 0.08% Mg have frequently exhibited hypomagnesemia (plasma less than 1.0 mg Mg/100 ml), but may not develop grass tetany. Calving, lactation, cold weather, or other stress may often place cattle in tetany when on feeds having low Mg concentrations. Bohman et al. (1977), after an intensive study of the forage chemical composition in relation to the tetany incidence in Nevada (Table 12), made the following recommendations: hay containing <0.12, 0.12 to 0.18, or >0.18% Mg was considered to have a high, marginal, or no tetany hazard, respectively, when consumed by livestock, particularly beef cows in early lactation.

RESEARCH NEEDS

Efforts in predicting the general grass tetany hazard have utilized information on forage N, K, Mg, and soluble carbohydrate levels. This information, coupled with weather conditions favoring a rapid flush of growth, has been helpful in alerting producers to impending occurrences of grass tetany.

Modeling the soil-plant-animal system would help us better understand the relationship between the many involved factors. Modeling is primarily a research tool enabling us to quantitatively test concepts and relationships. However, much progress in understanding the etiology of grass tetany will be made by studying small segments of this complex problem. Some of these research needs are identified below.

Table 12. Magnesium, Ca, K, and N concentrations of cured Nevada hays from areas where grass tetany was known to occur and other areas where it did not occur (Bohman et al., 1977)

Nevada hay	No. samples	Mg†	Ca	K	N
		%			
Oat hay					
Tetany prone	1	0.04	0.11	0.74	0.87
Not prone	11	0.28 (0.20–0.42)	0.90	2.77	2.02
Great Basin wildrye					
Tetany prone	2	0.08 (0.02–0.14)	0.39	1.23	1.00
Not prone	2	0.12 (0.11–0.13)	0.36	1.34	1.09
Native meadow					
Tetany prone	111	0.12 (0.04–0.25)	0.52	1.43	1.38
Not prone	67	0.22 (0.08–0.63)	0.70	1.70	1.55
Alfalfa and smooth brome					
Tetany prone	7	0.16 (0.07–0.23)	0.88	1.59	2.00
Not prone	10	0.27 (0.16–0.50)	1.45	1.98	2.48
Alfalfa					
Tetany prone	11	0.15 (0.09–0.21)	1.01	1.80	2.42
Not prone	430	0.29 (0.13–1.01)	1.91	2.53	3.03

† Data in parentheses are the ranges in Mg concentrations.

1) Determine the effect of soil pH, K, Mg, Ca, and Al levels on the availability and uptake of K, Ca, and especially Mg by forages.
2) Determine the mineral uptake characteristics of various forage species in relation to soil and climatic factors.
3) Determine the relationship of soil water and soil oxygen to K, Ca, and Mg absorption and translocation in various forages.
4) Determine Mg absorption, translocation, and partitioning in various forage grasses. This will require development of Mg fractionation techniques. Determine the relationship between these Mg fractions and Mg absorption, retention, and excretion by the animal.
5) Determine plant components responsible for the complexation of Mg secreted back into the digestive tract.
6) Determine mineral absorption and accumulation by C_3 and C_4 grasses grown under different N and K rates. Determine Mg distribution in these plants. Perhaps C_4 plants have characteristics, other than growing during warmer weather, that would help us understand the etiology of grass tetany.
7) Determine if the glutaraldehyde treatment of forage (used to prevent loss of stromal protein from chloroplast) will affect the rate of Mg release from the chlorophyll molecule and the ultimate Mg availability to the animal.
8) Determine HFA accumulation in several grass and legume cultivars as related to soil N, soil K, temperature, light intensity, C_3 vs. C_4, and stage of maturity.
9) Determine organic acid profiles and accumulations in several

grasses and legume cultivars as related to soil N, soil K, temperature, light intensity, C_3 vs. C_4, and stage of maturity. Will appreciable Mg complexation by the acids occur when animals begin grazing a tetanigenic pasture? What effect will dietary K have on the rate of organic acid decomposition in the rumen?

REFERENCES

Akin, D. E., and D. Burdick. 1977. Rumen microbial degradation of starch-containing bundle sheath cells in warm-season grasses. Crop Sci. 17:529–533.

Alston, A. M. 1972. Availability of magnesium in soils. J. Agric. Sci. Camb. 79:197–204.

Amos, R. L., G. J. Crissman, R. F. Keefer, and D. J. Horvath. 1975. Serum magnesium levels of ewes grazing orchardgrass topdressed with dolomite or calcite. J. Anim. Sci. 41: 198–202.

Arroyo-Aguilu, J. A., and J. Coward-Lord. 1975. Mineral composition of ten tropical forage grasses in Puerto Rico. J. Agric. Univ. P. R. 58:426–436.

Baker, B. S., and R. L. Reid. 1977. Mineral content of forage species grown in central West Virginia on various soil series. W. Va. Univ. Tech. Bull. 657.

Baker, D. E. 1971. A new approach to soil testing. Soil Sci. 112:381–391.

Baker, D. E. 1972. Soil chemistry of magnesium. p. 1–39. *In* J. B. Jones, M. C. Blount, and S. R. Wilkinson (ed.) Magnesium in the environment: Soils, crops, animals, and man. The Taylor County Printing Co., Reynolds, Ga.

Baker, D. E. 1973. A new approach to soil testing: II. Ionic equilibria involving H, K, Ca, Mg, Mn, Fe, Cu, Zn, Na, P, and S. Soil Sci. Soc. Am. Proc. 37:537–541.

Baker, D. O., and R. D. Gould. 1976. A survey of incidence of deaths from hypomagnesaemic grass tetany and of some management factors possibly related to their occurrence in beef cows in the Wairarapa. N.Z. J. Exp. Agric. 4:51–55.

Banwart, W. L., and W. H. Pierre. 1975. Cation-anion balance of field-grown crops. I. Effects of nitrogen fertilization. Agron. J. 67:14–19.

Barta, A. L. 1973. Effect of nitrogen and potassium fertilization on organic acids of *Bromus inermis* L. and *Dactylis glomerata* L. Crop Sci. 13:113–114.

Barta, A. L. 1975. Higher fatty acid content of perennial grasses as affected by species and by nitrogen and potassium fertilization. Crop Sci. 15:169–171.

Barta, A. L., E. M. Kohler, and J. F. Underwood. 1973. A study of the grass tetany syndrome in Ohio. Ohio Agric. Res. Dev. Cent., Res. Circ. No. 193.

Batey, T. 1967. The ratio of K to Mg in the soil in relation to plant growth. p. 143–146. *In* W. Dermott and D. J. Eagle (technical editors). Soil potassium and magnesium. Technical Bulletin No. 14. Ministry of Agriculture, Fisheries and Food. Her Majesty's Stationery Office, London. 195 p.

Beckett, P. 1972. Critical cation activity ratios. Adv. Agron. 24:379–412.

Beeson, K. C. 1959. Magnesium in soils—sources, availability, and zonal distribution. p. 1–11. *In* D. J. Horvath (ed.) Magnesium and agriculture, symp. proc., West Virginia Univ. W. Va. Agric. Exp. Stn., Morgantown. 217 p.

Birch, J. A., and K. M. Wolton. 1961. The influence of magnesium applications to pasture on the incidence of hypomagnesaemia. Vet. Rec. 73:1169–1173.

Black, C. C., and B. C. Mayne. 1970. P_{700} activity and chlorophyll content of plants with different photosynthetic carbon dioxide fixation cycles. Plant Physiol. 45:738–741.

Blevins, D. G., A. J. Hiatt, and R. H. Lowe. 1974. The influence of nitrate and chloride uptake on expressed sap pH, organic acid synthesis, and potassium accumulation in higher plants. Plant Physiol. 54:82–87.

Bohman, V. R., A. L. Lesperance, G. D. Harding, and D. L. Grunes. 1969. Induction of experimental tetany in cattle. J. Anim. Sci. 29:99–102.

Deuel, H. J., Jr. 1955. The lipids, their chemistry and biochemistry. II. Biochemistry, digestion, absorption, transport, and storage. Interscience Publ., New York.

deWit, C. T., W. Dijkshoorn, and J. C. Noggle. 1963. Ionic balance and growth of plants. Versl. Landbouwk. Onderz. NR. 69.15, Wageningen, the Netherlands.

Dickmann, D. I. 1971. Chlorophyll, ribulose-1, 5-diphosphate carboxylase, and Hill reaction activity in developing leaves of *Populus deltoides*. Plant Physiol. 48:143–145.

Dijkshoorn, W. 1973. Organic acids and their role in ion uptake. p. 163–188. *In* G. W. Butler and R. W. Bailey (ed.) Chemistry and biochemistry of herbage, Vol. 2. Academic Press, New York.

Dijkshoorn, W., D. J. Lathwell, and C. T. deWit. 1968. Temporal changes in carboxylate content of ryegrass with stepwise change in nutrition. Plant Soil 29:369–390.

Doll, E. C., and R. E. Lucas. 1973. Testing soils for potassium, calcium, and magnesium. p. 133–151. *In* L. M. Walsh and J. D. Beaton (ed.) Soil testing and plant analysis. Soil Sci. Soc. Am., Inc., Madison, Wis.

Elkins, C. B., R. L. Haaland, and C. S. Hoveland. 1977. Tetany potential of forage species as affected by soil oxygen. p. 588–594. *In* Proc. 13th Int. Grassland Congr., Leipzig, G.D.R., May 18–27, 1977.

Elkins, C. B., and C. S. Hoveland. 1977. Soil oxygen and temperature effect on tetany potential of three annual forage species. Agron. J. 69:626–628.

Fine, L. O., and D. G. Shannon. 1976. Growth and composition of sudangrass on high-calcium, low-magnesium soil. Agron. J. 68:671–674.

Fleming, A. L., J. W. Schwartz, and C. D. Foy. 1974. Chemical factors controlling the adaptation of weeping lovegrass and tall fescue to acid mine spoils. Agron. J. 66:715–718.

Fleming, G. A. 1973. Mineral composition of herbage. Vol. 1. p. 529–566. *In* G. W. Butler and R. W. Bailey (ed.) Chemistry and biochemistry of herbage. Academic Press, New York.

Fleming, G. A., and W. E. Murphy. 1968. The uptake of some major elements by grass as affected by season and stage of maturity. J. Br. Grassl. Soc. 23:174–184.

Follett, R. F., J. F. Power, D. L. Grunes, D. A. Hewes, and H. F. Mayland. 1975. Potential tetany hazard of N-fertilized bromegrass as indicated by chemical composition. Agron. J. 67:819–824.

Follett, R. F., J. F. Power, D. L. Grunes, and C. A. Klein. 1977. Effect of N, K, and P fertilization, N source, and clipping on potential tetany hazard of bromegrass. Plant Soil 48: 485–508.

Fontenot, J. P. 1972. Magnesium in ruminant animals and grass tetany. p. 131–151. *In* J. B. Jones, M. C. Blount, and S. R. Wilkinson (ed.) Magnesium in the environment: Soils, crops, animals, and man. The Taylor County Printing Co., Reynolds, Ga.

Fontenot, J. P., M. B. Wise, and K. E. Webb, Jr. 1973. Interrelationships of potassium, nitrogen, and magnesium in ruminants. Fed. Proc. 32:1925–1928.

Fowler, H. D. 1963. Grass tetany and histamine. Nature 197:619.

Foy, C. D., H. N. Lafever, J. W. Schwartz, and A. L. Fleming. 1974. Aluminum tolerance of wheat cultivars related to region of origin. Agron. J. 66:751–758.

Frederick, L. R. 1956. The formation of nitrate from ammonium nitrogen in soils: I. Effect of temperature. Soil Sci. Soc. Am. Proc. 20:496–500.

Garner, G. B., S. R. Shaffer, and W. H. Pfander. 1974. Effect of organic acids on Ca and Mg metabolism. J. Anim. Sci. 39:239. (Abstr.)

Garton, G. A. 1969. Digestion and absorption of lipids in the ruminant. Proc. Nutr. Soc. 28: 131–158.

Grace, N. D., and E. Davies. 1975. The distribution of Mg in the digesta of sheep fed fresh pasture. Proc. N.Z. Soc. Anim. Prod. 35:47–50.

Grace, N. D., and G. F. Wilson. 1972. Grass tetany. II. Some observations on plasma levels of Mg, Ca, and P in dairy cows and sheep grazing rye grass and white clover pastures. N.Z. J. Agric. Res. 15:72–78.

Bohman, V. R., D. M. Stuart, and E. I. Hackett. 1977. The mineral composition of Nevada hays as related to grass tetany. p. 137–140. *In* Proc. Western Sec., Am. Soc. Anim. Sci. Brigham Young Univ., Provo, Utah.

Boland, R. L., G. B. Garner, K. H. Asay, and C. J. Nelson. 1976. Organic acid composition of tall fescue leaves from diverse genotypes. Crop Sci. 16:677–679.

Brady, N. C. 1974. The nature and properties of soils, 8th Ed. MacMillan Publ. Co., New York.

Brewster, J. L., and P. B. Tinker. 1970. Nutrient cation flows in soil around plant roots. Soil Sci. Soc. Am. Proc. 34:421–426.

Brougham, R. W., and A. C. Glenday. 1969. Weather fluctuations and the daily rate of growth of pure stands of three grass species. N.Z. J. Agric. Res. 12:125–136.

Brown, W. V. 1977. The Kranz syndrome and its subtypes in grass systematics. Mem. Torrey Bot. Club 23(3):1–100 (entire issue).

Burau, R., and P. R. Stout. 1965. Trans-aconitic acid in range grasses in early spring. Science 150:766–767.

Burt, A. W. A., and D. C. Thomas. 1961. Dietary citrate and hypomagnesaemia in the ruminant. Nature 192:1193.

Camp, B. J., J. W. Dollahite, and W. L. Schwarz. 1968. Biochemical changes in sheep given transaconitic acid. Am. J. Vet. Res. 29:2009–2015.

Campbell, C. A., V. O. Biederbeck, and F. G. Warder. 1971. Influence of simulated fall and spring conditions on the soil system: II. Effect on soil nitrogen. Soil Sci. Soc. Am. Proc. 35:480–483.

Care, A. D., L. E. Vowles, S. O. Mann, and D. B. Ross. 1966. Factors affecting magnesium absorption in relation to the aetiology of acute hypomagnesaemia. J.Agric. Sci. Camb. 68:195–204.

Christenson, D. R., R. P. White, and E. C. Doll. 1973. Yields and magnesium uptake by plants as affected by soil pH and calcium levels. Agron. J. 65:205–206.

Christian, K. R., and V. J. Williams. 1960. Attempts to produce hypomagnesaemia in dry non-pregnant sheep. N.Z. J. Agric. Res. 3:389–398.

Claassen, M. E., and G. E. Wilcox. 1974. Comparative reduction of calcium and magnesium composition of corn tissue by NH_4-N and K fertilization. Agron. J. 66:521–522.

Claassen, N., and S. A. Barber. 1977. Potassium influx characteristics of corn roots and interaction with N, P, Ca, and Mg influx. Agron. J. 69:860–864.

Clark, R. B. 1977. Effect of aluminum on growth and mineral elements of Al-tolerant and Al-intolerant corn. Plant Soil 47:653–662.

Committee on Mineral Nutrition, The Hague. 1973. Tracing and treating mineral disorders in dairy cattle. Center for Agricultural Publishing and Documentation, Wageningen, the Netherlands.

Cox, W. J., and H. M. Reisenauer. 1973. Growth and ion uptake by wheat supplied nitrogen as nitrate, or ammonium, or both. Plant Soil 38:363–380.

Cox, W. J., and H. M. Reisenauer. 1977. Ammonium effects on nutrient cation absorption by wheat. Agron. J. 69:868–871.

Daniel, K., R. L. Reid, and G. A. Jung. 1969. Mineral balance of lactating goats on fertilized hays. J. Anim. Sci. 29:179–180. (Abstr.)

Davies, R. I., Chairman. 1971. Residual value of applied nutrients. Technical Bulletin No. 20. Ministry of Agriculture, Fisheries and Food. Her Majesty's Stationery Office, London. 335 p.

Dawson, R. M. C., and Norma Hemington. 1974. Digestion of grass lipids and pigments in the sheep rumen. Br. J. Nutr. 32:327–340.

Dennis, E. J. 1971. Magnesium deficiency and grass tetany. Is aluminum a key? Fert. Solutions 15(2):44, 46, 50, 51, 52, 54.

Dermott, W., and D. J. Eagle, ed. 1967. Soil potassium and magnesium. Technical Bulletin No. 14. Ministry of Agriculture, Fisheries and Food. Her Majesty's Stationery Office, London. 195 p.

Deuel, H. J., Jr. 1955. The lipids, their chemistry and biochemistry. II. Biochemistry, digestion, absorption, transport, and storage. Interscience Publ., New York.

deWit, C. T., W. Dijkshoorn, and J. C. Noggle. 1963. Ionic balance and growth of plants. Versl. Landbouwk. Onderz. NR. 69.15, Wageningen, the Netherlands.

Dickmann, D. I. 1971. Chlorophyll, ribulose-1, 5-diphosphate carboxylase, and Hill reaction activity in developing leaves of *Populus deltoides*. Plant Physiol. 48:143–145.

Dijkshoorn, W. 1973. Organic acids and their role in ion uptake. p. 163–188. *In* G. W. Butler and R. W. Bailey (ed.) Chemistry and biochemistry of herbage, Vol. 2. Academic Press, New York.

Dijkshoorn, W., D. J. Lathwell, and C. T. deWit. 1968. Temporal changes in carboxylate content of ryegrass with stepwise change in nutrition. Plant Soil 29:369–390.

Doll, E. C., and R. E. Lucas. 1973. Testing soils for potassium, calcium, and magnesium. p. 133–151. *In* L. M. Walsh and J. D. Beaton (ed.) Soil testing and plant analysis. Soil Sci. Soc. Am., Inc., Madison, Wis.

Elkins, C. B., R. L. Haaland, and C. S. Hoveland. 1977. Tetany potential of forage species as affected by soil oxygen. p. 588–594. *In* Proc. 13th Int. Grassland Congr., Leipzig, G.D.R., May 18–27, 1977.

Elkins, C. B., and C. S. Hoveland. 1977. Soil oxygen and temperature effect on tetany potential of three annual forage species. Agron. J. 69:626–628.

Fine, L. O., and D. G. Shannon. 1976. Growth and composition of sudangrass on high-calcium, low-magnesium soil. Agron. J. 68:671–674.

Fleming, A. L., J. W. Schwartz, and C. D. Foy. 1974. Chemical factors controlling the adaptation of weeping lovegrass and tall fescue to acid mine spoils. Agron. J. 66:715–718.

Fleming, G. A. 1973. Mineral composition of herbage. Vol. 1. p. 529–566. *In* G. W. Butler and R. W. Bailey (ed.) Chemistry and biochemistry of herbage. Academic Press, New York.

Fleming, G. A., and W. E. Murphy. 1968. The uptake of some major elements by grass as affected by season and stage of maturity. J. Br. Grassl. Soc. 23:174–184.

Follett, R. F., J. F. Power, D. L. Grunes, D. A. Hewes, and H. F. Mayland. 1975. Potential tetany hazard of N-fertilized bromegrass as indicated by chemical composition. Agron. J. 67:819–824.

Follett, R. F., J. F. Power, D. L. Grunes, and C. A. Klein. 1977. Effect of N, K, and P fertilization, N source, and clipping on potential tetany hazard of bromegrass. Plant Soil 48: 485–508.

Fontenot, J. P. 1972. Magnesium in ruminant animals and grass tetany. p. 131–151. *In* J. B. Jones, M. C. Blount, and S. R. Wilkinson (ed.) Magnesium in the environment: Soils, crops, animals, and man. The Taylor County Printing Co., Reynolds, Ga.

Fontenot, J. P., M. B. Wise, and K. E. Webb, Jr. 1973. Interrelationships of potassium, nitrogen, and magnesium in ruminants. Fed. Proc. 32:1925–1928.

Fowler, H. D. 1963. Grass tetany and histamine. Nature 197:619.

Foy, C. D., H. N. Lafever, J. W. Schwartz, and A. L. Fleming. 1974. Aluminum tolerance of wheat cultivars related to region of origin. Agron. J. 66:751–758.

Frederick, L. R. 1956. The formation of nitrate from ammonium nitrogen in soils: I. Effect of temperature. Soil Sci. Soc. Am. Proc. 20:496–500.

Garner, G. B., S. R. Shaffer, and W. H. Pfander. 1974. Effect of organic acids on Ca and Mg metabolism. J. Anim. Sci. 39:239. (Abstr.)

Garton, G. A. 1969. Digestion and absorption of lipids in the ruminant. Proc. Nutr. Soc. 28: 131–158.

Grace, N. D., and E. Davies. 1975. The distribution of Mg in the digesta of sheep fed fresh pasture. Proc. N.Z. Soc. Anim. Prod. 35:47–50.

Grace, N. D., and G. F. Wilson. 1972. Grass tetany. II. Some observations on plasma levels of Mg, Ca, and P in dairy cows and sheep grazing rye grass and white clover pastures. N.Z. J. Agric. Res. 15:72–78.

Gross, C. F. 1973. Managing magnesium-deficient soils to prevent grass tetany. Soil Conserv. Soc. Am. Proc. Vol. 28. Soil Conservation Society of America, Ankeny, Iowa.

Gross, C. F., and G. A. Jung. 1978. Magnesium, Ca, and K concentration in temperate-origin forage species as affected by temperature and Mg fertilization. Agron. J. 70:397–403.

Grunes, D. L. 1967. Grass tetany of cattle as affected by plant composition and organic acids. p. 105–110. *In* Proc. Cornell nutrition conference for feed manufacturers. (Buffalo, NY). Cornell Univ., Ithaca, N.Y.

Grunes, D. L. 1973. Grass tetany of cattle and sheep. p. 113–140. *In* A. G. Matches (ed.) Anti-quality components of forages. Crop Sci. Soc. Am., Madison, Wis.

Grunes, D. L., and H. F. Mayland. 1975. Controlling grass tetany. USDA Leaflet No. 561. U.S. Government Printing Office, Washington, D.C.

Grunes, D. L., P. R. Stout, and J. R. Brownell. 1970. Grass tetany of ruminants. Adv. Agron. 22:331–374.

Grunes, D. L., J. F. Thompson, J. Kubota, and V. A. Lazar. 1968. Effect of Mg, K, and temperature on growth and composition of *Lolium perenne*. Int. Congr. Soil Sci. Trans. 9th (Adelaide, Australia) II:597–603.

Hannaway, D. B., and J. H. Reynolds. 1976. Seasonal changes in minerals, protein, and yield of tall fescue forage as influenced by nitrogen and potassium fertilization. Tenn. Farm Home Sci. Prog. Rep. 98:14–17.

Hatch, M. D., C. B. Osmond, and R. O. Slatyer. 1971. Photosynthesis and photorespiration. Wiley-Interscience, New York.

Head, M. J., and J. A. F. Rook. 1957. Some effects of spring grass on rumen digestion and the metabolism of the dairy cow. Proc. Nutr. Soc. 16:25.

Henry, P. R., W. H. Smith, and M. D. Cunningham. 1977. Effect of histamine and ammonia on hypomagnesemia in ruminants. J. Anim. Sci. 44:276–281.

Hight, G. K., D. P. Sinclair, and R. J. Lancaster. 1968. Some effects of shading and nitrogen fertilizer on the chemical composition of freeze-dried and oven-dried herbage fed to sheep. N.Z. J. Agric. Res. 11:286–302.

Hill, R. R., Jr., and S. B. Guss. 1976. Genetic variability for mineral concentrations in plants related to mineral requirements of cattle. Crop Sci. 16:680–685.

Hogg, D. E., and F. D. Dorofaeff. 1976. Residual effects of various Mg fertilizers on grassland. N.Z. J. Exp. Agric. 4:127–133.

Horvath, D. J., and J. R. Todd. 1968. Magnesium supplements for cattle. Proc. 23 Texas Nutr. Conf. Texas Agric. Exp. Stn., College station. p. 96–104.

House, W. A., and R. J. Bird. 1975. Magnesium tolerance in goats fed two levels of potassium. J. Anim. Sci. 41:1134–1140.

House, W. A., and H. F. Mayland. 1976. Magnesium utilization in wethers fed diets with varying ratios of nitrogen to readily fermentable carbohydrate. J. Anim. Sci. 43:842–849.

House, W. A., and D. Van Campen. 1971. Magnesium metabolism of sheep fed different levels of potassium and citric acid. J. Nutr. 101:1483–1492.

Jolley, L. C., and D. D. Leaver. 1974. Grass tetany. The mineral species and status of 16 pastures in northeastern Victoria and New South Wales. Aust. Vet. J. 50:98–104.

Jones, E. 1963. Studies of the magnesium content of mixed herbage and some individual grass and clover species. J. Br. Grassl. Soc. 18:131–138.

Jones, J. B. 1972. Magnesium as a limiting factor for crop production in Georgia. p. 331–350. *In* J. B. Jones, M. C. Blount, and S. R. Wilkinson (ed.) Magnesium in the environment: Soils, crops, animals, and man. The Taylor County Printing Co., Reynolds, Ga.

Kemp, A. 1960. Hypomagnesaemia in milking cows: The response of serum magnesium to alterations in herbage composition resulting from potash and nitrogen dressings on pasture. Neth. J. Agric. Sci. 8:281–304.

Kemp, A., W. B. Deijs, O. J. Hemkes, and A. J. H. van Es. 1961. Hypomagnesaemia in milking cows: Intake and utilization of magnesium from herbage by lactating cows. Neth. J. Agric. Sci. 9:134–149.

. Grass tetany hazard of cereal forages
5–667.

. Chemical composition of *Agropyron*
441–446.

orence, D. A. Hewes, and P. K. Joo.
lated to forage quality indices of grass

. Higher fatty acid composition of im-
. J. 68:979–982.

Spectral, physical, and electron trans-
esophyll cells and bundle sheath cells
:600–605.

ffects of applied N, K, and Mg on the
9:389–397.

urces of magnesium for grassland. J.

inter wheat with special reference to

1968. Effect of magnesium fertilisers
ture on Hamilton clay loam. I. Mag-
0.

973a. Effect of some magnesium ferti-
u sandy loam. N.Z. J. Exp. Agric. 1:

K. Cottier. 1973b. Effect of potassi-
on uptake of magnesium by pasture
lc. 1:329–347.

. Some factors governing the availa-
ric. 2:277–319.

lew Zealand soils. II. Distribution of
n soil groups. N.Z. J. Agric. Res. 18:

. W. Graham. 1966. Chemical com-
f breeding cows. N.Z. J. Agric. Res.

wheat plant at different stages of de-
1–167.

emistry of dietary calcium and mag-

letson. 1974. Degradation of higher
ollowing drying and storage. J. Sci.

ss tetany. IV. Relationships between
d herbages. N.Z. J. Agric. Res. 16:

f calcium and magnesium by the or-
I. The organic acids, lignin and cell
gric. 22:393–396.

f calcium and magnesium by the or-
. II.* Complexing of Ca^{2+} and Mg^{2+}
Agric. 22:397–402.

Effect of form and level of nitrogen

magnesium in ryegrass. Some differ-
o shoots. Plant Soil 44:623–637.

Murray, R. B., H. F. Mayland, and P. J. Van Soest.
cattle of grasses on cheatgrass range in southern I
p. Intermtn. For. and Range Exp. Stn., Ogden, U

Nason, Alvin, and W. D. McElroy. 1963. Modes of a
p. 451–536. *In* F. C. Steward (ed.) Plant physi
plants. Academic Press, New York.

Nelson, W. E., and J. B. Jones. 1972. Evaluation of m
225. *In* J. B. Jones, M. C. Blount, and S. R. Will
ment: Soils, crops, animals, and man. The Tayl

Neumark, H., and A. Tadmor. 1968. The effect of his
acid on food intake and rumen motility, when
Agric. Sci. Camb. 71:267–270.

Nielsen, K. F., and R. K. Cunningham. 1964. The ef
level of nitrogen on growth and chemical compo
Am. Proc. 28:213–218.

Noller, C. H., and C. L. Rhykerd. 1974. Relationship
composition of forage to animal health and perf
(ed.) Forage fertilization. Am. Soc. Agron., Madi

Okolo, T. O. 1977. Serum, calcium, magnesium, fre
tating cows. Diss. Abstr. 77:431-B.

Okolo, T. O., J. A. Boling, N. Hay, and N. W. Brad
and FFA in hypomagnesemic beef cows. J. Anim.

Oliver, S., and S. A. Barber. 1966. An evaluation of th
Ca, Mg, K, and Na to soybean roots (*Glycine max*

O'Sullivan, M. 1968. Grass tetany—effects of enviro
tamine levels. J. Sci. Food Agric. 19:12–15.

Powell, K., R. L. Reid, and J. A. Balasko. 1978. Perfor
smooth brome, orchardgrass, and tall fescue pa
digestibility and chemical composition. J. Anim. S

Powley, G., A. D. Care, and C. L. Johnson. 1977.
faecal magnesium excretion from sheep eating gra
concentrations. Res. Vet. Sci. 23:43–46.

Price, N. O., and W. W. Moschler. 1970. Residual lin
ments in barley, fescue, and oats. J. Agric. Food C

Prior, R. L., D. L. Grunes, R. P. Patterson, F. W. Sm
1973. Partition column chromatography for quan
acids. J. Agric. Food Chem. 21:73–77.

Reid, R. L., K. Daniel, and J. D. Bubar. 1974. Min
maintained on orchardgrass fertilized with diff
elements, over a five-year period. Vol. 3, Part 1.
A. P. Movsissyants (ed.) Proc. XII Int. Grassl. Con

Reid, R. L., and G. A. Jung. 1974. Effect of element
value of forage. *In* D. Mays (ed.) Forage fertilizat

Reid, R. L., G. A. Jung, and C. F. Gross. 1978a. Gras
eastern United States. *In* Proc. int. hill land symp
town, W. Va. (in press).

Reid, R. L., G. A. Jung, I. J. Roemig, and R. E. Koche
and guinea pigs fed Mg-fertilized grass and legume

Reid, R. L., A. J. Post, and G. A. Jung. 1970. Mineral
Agric. Exp. Stn. Bull. 589T. 35 p.

Roberts, S., and W. H. Weaver. 1974. Magnesium a
sudan grass as influenced by potassium, calcium,
Anal. 5:303–312.

Robertson, J. A., and J. C. Hawke. 1965. Studies on ru
hydrate on ammonia levels in the rumen of pastur
bated with ryegrass extracts. J. Sci. Food Agric. 16:

Murray, R. B., H. F. Mayland, and P. J. Van Soest. 1978. Growth and nutritional value to cattle of grasses on cheatgrass range in southern Idaho. USDA-FS Res. Pap. INT-199, 57 p. Intermtn. For. and Range Exp. Stn., Ogden, Utah.

Nason, Alvin, and W. D. McElroy. 1963. Modes of action of the essential mineral elements. p. 451–536. *In* F. C. Steward (ed.) Plant physiology. Vol. III. Inorganic nutrition of plants. Academic Press, New York.

Nelson, W. E., and J. B. Jones. 1972. Evaluation of magnesium soil testing methods. p. 217–225. *In* J. B. Jones, M. C. Blount, and S. R. Wilkinson (ed.) Magnesium in the environment: Soils, crops, animals, and man. The Taylor County Printing Co., Reynolds, Ga.

Neumark, H., and A. Tadmor. 1968. The effect of histamine combined with formic or acetic acid on food intake and rumen motility, when infused into the omasum of a ram. J. Agric. Sci. Camb. 71:267–270.

Nielsen, K. F., and R. K. Cunningham. 1964. The effects of soil temperature and form and level of nitrogen on growth and chemical composition of Italian ryegrass. Soil Sci. Soc. Am. Proc. 28:213–218.

Noller, C. H., and C. L. Rhykerd. 1974. Relationship of nitrogen fertilization and chemical composition of forage to animal health and performance. p. 363–394. *In* D. A. Mays (ed.) Forage fertilization. Am. Soc. Agron., Madison, Wis. 621 p.

Okolo, T. O. 1977. Serum, calcium, magnesium, free fatty acids, and urea nitrogen in lactating cows. Diss. Abstr. 77:431-B.

Okolo, T. O., J. A. Boling, N. Hay, and N. W. Bradley. 1976. Serum Ca, Mg, K, glucose, and FFA in hypomagnesemic beef cows. J. Anim. Sci. 43:329. (Abstr.)

Oliver, S., and S. A. Barber. 1966. An evaluation of the mechanisms governing the supply of Ca, Mg, K, and Na to soybean roots (*Glycine max*). Soil Sci. Soc. Am. Proc. 30:82–86.

O'Sullivan, M. 1968. Grass tetany—effects of environment and fertilizers on pasture histamine levels. J. Sci. Food Agric. 19:12–15.

Powell, K., R. L. Reid, and J. A. Balasko. 1978. Performance of lambs on perennial ryegrass, smooth brome, orchardgrass, and tall fescue pastures. II. Mineral utilization *in vitro* digestibility and chemical composition. J. Anim. Sci. 46:1503–1514.

Powley, G., A. D. Care, and C. L. Johnson. 1977. Comparison of the daily endogenous faecal magnesium excretion from sheep eating grass with high sodium or high potassium concentrations. Res. Vet. Sci. 23:43–46.

Price, N. O., and W. W. Moschler. 1970. Residual lime effect in soil on certain mineral elements in barley, fescue, and oats. J. Agric. Food Chem. 18:5–8.

Prior, R. L., D. L. Grunes, R. P. Patterson, F. W. Smith, H. F. Mayland, and W. J. Visek. 1973. Partition column chromatography for quantitating effects of fertilization on plant acids. J. Agric. Food Chem. 21:73–77.

Reid, R. L., K. Daniel, and J. D. Bubar. 1974. Mineral relationships in sheep and goats maintained on orchardgrass fertilized with different levels of nitrogen with microelements, over a five-year period. Vol. 3, Part 1. p. 426–437. *In* V. G. Iglovikov and A. P. Movsissyants (ed.) Proc. XII Int. Grassl. Congr., Moscow, U.S.S.R.

Reid, R. L., and G. A. Jung. 1974. Effect of elements other than nitrogen on the nutritive value of forage. *In* D. Mays (ed.) Forage fertilization. Am. Soc. Agron., Madison, Wis.

Reid, R. L., G. A. Jung, and C. F. Gross. 1978a. Grass tetany as a metabolic problem in the eastern United States. *In* Proc. int. hill land symp. West Virginia Univ Press, Morgantown, W. Va. (in press).

Reid, R. L., G. A. Jung, I. J. Roemig, and R. E. Kocher. 1978b. Mineral utilization by lambs and guinea pigs fed Mg-fertilized grass and legume hays. Agron. J. 70:9–14.

Reid, R. L., A. J. Post, and G. A. Jung. 1970. Mineral composition of forages. W. Va. Univ. Agric. Exp. Stn. Bull. 589T. 35 p.

Roberts, S., and W. H. Weaver. 1974. Magnesium accumulation and mineral balance in sudan grass as influenced by potassium, calcium, and sodium. Commun. Soil Sci. Plant Anal. 5:303–312.

Robertson, J. A., and J. C. Hawke. 1965. Studies on rumen metabolism. IV. Effect of carbohydrate on ammonia levels in the rumen of pasture-fed cows and in rumen liquors incubated with ryegrass extracts. J. Sci. Food Agric. 16:268–276.

Rook, J. A. F., and R. C. Campling. 1962. Magnesium metabolism in the dairy cow. 4. The availability of the magnesium in various feeding stuffs. J. Agric. Sci. 59:225–232.

Rosero, O., R. E. Tucker, G. E. Mitchell, Jr., G. T. Schelling, and W. C. Templeton, Jr. 1975. Magnesium balance in sheep fed early spring dehydrated forages. J. Anim. Sci. 41:415. (Abstr.)

Sabbe, W. E., L. Hilman, D. Scott, and R. Maples. 1972. Status of magnesium in certain Arkansas field and forage crops. p. 291–307. *In* J. B. Jones, Jr., M. C. Blount, and S. R. Wilkinson (ed.) Magnesium in the environment: Soils, crops, animals, and man. The Taylor County Printing Co., Reynolds, Ga.

Salmon, R. C. 1964. Cation-activity ratios in equilibrium soil solutions and the availability of magnesium. Soil Sci. 98:213–221.

Scotto, K. C., V. R. Bohman, and A. L. Lesperance. 1971. Effect of oral potassium and sodium chloride on plasma composition of cattle: A grass tetany related study. J. Anim. Sci. 32:354–358.

Simesen, M. G. 1959. Experimental hypomagnesaemia. Comm. 16th Int. Vet. Congr., Madrid 2:85–87.

Sleper, D. A., G. B. Garner, K. H. Asay, R. Boland, and E. E. Pickett. 1977. Breeding for Mg, Ca, K, and P content in tall fescue. Crop Sci. 17:433–438.

Smith, R. H. 1969. Absorption of major minerals in the small and large intestine of the ruminant. Proc. Nutr. Soc. 28:151–160.

Smith, R. H., and A. B. McAllan. 1966. Binding of magnesium and calcium in the contents of the small intestine of the calf. Br. J. Nutr. 20:703–718.

Stillings, B. R., J. W. Bratzler, L. F. Marriott, and R. C. Miller. 1964. Utilization of magnesium and other minerals by ruminants consuming low and high nitrogen-containing forages and vitamin D. J. Anim. Sci. 23:1148–1154.

Storry, J. E. 1961. Studies on calcium and magnesium in the alimentary tract of sheep. J. Agric. Sci. Camb. 57:103–109.

Stout, P. R., J. Brownell, and R. G. Burau. 1967. Occurrences of *trans*-aconitate in range forage species. Agron. J. 59:21–24.

Stout, W. L., D. P. Belesky, G. A. Jung, R. S. Adams, and B. L. Moser. 1977. A survey of Pennsylvania forage mineral levels with respect to dairy and beef cow nutrition. Pa. Agric. Exp. Stn., Prog. Rep. 364.

Stuart, D. M., H. F. Mayland, and D. L. Grunes. 1973. Seasonal changes in *trans*-aconitate and mineral composition of crested wheatgrass in relation to grass tetany. J. Range Manage. 26:113–116.

Sykes, A. R., A. C. Field, and J. Slee. 1969. Cold exposure of Southdown and Welsh mountain sheep. III. Changes in plasma calcium, phosphorus, magnesium, sodium, and potassium levels. Anim. Prod. 11:91–99.

Teel, M. R. 1966. Nitrogen-potassium relationships and their influence on some biochemical intermediates and quality of crude protein in forages. p. 465–480. *In* Potassium symp. 1966. Brussels, Belgium. Potash Inst., Berne, Switzerland.

't Hart, M. L. 1960. Factors influencing the incidence of hypomagnesaemia: II. The influence of meteorological conditions and fertilizer treatment on pasture in relation to hypomagnesaemia. Proc. Br. Vet. Assoc. The Victoria Hall, London. p. 88–95.

Thill, J. L., and J. R. George. 1975. Cation concentrations and K to Ca+Mg ratio of nine cool-season grasses and implications with hypomagnesaemia. Agron. J. 67:89–91.

Tingle, J. N., and C. R. Elliott. 1975. Forage yield and quality of cultivated perennial grasses harvested at the early heading stage. Can. Plant Sci. 55:271–278.

Todd, J. R. 1962. Magnesium in forage plants. III. Magnesium distribution in pastures of low magnesium content. J. Agric. Sci. 58:277–279.

van Tuil, H. D. W., J. E. M. Lampe, and W. Dijkshoorn. 1964. The possibility of relating the ash alkalinity to the organic-salt content. Jaarboek I.B.S. (Yearbook for the Institute for Biological and Chemical Research on Field Crops and Herbage), Wageningen, the Netherlands 250:157–160.

van't Klooster, A. Th. 1967. The state of calcium, magnesium, and some other minerals in gut contents and faeces of ruminants in relation to their absorption. Meded. Landbouwhogesch. Wageningen, the Netherlands. 67-5. 136 p.

Wilcox, G. E., and J. E. Hoff. 1974. Grass tetany: An hypothesis concerning its relationship with ammonium nutrition of spring grasses. J. Dairy Sci. 57:1085–1089.

Wilkinson, S. R., J. A. Stuedemann, J. B. Jones, W. A. Jackson, and J. W. Dobson. 1972. Environmental factors affecting magnesium concentrations and tetanigenicity of pastures. p. 153–175. *In* J. B. Jones, M. C. Blount, and S. R. Wilkinson (ed.) Magnesium in the environment: Soils, crops, animals, and man. The Taylor County Printing Company, Reynolds, Ga.

Wilkinson, S. R., J. A. Stuedemann, D. J. Williams, J. B. Jones, R. N. Dawson, and W. A. Jackson. 1971. Recycling broiler house litter on tall fescue pastures at disposal rates and evidence of beef cow health problems. p. 321–324, 328. *In* Livestock waste management and pollution abatement. Int. symp. livestock wastes proc. (Columbus, Ohio). Am. Soc. Agric. Eng., St. Joseph, Mich.

Wilson, G. F., C. S. W. Reed, L. F. Molloy, A. J. Metson, and G. W. Butler. 1969. Grass tetany. 1. Influence of starch and peanut oil supplements on plasma magnesium, calcium, and phosphorus levels in grazing dairy cows. N.Z. J. Agric. Res. 12:467–488.

Wind, I. J. 1958. Relationship between the mineral composition of pasture and grass tetany and other mineral disorders. p. 93–123. *In* Control of diseases in cattle and sheep at pasture. European Productive Agency of Organizations for European Economic Cooperation, Rue Andre-Pascal, Paris 16.

Wind, J., W. B. Deijs, and A. Kemp. 1966. Higher fatty acids in feed and their possible role in hypomagnesaemia on pastures. Jaarboek Instituute voor Biologisch en Scheikungid Onderzoek val Landbouwgewassen. Wageningen, the Netherlands. 322:91–100.

Wright, D. E. 1971. Citric acid metabolism in the bovine rumen. Appl. Microbiol. 21:165–168.

Wright, D. E., and J. E. Wolff. 1969. *Trans*-aconitic acid and the magnesium status of guinea pigs and sheep. N.Z. J. Agric. Res. 12:287–292.

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