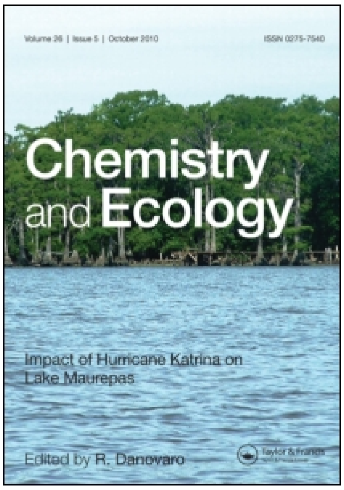

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THE NUTRIENT STATUS OF SOME GRAMINACEOUS SPECIES IN BRITAIN. 2. *DESCHAMPSIA FLEXUOSA* (L.) TRIN.

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Above-ground biomass of *Deschampsia flexuosa* from 40 sites throughout Britain was analysed for concentrations of elements (N, P, K, Ca, Mg, Fe, Mn, Cu, Zn and Na), with matching analyses of nutrient levels in the soils, together with pH and LOI. Seasonal variation in the nutrients was also studied in detail at one of the sites. The grass was found on acid sites ranging between pH 3.1 and 4.7. The soil humus content varied widely, and there were significant correlations between that and elements (N, P, K, Ca, Mg, Zn and Na) in the soil. Concentrations of zinc and manganese in the plant material were the only elements that significantly correlated with extractable levels in the soils. Tissue concentrations of nitrogen, phosphorus, and potassium declined throughout the growing season, whereas the other elements showed a tendency to build up until the end of September. Calcium, magnesium and manganese concentrations then declined as growth ceased. The results are compared with above-ground concentrations of minerals in other plants and the growth strategy of this perennial grass.

Keywords: Deschampsia flexuosa; plant nutrients; seasonal variation; soil status

Abbreviations: RSD = relative standard deviation; LOI = loss on ignition

1. INTRODUCTION

Deschampsia flexuosa (L.) Trin. (wavy hair-grass) is a perennial grass which grows on acid heaths, moors and in open woodlands, and

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occurs abundantly and widely throughout the British Isles. It occurs more frequently on highly organic, dry acid soils. The tussocks grow to a height of between 25 and 100 cm (Clapham *et al.*, 1987), produce flowers in June and July and sheds seeds shortly after ripening in August or September (Grime *et al.*, 1988). Leaves are generally long-lived, and remain green during the winter months. Tussocks reproduce by underground rhizomes or by seed.

D. flexuosa is a major component of lowland heaths throughout much of lowland Britain whilst other grasses are typically sub-ordinate in *D. flexuosa* grasslands (Rodwell, 1992). *D. flexuosa* and *Molinea caerulea* occur together in the forest ecosystem on grass moor, although *D. flexuosa* prefers drier locations (Markert, 1996). The abundance of *D. flexuosa* declines in favour of *M. caerulea* when nutrient availability increases (Aerts, 1989). The species is known to tolerate shade and low pH (Hogbom and Hogberg, 1991). Grassland dominated by *D. flexuosa* is characteristic of free-draining base-poor soils. However, *D. flexuosa* is tolerant of increasing nitrogen supplies, either as nitrate or ammonia (Rorison, 1985), but in dense canopy shade, the grass is not able to dilute nitrogen by increasing growth (Hogbom and Hogberg, 1991).

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 to assemble comparative information on the chemical composition of selected species in Britain and to examine inter-relationships between the nutrient content of individual species. In an earlier publication, data were reported on the nutritional status of *Molinea caerulea* in Britain (Rowland *et al.*, 1999). This paper is the second in a series evaluating the nutrient status of four different common graminaceous species. The objectives were to study the seasonal pattern of foliar micro- and macro-nutrients in *D. flexuosa* and the relation with soil nutrients and site characteristics at 40 sites distributed throughout Britain.

2. METHODS AND MATERIALS

For a fuller description of method protocols see Rowland *et al.* (1999). Sites were selected where *D. flexuosa* was defined as either dominant or co-dominant, and the site was free from any disturbance or pollution. Site characteristics were also noted.

2.1. Sampling and Preparation of *Deschampsia flexuosa*

D. flexuosa was sampled from habitat types of 40 different undisturbed sites between sea-level and 400 m altitude throughout Britain (Fig. 1). Where the altitude was recorded, 7 of the sites were below 50 m, 7 were between 50 and 100 m, 9 were between 100 and 200 m, 3 sites were between 200 m and 300 m, and the remaining 3 above 300 m. Green shoots were collected from 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 from 40 sites in total. 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 Bigland, Cumbria (SD362833) at monthly intervals over the growing season from the end of April until the beginning of November in 1969.

2.2. Soil Sampling

Ten random sampling points were selected at each location, and a 15 cm diameter core of soil was collected with a trowel from the 0–15 cm layer, after removal of *D. flexuosa* 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; the soil was sieved to less than 2 mm. Sub-samples of soil 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.

2.3. Chemical Analysis

Methods are described in detail in Allen (1989) and Grimshaw (1989). The elements determined were N, P, K, Ca, Mg, Fe, Mn, Cu, Zn and Na in the plant tissues. The pH, loss on ignition (LOI), total nitrogen and acetic acid extractable nutrients phosphate, calcium, magnesium, iron, manganese, copper, zinc and sodium were determined in soil samples collected at each site.

FIGURE 1 Distribution map of sampling sites in Britain.

3. RESULTS

3.1. Site Characteristics and Habitats

D. flexuosa was sampled from a variety of locations and habitats (Fig. 1) ranging from deciduous or mixed woodland, coniferous woodland, lowland grassland, bog/fen (1 site), hill grassland to upland heath. Approximately 65% were in habitats associated with coniferous or mixed deciduous woodland, with some degree of shading. The height of the aerial shoots at the end of July was between 10 and 20 cm at the majority of sites.

At 50% of the sites, *D. flexuosa* was sampled as the dominant species. In some cases, however, samples were collected where it was categorised as co-dominant with other species. Samples were collected from woodland edges or in the proximity of trees, beneath oak, birch and beech. Surveyors recorded *D. flexuosa* growing in grass mixtures together with *Nardus stricta*, *Deschampsia caespitosa* and *Festuca ovina*. At one site *Calluna vulgaris* was present, and occasionally *D. flexuosa* was collected from sites where *Pteridium aquilinum* or *Vaccinium myrtillus* were also dominant.

3.2. Between-site Variation in Nutrient Concentrations in Shoots of *Deschampsia flexuosa*

Table I lists the mean and median concentrations of nutrients in the aerial parts of *D. flexuosa*. These values provide an overall picture of the nutrient status of the species. In comparison with other species of grass collected in the "Vegetation Nutrient Survey", the concentrations of the elements nitrogen, calcium, magnesium, iron and sodium in *D. flexuosa* were relatively low, and were close to the mean for the elements phosphorus, potassium, copper and zinc. The species had a relatively high manganese content. The mean ratio of P : N in the aerial parts was 1 : 9, ranging from 1 : 5 to 1 : 14. The ratio of Ca : P was 1.1, ranging from 0.5 to 2.1.

Concentrations of the macro-nutrients nitrogen, phosphorus, potassium, calcium and magnesium in the plant tissues showed that inter-site variability was similar for all of them, with the highest concentrations 2–3 times the lowest and coefficients of variation

TABLE I Nutrient concentrations in *Deschampsia flexuosa* aerial shoots and in 21 other grasses sampled throughout Britain (%, or $\mu g\ g^{-1}$ for Cu and Zn)

	Mean	σ	*RSD*	*Median*	*Minimum*	*Maximum*	*Ratio max : min*	*Mean of* 21 *grass species*
N	1.42	0.30	22	1.46	0.773	2.25	2.9	1.62
P	0.160	0.041	25	0.155	0.079	0.251	3.2	0.176
K	2.11	0.51	24	2.12	1.13	3.27	2.9	1.95
Ca	0.148	0.034	23	0.138	0.088	0.234	2.7	0.319
Mg	0.110	0.020	18	0.108	0.072	0.153	2.1	0.143
Fe	0.0085	0.0044	52	0.006	0.0036	0.0200	5.6	0.0141
Mn	0.0431	0.0145	34	0.040	0.0133	0.0779	5.9	0.0189
Cu	5.87	5.64	96	4.16	2.33	27.2	12	6.49
Zn	36.3	29.0	80	30.0	13.8	201	15	33.7
Na	0.0175	0.0416	240	0.008	0.0007	0.268	380	0.197
Sum of Concentrations	4.0							4.4

(RSD = % relative standard deviation).

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

Plant				
Ca/Mg	Mg/P	Mg/N	**K/Mg**	**K/N**
Ca/Zn	**Fe/Cu**	P/N	**K/P**	
Soil				
LOI/Na	**Na/K**	**K/Mg**	**Ca/N**	**Zn/N**
LOI/K	Na/Ca	**K/Zn**	Mg/Fe	**P/N**
LOI/Ca	**Na/Mg**	**K/P**	**Mg/Zn**	pH/Mn
LOI/Mg	Na/Zn	**K/N**	**Mg/P**	
LOI/Zn	**Na/P**	**Ca/Mg**	**Mg/N**	
LOI/P	**Na/N**	**Ca/Zn**	Fe/N	
LOI/N	**K/Ca**	**Ca/P**	**Zn/P**	
Plant/Soil				
K/-Ca	Mn/Mn	Na/pH		
K/-P	**Zn/Zn**			
Ca/-Fe	**Zn/Ca**			
Na/-Fe	Na/Mg			
Mg/-Fe	**Na/Fe**			

Bold correlations indicate significance at $p < 0.001$.

less than 25%. Other elements were more variable, especially the trace elements copper and zinc and the non-essential element sodium, with the highest concentrations being 12, 15 and 380 times the lowest respectively. Coefficient of variation for manganese was in the region of 35% but exceeded 50% for other trace elements iron, copper, zinc and the non-essential element sodium.

Very few of the measured plant nutrients were correlated with each other. Only 9 of the possible 45 macro- and micro-nutrient relationships were inter-correlated (Tab. II). Of these, perhaps the most interesting from an ecological point-of-view, are the positive correlations between nitrogen and phosphorus, and between calcium and magnesium, and those between potassium and phosphorus, nitrogen and magnesium.

3.3. Seasonal Variation in the Nutrient Concentrations of *Deschampsia flexuosa* Shoots

Regular sampling of aerial shoots from *D. flexuosa* during the growing season revealed several distinctive seasonal patterns of tissue concentration (Fig. 2). Nitrogen and phosphorus concentrations were

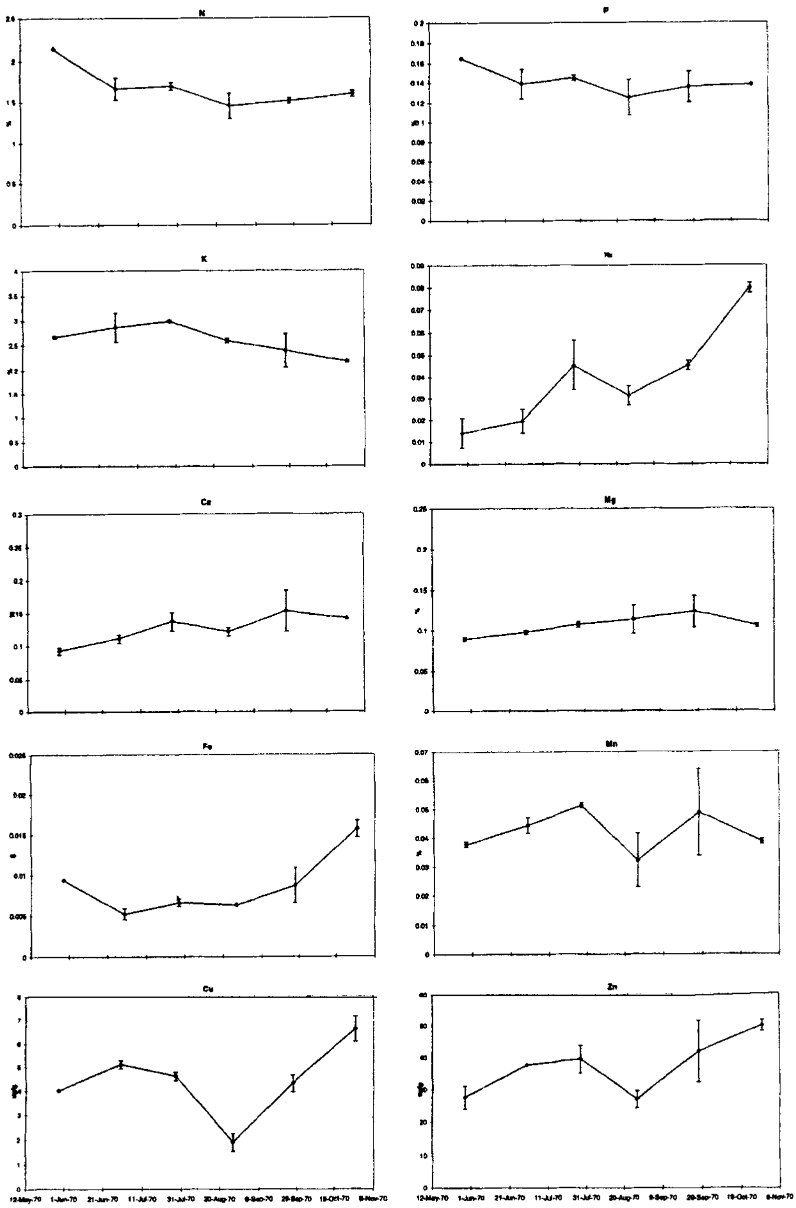

FIGURE 2 Seasonal pattern of macro- and micro-nutrients in *Deschampsia flexuosa* at Bigland, Cumbria. Error bars show $\pm\sigma$ for $n = 3$.

high in late spring and then gradually decreased, presumably due to dilution in the expanding leaf volume, to a constant value from the end of August onwards. Magnesium and calcium concentrations continued to increase slowly until the end of September. Potassium concentrations varied little until July and then declined; iron and sodium concentrations increased during the growing season; manganese, copper and zinc showed no clear trends. Calcium, magnesium and manganese concentrations in aerial growth declined at the end of October as the elements were withdrawn at the end of the growing season.

3.4. Soil Nutrient Status of *Deschampsia flexuosa* Sites

Soils under *D. flexuosa* were mainly organic, brown earth or loam, and were usually classified as well drained. A summary of the nutrient status of the soils is contained in Table III. Soils were acid with pH values ranging from 3.1 to 4.7 (mean and median value = 3.9). The humus content (measured as LOI) of the top 15 cm layer, sampled after removal of the litter layer, ranged from 2 to 92% with a mean of 26%, and median of 19%. The nitrogen status of the soil also varied significantly from poor (0.1%) to fertile (2.5%).

Thirty-one of the 66 measured soil parameter relationships were positively inter-correlated, and many of the correlations were significant at $p < 0.001$ (Tab. II). Many of the macronutrients themselves were positively correlated with each other. For example, LOI was correlated with nitrogen, extractable phosphate, potassium, calcium

TABLE III Nutrient concentrations in soil collected in *Deschampsia flexuosa* habitats in Britain (% or mg 100 g^{-1} for extractable (Ex) nutrients)

	Mean	σ	*RSD*	*Median*	*Minimum*	*Maximum*
pH	3.90	0.43	11	3.93	3.1	4.7
LOI	26.1	21.5	82	18.7	2.14	91.7
Kjeldahl N	0.716	0.571	100	0.451	0.089	2.47
Ex-P	1.70	1.77	80	0.887	0.385	9.40
Ex-K	15.6	13.2	85	11.5	1.27	65.9
Ex-Ca	40.3	42.7	110	29.2	1.94	202
Ex-Mg	11.9	10.5	89	7.65	1.14	44.2
Ex-Fe	8.45	8.36	99	6.53	1.35	45.3
Ex-Mn	4.36	5.26	120	2.67	0.080	22.5
Ex-Cu	0.096	0.277	290	0.0243	0.007	1.73
Ex-Zn	1.16	0.96	83	0.800	0.090	4.34
Ex-Na	4.78	5.21	110	2.85	0.29	26.9

and magnesium. Soil pH was only correlated with extractable manganese. Although, pH was not correlated with extractable calcium, magnesium or iron, this may be due to the fairly narrow range of soil pH and acidic conditions where *D. flexuosa* occurs. Trace or micronutrients did not generally show any correlation with LOI, and only 9 of the significant correlations featured the micro-nutrients, indicating that in semi-natural plant communities, micro-nutrients are not important in determining plant distribution.

3.5. Plant–Soil Relationships

Ten of the possible 120 macro- and micro-nutrient correlations between the soil nutrients and the *D. flexuosa* aerial tissue concentrations were significant, some at $p < 0.001$ (Tab. II). Acetic acid extractable measures of zinc and manganese in the soil correlated with the concentration of that element in the deciduous grass. None of the plant nutrients was directly related to soil organic matter content (LOI). Sodium was the only element where shoot tissue concentrations were correlated with soil pH.

4. DISCUSSION

4.1. Site Characteristics and Habitats

In an early Biological Flora of the British Isles, Scurfield (1954) provided an account of habitats and communities where *D. flexuosa* typically occupies. The sampling strategy employed in the "Vegetation Nutrient Survey" enabled the selection of sites which are typical for this species, *i.e.*, from moorland, woodland, hill pasture and lowland heath communities. Retrospectively, using Rodwell's (1992) distribution map, it is possible to confirm that the sampling site locations (Fig. 1) selected for this survey were representative the main *D. flexuosa* grasslands in Britain.

4.2. 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) derived a comparative index of the sum of the mean macro- and micro-nutrient concentrations in above-ground plant tissues. The total mineral content, the sum of macro- and micro-nutrients, in *D. flexuosa*, derived from sites distributed throughout Britain, was 4.0% (see Tab. I), intermediate between the mean for all grass species (4.4) and the deciduous grass *M. caerulea* (3.6%).

Grimshaw and Allen (1987) also 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. *D. flexuosa* coefficients of skewness were significant and positive for the trace elements, iron, copper and zinc, and also for calcium and sodium ($p < 0.05$). The pattern for sodium was extremely skewed, as confirmed by the large difference between the mean and median values (Tab. I). Except for calcium and iron, the coefficients of kurtosis for the *D. flexuosa* data were also significant for these elements, too. Outlying values ($> +/-4\sigma$) were detected for zinc and sodium, the exceptionally high concentrations of zinc were noted in foliage from a site where the available zinc concentration in the soil was exceptionally high.

Table I shows that *D. flexuosa* nutrient concentrations in leaves are in the order: K > N > P > Ca > Mg > Mn > Na > Fe > Zn > Cu. This exactly mirrors the order in 21 other grass species, unlike for the deciduous grass, *M. caerulea*, where nitrogen concentrations exceed potassium, and phosphorus concentrations exceed calcium and magnesium (Rowland *et al.*, 1999). The phosphorus: nitrogen ratio of 1 : 19 is mid-range for plants, and reflecting balanced nitrogen and phosphorus foliar concentrations. Across a broad range of species, Thompson *et al.* (1997) reported that the ratio of plant phosphorus: nitrogen ratio ranged from 1 : 5 up to 1 : 15 for non-legume plants. The calcium: phosphorus ratio in *D. flexuosa*, 0.5 at the first sampling, was stable (1.1) throughout the rest of the growing season until the end of October. In relation to animal nutrition, Fleming (1973) discussed the importance of the calcium: phosphorus ratio in pasture vegetation, and reported that values between 0.5 and 2.0 are desirable.

A similar data set of *D. flexuosa* from a more localised region in Derbyshire, mainly collected between 1970 and 1979, was published recently by Thompson *et al.* (1997). Mean elemental concentrations of nitrogen, phosphorus and calcium were slightly higher, manganese and magnesium were similar, and potassium slightly lower. The concept of a reference plant material with computed elemental concentrations was introduced by Markert (1992). This approach enables the elemental composition of different plant species to be easily compared. It appears that the values reported by him are derived from a single sample of each species, and for *D. flexuosa*, much lower nutrient concentrations for potassium, calcium and manganese were reported. However, the comparisons highlight that *D. flexuosa* is a plant low in nutrients with notable enrichments of silicon and enzymatically active heavy metals and low in alkaline earth metals (Markert, 1996). By comparing data with mean values for other grass species (Tab. I) we can show that this species is significantly lower in calcium and magnesium, and significantly higher in manganese.

There were relatively few between-site inter-element correlations for *D. flexuosa* at the 40 sites samples in Britain. Six of the nine inter-element relationships involved nitrogen, phosphorus and potassium. In contrast, Garten (1976) discovered significant between-species inter-element correlations for the elements phosphorus, potassium, nitrogen, calcium and magnesium for 54 species growing in the field. Similarly, there were many inter-element correlations between 13 different species (Markert, 1996).

4.3. Seasonal Variation in Nutrient Concentrations of *Deschampsia flexuosa* Shoots

Our seasonal study indicates that the macronutrients calcium and magnesium are relatively immobile. Iron and sodium exhibit similar properties, *i.e.*, they both increase over the whole growing season. Most plant nutrients are not withdrawn from foliar organs during the growing season between May and the beginning of November. Seasonal trends in the nutrient concentration in *D. flexuosa* were similar to those reported for the deciduous grass, *M. caerulea* (Rowland *et al.*, 1999), except in copper which increased in *D. flexuosa*, whereas shoot concentrations decreased throughout the growing season in

M. caerulea. The main differences were in the overall seasonal nutrient variation; average variation of nitrogen, phosphorus and potassium was 17% for *D. flexuosa*, compared with 36% for the deciduous *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 *D. 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 $\mu g\ g^{-1}$.

4.4. Soil Nutrient Status of *Deschampsia flexuosa* Sites

Data from the "Vegetation Nutrient Survey" confirm the experimental finding of Grime *et al.* (1988) that *D. flexuosa* is mostly restricted in Britain to sites with pH < 5.0. However, 40% of the randomly selected sampling sites in this study had a pH below 3.9, so there may be some differences between optimal conditions relating to natural growth data and those data reported from experimental manipulation of soil. Hackett (1965) reported that although low pH was not found to be harmful, optimal growth occurred at pH 5.7, a value well above the mean value reported for this species in Britain. We found three sites in Britain where the healthy community survived in soil with pH values in the region of 3.2. In contrast, in an experiment where the pH was reduced by artificial manipulation, Balsbergpahlsson (1995) induced injury symptoms which became more intense in the highest acidity treatment (pH 3.2). He concluded that his results corresponded with field observations in beech forests in southern Sweden.

There were correlations of all the major nutrients with organic matter content (measured as LOI) at the sampled sites. This demonstrates 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. Differing supplies of calcium, iron, manganese and potassium had only insignificant effects on growth, whilst Balsberg-pahlsson (1995) also reported that concentrations of copper, zinc and iron did not reach toxic levels in the extremely acid soil.

4.5. Relation Between Soil Nutrient Status and *Deschampsia flexuosa* Tissue Concentrations

Levels of mineral nutrients in the leaf tissue tend to be characteristic of the species, there being much less variation in the mineral concentrations in the tissues than in the soils (Jefferies and Willis, 1964). In this study of *D. flexuosa*, which thrives on acidic soils, tissue sodium was the only element correlated with soil pH (as in *M. caerulea*). In a study of 83 herbaceous species, Thompson *et al.* (1997) reported that only calcium and manganese in the plant tissues were consistently correlated with soil pH. So lack of a significant correlation between calcium and manganese concentrations in shoots and soil pH was probably due to the relatively low range of pH in the studied sites. The lack of correlation between nitrogen, phosphate and potassium concentrations in soil and plant tissue concentrations may indicate that rapid shoot growth in the spring is supported more from stored nutrients. The only relationships between the elemental plant and soil concentrations in *D. flexuosa* were established for zinc and manganese, in contrast to *M. caerulea* where significant correlations were also evident in calcium and magnesium (Rowland *et al.*, 1999).

It appears that the soil: plant relationships will need to be examined at the plant family level when all the graminaceous species data is available in more detail. For example, Clusner Godt (1990) reported that the relationships between the mineral elements (K, Ca and Mg) in leaves and the concentrations of soil nutrients or other soil factors show significant correlations for the majority of plant families. In summary (Clusner Godt, 1990), magnesium in leaves was most influenced by potassium and calcium concentrations in the surface soil, leaf calcium related to soil calcium, magnesium and pH, and potassium in leaves was most influenced by soil potassium, calcium, magnesium and nitrogen. These relationships were not evident in our data compiled for a single species.

5. CONCLUSION

Mean concentrations in *D. flexuosa* shoots were derived from a wide geographical area and related to soil nutrient measurements. In addition, we followed seasonal changes in the above-ground tissue concentrations of a full range of macro- and micro-nutrients. *D. flexuosa* shoots contain a lower mineral content than the mean value for other grass species in Britain, but a higher nitrogen status. This comprehensive data-set provides a baseline against which to assess ecological factors and change.

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