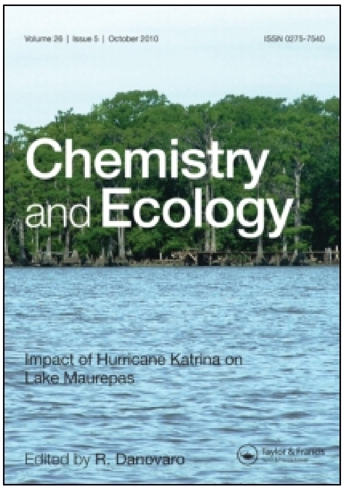

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THE NUTRIENT STATUS OF SOME GRAMINACEOUS SPECIES IN BRITAIN. 1. *MOLINIA CAERULEA* (L.) MOENCH

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Above-ground biomass biomass of *Molinia caerulea* from 36 sites throughout Britain was analysed for concentrations of elements (N, P, K, Ca, Mg, Fe, Mn, Cu, Zn and Na), with matching analyses of soil nutrients, together with pH and LOI. Between-year and seasonal variation in the nutrients was also studied at one of the sites. The grass was found on acid sites ranging between pH 3.1 and 5.8. The soil humus content varied widely, and there were significant correlations between that and elements (N, P, K, Ca, Mg and Na) in the soil. Concentrations of calcium, magnesium, zinc and manganese in the plant material were significantly correlated with extractable levels in the soils. Between year variation in the plant nutrient concentrations at one site was of a similar order to variation between the sites. Generally there was less variation in nitrogen, phosphorus and potassium tissue levels than in calcium, magnesium, zinc and copper. Iron and sodium were the most variable. Tissue concentrations of nitrogen, phosphorus, potassium and copper declined throughout the growing season, whereas magnesium, calcium and iron built up until August/September after which a decline set in as the leaves senesced. The results are discussed in relation to the importance of standardizing the time of sampling, in comparison with concentrations of tissue levels in other plants and the growth strategy of this deciduous grass.

Keywords: *Molinia caerulea*; plant nutrients; seasonal variation; soil status

Abbreviations: RSD, relative standard deviation

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1. INTRODUCTION

It is commonly recognised that soil nutrient factors have a profound effect on the botanical composition of grassland (Pegtel, 1987), with the increase in soil fertility resulting in the gradual replacement of slow-growing species by those with more rapid growth and higher nutrient demand. Although plant tissue analysis data are often used as a measure of the nutrient status of plant species (Davy and Taylor, 1975; Chapin and Van Cleve, 1989), details relating to seasonal variation, especially for trace micro-nutrients, annual changes over long periods and soil: plant nutrient data are still relatively sparse. Large comparative surveys have been made of major and minor plant nutrient composition (*e.g.*, Foulds, 1993), although there is relatively little information available on the background concentrations, distributions or fluxes of trace elements in natural or semi-natural ecosystems (Adriano, 1986).

A large-scale project was initiated to determine the nutrient composition of plant species in Britain. The objectives of the 'Vegetation Nutrient Survey', of which this study forms a part, were:

(1) to assemble between-site and seasonal information on the chemical composition of selected species in Britain as a means of assessing their nutrient status;
(2) to examine inter-relationships between the nutrient content of individual species and the temporal and spatial distribution, in relation to habitat and soil factors;
(3) to evaluate between-plant nutrient relationships of different species on similar habitats, soil types and geographic locations.

Molinia caerulea (L.) Moench (purple moor grass), the subject of this paper, is a deciduous grass which grows in fens, heaths and moors and occurs widely throughout the British Isles. The area of land on which it is the dominant species has been estimated at around 600 000 ha or 10% of the uplands (Bunce and Barr, 1988). The tussocks, which can be large, grow to a height of between 15–150 cm, (Clapham *et al.*, 1987). Shoots develop from buds of the previous season. The stems elongate during May and June, and in late June or early July, the second series of leaves open. The inflorescences expand to open in late July or early August, and by September, the first series of leaves are dead. By November all the leaves are dead, leaving a prominent swollen club-shaped basal internode. Because *M. caerulea* is unusual in being a deciduous grass, it is of particular interest to know how the nutrients recycle within the plant, and the extent and seasonal pattern of exchange between the plant and soil (Loach, 1968).

Studies have been made to compare or contrast *M. caerulea* productivity with two or three species at one site in relation to nutrient availability (Nazrulislam and Rorison, 1981; Berendse and Aerts, 1984; Heil and Bruggink, 1987; Aerts, 1989; Vanvuuren and Berendse, 1993). Although *M. caerulea* tends to occur on nutrient poor soils, it can replace *Calluna vulgaris* and *Deschampsia flexuosa* when nutrient availability increases (Aerts, 1989). It also out-competes *Erica tetralix* under these conditions (Aerts and Berendse, 1988). Higher nitrogen deposition in the Netherlands may partly explain why maximum above ground productivity there is twice as high as in Britain (Aerts, 1989). *M. caerulea* also exhibited more vigorous growth and greater vegetative development in a moorland habitat than on a calcium-rich alkaline waste tip (Abusalim *et al.*, 1995). Loach (1968) studied a range of wet heath habitats and found that *M. caerulea* was most abundant where nutrient levels were highest.

In general, however, there appear to be few data on soil nutrient status from sites where it occurs naturally and is not subject to fertilizer applications. This paper records a detailed study of the seasonal pattern of foliar micro- and macro-nutrients in *M. caerulea* and the relation with soil nutrients and site characteristics at 36 sites distributed throughout Britain.

2. METHODS AND MATERIALS

2.1. Criteria for Selection of Sampling Sites in the Vegetation Nutrient Survey

(1) Vegetation on the surveyed sites was to be composed mainly of higher plants, although ferns and one or two bryophytes could be present;

(2) the species in the sampled area was to be the dominant or co-dominant;

(3) the habitat was to be generally widespread throughout Britain, although it might be restricted to a geographical region;
(4) certain disturbed sites were avoided *e.g.*, roadside verges, and areas subject to 'contamination' by fertilizers, herbicides or pollution.

2.2. Sampling and Preparation of *M. caerulea*

M. caerulea was sampled from 36 habitats at undisturbed sites between 30 and 300 m altitude, throughout Britain (Fig. 1). Green shoots were collected from between 5 and 10 tussocks, sufficient to fill a 1-litre paper bag. Samples were collected between 19 July and 10 August in three years: 1969, 1970 and 1974. Three replicate samples were collected from each site to provide independent samples for analysis.

In order to evaluate the seasonal pattern of nutrient concentrations in the biomass, triplicate samples were collected from Roudsea Wood, Cumbria (SD330820) at monthly intervals over the growing season from the end of April until the beginning of November in 1969. For a more detailed assessment of between-year variation, *M. caerulea* samples from Roudsea Wood were collected each year for a period of 15 years.

Plant material was dried for 24 h at 40°C, and then ground to less than 0.7 mm, using a Christy and Norris mill. Ground samples were dried at 105°C for 3 hours prior to analysis. All results were expressed on a dry weight basis.

2.3. Soil Sampling

Ten random sampling points were selected at each site, and a 15 cm diameter core of soil was collected with a trowel from the 0 – 15 cm layer, after removal of *M. caerulea* and other plant litter. Two samples for chemical analysis were created by bulking five of the cores.

Samples were dried for 24 h at 40°C; air dry material was sieved to less than 2 mm. Sub-samples of material were analysed to determine the residual moisture by drying for 3 h at 105°C, and correction factors were applied to convert the data to a dry weight basis.

2.4. Chemical Analysis

The elements determined were elements (N, P, K, Ca, Mg, Fe, Mn, Cu, Zn and Na), although trace elements were not determined on the soil from the site at Church Stile Wood, Wasdale, Cumbria, NY127044.

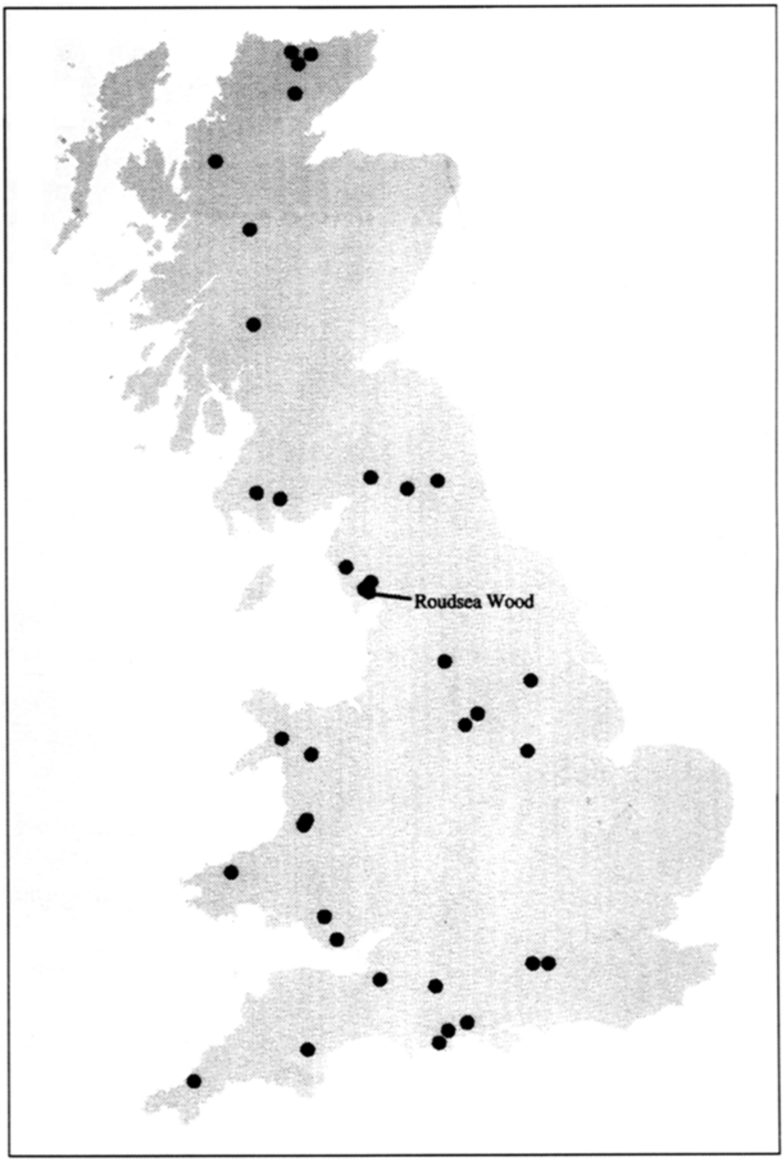

FIGURE 1 Distribution map of sampling sites for *Molinia caerulea* in Britain.

2.4.1. Determination of Nutrients in Plant Material

Methods are described in detail in Allen (1989). Samples were acid digested by the peroxide-sulphuric acid modified Kjeldahl digestion method (Parkinson and Allen, 1975). Potassium and sodium were determined by flame emission. Calcium and magnesium were determined by atomic absorption spectrophotometry, with the addition of lanthanum releasing agent (Grimshaw, 1989). Nitrogen, phosphorus, and iron were determined by continuous flow colorimetry (see below for specific methods). Manganese, copper and zinc were determined by atomic absorption spectrophotometry.

2.4.2. Determination of Nutrients in Soil

Methods are described in detail in Grimshaw (1989). The pH was measured in a 1 : 2 slurry with deionised water. Loss on ignition (LOI) was determined by igniting air dry material for 2 h at 550°C. Total nitrogen was determined, following Kjeldahl digestion, by indophenol blue continuous flow colorimetry. For elements (P, K, Ca, Mg, Fe, Mn, Cu, Zn and Na) the 2.5% acetic acid extractable fraction (5 g air dry soil plus 125 ml extractant) was determined using methods outlined above for plant material. Extractable phosphate was determined using molybdenum blue continuous flow colorimetry, and iron was determined by bathophenanthrolein continuous flow colorimetry.

2.5. Statistical Analysis

Means, medians, standard deviations and correlation coefficients were computed in Microsoft Excel version 5. Principal components analysis calculations were generated in SYSTAT. Standardized weightings above 0.75 were used to define the grouping of nutrients.

3. RESULTS

3.1. Site Characteristics and Habitats

M. caerulea was sampled from a variety of locations and habitats (Fig. 1) ranging from coniferous woodland, lowland heath, bog/fen, hill grassland, deciduous or mixed woodland and upland heath.

At the majority of sites, it was sampled as the dominant species. In some cases, however, samples were collected where it was categorized as abundant or co-dominant with other species. Surveyors recorded *M. caerulea* growing in grass mixtures together with *Agrostis capillaris*, *Deschampsia flexuosa* and *Holcus lanatus*. At 5 sites, *Calluna vulgaris* was present, and occasionally *M. caerulea* was collected from sites where *Erica tetralix* or *Eriophorum vaginatum* were also dominant. We also found dominant swards of *M. caerulea* in areas where *Sphagnum* spp. or *Pteridium aquilinum* were present. Samples were collected from woodland edges with *Galium* spp. present, or in the proximity of trees, beneath spruce, oak, rowan, willow or birch.

3.2. Between-site Variation in Nutrient Concentrations in *M. caerulea* Shoots

Table I lists the mean concentrations of all the nutrients in the aerial parts of *M. caerulea* from 36 sites. These values provide an overall picture of the nutrient status of the species. In the range of nutrient concentrations in the species of grasses collected in the Vegetation Nutrient Survey, the elements (P, K, Ca, Fe and Na) in *M. caerulea* were relatively low, copper and magnesium were close to the mean and nitrogen, manganese and zinc were relatively high. The mean ratio of P:N in the aerial parts was 1:15, ranging from 1:10 up to 1:25. The ratio of Ca:P was 1.3, ranging from 0.6 up to 2.7.

Concentrations of the macronutrients nitrogen, phosphorus, potassium, calcium and magnesium in the plant tissues showed a similar

TABLE I Nutrient concentrations of *Molinia caerulea* aerial shoots and of 21 other grasses sampled throughout Britain (% or $\mu g\,g^{-1}$ for copper and zinc)

	Mean	*σ*	*%RSD*	*Median*	*Min.*	*Max.*	*Ratio max:min*	*Mean of grasses*
N	1.81	0.263	14	1.80	1.17	2.34	2	1.62
P	0.118	0.021	18	0.119	0.065	0.183	3	0.176
K	1.26	0.199	16	1.26	0.802	1.71	2	1.95
Ca	0.167	0.049	29	0.159	0.100	0.321	3	0.319
Mg	0.135	0.038	28	0.132	0.059	0.217	4	0.143
Fe	0.00769	0.0028	36	0.00697	0.0044	0.0161	4	0.0141
Mn	0.0271	0.0107	39	0.0254	0.0053	0.0492	9	0.0189
Cu	5.63	1.72	31	5.25	2.97	11.8	4	6.49
Zn	44.1	54.3	123	31.1	17.3	348	20	33.7
Na	0.027	0.021	78	0.020	0.002	0.096	48	0.197
n	36							
Total	3.6							4.4

(RSD = relative standard deviation).

range of inter-site variability, with the highest concentrations 2–4 times the lowest. Inter-site coefficients of variation for nitrogen, phosphorus, and potassium were less than 20%, and for manganese and calcium between 20 and 30%. Other elements were more variable, especially the trace element zinc and the non-essential element sodium, with the highest concentrations being 20 and 48 times the lowest. Inter-site variation for iron, manganese and copper was in the region of 30–40% and sodium and zinc more than 70%.

Very few of the measured plant nutrients were correlated with each other. Only 6 of the possible 90 macro- and micro-nutrient relationships were inter-correlated (Tab. II). Standard normal distributions would predict that approximately 5% of relationships, more or less the number we found, would have occurred by chance. However, positive correlations were noted between nitrogen and phosphorus and between calcium and magnesium, which are likely to be of ecological interest. Principal component analysis of the plant nutrient highlighted the first component to involve calcium, magnesium and iron, where the first two contrasted with iron, and this component accounted for 23% of the variation in the data. Nitrogen, phosphorus, and copper made up component 2, and potassium, calcium and sodium formed component 3. Fifty-four percent of the variation in the data was accounted for by the three components.

TABLE II Significant correlations within plant nutrient concentrations, soil parameters and between plant and soil measures ($p < 0.05$)

	Correlations of plant nutrients			
Na/Ca	*Ca/Mg*	*Mg/Fe*	*Fe/Cu*	*Cu/P*
P/N				
	Correlations of soil nutrients			
LOI/Na	**LOI/K**	LOI/Ca	**LOI/Mg**	**LOI/P**
LOI/N	**Na/Mg**	**Na/P**	**Na/N**	K/Mg
Na/K	K/N	Ca/Mg	Ca/N	**Mg/P**
K/P	**Mg/N**	**Fe/Cu**	Cu/Zn	P/N
pH/Mn	pH/Zn			
	Correlations between plant and soil nutrients			
Na/pH	Na/Ca	**Na/Mn**	K/N	**Ca/Ca**
Mg/Mg	Fe/Mg	Fe/N	**Mn/Mn**	Cu/P
Zn/Cu	**Zn/Zn**	Mg/LOI	Mg/P	Mg/N
Fe/LOI	Cu/LOI	Cu/Na	P/LOI	Ca/Mg
Cu/Mg				

Bold correlations indicate significance at $p < 0.001$.

3.3. Between-year Variation in Nutrient Concentrations of *M. caerulea* Shoots

To assess the year-to-year variation, and to determine the value of tissue concentrations in aerial growth at a single point in time as an index of plant nutrient status, we sampled *M. caerulea* aerial growth from the same site at Roudsea Wood over a period of 15 years. There were no marked changes in the 10 macro- or micro-nutrients over the whole period. There were 5 successive years between 1976 and 1981 when the nitrogen concentration was lower than in the previous year. However, in the following two years the concentrations returned to the pre-1976 level. The scale of between-year variation was of a similar order to that of inter-site variation, and the spread of data was again lower for macro- than micronutrients. The coefficient of variation for nitrogen, phosphorus and potassium was less than 10% (Tab. III), calcium, manganese, magnesium, zinc and copper, between 10 and 20%, and only iron and sodium exceeded 30%.

3.4. Seasonal Variation in Nutrient Concentrations of *M. caerulea* Shoots

Regular sampling of aerial shoots from *M. caerulea* tussocks during the growing season, also at Roudsea Wood, revealed several distinctive seasonal patterns of tissue concentration (Fig. 2). Nitrogen,

TABLE III Mean nutrient concentrations of *Molinia caerulea* shoots sampled at Roudsea Wood over a 15 year period (% or $\mu g\,g^{-1}$ for copper and zinc)

	Mean	σ	*%RSD*
N	1.89	0.15	8
P	0.123	0.010	8
K	1.65	0.16	10
Ca	0.121	0.013	11
Mg	0.146	0.021	14
Fe	0.0067	0.0020	30
Mn	0.0158	0.0027	17
Cu	6.47	1.20	19
Zn	32.1	5.92	18
Na	0.0151	0.0059	39

(RSD = relative standard deviation).

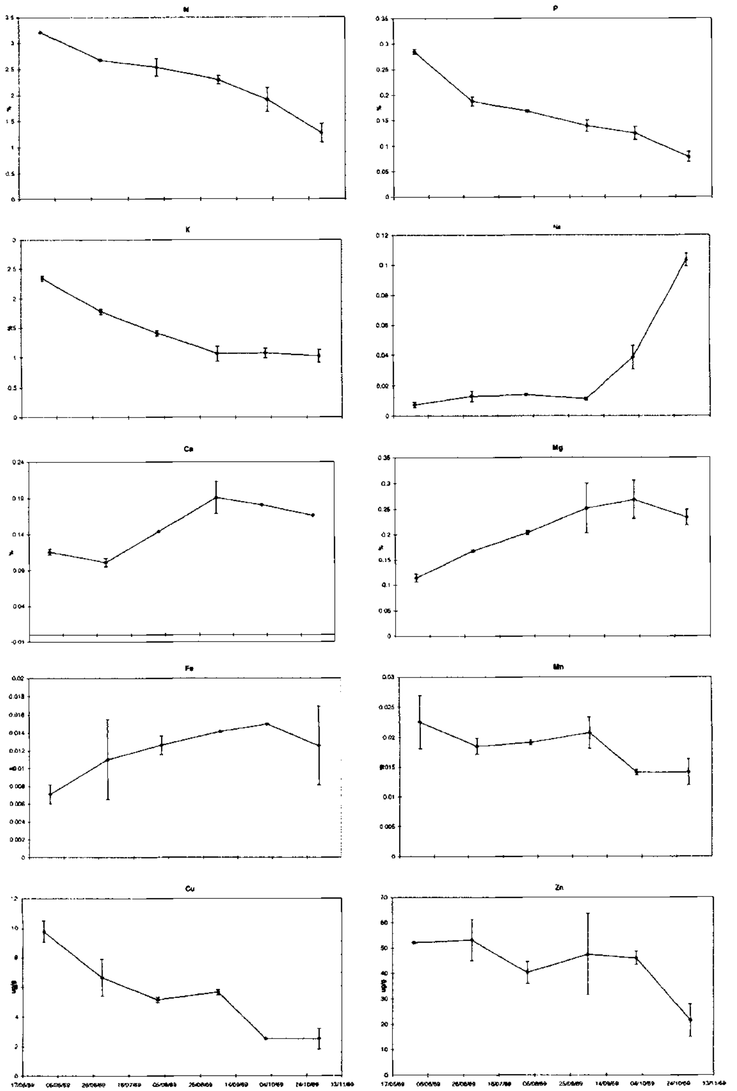

FIGURE 2 Seasonal pattern of macro- and micro-nutrients in *Molinia caerulea* at Roudsea Wood, Cumbria. Error bars show ± σ for $n = 3$.

phosphorus, potassium and copper concentrations were high in late spring and then gradually decreased, presumably due to dilution in the expanding leaf volume, to a fairly constant value from the end of

August onwards. Magnesium and iron concentrations continued to build up until the end of September, from when they gradually started to decline. The maximum tissue concentration of calcium occurred at the end of August onwards. Manganese and zinc concentrations varied little during the growing season, but then declined in the autumn as the leaves began to senesce. Sodium concentrations remained low at around 0.01% to the end of August, and then between August and the end of October, increased dramatically by about ten-fold.

3.5. Soil Nutrient Status of *M. caerulea* Sites

Soils under *M. caerulea* were found to be mainly organic or podzolised, and were usually either water-logged or poorly drained. A summary of the nutrient status of the soils is contained in Table IV. Soils were acid, with pH values ranging from 3.1 to 5.8 (mean 4.2, median 4.0). The humus content (measured as LOI) of the top 15 cm layer, sampled after removal of the litter layer, ranged from 9 to 98% with a mean of 47%, and median of 40%. The nitrogen status of the soil also varied significantly from poor (0.2%) to a higher fertility status (2.6%). One unusual site was on a sandy soil of low LOI (4%) and very low nitrogen content (0.07%).

In contrast to the plant nutrient concentrations, twenty-two of the 144 measured soil parameter relationships were positively

TABLE IV Nutrient concentrations of soil collected beneath *Molinia caerulea* habitats in Britain (% or mg 100 g^{-1} for extractable (Ex) nutrients)

	Mean	*σ*	*Median*	*Minimum*	*Maximum*
pH	4.17	0.685	3.99	3.08	5.76
LOI	47.2	32.4	39.6	4.03	98.2
Kjeldahl N	1.24	0.78	1.22	0.07	2.63
Ex-P	2.49	2.92	1.16	0.25	14.2
Ex-K	23.4	21.1	17.3	2.01	95.4
Ex-Ca	81.9	93.1	49.6	1.25	480
Ex-Mg	31.2	32.9	18.7	0.62	122
Ex-Fe	7.02	7.58	5.43	0.55	35.0
Ex-Mn	5.94	9.52	1.82	0.00	38.1
Ex-Cu	0.09	0.22	0.03	0.00	1.17
Ex-Zn	3.29	11.6	1.01	0.14	69.7
Ex-Na	14.1	14.7	9.13	0.50	53.4

inter-correlated, and many of the correlations were significant at $p < 0.001$ (Tab. II). The most important factor in the soil budget, assessed by the greatest number of significant correlations ($p < 0.001$), appeared to be the organic matter content (LOI), which was correlated with the soil macro-nutrients, (N, P, K, Ca, Mg) and also with sodium. Many of the macronutrients themselves were positively correlated with each other. For example, soil extractable phosphate was correlated with LOI, nitrogen, extractable potassium and magnesium. Soil pH was only correlated with extractable manganese and zinc. The pH was not correlated with extractable calcium, magnesium or iron, although this may be attributable to the fairly narrow range of soil pH and acidic conditions where *M. caerulea* occurs. Trace or micronutrients did not generally show any correlation with LOI, and only 4 of the 22 significant correlations featured the micronutrients.

Plant growth and distribution is generally related to the availability of macronutrients released in decomposition of soil organic matter. Principal component analysis of the soil nutrient values demonstrated a high degree of correlation between certain of the variables. The first component, LOI, nitrogen, and extractable phosphate, potassium, manganese and sodium accounted for 37% of the variation. Extractable copper, manganese and pH made up component 2, and extractable iron together with copper component 3. These 3 components accounted for 69% of the variation in the data.

3.6. Plant-soil Relationships

Twenty-one of the possible 120 macro- and micro-nutrient correlations between the soil nutrients and the *M. caerulea* aerial tissue concentrations were significant, some at $p < 0.001$. Acetic acid extractable measures of calcium, magnesium, zinc and manganese in the soil correlated with the concentration of that element in the deciduous grass. Magnesium was the only plant nutrient that was positively correlated to soil organic matter content (LOI), although plant phosphorus, iron and copper were all negatively correlated. Tissue concentrations of sodium were the only ones to show a correlation with soil pH.

4. DISCUSSION

4.1. Plant Nutrient Concentrations

The 'Vegetation Nutrient Survey' was designed to evaluate the nutrient status of common native plants. In order to establish an accurate indication of plant nutrient status, plants were sampled from sites only where there was no sign of disturbance or agricultural activity. From an early evaluation of data from the survey, Grimshaw and Allen (1987) produced a comparative index that was derived from the sum of the mean macro- and micro-nutrient concentrations in above-ground plant tissues. This sum in *M. caerulea*, derived from sites distributed throughout Britain, was 3.6% (see Tab. I), and was similar to that derived for other grasses, such as *Deschampsia flexuosa* (4.0%) and *D. caespitosa* (4.2%). In contrast, the mineral content index derived for the shrub, *Calluna vulgaris*, is lower (2.5%) and for the opportunistic forb, *Chamaenerion angustifolium*, much higher (6.8%).

Grimshaw and Allen (1987) examined the skewness and kurtosis (the length and height of the tail in the frequency distribution) of the tissue nutrient contents, and discussed how this might affect the variance. *M. caerulea* coefficients of skewness were significant and positive for the trace elements iron, copper and zinc, and also for calcium and sodium ($p < 0.05$). In comparisons of 15 native species, they noted that micronutrient distributions are often more skewed than those of macronutrients. The coefficients of kurtosis for the *M. caerulea* data were also significant for these elements too, and for phosphorus. One outlying value ($> +/-4\sigma$) was detected for zinc, from a site where the available zinc concentration was high.

Table I shows that *M. caerulea* nutrient concentrations in shoots are in the order: N > K > Ca > Mg > P > Mn > Na > Fe > Zn > Cu. The mean nutrient values for 21 grass species analysed in the overall general survey also follow this pattern, except that phosphorus concentrations exceed magnesium. Our data support the findings of Foulds (1993), who surveyed the nutrient content of south Australian foliage. The plant nutrient concentrations were ranked in a similar order.

The ratio for *M. caerulea* for plant P:N of 1:15 is at the lower limit of the range for plants, and reflects both a higher than average nitrogen concentration and a lower than average phosphorus concentration. Across a broad range of species, Thompson *et al.* (1997) reported that the ratio of plant P:N concentrations ranged from 1:5 up to 1:15 for non-legume plants. Vascular plants appear to require a very similar balance of nutrient supply for optimal growth (Ingestad, 1982), and therefore there should be a similar ratio of nutrient concentrations in tissue unless some element is limiting growth. Variations in the P:N ratio may therefore indicate nutrient limitation in plants (Chapin and Van Cleve, 1989), reflecting either deficiencies or temporary storage of one nutrient in excess of plant demand. The ratio of 1:15 for *M. caerulea* probably reflects the strategy of storage of nitrogen in the basal internode during the winter period, and subsequent recycling during the spring and summer.

The Ca:P ratio in *M. caerulea*, a deciduous grass, increased throughout the growing season from 0.4 in May, up to 2.1 at the end of October. In relation to animal nutrition, Fleming (1973) discussed the importance of the Ca:P ratio in pasture vegetation, and reported that values between 0.5 and 2.0 are desirable. He considered the possibility of a ratio outside this range to be greatest during the summer months; this was not the case for *M. caerulea*, where the ratio increased throughout the growing season.

We found a range of copper concentrations of between 3 and 12 $\mu g\ g^{-1}$ in the plant tissues. It is perhaps interesting to note that, although there were only 6 correlations between plant tissue macro- and micronutrients in our studies of *M. caerulea*, one of these was a positive correlation between copper and phosphorus. Smilde (1973) reported that high concentrations of phosphorus can accentuate copper deficiency in trees. Copper is required in very low amounts by plants; concentrations in the range between 5 and 20 $\mu g\ g^{-1}$ in plant tissue is considered adequate for normal growth (Jones, 1972). Outside this small range, it is considered to be either deficient or toxic. The median range for grasses, primarily from agricultural areas, however, was reported by Kubota (1983) to be lower than for legumes (median 4 $\mu g\ g^{-1}$; range = 1 to 16 $\mu g\ g^{-1}$).

4.2. Between-year and Seasonal Variation in Nutrient Concentrations in *M. caerulea* Shoots

Annual mean nutrient concentrations in aerial shoots (Tab. III) from an undisturbed site over a 15 year period for *M. caerulea* indicate extremely small variation in nutrient status for nitrogen, phosphorus and potassium. Under natural conditions, environmental variables, notably temperature, light intensity and ion availability, would be expected to affect the rates of ion absorption, tissue concentrations and growth rates. In the early stages of leaf development in the spring, nitrogen, phosphorus and potassium leaf concentrations are relatively high due to the supply of nutrients from the soil, the rhizome and basal internode. As growth proceeds, demand for nutrients increases the store of nutrients is rapidly depleted and tissue concentrations in *M. caerulea* shoots decrease. In an early study to evaluate seasonal variation in moorland species, Thomas and Trinder (1947) noted some clear patterns for phosphorus, potassium and calcium. We have been able to confirm that phosphorus and potassium decrease throughout the growing season, in contrast to calcium, which increases. However, they were not able to establish such clear trends as we found for other ions (Mg, Fe, Mn or Cu), but the pattern we detected for magnesium and copper is apparent in their data. Old basal internodes appear to be storage organs, as suggested by Thornton and Millard (1993), for major nutrients as they decline during the season, and then increase in November (Loach, 1968).

Our seasonal study of *M. caerulea* confirms that calcium is relatively immobile (Langkamp and Dalling, 1982). Magnesium and iron exhibit similar properties *i.e.*, they increase over the whole growing season and only decline slightly at the final sampling at the end of October, as senescence sets in. Most plant nutrients are withdrawn from foliar organs with lesser efficiency than phosphorus. Iron, manganese, zinc and copper have variable mobilisation as indicated by the lack of smooth trends in the seasonal patterns of nutrient concentrations in shoots (Fig. 2).

Aerts (1989) reported seasonal trends in nitrogen and phosphorus concentration of leaves, culms, panicles, leaf sheaths, basal internodes and cord roots. In *M. caerulea* however, the results only covered the period from August to November from one site in central Netherlands. Leaf nitrogen content declined from 2% in August to 0.5% in November. Basal internodes and cord roots increased slightly over this period (0.6% to 1.0% and 1.0% to 1.4% respectively) as nutrients were translocated back prior to senescence and abscission of the dead shoots above the internode. The decline in leaf phosphorus was even more marked, from 0.06% to 0.01% in the three months. Again basal internodes and cord roots were the only two components to show an increase in phosphorus concentration (0.03 to 0.06%). Other species show a similar trend *e.g.*, nitrogen and phosphorus decline during the growing season in *Chamaenerion angustifolium* (Thompson *et al.*, 1997).

Trends in the mineral concentration of *M. caerulea* for the macronutrients between May and August were similar to those described by Marks and Taylor (1972) for *Rubus chamaemorus*, a plant that is deciduous and found in similar wet, acidic habitats to *M. caerulea*. The rates of change appear to be much greater for *R. chamaemorus*, as initial concentrations, or maximum concentrations were much higher than in *M. caerulea*.

The majority of studies on seasonal nutrient patterns in plants, focus on major nutrients (Thomas and Trinder, 1947; Aerts, 1989). One exception to this was an investigation of seasonal patterns for zinc, cadmium and lead in *M. caerulea* and *Deschampsia flexuosa* (Badsha and Badsha, 1988). Fluctuations were partly due to rainfall patterns, and to the presence of dry foliage material subjected to longer term exposure to airborne contamination. Zinc levels showed differences between tissues which varied at different times of year, with shoot and leaf concentrations stable between April and September at around 150–160 $\mu g\,g^{-1}$, declining in October and November to about 90 $\mu g\,g^{-1}$. We found a similar trend in zinc concentrations in *M. caerulea* throughout the growing season, declining from 50 $\mu g\,g^{-1}$ to 20 $\mu g\,g^{-1}$ in the autumn.

4.3. Soil Nutrient Status of *M. caerulea* Sites

At undisturbed *M. caerulea* sites, relationships for all the major nutrients with organic matter content (measured as LOI), demonstrate that the size of the organic pool and its rate of turn-over is probably the main factor for estimating the soil nutrient status. Dickinson (1984) concluded that nutrient availability in grassland soils is largely dependent upon the rate of decomposition of organic residues in the soil or litter layer.

There are very few data concerning plant distribution in relation to micro-nutrients at a non-toxic level. The solubility, mobility and availability of copper to plants is largely dependent on soil pH

(Adriano, 1986). The availability of copper is drastically reduced at a soil pH above 7. It is more available below pH 6 (Locascio, 1978) and especially below pH 5 (Lucas and Knezek, 1972). In our study, none of the soils had a pH greater than 6, and only 4 sites were between pH 5 and 6 which may explain the lack of correlation between either soil pH or extractable soil copper and plant tissue copper concentrations. However, we did find a relationship between soil copper and plant productivity as measured by the mean height of the *M. caerulea* stand. Similarly, the availability of zinc becomes very low above pH 7 and it is reported as generally low in organic soils (Adriano, 1986). We found a positive correlation between pH and extractable zinc, but no correlation with organic matter.

The availability of manganese and iron to plants is largely governed by the supply of H^+, as acidic conditions favour the mobility of soil manganese and iron. There was a correlation between soil pH and extractable manganese in the organic and poorly drained podzolic soils at the *M. caerulea* sites. Marked increases in the availability of manganese should be expected when the pH decreases below 5.5 (Lucas and Knezek, 1972). Water-logging also leads to increased levels of soluble Mn^{2+} and Fe^{2+} (Jones, 1971), but soil water content was not measured in this study.

4.4. Relation between Soil Nutrient Status and *M. caerulea* Tissue Concentrations

In this study of *M. caerulea*, which thrives on acidic soils, tissue sodium was the only value to correlate with soil pH. Lack of a significant correlation of calcium and manganese concentrations in shoots with soil pH was probably due to the relatively low range of pH in the studied sites. In a study of 83 herbaceous species, Thompson *et al.* (1997) reported that only calcium and manganese in the tissues were consistently correlated with soil pH.

Plant productivity, determined by the height of the *M. caerulea* community, showed a negative relationship with calcium and iron. Four of the nutrients studied showed positive correlations between extractable soil concentrations and levels measured in the plant tissues in late summer; these were calcium, magnesium, manganese and zinc. It is perhaps not surprising that none of the three major nutrients showed this relationship, because of the difficulties in obtaining suitable measures of these labile soil nutrients. Soil water status and seasonal patterns of variation in soil nutrient levels probably have a greater influence on plant tissue concentrations for the three major nutrients. These would not be adequately detected in a single determination by digestion or extraction. Patterns of uptake are known to vary between species, and are not necessarily related empirically to available nutrients measured by conventional soil analysis (Hayati and Proctor, 1991).

The lack of correlation between the measures of soil availability for nitrogen, phosphorus and potassium and plant tissue concentrations may indicate that rapid shoot growth in the spring is supported more from stored nutrients, translocated back from the internode, than from concurrent absorption from the soil. Our soil data indicate that *M. caerulea* is adapted to survive in a range of different soils and nutrient supply conditions. Plants adapted to live in infertile habitats maximise nutrient uptake (Chapin, 1980) and species exhibit low absorption rates *i.e.*, only a relatively small increase in absorption occurs in response to increasing nutrient supply. When grown under comparable conditions, slow growing species from infertile habitats have higher tissue concentrations of a limiting nutrient than do rapidly growing species.

Fertilizer experiments (Aerts and Berendse, 1988) indicate that phosphate is the limiting nutrient for *Calluna vulgaris* and other ericaceous species, as they appear unable to compete with *M. caerulea* where soil phosphate availability is low. Therefore, according to Chapin (1980), *C. vulgaris* for example might be expected to have higher tissue concentrations than *M. caerulea.* Grimshaw and Allen (1987) in reporting mean values from 15 species from this survey show that the mean phosphorus concentration in *C. vulgaris* current year's growth is slightly lower (0.10%P) than that in the shoots of *M. caerulea* (0.12%P). Although the mineral composition in general is lower for *C. vulgaris*, the plant tissue concentration of calcium (0.32%) is double the mean value for *M. caerulea* (0.16%).

5. CONCLUSIONS

Mean concentrations in *M. caerulea* shoots were derived from a wide geographical area and related to soil nutrient measurements. In addition we have determined annual variation from one site over a period of 15 years and followed seasonal changes in the above-ground tissue concentrations of a full range of macro- and micro-nutrients. *M. caerulea* tends to be little grazed by sheep, but in grazed situations, particularly if fertilizers are applied, *Agrostis* spp. are favoured at the expense of *M. caerulea* (Grant *et al.*, 1996). *M. caerulea* shoots contain a lower mineral content than the mean value for other grass species in Britain. *Eriophorum vaginatum* and *Nardus stricta*, two species that exist in similar habitats to *M. caerulea* but with contrasting growth strategies, have a lower mineral concentration in their shoots. This comprehensive data set provides a baseline against which to assess ecological factors and change.

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