6 Mineral Nutrition[1]

H. F. MAYLAND

USDA-ARS
Kimberly, Idaho

S. R. WILKINSON

USDA-ARS
Watkinsville, Georgia

Many reviews have been published on plant mineral nutrition. Some of these are specific for forages. Fertilization of forages, including cool-season grasses was reviewed in a book edited by Mays (1974). Wilkinson and Mays (1979) reviewed the mineral nutrition of tall fescue, and Turner (1993) discussed nutrient deficiencies and toxicities of turfgrass. The most thorough treatment of mineral nutrition of higher plants was provided by Marschner (1986). The chemical composition of cool-season grasses was presented in Spedding and Diekmahns (1972). Shuman (1994) provides information on uptake, translocation, and enzyme activity of mineral elements. Trace elements in soils and plants were thoroughly discussed by Kabata-Pendias and Pendias (1992). Barber (1995) has published a mechanistic approach to soil nutrient bioavailability. Graham and Webb (1991) reviewed the role of micronutrients and disease resistance and tolerance in plants. Nicholas and Egan (1975), Reid and Horvath (1980), and Spears (1994) provided excellent reviews of minerals in the soil–forage plant–animal system. This chapter presents details about minerals in the soil/cool-season grass/animal system compiled for those interested in production and herbage utilization of cool-season grasses.

ELEMENTAL REQUIREMENTS

Plants

Plant growth is dependent upon available water, solar radiation, C, H, O, and at least 13 mineral elements (Marschner, 1986). Six of these (N, K, Ca, Mg, P, and S) are macronutrients. They normally occur in plants at concentrations greater than 1 g kg^{-1} (30 mmol kg^{-1}) level (Table 6–1). The remaining seven

[1] Common names for plants have been used throughout the chapter. Refer to the appendix for the scientific name.

Copyright © 1996 American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, 677 S. Segoe Rd., Madison, WI 53711, USA. *Cool-Season Forage Grasses*, Agronomy Monograph no. 34.

Table 6-1. "Normal" concentrations of elements in cool-season grass herbage that are sufficient for adequate growth in plants, arranged in order of the relative abundance in plant tissue.

Element	Symbol	Probable form for absorption‡	Concentration¶		
			μmol kg^{-1} DM§	mg kg^{-1} DM	g kg^{-1} DM
Iodine†	I	I^-	1	0.1	--
Molybdenum	Mo	MoO_4^{2-}	1	0.1	--
Nickel	Ni	Ni^{2+}	1	0.1	--
Selenium†	Se	SeO_3^{2-}, SeO_4^{2-}	1	0.1	--
Cobalt†	Co	Co^{2+}	3	0.2	--
Chromium†	Cr	Cr^{6+}, Cr^{3+}	4	0.2	--
Copper	Cu	Cu^{2+}, Cu^+	100	6	--
Zinc	Zn	Zn^{2+}	300	20	--
Manganese	Mn	Mn^{2+}	1 000	50	--
Boron	B	H_3BO_3	2 000	20	--
Iron	Fe	Fe^{2+}, Fe^{3+}	2 000	100	--
Chlorine	Cl	Cl^-	3 000	100	--
Sodium†	Na	Na^+	13 000	300	--
Sulfur	S	SO_4^{2-}, SO_2	60 000	--	2
Phosphorus	P	$H_2PO_4^-$, HPO_4^{2-}	60 000	--	2
Magnesium	Mg	Mg^{2+}	80 000	--	2
Calcium	Ca	Ca^{2+}	100 000	--	4
Silicon†	Si	$Si(OH)_4$	200 000	--	5
Potassium	K	K^+	500 000	--	20
Nitrogen	N	NH_4^+, NO_3^-	2 000 000	--	25
Oxygen	O	O_2, H_2O	30 000 000	--	430
Carbon	C	CO_2, HCO_3^-	40 000 000	--	450
Hydrogen	H	H_2O	60 000 000	--	55

† Requirement not established for cool-season grasses, but these elements are required for animal nutrition.
‡ Data adapted from Follett and Wilkinson (1995).
§ DM = dry matter.
¶ Data are for cool-season grasses (Mayland, unpublished).

micronutrients or trace elements (B, Cl, Cu, Fe, Mn, Mo, and Zn) normally occur in plants at concentrations less than 3 mg kg^{-1}. Trace amounts of other elements (e.g., Co, Na, Ni, and Si) may be beneficial for plants (Marschner, 1986). For example, Si is commonly found in many cool-season grasses as an important structural component of cell walls, trichomes, and rasplike leaf margins. Silicon in grasses provides protection against various herbivory (McNaughton et al., 1985). Nickel has been identified as required for plants in ultrasmall amounts (Brown et al., 1990).

For an element to be essential for the growth of plants. it should meet the following three criteria (Marschner, 1986):

1. The organism cannot complete its life cycle without the element.
2. The function of the element must not be replaceable by another element.
3. The function of the element must be direct. For example, it must be part of an essential plant constituent such as an enzyme or be required for metabolism.

Table 6–2. Nutrient element concentrations in cool-season grasses in relation to ruminant requirements (see discussion for interactions).†

Element	Cool-season grasses		Dietary requirements§	
	Critical minimum‡	Normal range	Sheep	Cattle
	g kg^{-1}			
Ca	<2	3–6	3–4	3–4
Cl	0.3–1.2	1–5	1	2
Mg	1	1–3	1	2
N	25–35	20–40	10–15	10–15
P	2–3	2–4	2	2
K	20–30	20–50	3	8
Si	NR¶	2–20	NR	NR
Na	NR	<1–3	1	1–2
S	2–3	1–3	1–2	1–2
	mg kg^{-1}			
B	<3	5–15	NR	NR
Cu	4	5–30	5–6	7–10
F	NR	1–20	NR	NR
Fe	<50	50–150	40	40
Mn	20	30–100	25	25
Mo	<0.1	0.1–2	<0.1	<0.1
Zn	10–14	15–60	25	25
	μg kg^{-1}			
Co	NR	50–300	100	60
Cr	NR	200–1000	Trace	Trace
I	NR	40–800	500	500
Ni	--	200–1000	100–800	100–800
Se	NR	10–500	30–200	40–300

† Herbage data are generalized from Fageria et al. (1991), Gough et al. (1979), Jones and Thomas (1987), Marschner (1986), Mayland (1986, unpublished), Mays (1974), Murray et al. (1978), and Reid et al. (1970). Animal data are generalized from Grace (1994), Grace and Clark (1991), Jones and Thomas (1987), NRC (1984, 1985, 1989). Fluorine while not required by animals is beneficial to bones and teeth. See Table 6–4 for additional considerations.

‡ Growth is reduced when test values are less than those shown for plants at vegetative to boot stage.

§ Dietary requirements are for growing sheep and lactating cattle. Requirements may be different for other animal classes.

¶ NR = not required for nutrition.

The second criterion may be too restrictive. For example, Cl is necessary for growth in higher plants; but other halides (e.g., Br at higher concentrations) can substitute for Cl. Thus, Br functions in plant metabolism. The term "functional nutrient" can include any mineral element that functions in plant metabolism, whether or not its action is specific.

Animals

The cool-season grasses, when grown for forage, often serve as the sole source of energy, proteins, fats, vitamins, and most minerals for grazing animals. Thus, forage producers must consider mineral nutrient needs for both plant growth

and animal maintenance and production. Mineral elements required by animals include the macroelements Ca, Cl, K, Mg, N, Na, P, and S; the trace elements Co, Cu, Fe, I, Mn, Mo, Se, and Zn; and the ultra-trace elements Cr, Li, and Ni (NRC, 1984, 1985, 1989). Some elements like Cr, Cl, Fe, K, Li, Mo, and Ni are generally present in the herbage at levels exceeding animal requirements (Table 6–2).

The list of macroelements for livestock, is like that for the grasses, but with the addition of Cl and Na. These two elements are generally supplemented to animals as NaCl salt. The salt matrix also may contain Co, Cu, Fe, I, Se, and Zn to supplement mineral levels in the herbage. Iodine deficiency is often encountered in the interior of large continental land masses like the northern half of the USA and Canada. Thus I is often added to salt for human and livestock use.

Drinking water may provide additional Zn, because of flow through or storage in galvanized metal pipe and water troughs. Dust contamination (exogenous) on herbage may contain sufficient amounts of Fe, Mn and other elements, to complement that absorbed by the plant (endogenous) and thereby meet animal requirements for them (Mayland et al., 1977). The direct ingestion of soil from select natural areas known as salt licks also may supplement the intake of some minerals.

GROWTH (YIELD) RESPONSE: PRINCIPLES

Law of the Minimum

The amount of plant growth in a given environment depends on quantity and balance of growth-determining factors, with the least optimum factor limiting growth. This concept is the Principle of Limiting Factors or Liebig's Law of the Minimum and is extremely useful. However, two additional aspects must be considered. First, Liebig's Law of the Minimum applies to conditions where inflows and outflows of energy, minerals, and other factors are balanced (steady-state condition); e.g., where forage growth is limited by N, a sudden increase in available N may remove N as the limiting factor. During the transitional period to a new production level, the next limiting factor or factors may be difficult to identify until a new steady-state condition is established. Second, factors interact to modify effects of individual factors. Thus, when solar radiation, temperature and soil water are nonlimiting, fertilizer requirements are higher than when such factors are limiting. Pasture-, range-, or forage-land productivity is controlled primarily by temperature, water (rainfall), soil fertility, and defoliation (grazing) management.

All green plants require the same essential elements for growth. Various forage plants differ in their abilities to extract nutrients from the soil in required amounts because of differences in their responses to the range of soil and climatic conditions. Forage yield multiplied by nutrient concentration equals nutrient uptake. Yield is usually the most important factor in nutrient removal by forage crops. Nutrient removal is an important part of plant-nutrient requirement (fertilizer requirement).

Table 6–3. Deficient, critical, and adequate levels of NH_4HCO_3-DPTA-extractable macro- and micronutrients in alkaline soils as determined necessary for growth of cool-season grasses and cereal forages (Mayland, 1983).

Nutrient	Nutrient concentration extracted from soil		
	Deficient	Critical	Adequate
	mg kg^{-1}		
P	<3	4–7	8–11
P†	(7)	(8–14)	(15–22)
K‡	<60	61–120	>120
Zn	<0.9	1–1.5	>1.5
Fe	<2	2–4	>4
Cu	<0.5	0.5	>0.5
Mn	<1.8	1.8	>1.8

† Values in parenthesis are for $NaHCO_3$-extractable soil P.
‡ Similar ranges were identified for ammonium-acetate-extractable K.

Fertilizer and Plant Nutrient Requirements

Fertilizer requirement is the amount of a nutrient needed (beyond that supplied by the soil) to increase plant growth to a desired or optimum level (external nutrient requirement). The amount of soil nutrient available to the plant may be determined by various chemical or biological tests. Chemical extractants and procedures vary in different geographic regions. Soil test extractants and procedures are calibrated to provide reliable indication of the particular nutrient status of groups of soils. The reader is referred to Brown (1987) for detailed discussion of soil testing to evaluate external plant nutrient status. Specific soil test values for various levels of nutrient sufficiency should be obtained from organizations having responsibility for that geographic region. Internal nutrient requirements are those concentrations needed in plant tissue for a given yield level. Yield levels often are expressed as a percentage of maximum, for that environment (Table 6–3).

Crop yield and quality responses, as a function of nutrient input or plant concentration, may be separated into four zones: *deficiency*, or inadequate to complete a life cycle; *critical nutrient range* (CNR), where near maximum yields are obtained with minimum amounts of nutrients; *adequacy*, where no further changes in yield occur; and *yield depression*, where yield decreases occur with increasing nutrient concentrations (Fig. 6–1). Yield depression may be caused by nutrient toxicity, imbalance, or antagonism leading to deficiency of another nutrient. The reader is referred to Black (1993) for a comprehensive discussion of soil fertility evaluation and control. Relationships between concentrations in plant tissue and yield increases from adding fertilizer also are described succinctly in Beeson and Matrone (1976).

Research that covers the full range of response is important for biological, economic, and environmental reasons. Plant and soil analyses help prevent yield and stand losses while identifying optimum fertilization practices allowing the achievement of full production potential of the soil, crop, and environment. Such

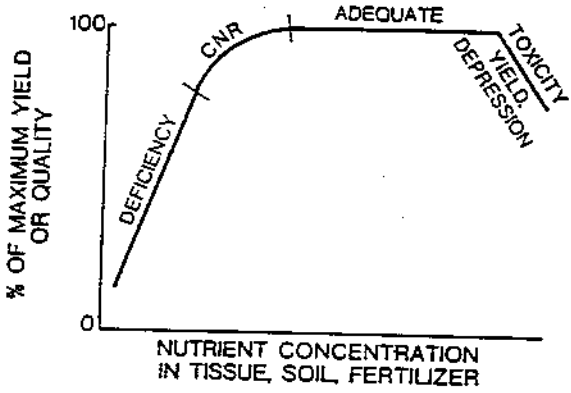

Fig. 6–1 Conceptual yield response to increasing levels of an essential nutrient measured in tissue, soil, or fertilizer. Plant response to increasing nutrient levels; progresses from deficient nutrient range, to critical nutrient range (CNR), adequate nutrient range, and finally to yield depression because of excess nutrient.

analyses help diagnose nutrient excesses, conserve nonrenewable resources, and prevent negative impacts on the environment caused by overfertilization.

Animal performance and health also are important criteria in evaluating fertilizer requirement. Yields of animal products are controlled by the effective utilization of increased forage yield and forage quality produced by the fertilizer.

Cation-Anion Balance

Biological systems such as plant cells, tissues, and soil systems operate under the principle of electrical neutrality. That is, the total sum of anion equivalents in plant tissue is equal to the sum of cation equivalents. Since the uptake of ions like NO_3^- or K^+ is rapid, while the uptake of ions like Ca^{2+} or SO_4^{2-} is slow, cations and anions are removed from the soil in unequal amounts. These cation–anion imbalances are compensated within plant tissue by the degradation, or accumulation of organic acids, particularly malate (Mangel & Kirkby, 1987).

Ionic balance is maintained within the soil by H^+, or OH^- (HCO_3^-) accumulation (Mengel & Kirkby, 1987). This aspect of mineral nutrition can significantly affect mineral composition and organic acid composition. For example, the application of K_2SO_4 fertilizer can result in more rapid uptake of K than SO_4^{2-}, creating an imbalance compensated within the plant by the production of organic anion equivalents (malic acid). On the other hand, KCl fertilizer may not result in this cation–anion imbalance because K and Cl uptake rates are similar. These cation–anion relationships in grass may affect growth rates, mineral concentrations, and concentrations of organic acids in the plant. These can affect Mg uptake by the plant and bioavailability of herbage Mg to the grazing animal.

Reduced bioavailability of Mg may cause grass tetany (Hypomagnesemia) in grazing animals. Among the noninfectious diseases, economic losses from this disorder are probably second only to bloat in ruminants. Grunes et al. (1985) found that high rates of N and K fertilization or high rates of broiler litter fertilization more than doubled malate concentrations in 'Kentucky 31' tall fescue,

Table 6-4. Critical element concentrations in immature leaves of perennial ryegrass (adapted from Smith et al., 1985).†

Element	Elemental concentration	
	90% maximum yield	99% maximum yield
	g kg^{-1} DM‡	
N (kjeldahl)	32	44
Nitrate-N	0.5	1.0
K	28	38
P	2.1	4.4
S	1.8	2.5
Mg	0.7	1.0

† Plants were grown in glasshouse under conditions suitable for maximum vegetative growth and harvested at grazing height of 4 to 15 cm.
‡ DM = dry matter.

thus increasing the grass tetany potential of the grass. Grass tetany is discussed further under antiquality components.

Chemical Tests

Bioavailability testing of soil elements has concentrated on cultivated crops and legumes. Critical soil test levels of several elements are shown in Table 6.3 for cool-season grasses and cereal forages grown on alkaline soils. More reliable measures of mineral element availability depend on plant tissue analysis (Table 6–4). Data for critical, adequate and high nutrient concentration in tissue are shown in Table 6–5.

Several studies have assessed the fertilizer influence on animal dietary requirements (Lightner et al., 1983; Reid et al., 1984). Their test values are similar to those shown in Table 6–5.

Table 6–5. Critical, adequate, and high nutrient ranges in whole-plant tissue for growth of cool-season grasses and cereal forages (Mayland, 1983).

Nutrient	Nutrient concentration in tissue		
	Critical	Adequate	High
	g kg^{-1}		
N	1.5–2.0	2.1–3.0	>3.0
P	0.15–0.20	0.21–0.5	>0.5
K	1.2–1.5	1.6–2.5	>2.5
Ca	<0.20	0.20–0.5	>0.5
Mg	<0.13	0.14–0.4	>0.4
S	0.15–0.19	0.2–0.4	>0.4
	mg kg^{-1}		
Zn	10–14	20–50	50–300
B	<3	3–40	41–50
Mn	15–20	20–100	100–250
Fe	<20	20–250	>250
Cu	3–5	6–15	16–30

Fertilization to Maintain Grass/Legume Associations

Cool-season grass–legume associations are particularly important in ruminant livestock production. The legume provides high quality feed. The legume–*Rhizobium* association fixes atmospheric N for use by the alfalfa and by companion grass. The grass provides quality and quantity of feed. Effective transfer of fixed N from the legume to the grass occurs primarily through legume residue decomposition and transfer by the grazing animal through its excreta (Russelle, 1992). The quantity of N available, however, is often less than that required for maximum grass production. Active and passive release of soluble N materials occur from the legume. And there are genetic differences within crested wheatgrass, and presumably other grass species, that affect the competitiveness of their ability to scavenge the N released by the legume (Asay & Mayland, 1991).

Plant nutrients are absorbed by plant roots from soil solution. Their occurrence at the absorbing surface of the root is determined by mass flow, diffusion, and extension of roots into new soil volumes. The amount of nutrient arriving at the root surface by mass flow depends on the concentration of nutrients in the water that moves to the root surface as a result of water use by the plant (Barber, 1984). The amount arriving by diffusion depends on temperature, the diffusion coefficient of the nutrient, the concentration gradient between the soil mass and root surface, soil water content, porosity and tortuosity of the soil, and total root surface area available for absorption. Root extension into unexplored soil areas increases both amount and rate of nutrient supply. The amount absorbed is a function of the concentration arriving at the root surface.

Since grass-legume associations occupy the same soil volume, competition exists for water and nutrients contained in the shared root zone. Cool-season grasses and legumes may differ greatly in their root morphology, growth rates, and physiology (Mengel & Kirkby, 1987; Barber, 1984). Generally, grasses have fibrous, extensively branched root systems that permeate the soil. In contrast, legumes have sparsely branched tap roots that do not intensively exploit soil volumes. Consequently, root surface areas of grasses in the fertile top soil volume are generally much greater than root surface areas of legumes. However, soil biota and abiotic conditions may modify root morphology and extent to a high degree.

Because of the *Rhizobium*–legume association, legumes have a competitive advantage over grasses on N-deficient soils. However, grasses have a competitive advantage in P- or K-deficient soils because of their greater root surface area and root exploitation of a larger soil volume. Presence of vesicular arbuscular mycorrhizae (VAM) in association with roots can effectively increase root surface area, increasing nutrient and water scavenging ability. The VAM are considered more helpful to tap-rooted forage species such as legumes than for fibrous rooted species such as grasses. They also may be more important for warm-season than for cool-season grasses (Hetrick et al., 1988).

Fertilizer requirements of cool-season legumes for P in competition with cool-season grasses also may be higher than for cool-season grasses (Wilkinson & Lowrey, 1973). Fertilization for maintenance of grass–legume associations usually requires higher P fertilization to meet the P requirements of the associa-

tion than for grass monoculture. The concentrations of P in legume tissue are often higher and the ability to obtain the P from the soil may be lower for tap-rooted legumes, hence the greater significance of P fertilization for legumes in association with grasses (Wilkinson & Lowrey, 1973).

Nitrogen fertilization stimulates cool-season grass growth and increases grass competitiveness. This sometimes results in unwanted shifts in grass/legume association balance to fewer legumes (Stern & Donald, 1962). Build-up of N in the soil from biologically fixed N also may encourage grasses to the detriment of the legume. About 20 to 30% legume in association with cool-season grass may be desirable for longevity of the mixed stand. Such an association provides sufficient transfer of N to sustain grass growth without stimulation of the grass to the detriment of the legume (maintenance of the grass in a slightly N-deficient mode). Potassium fertilization to meet the legume requirement is essential. The ability of grasses to absorb K far in excess of their needs, sometimes to the point where insufficient available K remains in the soil for the legume, is an important factor affecting fertilization to maintain grass–legume associations (Follett & Wilkinson, 1995).

Mineral and forage quality data are presented for samples of hay and silage analyzed by the Dairy Herd Improvement Association (DHIA) forage lab in Ithaca, New York (Table 6–6). Since 80% of the samples originated from New York and the Northeast, it is assumed that cool-season grasses are the dominant grasses analyzed. The data show the relative value of legume vs. grass herbage. Except for Na, Mn, Zn, and NO_3^-, legumes have higher concentrations of minerals than grasses.

GRASS TOLERANCE TO SOIL CONDITIONS

Soil Acidity

The impact of soil acidity on cool-season grass growth is dependent on many factors besides the species and cultivar of grass. Soil acidity may be detrimental to plant growth because of direct or indirect effects of pH. The indirect effects are: (i) increased solubility of toxic elements, (ii) decreased availability of essential nutrients, and (iii) repressed activity of desirable soil microorganisms (Pearson & Hoveland, 1974). For example, a combination of Al and Mn toxicity and Ca deficiency could occur simultaneously (Fig. 6–2).

The potential for Al toxicity at low pH is greatest on silt loam and clay soils because of the Al present in the clay mineral fractions of the soil. Soils vary widely in Mn content, thus Mn toxicity at low soil pH depends on presence of Mn in the soil. Calcium deficiencies also may be a problem with acid soils. Increasing soil pH by liming may enhance root growth, nutrient absorption, reduce solubility of Al, Mn and Fe, and stimulate mineralization of organic matter and enhance nutrient turn-over rates. The increased mineralization associated with soil bacteria can improve P, S, and N availability to the grass.

For grass–legume associations, decreasing soil acidity normally enhances nodulation of legume roots and provides improved N nutrition for the sward. In

Table 6-6. Forage composition ($\bar{x} \pm s$) of several hay and silage types analyzed by the Northeast DHIA Forage Lab, Ithaca, New York, during the period 1 May 1991 to 30 April 1992 (published with permission of P.K. Sirois, Forage Laboratory Manager).

	Hay		Silage	
	Legume	Grass	Legume	Grass
No. samples†	2287	2061	2608	1257
	g kg^{-1}			
Dry matter (DM)	910 ± 16	920 ± 13	440 ± 117	395 ± 121
Ca	14.3 ± 2.9	6.1 ± 2.3	13.8 ± 2.7	7.0 ± 2.6
Mg	2.9 ± 0.7	2.0 ± 0.6	2.7 ± 0.5	2.1 ± 0.6
P	2.6 ± 0.5	2.3 ± 0.6	3.1 ± 0.5	2.8 ± 0.6
K	23.4 ± 5.3	18.9 ± 5.2	28.8 ± 5.8	24.1 ± 6.8
S	2.8 ± 0.6	2.2 ± 0.9	2.9 ± 1.1	2.3 ± 0.7
Cl	4.7 ± 1.8	4.4 ± 2.9	5.8 ± 2.2	5.4 ± 2.1
	mg kg^{-1}			
Na	71 ± 74	370 ± 740	360 ± 430	460 ± 870
Fe	330 ± 3600	171 ± 174	350 ± 376	624 ± 2030
Zn	24 ± 9	31 ± 17	27 ± 7	34 ± 17
Cu	9 ± 5	10 ± 6	9 ± 3	10 ± 5
Mn	37 ± 21	79 ± 52	44 ± 22	74 ± 46
Mo	2.3 ± 1.5	1.2 ± 0.8	1.8 ± 0.8	1.6 ± 0.9
Nitrate as N	90 ± 70	110 ± 140	140 ± 140	110 ± 140
	g kg^{-1}			
Total N	30.6 ± 4.2	17.6 ± 4.8	32.5 ± 4.8	21.8 ± 5.3
Protein solubility	324 ± 51	290 ± 49	543 ± 86	471 ± 105
ADF	324 ± 45	379 ± 36	358 ± 52	396 ± 46
NDF	418 ± 62	615 ± 64	453 ± 68	599 ± 75
Ash	85 ± 8	64 ± 11	94 ± 16	79 –
Nonstructural carbohydrates	272 ± 51	182 ± 5	230 ± 47	167 ± 53
Relative feed value‡	145 ± 28	91 ± 13	129 ± 28	92 ± 17

† Number of samples for dry matter (DM), Ca, Mg, P, K, acid detergent fiber (ADF), neutral detergent fiber (NDF), and nonstructural carbohydrates (NSC). Remaining data are for ≤35% of that number. Fifty-five percent of samples originated from New York, 25% from other northeastern states, and 20% from other areas of the USA. Data are reported on DM.

‡ Relative feed value (RFV) is a dimentionless parameter. RFV = [(digestible dry matter (DDM) × dry matter intake (DMI))/1.29]; where DDM = (88.9 − 0.779) and DMI = 120/NDF%.

summary, cool-season grasses are not sensitive to the direct effect of soil pH (H^+) until it approaches three. It is the secondary effect of increased levels of soluble toxic elements, decreased essential nutrient availability, and reduced microbiological activity may affect yield and quality of cool-season grasses. The optimum pH range varies from 4.1 to 7.4 and is mainly determined by indirect effects rather than direct effects (Mengel & Kirkby, 1987; Pearson & Hoveland, 1974). Fageria et al. (1991) identified several cool-season grasses that tolerate acid soil. Those adapted to soil pH <4.5 included redtop, chewings fescue, and red fescue. Species adapted to soil pH 5 to 6 included orchardgrass, tall fescue, smooth bromegrass, perennial ryegrass, timothy, Kentucky bluegrass, reed canarygrass, and tall oatgrass.

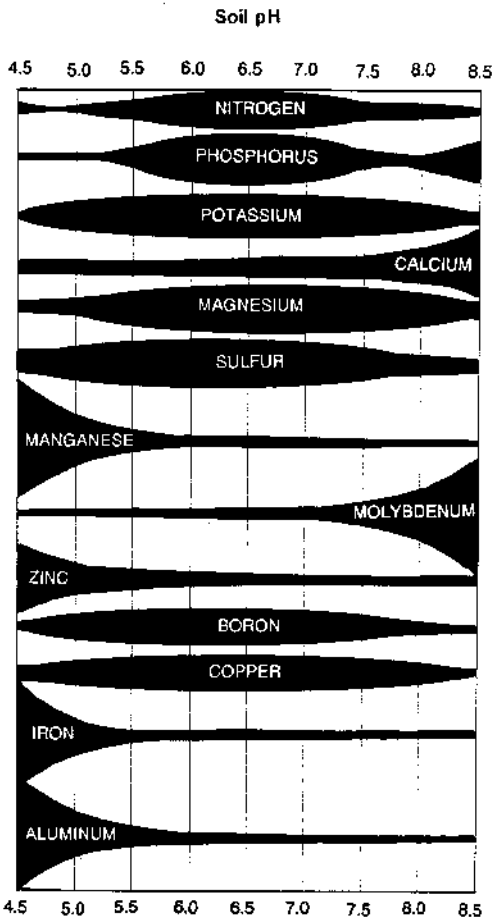

Fig. 6–2. The relative availability of 12 essential plant nutrients and Al in well-drained mineral soils. General effect of pH on element availability.

Soil Salinity

Soil pH >7.0 is caused by excess bases (Ca, Mg, Na, and K) in the soil solution. High pH affects mineral availability (Fig. 6–2). Deficiencies of Fe, Zn, Mn, and to some extent P, may occur in cereal forages and other cool-season grasses as soil pH increases and nutrient availability decreases (Fig. 6–2).

Soil salinity, resulting from an excess of these soluble salts is measured as the electrical conductivity (EC) of the saturation–soil–paste extract. Saline soils are those soils having an EC >4 dS m^{-1}. An EC of this magnitude may cause reduced crop production because of increased osmolality of the soil water (Maas, 1986). Plants, including cool-season grasses, have been classified by their relative salinity tolerance (Table 6–7).

Table 6–7. Relative salt tolerance of cool-season grasses (adapted from Maas, 1986).

Common name	Electrical conductivity of saturated soil extract: Threshold† dS/m	Slope‡ %/dS/m
Moderately sensitive		
Bentgrass	--	--
Bromegrass, smooth	--	--
Foxtail, meadow	1.5	9.6
Oatgrass, tall	--	--
Oat forage	--	--
Orchardgrass	1.5	6.2
Rye forage	--	--
Timothy	--	--
Moderately tolerant		
Barley forage	6.0	7.1
Brome, mountain	--	--
Fescue, tall	3.9	5.3
Fescue, meadow	--	--
Hardinggrass	4.6	7.6
Reed canarygrass	--	--
Rescuegrass	--	--
Ryegrass, Italian	--	--
Ryegrass, perennial	5.6	7.6
Wheat forage	4.5	2.6
Wheatgrass, intermediate	--	--
Wheatgrass, Siberian crested	3.5	4.0
Wheatgrass, slender	--	--
Wheatgrass, western	--	--
Wildrye, beardless	2.7	6.0
Wildrye, Canada	--	--
Tolerant		
Alkaligrass, nuttail	--	--
Wheatgrass, standard crested	--	--
Wheatgrass, fairway crested	7.5	6.9
Wheatgrass, tall	7.5	4.2
Wildrye, Altai	--	--
Wildrye, Russian	--	--

† Threshold = the maximum allowable salinity without yield reduction below that for nonsaline conditions.

‡ Slope = the percentage yield decrease per unit increase in salinity beyond the threshold.

Soil Alkalinity

Alkalinity refers to the proportion of soluble Na in the soil solution. Alkaline soils are most often encountered in semiarid areas and have an exchangeable sodium percentage (ESP) >15%. Reported alkalinity tolerance of plants is often similar to the relative salinity tolerance (Maas, 1986). That occurs because most of the salinity tests have used NaCl.

Grass Tolerance of Wet Soils

Perennial grasses also vary in their tolerance to poorly drained soil conditions. In addition to saturated soil conditions, with accompanying reduced O_2

Table 6–8. Perennial cool-season grasses tolerant (T) of soil-water salinity (dS/m) and spring flooded or poorly drained soil conditions (adapted from Gayton, 1990).

	Flooding period and salinity level in dS/m							
	<2 wk		2–5 wk			5–8 wk		Peat or poorly drained soil
	2–6	6–15	<2	2–6	6–15	<2	2–6	
Altai wildrye	T	T	T	T	T			
Bromegrass	T	T	T	T				T
Crested wheatgrass	T	T						
Reed canarygrass	T		T	T		T	T	T
Russian wildrye	T	T						
Slender wheatgrass	T	T	T	T	T	T	T	T
Tall wheatgrass	T	T	T	T	T	T	T	T
Timothy			T			T		T

diffusion, such soils may have varying degrees of salinity. The tolerance of several cool-season grasses to both salinity and spring flooded or poorly drained soil conditions is shown in Table 6–8.

Plant Genetic Variation for Ion Uptake/Tolerance

Genetic variability in mineral element uptake by plants was examined by Vose (1990). Variability in Se concentrations in tall fescue was reported by McQuinn et al. (1991). Variability also has been found in Ca, Mg, and K concentrations within several genera of cool-season grasses (Sleper et al., 1989; Asay & Mayland, 1990). A high-Mg line of Italian ryegrass has been shown to reduce the risk of grass tetany in grazing sheep (Moseley & Griffiths, 1984). Further selection for high Mg lines within other cool-season grasses also may reduce the risk of grass tetany.

MINERAL CYCLING

Essential plant nutrients for cool-season grass production may cycle from soil to plant to animal to the atmosphere and back to the soil. The extent and rate of return of nutrients back to the pool of available soil nutrients greatly affect fertilizer requirements of grazed pastures. Inputs to the cycle occur from fertilizers and manures, the atmosphere (biological N fixation, deposition), soil minerals, and organic matter. Losses may occur through harvest of animal or plant products, transfer of nutrients within the pasture with animal excreta, fixation and precipitation of nutrients in soil, volatilization, leaching, soil erosion, and surface runoff.

A graphic model of a mineral nutrient cycle for a pasture ecosystem is portrayed in Fig. 6–3. Essential features of nutrient cycles are soil, plant, animal and atmospheric nutrient pools; rate and quantity of nutrients moving between these pools; and inputs and outputs. Mineral nutrients cycle on global, regional, and pasture ecosystem scales; they also cycle within soil, plant, animal and atmospheric pools. Each mineral element cycle has unique features, which are dis-

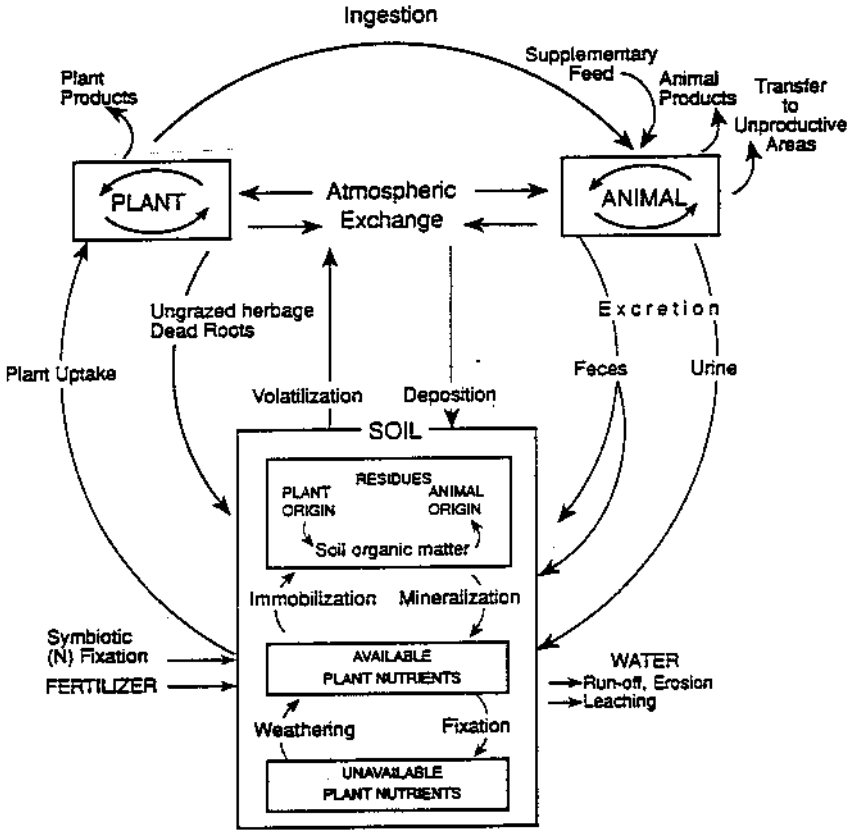

Fig. 6–3. Mineral cycling in soil–plant–animal continuum (from Follett & Wilkinson, 1995).

cussed in more detail in Wilkinson and Lowrey (1973), Schimel (1986), Power (1986), Gillingham (1987), Nguyen and Goh (1992), Russelle (1992), and Follett and Wilkinson (1995).

The soil compartment for pasture ecosystems includes a labile pool of nutrients available for plant root uptake in dynamic equilibrium with nutrients in residues and in unavailable forms (inorganic and organic). Plant roots absorb nutrients from the available soil pool and translocate them to herbage. Nutrients in herbage consumed by grazing animals are used either by the animal or excreted as feces or urine and returned to the soil. When nutrients are released from excreta and herbage residues to the available nutrient pool in the soil, the nutrients have been recycled. Portions of some elements like N, S, and Se may be respired by plants and animals and volatilized from decomposing soil organic matter or animal excreta (Wilkinson, 1983).

Energy flow (temperature, solar radiation, energy, and potential for biomass accumulation), hydrologic cycles (flows and storage of water), and nutrient cycles are interconnected and interdependent. Climate and weather patterns affect energy flows, water movement and use, and nutrient use and movement. This interconnectedness and interdependence underscores the complexity of pas-

ture ecosystems and confirms that changes in pasture ecosystem management may have unforeseen effects. Holistic approaches are necessary for appropriate management of pasture ecosystems.. Such approaches are required to accurately determine the plant nutrient requirements of the vast number and types of pasture ecosystems that exist or that may be developed.

Soil Nutrient Pools

The indigenous nutrient supply to the available soil pool is controlled by soil factors such as type and amount of clay mineral, amount and quality of soil organic matter, and characteristics of original parent materials. Together these components determine the exchangeable and the mineralizable fractions of the available nutrient pool in the soil. These fractions supply the soluble nutrient pool from which roots absorb soil nutrients. The relative contribution of each to the available nutrient pool is related to soil texture (proportions of sand, silt, and clay), type of clay, type of parent material, climatic factors of temperature and rainfall, and cropping history.

Organic matter becomes more important for plant growth in coarse-textured soils, but is an integral, vital part of all nutrient cycles as a reservoir of nutrients. It also improves and maintains favorable soil physical conditions. Soil organic matter is maintained and increased by the return of residues of plant and animal origin. The importance of residue return has been confirmed extensively, but has received little attention in cool-season forage grass production systems. Soil in each specific ecosystem has a given residue cycling intensity needed to maintain soil organic matter and ecosystem productivity. This can occur under grazing (Hoglund, 1985). For example, soil N was lost from pasture when overgrazing by sheep left less than 830 kg ha^{-1} residual live DM.

Role of Soil Organisms

Soil microfauna and microflora play a major role in nutrient cycling. Release of nutrients from plant and animal residue is dependent on microbial activity. Soil bacteria use the more readily available soluble or degradable organic substrates. Fungi and actinomycetes decompose materials such as cellulose, hemicellulose, and lignin. Dung beetles (*Scarabaeidae* family), earthworms (*Lumbricid*) (Martin & Charles, 1979), and other soil fauna increase the decomposition rates of feces and plant litter by mixing them with soil (Fincher et al., 1981). The conversion of soil organic matter, or organic residue N to mineral N (NH_4–N, or NO_3–N) is mediated by microbial activity, as is the reverse process of reducing NO_3^- to N_2O, or N_2 (denitrification). Other elements also undergo similar processes of mineralization mitigated by plant, animal, and microorganism activity.

Rhizobium bacteria fix N_2 in symbiosis with leguminous plants which actively or passively release N to companion cool-season grasses (Asay & Mayland, 1991). Soil microorganisms also influence availability of plant nutrients by altering soil pH through the release of H^+ or HCO_3^-. Soil pH may influence type of microbial activity with fungi being encouraged more at acid pH and bacteria at less acid pH.

Soil microorganism activity depends on soil temperature and moisture. Microbial and soil fauna activity, with sufficient substrate (food or energy), is much higher in moist-subtropical regions than in semiarid temperate regions. Activity of microflora in grassland soils is more likely to be limited by availability of N. While in cultivated cropland, C is more likely to be limiting (Schimel, 1986). Pesticide use on pastures may slow the rate of nutrient return if certain populations of soil organisms are adversely affected (Keogh, 1979). At any time, soil-microbial biomass contains much of the actively cycling N of the soil and represents an available pool of nutrients capable of rapid turnover (Bristow & Jarvis, 1991).

Role of the Grazing Animal

Grazing animals in pasture ecosystems affect primary productivity (plant growth) in several ways. These include defoliation, traffic patterns, herbage fouling, and distribution of excreta. Meanwhile, nutrients in the forage are partitioned to body weight, feces, and urine. Defoliation by grazing animals prevents senescence of plant tissue. Grazing removes nutrients in animal products and changes the nutrient pathways from internal plant recycling or leaf fall to return as feces and urine. Grazing increases light penetration into the canopy by partial defoliation, and through selective grazing may promote one species over another. This may alter the botanical composition.

Animal traffic compacts soil, sometimes making its physical characteristics for plant growth less desirable. Fouling of herbage with feces reduces its acceptability for grazing, thereby resulting in increased forage maturity and reduced quality and/or degree of consumption by grazers. Urine causes only a temporary unacceptability of herbage. Nutrient turnover rates and microbial activity may be reduced or enhanced by the redistribution of nutrients by grazing animals moving around the paddock.

Partitioning of ingested Nitrogen, Phosphorus, and Potassium to Animal Products

Nutrient balances within animals are determined by measuring nutrient intake in the forage eaten minus that retained in products (milk, liveweight gain, wool), and that excreted in dung and urine. Nutrient retention is greatest in actively growing livestock and least in mature livestock. Nitrogen retention estimates range from 8% of dietary intake (DMI) for weight gain to 20% for high milk-producing cows. Such estimates are only approximate because level of dietary N, age and type of animal, etc., also impact N retention. Nitrogen is excreted in both urine and feces. The proportion of total N excreted in urine increases linearly with increasing N consumption. The relationship appears similar for either legume or grass N diets (Jarvis et al., 1989).

Phosphorus is excreted mainly in feces and the proportion of total P excreted as organic P is relatively constant over the range of 1 to 4 g kg^{-1} in the diet, while the proportion of inorganic P increases. Therefore, the higher the P concentration of the diet, the greater the concentration of inorganic P in the fe-

ces, and the higher its availability for plant growth. Potassium is mainly excreted in urine (50–90%) (Wilkinson & Lowrey, 1973).

Sulphur excretion patterns, in relation to S concentrations of forage eaten, are similar to those of N. About 1.1 g S kg^{-1} of feed eaten appears in feces, while for N about 8 g N kg^{-1} of feed eaten appears in feces. Thus increasing amounts of S, as sulfate (SO_4^{2-}), in the urine, increase the availability of S for plant uptake or leaching. Grazing animals increase recycling rates of S, and accelerate losses of S from the ecosystem by leaching, particularly of urinary forms of S (Nguyen & Goh, 1992).

Animal Type, Behavior and Distribution of Excreta

Animal species, age, size, and sex affect herbage and nutrient retention, ability to graze close and selectively (Arnold & Dudzinski, 1978). Animal mobility and behavior affects the spatial redistribution of nutrients, whereas return of nutrients in plant residues remain in place. Sheep tend to be more gregarious than cattle, and enhance localization of excretal nutrient returns at camp sites and bedgrounds. Sheep may use more of the available forage grown.

Animals on range use forage to a higher degree near watering points (Arnold & Dudzinski, 1978). Greater density of dung in areas near watering and shade points has frequently been observed (Wilkinson et al.,1989; Peterson et al.,1956). Wilkinson et al. (1989) found annual transport of K to areas near watering points equivalent to 59% of the fertilizer K applied when steers were grazing endophyte-infected tall fescue. Similar trends in soil-profile NO_3^- also were observed. West et al. (1989) documented large accumulations of extractable P and exchangeable K near watering points, compared to other areas. Rowarth et al. (1992) found that sheep excreted a larger portion of consumed nutrients, including P, on relatively flat parts of pastures and depleted nutrient levels from steeper parts of hill pastures.

Even without transfer to unproductive areas such as woods, shade, watering points, fence lines, and cow paths, consumption and excretion of nutrients by ruminants results in gathering of nutrients from large areas of the pasture and return to smaller areas. This concentrating effect frequently means that nutrients cycled through livestock cannot be used efficiently by forage plants in these smaller areas.

On an annual basis, less than 35% of the pasture area receives excreted N and some areas receive one or more applications (overlapping of excreta) (Wilkinson & Lowrey, 1973), this uneven distribution means some pasture areas are underfertilized (depletion) and some overfertilized (accumulation). This uneven spatial distribution of excreta on pasture productivity is analogous to an uneven fertilizer distribution on yields. Factors affecting the use-efficiency of uneven fertilizer distribution are described by Welch et al. (1964). Uneven distribution also occurs with rotational grazing, but the magnitude of the losses to unproductive area may be smaller (Hilder,1966). Set-stocked animals may transfer more fertility to stock camps than rotationally grazed animals (Quin, 1982). Mathews et al. (1994) found that the effects of rotational grazing vs. continuous grazing on plant nutrient redistribution were considerably less important than

shade, water and supplemental feed source locations. Supplemental feeds fed grazing livestock may add a significant amount of additional nutrients via the excreta. This input increases nutrient-cycling and availability (Bennocchio et al., 1970).

Effectiveness of Nutrient Cycling

Potential control points for improving effectiveness of nutrient cycling in meeting pasture nutrient requirements involve three processes. These include: (i) increasing available nutrient pool size (gains in the cycling pool), (ii) increasing transport rate between component pools (turnover rates), and (iii) decreasing losses from the nutrient pool. Potential control of nutrient cycling in pasture ecosystems involves the following: soil selection, soil and pasture fertilization, soil management, pasture crop selection and management systems, and animal management systems. Nutrient recoveries are much higher for machine-cut and harvested forage than for grazed pastures on a field basis. However, nutrient recoveries overall may be less when the forage harvested is fed to cattle and excreta nutrients improperly recycled (Jarvis et al., 1989).

In much of Europe, cool-season grass pastures are heavily fertilized with N, and nitrate leaching has become a serious environmental problem affecting water quality. Cuttle and Scholefield (1994) have reviewed management options to limit nitrate leaching from grassland. Management steps included: monitoring N balances on each field, reducing fertilizer N application rates, increasing use of grass/arable crop rotations, and improving pasture management.

Plant Nutrient Sources

Essential plant nutrients, the probable form absorbed by plants, and their "normal" concentrations in plants are listed in Table 6–1. Essential plant nutrients have been classified as macronutrients or micronutrients depending primarily on the quantities of nutrients required. Micronutrient deficiencies in cool-season grasses are rare, and when they occur are primarily associated with abnormal or unusual soil conditions or involve antagonisms with other elements. This discussion will emphasize primarily macronutrients. Plant nutrients can be further classified as inorganic or organic. Inorganic fertilizers are usually chemical salts. Inorganic N sources include ammonium nitrate, 33% N; ammonium sulfate, 21% N; calcium nitrate, 15.5% N; sodium nitrate, 16.5%; anhydrous ammonia, 82% N; and N solutions, 27.5% N. Urea fertilizers, 46% N, while not inorganic are often included in this grouping.

Fertilizer P sources generally fall into four categories: (i) superphosphate (9% water-soluble P), made by treating ground rock phosphate with sulfuric acid; (ii) triple superphosphate (20% water-soluble P), made by treating rock phosphate with phosphoric acid; (iii) ammonium phosphates (7–23% water-soluble P, made by reacting NH_3 and phosphoric acid; and (iv) less soluble forms of P such as basic slag and ground rock phosphates. Finely ground rock phosphates may be effective in acid soils for supplying P to acid-tolerant forages; however, their effectiveness per unit of P supplied is usually lower than for normal superphosphate.

Fertilizer sources of K are mostly water soluble, and do not influence soil pH. The most common K fertilizer sources are muriate of potash (49.8% K), potassium sulfate (18.3% K + 17.6% S), potassium–magnesium sulfate (18.3% K + 22.7% S + 11.2% Mg), and potassium nitrate (36.5% K, 13% N). Obviously, potassium–magnesium sulfate is an excellent Mg source. Other important Mg sources are magnesium sulfate (10% Mg) and magnesium oxide (50% Mg). Choice of Mg fertilizers for cool-season grasses is influenced primarily by soil acidity, i.e., use of magnesium sulfate for more alkaline situations, and MgO for more acidic soil situations. Magnesium fertilizers are used more often to increase Mg concentrations of cool-season grasses than to increase yields. The use of dolomite limestone is recommended when both Mg and pH need to be increased (Mayland & Wilkinson, 1989).

Organic fertilizer sources include various synthetics such as urea forms, but predominantly are residues of plant and animal origin. As such, they are usually of low plant nutrient content except for C. Their high C content improves their value for use on soils having poor physical condition. Because of volatilization losses and slowly available N, their fertilizer equivalent N values are often one-half those of inorganic fertilizers. Equivalent N values for animal manures have been ranked from best to poorest as follows: poultry (broilers, turkey, hens), swine, dairy cattle, beef cattle, and horses. Much of the basis for this evaluation is founded in the original crude protein of the diet fed.

The P, K, Ca and Mg and micronutrients in animal manures have fertilizer equivalency values similar to inorganic fertilizers of similar concentration, except for organic P in manures. However, the relative abundance of other nutrients in manure enhances mineralization and consequent availability of P. There is an environmental problem developing because manure has been applied at rates to satisfy N requirements of crops. That problem is the accumulation of P in the soil surface from broadcast applications. This surface accumulation of P then becomes very susceptible to loss with surface water run-off and consequently could contribute to eutrophication in receiving waters. Manures from confined animal feeding operations often have large residual carryovers of feed additives. The most notable of these are Cu and Zn. Copper toxicity to sheep may be a potential problem if excessive rates of high Cu manure are applied to pastures where sheep graze. Poultry litter absorption on the surface of grass leaves could result in high availability of Cu for consumption by grazing livestock.

There is ongoing fertilizer research to develop fertilizers which release plant nutrients more nearly in phase with the fertilizer requirements of the cool-season grasses. The advantage of controlled release fertilizers resides more in better seasonal distribution of forage than in total yield of forage (Overman et al., 1989). Whether an advantage accrues from an environmental perspective depends on climatic factors of water balance and rates of application.

In regions of large population growth and/or industrial growth, there may be contributions of NH_4^+ or NO_3^- either by dry or wet deposition. These contributions can be substantial on a regional basis and impact water quality assessments through an increased background level. Primary elements of concern are N and S. These elements also are involved in the phenomenon of acid rain and its potential negative impact on the environment.

MODELS

Nutrient cycling models are useful in understanding the many interactions involved in nutrient movement within and between the soil, plant, air, and animal components of the ecosystem. These models may be particularly useful in developing grazing management and fertilization strategies. The cycling of N, P and S in grassland systems are described by Cole et al. (1987); Overman and Wilkinson (1992), Stewart and Sharpley (1987), and Thornley and Verbene (1989). Also, there are large models that simulate ecosystem productivity through nutrient, hydrologic, and plant–animal productivity submodels (Wight & Skiles, 1987). Many intensive or confined animal production areas are being required to develop comprehensive nutrient management plans. Currently, crop- and grassland are considered appropriate sites for application of manure and liquid animal waste. Adopting such plans will avoid excessive nutrient loading on such lands.

MINERALS AND ANIMAL HEALTH

Reid and Jung (1965) and Harris et al. (1989) discuss the influence of herbage minerals on palatability and digestion of grasses. Palatability affects total DM intake including mineral intake. The total intake and the interaction between several of the minerals may greatly impact the bioavailability of the minerals. The following points are made about each element that may in some way affect animal health (Grace, 1994; Grace & Clark, 1991). These points must be considered together with the information given in Table 6–2 on ruminant mineral requirements. All mineral elements, whether essential or nonessential, can adversely affect an animal if included in the diet at excessively high levels (Gough et al., 1979; NRC, 1980).

Calcium and Phosphorus

Milk fever or parturient paresis, is characterized by low blood Ca (<1.0 mmol L^{-1}). It occurs during late pregnancy and onset of lactation. This situation can occur even though herbage contains 4.4 g kg^{-1} DM. Animals must be treated parenterally with Ca for several days. Calcium/Phosphorus ratio of 2:1 (wt/wt) is ideal, but 8:1 has been tolerated. Animal nutritional guides generally discuss rations of Ca/P rather than absolute dietary concentrations.

Magnesium

Hypomagnesemic grass tetany is probably the most important metabolic problem in ruminants (Mayland, 1988). It is characterized by low blood plasma Mg concentrations (<0.4 mmol L^{-1}) and most assuredly by low urinary Mg concentrations (<0.8 mmol L^{-1}). Although 2 g Mg kg^{-1} DM is adequate to meet the Mg requirements in most situations, cows and ewes near parturition may need extra Mg (10–30 g Mg cow-d, 2–3 g Mg ewe-d).

Magnesium absorption by ruminants is reduced by high concentrations of herbage N and K and low concentrations of readily fermentable carbohydrates. The risk of grass tetany increases exponentially when the herbage K/(Ca + Mg)

increases above 2.3 (expressed as moles of charge basis). Prudent use of N and K fertilizers is warranted in order to minimize the risk of grass tetany (Mayland & Wilkinson, 1989). Aluminum in acid soil solutions also may inhibit Ca and Mg uptake by cool-season grasses, which will act to reduce Ca + Mg intake, and enhance susceptibility to grass tetany (Rengel & Robinson, 1989).

Potassium

Potassium levels of 28 g kg^{-1} DM in herbage (Tables 6–2, 6–4, and 6–5) will provide near maximum herbage yield. However, increases in solution K concentration will reduce uptake of both Ca and Mg by plants, even at solution K levels that result in less than maximum forage yield. Smith et al. (1985) reported that Mg concentrations leveled out at 1.9 g kg^{-1} when herbage contained ≥25 g K kg^{-1}; whereas Ca concentration continued to decrease to a low of 6 g kg^{-1} as forage K increased to 65 g K kg^{-1}. High herbage K levels also depress Mg and Ca absorption by ruminants. Prudent applications of fertilizer K are required to meet plant growth requirements, but not aggravate the risk of lowered Mg and Ca uptake by plants and absorption by animals.

However, K levels in dry-mature or winter grass (standing or harvested, but left in field) may be inadequate for cattle requirements. Minimum critical levels are in the range of 5 to 10 g kg^{-1}. This may occur because of weathering and leaching of K from the curing forage. During summer, 20 g K kg^{-1} DM may be desired to reduce heat stress in cattle.

Sulfur

Nitrogen/Sulfur ratios of 12:1 are recommended for ruminants. A blind staggers, or more correctly, polioencephalomalacea may be caused by ruminant animal ingestion of excess sulfate S. This occurs when ruminant organisms reduce SO_4 to the toxic H_2S form.

Nitrates

Nitrate (NO_3^-) accumulates in plant tissue because of luxuriant uptake of soil nitrate when plant metabolism of N is slow or even stopped. The condition is promoted by cool temperature, drought or physiological stress that slows growth. Upon ingestion by animals, plant NO_3^- is initially reduced to NO_2^- in the rumen and then to other nitrogenous forms (NH_4^+). If NO_2^- is absorbed by the animal, it will complex with blood hemoglobin to form a brownish colored methemoglobin which is toxic (Mayland & Cheeke, 1995). Ruminants may be conditioned to small increases in forage NO_3^-. Nevertheless, forages containing 3400 to 4500 mg N kg^{-1} as NO_3^- should be considered potentially toxic.

The uptake and accumulation of NO_3^- by grasses was demonstrated by Smith et al. (1985). They reported that when total N in grass increases from 30 g kg^{-1} to 66 g kg^{-1} DM, then NO_3–N increases linearly from 0.1 to an excess of 1.4 g kg^{-1}. [90% of maximum yield was achieved at 0.5 g kg^{-1} (Table 6–4).] Prudent use of N fertilizer is warranted.

Cobalt Copper Fluorine and Iodine

Cobalt requirements for sheep are about twice those for cattle. Lambs are most sensitive to Co deficiency. Copper availability is reduced in the presence of increased Mo, S, and Fe intake. The formation of thiomolybdates in the gut, reduce the absorption of Cu by the animal. Dietary Cu intake should be decreased in those areas where herbage Mo levels are extremely low. Copper requirements for cattle are about twice those for sheep. Dietary F levels of 1 to 2 mg F kg^{-1}, while not required by animals, are beneficial for high tooth and bone density. Concentrations of 4 to 6 mg F kg^{-1} will cause brown staining of tooth enamel and concentrations greater than 8 mg F kg^{-1} will reduce tooth and bone density and increase tendency for breakage. Drinking water is the primary source of F. High F is most often associated with thermal water. Animal performance can be good on pastures containing 0.3 mg I kg^{-1} DM. However, the northern half of the USA and Canada is generally I deficient. Salt (NaCl) is a common carrier of I for both human and domestic livestock. Dietary intakes of 1 to 2 mg I kg^{-1} DM must be considered in the presence of goitrogenic herbage like *Brassicas*.

Selenium

Selenium is unique in that it may occur in high to toxic (to animals) levels in herbage grown on Cretaceous geological soils, especially in the Central Plains of North America. In other areas, herbage Se concentrations may be inadequate for animal requirements. Dietary Se requirements range from 0.03 to as much as 1.0 mg Se kg^{-1} DM. The amount is dependent on the class of animal and levels of Vitamins E, S, and other factors present in the diet. The effect of Se is complemented to some extent by that of Vitamin E. High levels of dietary S will counter the availability of Se to ruminants. Whole blood Se concentrations should be >250 nmol L^{-1}.

Selenium is the only mineral whose supplementation is regulated. Effective 13 Sept. 1993, the U.S. Food and Drug Administration (FDA, 1993) permitted an increase of 0.1 mg Se kg^{-1} (as sodium selenite or sodium selenate) in complete feeds for animals. The use of Se boluses is not permitted. The U.S. Congress and President Clinton suspended the FDA action until 31 Dec. 1995 (Gloyd, 1994). Thus, during 1995, animal and fowl feeds could contain 0.3 mg Se kg^{-1} and the osmotic Se bolus for cattle could be used as a source of Se. The current status is that none of the controls consider the level of Se in naturally occurring feed stuffs. Selenium deficiency causes white muscle disease, ill thrift, and reduced fertility, in animals. Alkali disease and acute toxicosis (selenosis) may occur when animals ingest excess Se (>5 mg kg^{-1}).

Ultratrace Elements

The elements Al, As, Cr, Ni, Si, V, Sn are presumed essential for ruminants although research data are not available. If required, the dietary concentrations must be extremely low. Using the definition of essentiality for plants; one also might add Ba, Br, F, Rb, and Sr. We have measured <0.5 mg Cd kg^{-1} DM and 0.5 to 6 mg F kg^{-1} DM in grass herbage.

Silicon

Silicon uptake, and subsequent deposition on leaf-cell wall, and especially on the leaf perimeter provides physical support to the plant. Silicon deposits also reduce susceptibility to insect and fungal attack and also may affect animal preference (Shewmaker et al., 1989). Once eaten, Si reduces digestibility of forage by: (i) acting as a varnish on the plant cell wall and reducing accessibility to rumen microflora, (ii) complexing with trace elements like Zn and reducing their availability to rumen microflora, or (iii) complexing with some of the enzymes that are integrally involved in rumen metabolism.

Urolithiasis

Male sheep or cattle are more prone to kidney stones when the dietary Ca/P is less than 2:1 or ingested Si is high and water intake is limited. Supplementing Ca will reduce the incidence of this problem only if the stones are analyzed as containing high concentrations of P. Providing adequate and quality drinking water will reduce the incidence of silicosis.

Soil Contamination

Mineral element concentrations of analyzed herbage samples may be significantly biased by the presence of dust or soil adhering to the material. Such contamination is reflected by sample Fe concentrations >250 to 500 mg kg^{-1} DM (Mayland & Sneva, 1983). Soil contamination on herbage may elevate the intake of Fe, Mn, Se, Co, and other elements above the true elemental composition of the herbage. Direct soil ingestion by animals also may affect the intake of some mineral elements (Mayland et al., 1977).

SUMMARY

Discussions of mineral nutrition of cool-season grasses must include the element needs of both grass and grazing animal. Grasses require six macronutrients (N, K, Ca, Mg, P, and S) in concentrations exceeding 1 g kg^{-1} . They also require seven micronutrients (B, Cl, Cu, Fe, Mn, Mo, and Zn) in concentrations ranging from 0.1 to 100 mg kg^{-1} Some ultratrace elements like Ni, Co, Si, and Na also may be needed by cool-season grasses.

Grazing animals require eight macronutrients. This list includes the same six needed by plants plus Na and Cl. Animals require some of the same micronutrients as plants (Cu, Fe, Mn, Mo, and Zn) plus Co, I and Se. Animals also may require ultratrace quantities of Cr, Li, and Ni.

Cool-season grasses may exhibit macronutrient deficiencies but seldom suffer from micronutrient deficiencies. However, these grasses may not provide sufficient macronutrients (N, Ca, Mg, P, and S), micronutrients (Cl, Cu or Zn), or other elements (I, Na or Se) to meet animal needs. Paddocks of cool-season grasses are often fertilized with N and K. Grazing animals are generally supple-

mented with NaCl and also may receive additional amounts of I, Se, Zn, and Co trace mineral to supplement their forage diets. Ruminants also may receive supplementary Mg where there is considerable risk of grass tetany.

Often the cool-season grass diet will contain nutrient levels considered adequate, but the bioavailability of some minerals may be reduced because of interactions like K and Mg; Mo, Cu, and S; S and Se; and Cu and Zn. Split applications of K fertilizer will minimize the impact of high K levels on Mg availability to the plant and subsequent animal.

Grasses in some geographic areas contain sufficient mineral nutrients to maintain herbage growth, but there may be an insufficient amount of Cu, Mg, Se (not needed by plants), or Zn to meet animal requirements. For example, tall fescue is well adapted to many areas of the USA. Soils in these areas contain little plant-available Se and plants growing on them may not take up sufficient Se to meet animal requirements.

Knowledge of mineral element requirements of both cool-season grass and grazing animal provides essential information for both forage and animal production.

REFERENCES

Arnold, G.W., and M.L. Dudzinski. 1978. Ethology of free ranging domestic animals. Elsevier Sci. Publ., Amsterdam.

Asay, K.H., and H.F. Mayland. 1990. Genetic variability for elements associated with grass tetany in Russian wildrye. J. Range Manage. 43:407–411.

Asay, K.H., and H.F. Mayland. 1991. Genetic variances for dry matter yield, nitrogen content, and nitrogen yield in crested wheatgrass-alfalfa mixtures. J. Range Manage. 44:418–421.

Barber, S.A. 1984. Soil nutrient bioavailability: A mechanistic approach. John Wiley & Sons, Inc., New York.

Barber, S.A. 1995. Soil nutrient bioavailability: A mechanistic approach. 2nd ed. John Wiley & Sons, Inc., New York.

Beeson, K.C., and G. Matrone. 1976. The soil factor in nutrition, animal and human. Marcel Dekker, Inc., New York.

Bennocchio, S.S., M.F. Baumgardner, and G.O. Mott. 1970. Residual effect of grain-pasture feeding systems on the fertility of the soil under a pasture sward. Soil Sci. Soc. Am. Proc. 34:621–624.

Black, C.A. 1993. Soil fertility evaluation and control. CRC Press, Inc. Boca Raton, FL.

Bristow, A.W., and S.C. Jarvis. 1991. Effects of grazing and nitrogen fertiliser on the soil microbial biomass under permanent pasture. J. Sci. Food Agric. 54:9–21.

Brown, J.R. (ed.). 1987. Soil testing: Sampling, correlation, calibrations, and interpretation. SSSA Spec. Publ. 21. SSSA, Madison, WI.

Brown, P.H., R.M. Welch, and J.T. Madison. 1990. Effect of nickel deficiency on soluble anion, amino acid, and nitrogen levels in barley.Plant Soil 125:19–27.

Cole, C.V., J. Williams, M. Shafer, and J. Hanson. 1987. Nutrient and organic matter dynamics as components of agricultural production systems models. p. 147–166. *In* R.F. Follett et al. (ed.) Soil fertility and organic matter as critical components of production systems. SSSA Spec. Publ. 19. SSSA, Madison, WI.

Cuttle, S.P., and D. Scholefield. 1994. Management options to limit nitrate leaching from grassland. p. 138–156. *In* J.D. Etchevers (ed.) Vol. 5a. Commission 4. Symp. Trans., 15th World Congr. Soil Sci., Acapulco, Mexico. 10–16 July. Inst. Natl. Geogr. Stad. Inform. and Natl. Comm. Water, Mexico, City.

Fageria, N.K., V.C. Baligar, and C.A. Jones. 1991. Growth and mineral nutrition of field crops. Marcel Dekker, New York.

Fincher, G.T., W.G. Monson, and G.W. Burton. 1981. Effects of cattle feces rapidly buried by dung beetles on yield and quality of coastal bermudagrass. Agron. J. 72:775–779.

Follett, R.F., and S.R. Wilkinson. 1995. Nutrient management of forages. p. 55–82. *In* R.F Barnes et al. (ed.) Forages: The science of grassland agriculture. 5th ed. Iowa State Univ. Press, Ames, IA.

Food and Drug Administration. 1993. Food additives permitted in feed and drinking water of animals; Selenium. Fed. Reg. 56:47 962–47 973.

Gayton, D. 1990. Forage crop recommendations. Saskatchewan Advis. Counc. on Forage Crops, Saskatoon, Sask.

Gillingham, A.G. 1987. Phosphorus cycling in managed grasslands. p. 172–180. *In* R.W. Snaydon (ed.) Managed grasslands. Analytical studies (ecosystems of the world 17B). Elsevier Sci. Publ., Amsterdam.

Gloyd, J.S. 1994. Stay of selemiun amendments lifted. J. Am. Vet. Med. Assoc. 205:1639.

Gough, L.P., H.T. Shacklette, and A.A. Case. 1979. Element concentrations toxic to plants, animals, and man. U.S. Geol. Surv. Bull. 1466. U.S. Gov. Print. Office, Washington, DC.

Grace, N.D. 1994. Managing trace element deficiencies. AgResearch, N.Z. Pastoral Agric. Res. Inst., Palmerston North, NZ.

Grace, N.D., and R.G. Clark. 1991. Trace element requirements, diagnosis and prevention of deficiencies in sheep and cattle. p. 321–345. *In* T. Tsuda (ed.) Physiological aspects of digestion and metabolism in ruminants. Acad. Press, San Diego, CA.

Graham, R.D., and M.J. Webb. 1991. Micronutrients and disease resistance and tolerance in plants. p. 329–370. *In* J.J. Mortvedt et al. (ed.) Micronutrients in agriculture. 2nd ed. SSSA, Madison, WI.

Grunes, D.L., S.R. Wilkinson, P.K. Joo, W.A. Jackson, and R.P. Patterson. 1985. Effect of fertilization on the grass tetany potential and organic acid composition of tall fescue. p. 509–510. *In* H. Kirita (ed.) Proc. 15th Int. Grassl. Congr., Kyoto, Japan. 24–31 August. Sci. Counc. Japan, and the Japanese Soc. Grassl. Sci., Kyoto, Japan.

Harris, K.B., V.M. Thomas, M.K. Peterson, S.D. Kachman, and M.J. McInerney. 1989. Influence of minerals on rate of digestion and percentage degradable in vitro neutral detergent fiber. Nutr. Rep. Int. 40:219–226.

Hetrick, B.A.D., D.G. Kitt, and G.T. Wilson. 1988. Mycorrhizal dependence and growth habit of warm-season and cool-season tall grass prairie plants. Can. J. Bot. 66:1376–1380.

Hilder, E.J. 1966. Distribution of excreta by sheep at pasture. p. 977–981. *In* A.G.G. Hill (ed.) Proc. 10th Int. Grassl. Congr., Helsinki. 7–16 July. Finnish Grassl. Assoc. Publ., Helsinki.

Hoglund, J.H. 1985. Grazing intensity and soil nitrogen accumulation. Proc. N.Z. Grassl. Assoc. 46:65–69.

Jarvis, S.C., D.J. Hatch, and D.H. Roberts. 1989. The effects of grassland management on nitrogen losses from grazed swards through ammonia volatilization: The relationship in excretal returns from cattle. J. Agric. Sci. 112:202–215.

Jones, D.I.H., and T.A. Thomas. 1987. Minerals in pastures and supplements. p. 145–153. *In* R.W. Snaydon (ed.) Managed grasslands. Analytical studies (ecosystems of the world 17B). Elsevier Sci. Publ., Amsterdam.

Kabata-Pendias, A., and H. Pendias. 1992. Trace elements in soils and plants. 2nd ed. CRC Press, Boca Raton, FL.

Keogh, R.G. 1979. Lumbricid earthworm activities and nutrient cycling in pasture ecosystems. p. 49–51. *In* T.K. Crosby and P.F. Pottinger (ed.) Proc. 2nd Australas Conf. Grassl. Invertebr. Ecol., Palmerston, N.Z. 22–26 May 1978. Dep. Sci. Indust. Res., N.Z. Min Agric. Fish. N.Z. Gov. Print., Wellington, NZ.

Lightner, J.W., C.L. Rhykerd, D.B. Mentel, G.E. Van-Scoyoc, E.L. Hood, and C.H. Noller. 1983. Influence of NPK fertilization on Ca, and Mg in *Poa pratensis* L. with reference to dietary requirements of grazing cattle. Commun. Soil Sci. Plant Anal. 14:121–130.

Maas, E.V. 1986. Salt tolerance of plants. Appl. Agric. Res. 1:12–26.

Marschner, H. 1986. Mineral nutrition of higher plants. Acad. Press, San Diego, CA.

Martin, N.A., and J.C. Charles. 1979. Lumbricid earthworms and cattle dung in New Zealand pastures. p. 52–54. *In* T.K. Crosby and P.F. Pottinger (ed.) Proc. 2nd Australas Conf. Grassl. Invertebr. Ecol., Palmerston North, NZ. 22–26 May 1978. Dep. Sci. Indust. Res., and N.Z. Min. Agric. & Fish., NZ. Gov. Print., Wellington, NZ.

Mathews, B.W., L.E. Sollenberger, V.D. Nair, and C.R. Staples. 1994. Impact of grazing management on soil nitrogen, phosphorus, potassium, and sulfur distribution. J. Environ. Qual. 23:1006–1013.

Mayland, H.F. 1983. Assessing nutrient cycling in the soil/plant/animal system of semi-arid pasture lands. p. 109–117. *In* Nuclear techniques in improving pasture management. Proc. Advisory Group Meet., Vienna, Austria. 10–14 Nov. 1980. FAO/IAEA, Vienna.

Mayland, H.F. 1986. Factors affecting yield and nutritional quality of crested wheatgrass. *In* K.L. Johnson (ed.) Crested wheatgrass: Its values, problems andmyths. Proc. Symposium. Logan, UT. 3–7 Oct. 1983. Utah State Univ. Press, Logan, UT.

Mayland, H.F. 1988. Grass tetany. p. 511–523, 530–531. *In* D.C. Church (ed.) The ruminant animal: Its physiology and nutrition. Prentice-Hall, Englewood Cliffs, NJ.

Mayland, H.F., and P.R. Cheeke. 1995. Forage-induced animal disorders. p. 121–135. *In* R.F Barnes et al. (ed.) Forages. The science of grassland agriculture. 5th ed. Iowa State Univ. Press, Ames, IA.

Mayland, H.F., G.E. Shewmaker, and R.C. Bull. 1977. Soil ingestion by cattle grazing crested wheatgrass. J. Range Manage. 30:264–265.

Mayland, H.F., and F.A. Sneva. 1983. Effect of soil contamination on the mineral composition of forage fertilized with nitrogen. J. Range Manage. 36:266–288.

Mayland, H.F., and S.R. Wilkinson. 1989. Soil factors affecting magnesium availability in plant-animal systems: A review. J. Anim. Sci. 67:3437–3444.

Mays, D.A. (ed.). 1974. Forage fertilization. ASA, CSSA, and SSSA, Madison, WI.

McNaughton, S.J., J.L. Tarrants, M.M. McNaughton, and R.H. Davis. 1985. Silica as a defense against herbivore and a growth promoter in African grasses. Ecology 66:528–535.

McQuinn, S.D., D.A. Sleper, H.F. Mayland, and G.F. Krause. 1991. Genetic variation for selenium content in tall fescue. Crop Sci. 31:617–620.

Mengel, K., and E.A. Kirkby. 1987. Principles of Plant Nutrition, p. 138–143. 4th ed. Intl. Potash Inst., Bern, Switzerland.

Moseley, G., and D.W. Griffiths. 1984. The mineral metabolism of sheep fed high and low magnesium selections of Italian ryegrass. Grass Forage Sci. 39:195–199.

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. Intermountain For. & Range Exp. Stn., Ogden, UT.

National Research Council. 1980. Mineral tolerance of domestic animals. Natl. Acad. Press. Washington, DC.

National Research Council. 1984. Nutrient requirements of sheep. 6th ed. Natl. Acad. Press. Washington, DC.

National Research Council. 1985. Nutrient requirements of sheep. 6th ed. Natl. Acad. Press. Washington, DC.

National Research Council. 1989. Nutrient requirements of sheep. 6th ed. Natl. Acad. Press. Washington, DC.

Nicholas, D.J.D., and A.R. Egan. 1975. Trace elements in soil-plant-animal systems. Acad. Press, New York.

Nguyen, K., and M. Goh. 1992. Nutrient cycling and losses based on a mass-balance model in grazed pastures receiving long-term superphosphate applications in New Zealand. II. Sulphur. J. Agric. Sci. (Cambridge) 119:107–122.

Overman, A.R., D. Downey, and S.R. Wilkinson. 1989. Effect of applied nitrogen and harvest interval on nitrogen concentration in bahiagrass. Commun. Soil Sci. Plant Anal. 20:513–527.

Overman, A.R., and S.R. Wilkinson. 1992. Model evaluation for perennial grasses in the Southern United States. Agron. J. 84:523–529.

Pearson, R.W., and C.S. Hoveland. 1974. Lime needs of forage crops. p. 301–322. *In* D.A. Mays (ed.) Forage fertilization, ASA, CSSA, and SSSA, Madison, WI.

Peterson, R.G., H.L. Lucas, and W.W. Woodhouse, Jr. 1956. The distribution of excreta by freely grazing cattle and its effect on pasture fertility: I. Excreta distribution. Agron. J. 48:440–449.

Power, J.F. 1986. Nitrogen cycling in seven cool-season perennial grass species. Agron. J. 78:681–687.

Quin, B.F. 1982. The influence of grazing animals on nitrogen balance. p. 95–102. *In* P.W. Gander (ed.) Nitrogen balances in New Zealand ecosystems. DSIR, Palmerston North, NZ.

Reid, R.L., B.S. Baker, and L.C. Vona. 1984. Effects of magnesium sulfate supplementation and fertilization on quality and mineral utilization of timothy hays by sheep. J. Anim. Sci. 59:1403–1410.

Reid, R.L., and D.J. Horvath. 1980. Soil chemistry and mineral problems in farm livestock. A review. Anim. Feed Sci. Technol. 5:95–167.

Reid, R.L., and G.A. Jung. 1965. Influence of fertilizer treatment on the intake, digestibility, and palatability of tall fescue hay. J. Anim. Sci. 24:615–625.

Reid, R.L., A.J. Post, and G.A. Jung. 1970. Mineral composition of forages. West Virginia Agric. Exp. Stn. Bull. 589T.

Rengel, Z., and D.L. Robinson. 1989. Aluminum effects on growth and macronutrient uptake by annual ryegrass. Agron. J. 81:208–215.

Rowarth, J.S., R.W. Tillman, A.G. Gillingham, and P.E.H. Gregg. 1992. Phosphorus balances in grazed, hill-country pastures: The effect of slope and fertilizer input. N.Z. J. Agric. Res. 35:337–342.

Russelle, M.P. 1992. Nitrogen cycling in pasture and range. J. Prod. Agric. 5:13–23.

Schimel, F.S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry 2:345–350.

Shewmaker, G.E., H.F. Mayland, R.C. Rosenau, and K.H. Asay. 1989. Silicon in C-3 grasses: Effects on forage quality and sheep preference. J. Range Manage. 42:122–127.

Shuman, L.M. 1994. Mineral nutrition. p. 149–182. *In* R.E. Wilkinson. Plant-environment interactions. Marcel Dekker, Inc., New York.

Sleper, D.A., K.P. Vogel, K.R. Asay, and H.F. Mayland. 1989. Using plant breeding and genetics to overcome the incidence of grass tetany. J. Anim. Sci. 67:3456–3462.

Smith, G.S., I.S. Cornforth, and H.V. Henderson. 1985. Critical leaf concentrations for deficiencies of nitrogen, potassium, phosphorus, sulphur, and magnesium in perennial ryegrass. New Phytol. 101:393–409.

Spears, J.W. 1994. Minerals in forages. p. 281–317. *In* G.C. Fahey (ed.) Forage quality, evaluation, and utilization. ASA, CSSA, and SSSA, Madison, WI.

Spedding, C.R.W., and E.C. Diekmahns (ed.). 1972. Grasses and legumes in British agriculture. Bull. 49. Commonweal. Agric. Bur., Farnham Royal, Bucks., England.

Stern, W.R., and C.M. Donald. 1962. Light relationships in grass: clover swards. Aust. J. Agric. Res. 13:599–614.

Stewart, J.W.B., and A.N. Sharpley. 1987. Controls on dynamics of soil and fertilizer phosphorus and sulfur. p. 101–121. *In* R.F. Follett et al. (ed.) Soil fertility and organic matter as critical components of production systems. SSSA Spec. Publ. 19. SSSA, Madison, WI.

Thornley, J.H.M., and E.L.J. Verbene. 1989. A model of nitrogen flows in grassland. Plant, Cell Environ. 12:863–886.

Turner, T.R. 1993. Turfgrass. p. 187–196. *In* W.F. Bennett (ed.) Nutrient deficiencies & toxicities in crop plants. Am. Phytopath. Soc., St. Paul, MN.

Vose, P.B. 1990. Screening techniques for plant nutrient efficiency: Philosophy and methods. p. 283–289. *In* N. El Bassam et al. (ed.) Genetic aspects of plant mineral nutrition. Kluwer Acad. Publ., Amsterdam.

Welch, L.F., A.R. Bertrand, and W.E. Adams. 1964. How non-uniform distribution of fertilizer affects crop yields. Georgia Agric. Res. 5:315–316.

West, C.P., A.P. Mallarino, W.F. Wedin, and D.B. Marx. 1989. Spatial variability of soil chemical properties in grazed pastures. Soil Sci. Soc. Am. J. 53:784–789.

Wight, J.R., and J.W. Skiles. 1987. SPUR: Simulation of production and utilization of rangelands. USDA-ARS Document. Users Guide. no. 63. U.S. Gov. Print. Office, Washington, DC.

Wilkinson, S.R. 1983. Isotope-aided studies of nutrient cycling and soil fertility assessment in humid pasture systems. p. 81–92. *In* Nuclear techniques in improving pasture management. Proc. Advisory Group Meet., Vienna, Austria. 10–14 Nov. 1980. FAO/IAEA, Vienna.

Wilkinson, S.R., and R.S. Lowrey. 1973. Cycling of mineral nutrients in pasture ecosystems. p. 248–316. *In* G.W. Butler and W. Bailey (ed.) Chemistry and biochemistry of herbage. Vol. 2. Acad. Press, New York.

Wilkinson, S.R., and D.A. Mays. 1979. Mineral nutrition. p. 41–73. *In* R.C. Buckner and L.P. Bush (ed.) Tall fescue. ASA, Madison, WI.

Wilkinson, S.R., J.A. Stuedemann, and D.P. Belesky. 1989. Soil potassium distribution in grazed K-31 tall fescue pastures as affect by fertilization and endophytic fungus infection level. Agron. J. 81:508–512.

Reid, R.L., A.J. Post, and G.A. Jung. 1970. Mineral composition of forages. West Virginia Agric. Exp. Stn. Bull. 589T.

Rengel, Z., and D.L. Robinson. 1989. Aluminum effects on growth and macronutrient uptake by annual ryegrass. Agron. J. 81:208–215.

Rowarth, J.S., R.W. Tillman, A.G. Gillingham, and P.E.H. Gregg. 1992. Phosphorus balances in grazed, hill-country pastures: The effect of slope and fertilizer input. N.Z. J. Agric. Res. 35:337–342.

Russelle, M.P. 1992. Nitrogen cycling in pasture and range. J. Prod. Agric. 5:13–23.

Schimel, F.S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry 2:345–350.

Shewmaker, G.E., H.F. Mayland, R.C. Rosenau, and K.H. Asay. 1989. Silicon in C-3 grasses: Effects on forage quality and sheep preference. J. Range Manage. 42:122–127.

Shuman, L.M. 1994. Mineral nutrition. p. 149–182. *In* R.E. Wilkinson. Plant-environment interactions. Marcel Dekker, Inc., New York.

Sleper, D.A., K.P. Vogel, K.R. Asay, and H.F. Mayland. 1989. Using plant breeding and genetics to overcome the incidence of grass tetany. J. Anim. Sci. 67:3456–3462.

Smith, G.S., I.S. Cornforth, and H.V. Henderson. 1985. Critical leaf concentrations for deficiencies of nitrogen, potassium, phosphorus, sulphur, and magnesium in perennial ryegrass. New Phytol. 101:393–409.

Spears, J.W. 1994. Minerals in forages. p. 281–317. *In* G.C. Fahey (ed.) Forage quality, evaluation, and utilization. ASA, CSSA, and SSSA, Madison, WI.

Spedding, C.R.W., and E.C. Diekmahns (ed.). 1972. Grasses and legumes in British agriculture. Bull. 49. Commonweal. Agric. Bur., Farnham Royal, Bucks., England.

Stern, W.R., and C.M. Donald. 1962. Light relationships in grass: clover swards. Aust. J. Agric. Res. 13:599–614.

Stewart, J.W.B., and A.N. Sharpley. 1987. Controls on dynamics of soil and fertilizer phosphorus and sulfur. p. 101–121. *In* R.F. Follett et al. (ed.) Soil fertility and organic matter as critical components of production systems. SSSA Spec. Publ. 19. SSSA, Madison, WI.

Thornley, J.H.M., and E.L.J. Verbene. 1989. A model of nitrogen flows in grassland. Plant, Cell Environ. 12:863–886.

Turner, T.R. 1993. Turfgrass. p. 187–196. *In* W.F. Bennett (ed.) Nutrient deficiencies & toxicities in crop plants. Am. Phytopath. Soc., St. Paul, MN.

Vose, P.B. 1990. Screening techniques for plant nutrient efficiency: Philosophy and methods. p. 283–289. *In* N. El Bassam et al. (ed.) Genetic aspects of plant mineral nutrition. Kluwer Acad. Publ., Amsterdam.

Welch, L.F., A.R. Bertrand, and W.E. Adams. 1964. How non-uniform distribution of fertilizer affects crop yields. Georgia Agric. Res. 5:315–316.

West, C.P., A.P. Mallarino, W.F. Wedin, and D.B. Marx. 1989. Spatial variability of soil chemical properties in grazed pastures. Soil Sci. Soc. Am. J. 53:784–789.

Wight, J.R., and J.W. Skiles. 1987. SPUR: Simulation of production and utilization of rangelands. USDA-ARS Document. Users Guide. no. 63. U.S. Gov. Print. Office, Washington, DC.

Wilkinson, S.R. 1983. Isotope-aided studies of nutrient cycling and soil fertility assessment in humid pasture systems. p. 81–92. *In* Nuclear techniques in improving pasture management. Proc. Advisory Group Meet., Vienna, Austria. 10–14 Nov. 1980. FAO/IAEA, Vienna.

Wilkinson, S.R., and R.S. Lowrey. 1973. Cycling of mineral nutrients in pasture ecosystems. p. 248–316. *In* G.W. Butler and W. Bailey (ed.) Chemistry and biochemistry of herbage. Vol. 2. Acad. Press, New York.

Wilkinson, S.R., and D.A. Mays. 1979. Mineral nutrition. p. 41–73. *In* R.C. Buckner and L.P. Bush (ed.) Tall fescue. ASA, Madison, WI.

Wilkinson, S.R., J.A. Stuedemann, and D.P. Belesky. 1989. Soil potassium distribution in grazed K-31 tall fescue pastures as affect by fertilization and endophytic fungus infection level. Agron. J. 81:508–512.