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RELATIONSHIP BETWEEN SHOOT AND ROOT NUTRIENT CONCENTRATIONS FOR A RANGE OF TEMPERATE PASTURE AND CEREAL SPECIES

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Abstract. The relationships between shoot and root nutrient concentrations were determined using regression analysis for a range of temperate pastures species and cultivars grown in low ionic strength solution culture. Results from cereals were also included as a comparison. There were significant ($P<0.05$) differences in the relationships between the grass and cereal species, and the leguminous species. For a given shoot concentration, the root concentrations were higher in legumes for N, P, S, K, Mn, and Zn. Generally, the range of measured shoot concentrations from grass/cereal and legumes were similar (Figure 1). The exceptions were Ca, Mg and B, where legumes had higher shoot concentrations than the grasses/ cereal. For N, S, P, Mn, Zn, Cu, and Fe within the leguminous species, root concentrations for a given shoot concentration were lower when root K concentrations were <3%. Including other nutrients did not significantly improve the relationship except in wheat, where increasing root Ca concentrations increased root Mg concentrations, and increasing root Mg concentrations increased root Ca concentrations. The results from this study give an empirical method for estimating the root nutrient concentrations from shoot nutrient concentrations when modelling nutrient flows in pasture.

Introduction

Within a pastoral system, plant roots can be a sink (via uptake) or source (via senescence) of nutrients. In order to model the relative contribution of roots within a pastoral system, information on root mass and root nutrient concentrations is required. Since shoot concentrations are regularly measured in pastures, one approach is to estimate root concentrations from an empirical relationship with shoot concentrations.

Solution culture techniques for growing plants allow easy harvest of roots without problems due to soil contamination, and hence could give good estimations of root nutrient concentrations in actively growing roots. A wide range of pasture species and cultivars have been screened for Al tolerance using a low ionic strength solution culture technique (see Table 1). The nutrient concentrations used in the experimental soil solution mimicked those found in soil solution extracts from fresh soils (Edmeades *et al*., 1985; Blamey *et al*., 1991) as these have been shown to be important for the study of plant responses on acid soils (Edmeades *et al*., 1995). The majority of experiments with pasture species had varying solution Al concentrations. Thus the range in nutrient concentrations obtained were due to between experiment variation, or to variation when solution Al concentrations were varied. There were a series of experiments with wheat using the same technique where several factors relating to Al tolerance were investigated (see Table 1). These experiments give an indication of what factors may affect the relationship between shoot and root concentrations, and were also included in the analysis. In addition, the results from a set of experiments investigating the Al tolerance of different cereals were also included as a comparison with grass species.

From these sets of experiments empirical relationships between shoot and root nutrient concentrations were derived and are presented in this paper.

Table 1. Experiments shoot and root nutrient concentrations were collected from. The reference for experimental methods is also given. Plant concentrations reported in these references are either means or subsets of the full range of data used in this paper.

Species	Experiment	Reference
Grass	Al tolerance of temperate grasses *Agrostis tenuis*, *Bromus inermis*, *B. sitchensis*, *B. stamineus*, *B. wildenowii*, *Ehrharta calycina*, *Festuca arundinacea* (2 cv), *F. rubra*, *Lolium perenne* (7 cv), *L. hybridium* (7 cv), *L. multiflorum* (3 cv), *Holcus lanatus*, *Paspalum dilatatum*, *Phleum pratense*, *Panicum miliacium*)	Wheeler *et al*. (1992a) Wheeler (1995c)
Wheat	investigations using Al tolerant and sensitive lines of wheat (*Triticum aestivum*) into the effect of varying:	
	• ionic strength	Wheeler and Edmeades (1995a)
	• NO3/NH4 ratio	Wheeler (1995a)
	• solution concentrations of Al, Ca and Mg	Wheeler and Edmeades (1995b)
	• solution concentrations of Mn, Zn, Cu, Fe, B	Wheeler and Power (1995)
	• harvest times	Wheeler (1995b)
Cereal	Al tolerance of different cultivars of wheat (8 cvs), oats (*Avena sativa* 6 cv, *A. Byzantina*, *A. Strigosa*) and barley (*Hordeum vulgare*)	Wheeler *et al*. (1992b)
Legumes	Al tolerance of different species of legumes from the genus *Adesmia* (1 spp), *Dorycnium* (1 spp), *Lotus* (6 spp), *Medicago* (7 spp), *Melilotus* (1 spp), and *Trifolium* (14 spp)	Wheeler and Dodd (1995)
	Varying rates of N (NO_3, NH_4, total N), P, S, Ca, Mg, K in white clover (*Trifolium repens*)	Wheeler (1996)

Methods

Plants were grown in a low ionic strength nutrient solution culture technique in a temperature controlled (min. night 12 °C, min. day 18 °C, max. day 25 °C) glasshouse using artificial lights (average PAR 250 µE/m^2/s) to extend day length to 15 hours. The nominal concentration of nutrients in the basal nutrient solution were (µM) 450 Ca; 100 Mg; 300 K; 600 N (150 NH_4, 450 NO_3); 2.5 P; 550 S; 3 B; 0.5 Zn; 0.5 Mn and 0.1 Cu at pH 4.7. In experiments where Al tolerance was tested, solution Al concentrations typically varied between 0 and 50 µM, with most being less than 20 µM. Solution nutrient concentrations were maintained with monitoring and frequent additions as described by Wheeler and Follet (1991). Plants were typically harvested after about 4 weeks growth and separated into shoots and roots. For legumes, shoots included leaves and stolons. Plant concentrations were measured on shoots and roots using the methods described by Wheeler and Follett (1991).

The relationship between shoot and root concentrations for each nutrient was determined for each set of experiments (Table 1) using regression analysis. For the wheat set of experiments, the relationships for each nutrient were examined to determine whether any of the factors (varying ionic strength, NO_3/NH_4 ratio, harvest times, or Al tolerance of cultivars, or varying solution Ca, Mg, Mn, Zn, Cu, Fe or B concentrations,) had an effect on the relationship between shoot and root concentrations. The relationships for the other sets of experiments (cereals, grasses, legumes) were also examined as outlined above to determine whether the relationships differed between species, cultivars within a species, or between nil Al and plus Al treatments (including subsets of low, medium and high solution Al values). The relationships were also examined to determine whether there was any non-linearity.

Multiple and stepwise regression analysis was also performed to test whether the relationships could be improved by including more than one nutrient. When significant relationships were found, analysis was done on subsets of the data to test whether the relationships were stable, that is, whether similar relationships occurred for some subsets of the data.

Results

For a given nutrient, there were significant ($P < 0.05$) differences in the relationship between shoot and root concentrations between individual experiments. The differences between experiments tended to be larger for the trace nutrients Mn, Zn, Cu, Fe and Al than for the major nutrients (N, P, S, Ca, Mg, Na and K). Within the wheat set of experiments, the factors examined (see Table 1) had no consistent significant ($P > 0.05$) effect on the relationships. Within each set of experiments, there were no significant ($P > 0.05$) differences between the relationships determined in the absence and presence of Al.

There were statistically significant ($P < 0.05$) differences in the relationships between shoot and root concentrations of grass and cereals (wheat and cereal experiments in Table 1) species (monocotyledons), and the leguminous species (dicotyledons). Within these two groups, except where noted, there were generally no consistent significant ($P > 0.05$) differences between species, cultivars or treatments. In cases where non-linearity was found (mainly for K), examination of the data indicated that two discrete linear functions fitted as well or better than a continuous curvilinear function. In most cases, adding additional nutrients provided no significant improvements to the regression. However, some consistent deviations, whereby a subset of the data set had a different relationship, where observed (deviations). The relationships for the standard data set (data excluding those that gave deviations) and for the deviations are shown in Table 2 for grass/cereals and Table 3 for legumes. The relationships of the standard relationships in Table 2 and 3 are shown in Figures 1 for the major nutrients and Figure 2 for the minor nutrients.

For a given shoot concentration, the root concentrations were greater in legumes for N, P, S, K, Mn, and Zn. Generally roots and shoots had similar ranges of concentrations, the exception being Mn, Zn, Cu, Fe, and Al that were greater in the roots, possibly due to adsorption on the root surface. Generally, the range in measured shoot concentrations from grass/ cereals and legumes covered a similar range (Figures 1 and 2). The exception was Ca, Mg and B, where legumes had greater shoot concentrations than the grasses/cereals.

Table 2. The relationship between shoot (subscript s) and root (subscript r) concentrations (in % for N, S, P, Mg, Ca, K, otherwise ppm) for grass/cereals for the standard data set, and for deviations from that set (see text). The standard error of the observations, which gives a minimum estimate of the standard error for predicting root concentrations, is also shown. Standard errors of the estimated parameter values are shown in parenthesises, and are significant (P > 0.05) unless followed by ns (non-significant.

Standard data set Equation	SE_{obs}	Deviations Equation	SE_{obs}
$N_r = 1.893 + 0.301\ N_s$	0.62		
(0.025) (0.125)			
$S_r = 0.155 + 0.421\ S_s$	0.09		
(0.010) (0.019)			
$P_r = 0.041 + 0.857\ P_s$	0.15		
(0.013) (0.030)			
		Interaction in wheat	
$Mg_r = 0.021 + 0.634\ Mg_s$	0.11	$Mg_r = -0.069 + 0.586\ Mg_s + 0.521\ Ca_r$	0.10
(0.006) (0.030)		(0.009) (0.027) (0.037)	
		High fertility grasses	
		$Mg_r = 0.050 + 0.115\ Mg_s$	0.022
		(0.006) (0.137) ns	
		Interaction in wheat	
$Ca_r = 0.084 + 0.242\ Ca_s$	0.07	$Ca_r = 0.070 + 0.213\ Ca_s + 0.208\ Mg_r$	0.07
(0.006) (0.014)		(0.005) (0.009) (0.019)	
		High fertility grasses	
		$Ca_r = 0.112 + 0.066\ Ca_s$	0.022
		(0.009) (0.019)	
		High K concentrations (shoot K > 4.5%)	
$K_r = 0.931 + 0.294\ K_s$	0.41	$K_r = -2.740 + 1.094\ K_s$	0.36
(0.083) (0.019)		(0.684) (0.119)	
		Low concentrations (< 200 ppm)	
$Mn_r = -26 + 1.66\ Mn_s$	1522	$Mn_r = 28.3 + 1.132\ Mn_s$	70
(108)ns (0.109)		(12)ns (0.163)	
		Cultivars of *Lolium, Hordeum* and *Avena*	
		$Mn_r = 31.82 + 0.170\ Mn_s$	24
		(5.16) (0.062)	
$Zn_r = 1.1 + 2.801\ Zn_s$	734		
(52.9)ns (0.086)			
$Cu_r = -32.3 + 5.469\ Cu_s$	95		
(10.2) (0.422)			
$Fe_r = 155 + 8.11\ Fe_s$	855		
(76)ns (0.51)			
$B_r = 9.11 + 0.334\ B_s$	14		
(1.58) (0.006)			
$Al_r = 207 + 10.42\ Al_s$	1851		
(147)ns (0.64)			

Table 3. The relationship between shoot (subscript s) and root (subscript r) concentrations (in % for N, S, P, Mg, Ca, K, otherwise ppm) for temperate pasture legumes for the standard data set, and for deviations from that set (see text). Standard errors of the estimated parameter values are shown in parenthesises. The standard error of the observations, which gives a minimum estimate of the standard error for predicting root concentrations, is also shown. Standard errors of the estimated parameter values are shown in parenthesises, and are significant (P > 0.05) unless followed by ns (non-significant.

High plant K concentrations Equation	SE_{obs}	Low plant K concentrations Equation	SE_{obs}
		root K < 3%	
$N_r = 1.853 + 0.648\ N_s$	0.56	$N_r = 2.145 + 0.471\ N_s$	0.64
(0.444) (0.083)		(0.386) (0.078)	
		root K < 3%	
$S_r = 0.297 + 0.874\ S_s$	0.13	$S_r = 0.262 + 0.403\ S_s$	0.10
(0.059) (0.121)		(0.035) (0.082)	
		root K < 3%	
$P_r = 0.082 + 1.018\ P_s$	0.11	$P_r = 0.204 + 0.360\ P_s$	0.09
(0.035) (0.083)		(0.020) (0.075)	
$Ca_r = 0.173 + 0.103\ Ca_s$	0.10		
(0.020) (0.013)			
$Mg_r = 0.136 + 0.055\ Mg_s$	0.07		
(0.018) (0.047) ns			
		shoot K < 2.3%	
$K_r = -0.218 + 0.897\ K_s$	0.29	$K_r = 1.157 + 0.290\ K_s$	0.44
(0.094) (0.409)		(0.181) (0.049)	
		root K < 3%	
$Mn_r = -140 + 4.695\ Mn_s$	160	$Mn_r = 5.0 + 1.64\ Mn_s$	98
(41) (0.39)		(27) (0.24)	
		root K < 3%	
$Zn_r = 98.7 + 4.279\ Zn_s$	418	$Zn_r = 125 + 1.74\ Zn_s$	478
(98.6)ns (0.722)		(102)ns (0.48)	
		root K < 3%	
$Cu_r = -55.4 + 6.225\ Cu_s$	38	$Cu_r = 9.78 + 1.32\ Cu_s$	17
(9.0) (0.367)		(5.59)ns (0.323)	
		root K < 3%	
$Fe_r = 932 + 0.67\ Fe_s$	440	$Fe_r = 319 + 1.78\ Fe_s$	204
(192) (1.16)ns		(77) (0.48)	
$B_r = 14.52 + 0.286\ B_s$	9.3		
(2.6) (0.049)			
$Al_r = 431 + 4.256\ Al_s$	1398		
(176) (0.388)			

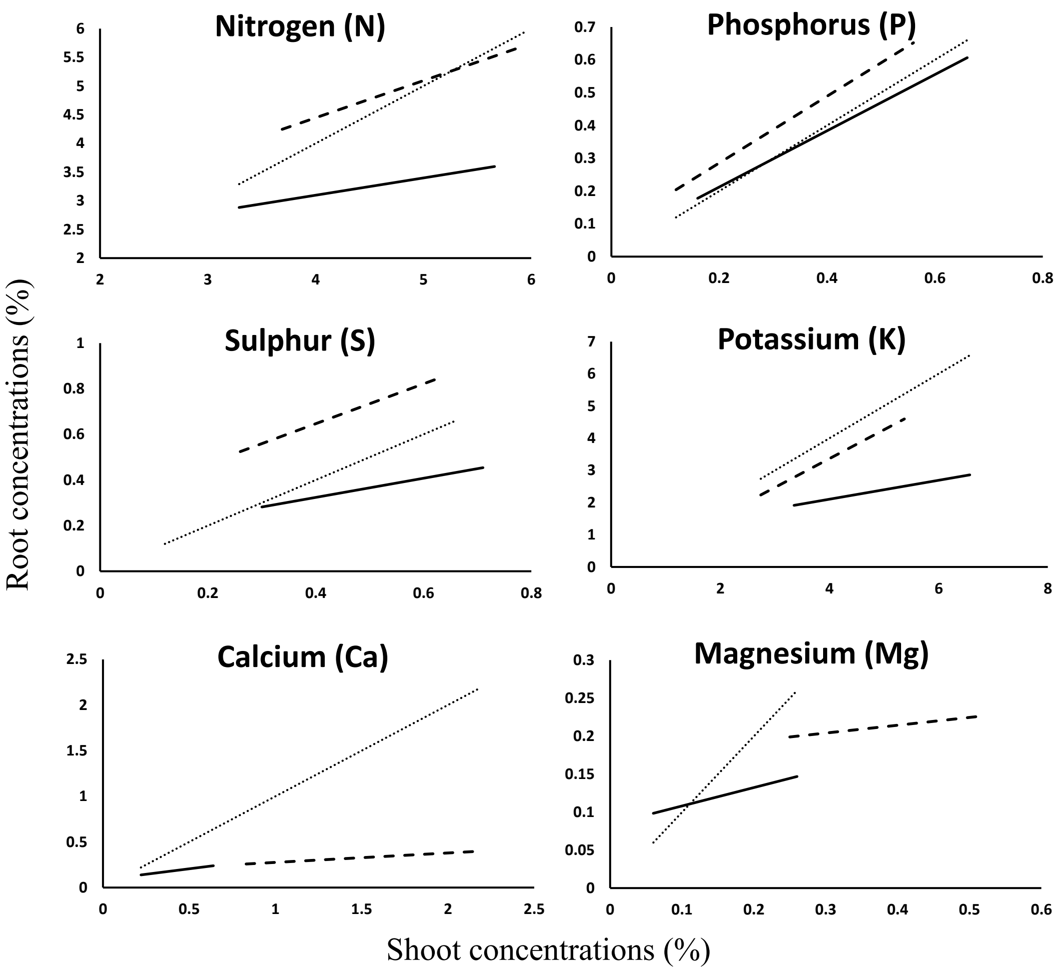

Figure 1. Relationship between shoot and root concentrations of major nutrients for grasses/cereals (solid line) and legumes (dashed line). The 1:1 line is shown as a dotted line. Regression lines are shown between the 10th and 90th percentile of shoot concentration data.

Regression equations for grass and cereal species

The slope of the relationship for K was lower when shoot K concentrations were less than 4.5% (Table 2). Also, regression analysis indicated that increasing root Ca concentrations increased root Mg concentrations, and increasing root Mg concentrations increased root Ca concentrations (Table 2). This interaction was verified using data from a series of Ca and Mg factorial experiments included in the wheat set of experiments (Wheeler and Edmeades 1995b).

There were generally no consistent differences between species of cereals or grasses. The exceptions were that the relationship for Ca and Mg for the high fertility grasses (cultivars and species of *Lolium* and *Bromus*, and cultivars of *Festuca arundinacea* (tall fescue)) had a lower slope than for the other grasses and cereals. The relationship for Mn for species and cultivars of *Lolium* (ryegrass), *Hordeum* (barley) and *Avena* (oats) had a lower slope than that for the other grasses and wheat.

In contrast to the other major nutrients, Na was higher in the roots than the shoots, and the slope of the relationship depended on the concentrations of other ions in solution. Hence no regression equation for Na is shown Table 2. In wheat, when shoot Na concentrations were greater than 0.1%, root Na concentrations were about 25 times that in the shoots when Na was added in the presence of Cl (when $MgCl_2$ or $CaCl_2$ was added, with Na as a contaminant). However, if Na was added in the absence of Cl (e.g. $NaNO_3$), or if Al was added irrespective of whether Cl was added, then root Na concentrations was about 6 times that in the shoots.

Regression equations for leguminous species
The regression equations for the relationships between shoot and root concentrations for the legume sets of experiments are shown in Table 3. For N, S, P, Mn, Zn, Cu and Fe, the data could be separated into 2 distinct groups depending on the root K concentrations (Table 3). This separation into 2 groupings did not occur if shoot K concentrations were used. The relationship for K was non-linear, with the slope being lower when shoots concentrations were < 2.3 % K. For Mg, no significant ($P > 0.05$) slope could be found.

Plant Na concentrations in both the shoots and roots were generally low (< 0.1%). Where higher Na concentrations occurred, the slope of the relationships depended on the form of Na that was added, such that, for a given shoot concentration, root Na concentrations were higher when Na was added as $NaNO_3$ than as Na_2SO_4 (slope 2.0, 0.15 respectively).

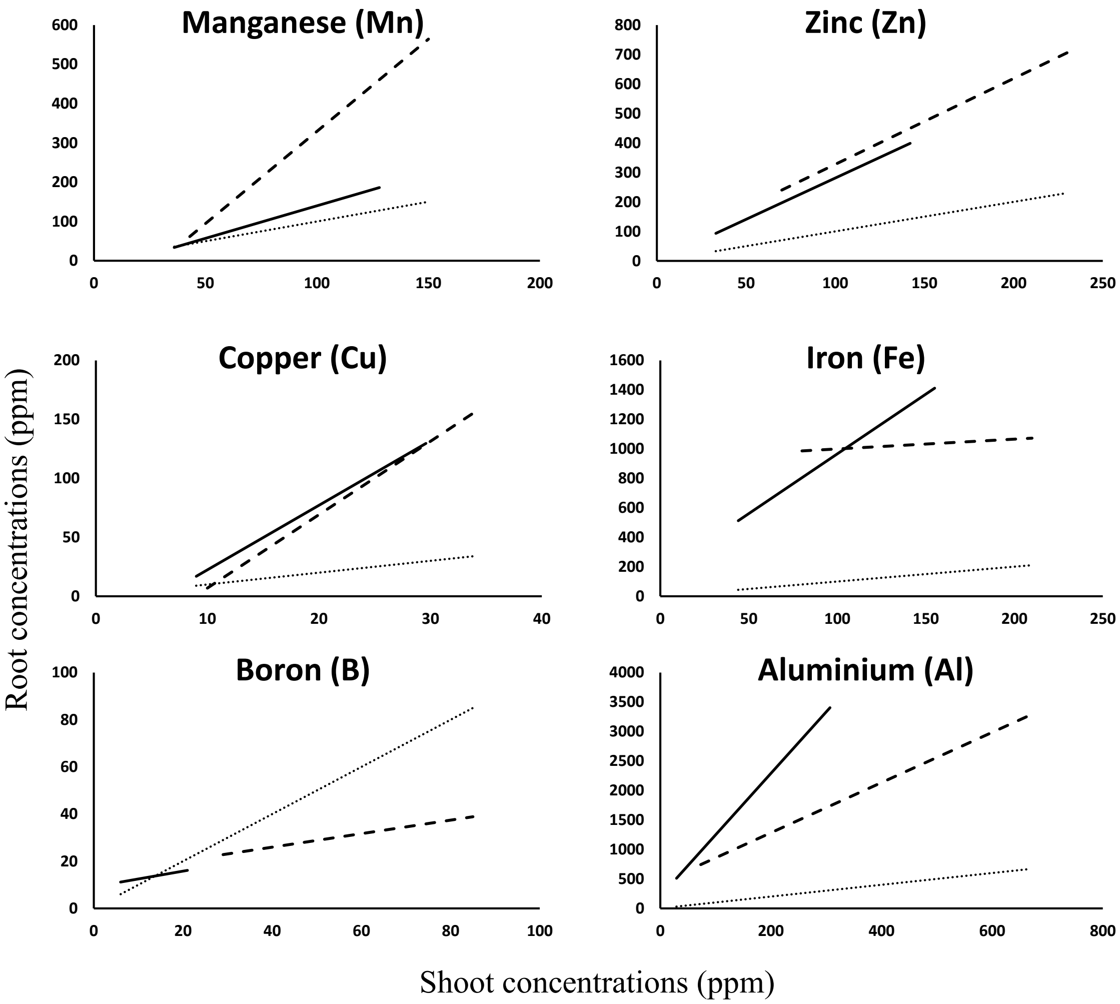

Figure 2. Relationship between shoot and root concentrations of minor nutrients for grasses/cereals (solid line) and legumes (dashed line). The 1:1 line is shown as a dotted line. Regression lines are shown between the 10th and 90th percentile of shoot concentration data

Discussion and conclusions

Despite the experiments being conducted under glasshouse conditions, there was considerable variation (as indicated by the high SE_{obs} shown in Tables 1 and 2) in estimating root concentrations from shoot concentrations using these regression equations. Some of this variation is due to both the slope and intercept differing between experiments for a given species, although the underlying reason for this variation is unknown. Some of this variation may be due to differences between species, and cultivars within species, that could not be reliably detected due to the limited range of data. The higher variation between experiments investigating trace nutrients could, in part, be due to precipitation or adsorption occurring on the root surface, with the amount of precipitation or adsorption differing between experiments in response to environmental conditions. As these root samples were not washed, surface adsorption of other nutrients may also have occurred leading to greater variation in the relationship between shoot and root concentrations.

Non-linear relationships were only noted for K. In general, only K concentrations decreased below the deficient levels reported by Cornforth and Sinclair (1984). The overall lack of non-linear relationships for other nutrients could be due to a lack of sufficiently low values for these nutrients.

The distribution of nutrients between shoots and roots was not affected by other nutrients except for Ca and Mg in wheat. It should be noted that factorial experiments were not conducted to allow this to be readily observed, and if such interactions occurred then they could have contributed to the variation noted above. In the roots of wheat, increasing root Ca increased root Mg, and vice versa (Table 2). In contrast, in the shoots there is normally a competitive effect of Ca on Mg, and vice versa (Wheeler and Edmeades 1995b). The absence of the competitive effect in the roots suggests that Ca and Mg are competing during transport from the roots to the shoots rather than at uptake.

Of the major plant nutrients, Na was the only one to have higher concentrations in the roots than the shoots, and for the relationship between shoot and root concentrations to be dependent on the form added to solution. Despite ryegrass and white clover being natrophiles that readily accumulate Na in the shoots (Smith *et al*. 1980), Na was higher in the roots than the shoots of grasses and cereals, and in legumes when added as nitrate, which is characteristic of natrophobes. Although these results indicate that it could be difficult to increase pasture Na concentrations by direct fertiliser applications, O'Connor *et al*. (1989) has demonstrated that this can occur.

The equations and ratios in this paper are based on whole shoot concentrations. In white clover, stolons have lower concentrations of N and P than the leaves (Hay *et al*. 1985) while in ryegrass, S concentrations were lower in closely cut than laxly cut material (Wheeler, unpublished data). Also, stems generally had lower nutrient concentrations than leaves in beans and squash grown using the same hydroponic technique (Wheeler and Follett 1991, Wheeler *et al*. 1992c). This indicates that the shoot concentrations may need to be adjusted if the regression equations shown in Tables 2 and 3 are used when shoot concentrations are measured from some harvestable portion of shoot yield rather than the complete shoot system.

The regression equations (Tables 2, 3) allow estimation of the distribution of nutrients between the shoots and roots when plant uptake is estimated in nutrient models. The consistent difference between the monocotyledons and dicotyledons means that initial estimates for other pasture species not included in this data set can be made on the basis of whether they are monocotyledons or dicotyledons. Distributions between shoots and roots have sometimes been estimated using a ratio. However, the significant constant term in most of the regression equations, or the non-linear relationships found for K, indicate that the use of ratios could be misleading, particularly at low or high plant concentrations.

Conclusions

The results from this study give an empirical method for estimating the root nutrient concentrations from shoot nutrient concentrations when modelling nutrient flows in pasture.

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