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Plant Seeds as Mineral Nutrient Resource for Seedlings—A Comparison of Plants from Calcareous and Silicate Soils

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Mineral nutrients of seeds constitute a significant source of essential elements to seedlings and developing individuals of vascular plants. In spite of their potential ecological significance, seed nutrient pools have attracted little attention with respect to calcifuge–calcicole behaviour of plants. The objectives of this study were, therefore, to compare concentrations of 13 macro- and micronutrients (K, Rb, Mg, Ca, Mn, Fe, Co, Cu, Zn, Mo, B, P and S) in seeds and leaves of 35 mainly herbaceous vascular plant species growing on both limestone (calcareous) and silicate (non-calcareous) soils. Concentrations of Rb and Co in seeds of plants originating from limestone soils were, on average, about half of those from silicate soils. Concentrations of Mn, Mg, Zn and P of seeds were, or tended to be, lower or slightly lower in limestone-soil plants, whereas mean Ca and Mo concentrations were higher. Comparing seed and leaf concentrations of the same species from limestone and silicate soils generally demonstrated a high P enrichment ratio, but a particularly low K enrichment ratio in seeds, valid for both types of soil. It was also apparent that Fe and Mn, micronutrients which are less readily solubilized and taken up by plants on limestone soils, had significantly higher seed:leaf concentration ratios in plants from limestone than from silicate soils, whereas the opposite was true for Ca. This indicates a 'strategy' to satisfy the demand of seedlings for elements which are less readily available in the soil.

Keywords: Seed, leaf, plant, nutrient, content, calcareous, silicate, acid, soil.

INTRODUCTION

Mineral nutrients of seeds constitute a significant source of several essential elements for seedlings and developing individuals of vascular plants. This is particularly true of the micronutrient Mo, the seed contents of which are sometimes adequate for normal development and growth during complete ontogenesis of the individual, or at least highly essential for its performance (Hewitt, Bolle-Jones and Miles, 1954; Brodrick and Giller, 1991; Brodrick *et al*., 1995). Adequate concentrations of Co in seeds were able to prevent chlorosis in *Lupinus angustifolius* L. (Medit.) cultivated without Co application (Robson and Mead, 1980). High levels of Mn in parent seed may counteract seed disorders in *Lupinus* spp. (Hocking *et al*., 1977) and the appearance of fungal diseases in cereals (McCay-Buis *et al*., 1995). Development and grain production in wheat (*Triticum* sp.), grown with deficient Mn or Zn, were positively related to seed contents of these elements (Marcar and Graham, 1986; Rengel and Graham, 1995*a*, *b*).

The seed content of macronutrients, although constituting only a small proportion of the total demand, may also be essential for plant establishment and growth. This is particularly true for phosphorus. Yields of annual pasture legumes were positively related to P concentrations of their seeds (Bolland and Paynter, 1990), and the early development of wheat seedlings was clearly favoured by a high seed-P concentration when plants were grown at P deficiency (De Marco, 1990). In the absence of an external P supply, seed-borne P ensured almost maximal root growth and development in young seedlings of several crop species (Schjoerring and Jensén, 1984).

It is apparent that plants utilize seed-derived mineral nutrient resources for their development. The efficiency of redistribution may, however, differ greatly among elements. In developing *Lupinus* spp., P, K and S were retrieved from cotyledons to the seedling axis with > 90 % efficiency, Mg, Fe, Zn and Mn with 59–90 %, but Ca with only 26–31 % efficiency (Hocking, 1980). In pasture grasses and legumes subjected to deficiencies of single nutrients, little growth of seedlings was obtained without external supply of elements demanded in large amounts (N, K), whereas about 60 % of the dry weight, compared to nutrient sufficient control plants, was produced without added P or Fe, and about 80 % without added S (Fenner and Lee, 1989). Seedling growth of *Senecio vulgaris* was most dependent on an external supply of Ca and least dependent on a supply of Fe and S; P, K and Mg were intermediate (Fenner, 1986*a*).

Seed nutrient pools in relation to calcifuge–calcicole behaviour of plants have attracted little attention, in spite of its potential ecological significance. Limestone soils of northern Europe are notoriously low in exchangeable or easily plant-available P and Fe, and sometimes other micronutrients, e.g. Mn. Calcicole plants have a much higher capacity than calcifuges to render less soluble forms of these elements available, e.g. by root exudation of suitable organic acids (Ström, Olsson and Tyler, 1994; Tyler and Ström, 1995).

Only a few studies have demonstrated that concentrations of mineral nutrients in seeds may be related to the soil and substrate supply. Seed content of Mo in *Phaseolus vulgaris* differed by one order of magnitude between soils rich and poor in this element (Brodrick *et al*., 1995). In an experiment on mineral allocation to reproduction in two species of *Sorghum*, concentrations of P, K and Mg in *S. halepense* seeds decreased significantly with decreasing supply of these elements (Benech Arnold, Fenner and Edwards, 1992). However, solution experiments with the weed *Senecio vulgaris* L. indicated that allocation of minerals to the seeds generally increased with nutrient shortage, though the seeds generally maintained the same concentration of nutrients (Fenner, 1986*b*). *Chionochloa* species from infertile soils tended to have a higher seed enrichment, compared to their vegetative parts, than seeds from fertile soils, mainly because shoot concentrations reflected the environmental supply (Fenner and Lee, 1989). Seeds of *Ricinus communis* L. from plants on poor sandy soil had adequate levels of nutrients when compared with seeds from plants growing on a fertile loam (Hocking, 1982).

Preferential allocation to seeds of elements limiting, or constituting a potential limitation, to growth on limestone soils, would be a strategy of importance to the survival and competitive power of plants on such soils. The objectives of this study are to compare mineral element concentrations of seeds and vegetative parts (leaves) of 35 species of (mainly herbaceous) plants, able to grow on limestone soils as well as on slightly–moderately acid, non-calcareous silicate soils. It is hypothesized that elements present in less available forms in limestone soils tend to be enriched in seeds compared to leaves in plants of such soils, thereby supporting the early stages of plant development under conditions of nutrient shortage or limited acquisition rates.

MATERIALS AND METHODS

Green leaves, when applicable, from the distal half of the shoots, were sampled from unfertilized sites with natural–seminatural vegetation in south Sweden. A total of 35 species, occurring on both calcareous and silicate soils were included. Of these species, six belong to the Asteraceae, five each to the Apiaceae and the Papilionaceae, three each to the Caryophyllaceae, Rosaceae and Polygonaceae, and the remaining ten to a variety of plant families (Table 1). The samples, consisting of leaves from ten–50 shoots (quantity according to size and leaf abundance of the species) were collected in July from a site characterized by purely silicate, more or less acidic soil (pH–H$_2$O = 4·5–6 in A horizon). A second sample of the same species was collected from a site with soil derived from limestone of Archaean, Cambro-Silurian or Cretaceous age (pH–H$_2$O = 7·5–8·5 in A horizon). Inflorescences containing mature seeds were collected from the same sites between July and November, according to seed maturation of the different species.

TABLE 1. *List of the 35 species included in the study, sampled both on calcareous and on acid silicate soils*

Achillea millefolium L.
Arctium tomentosum Mill.
Arenaria serpyllifolia L.
Artemisia campestris L.
Artemisia vulgaris L.
Cerastium semidecandrum L.
Filipendula ulmaria (L.) Maxim
Filipendula vulgaris Moench
Geum urbanum L.
Hypericum maculatum Cr.
Hypericum perforatum L.
Juncus conglomeratus L.
Laserpithium latifolium L.
Lathyrus niger (L.) Bernh.
Lathyrus sylvestris L.
Matricaria inodora L.
Medicago lupulina L.
Melilotus albus Desr.
Origanum vulgare L.
Pastinaca sativa L.
Phleum phleoides (L.) Karst.
Pimpinella saxifraga L.
Plantago lanceolata L.
Pleurospermum austriacum (L.) Hoffm.
Rosa canina L.
Rumex crispus L.
Rumex obtusifolius L.
Rumex thyrsiflorus Fingerh.
Sedum album L.
Silene nutans L.
Tanacetum vulgare L.
Torilis japonica (Houtt) Bernh.
Veronica spicata L.
Vicia dumetorum L.
Vincetoxicum hirundinaria

Leaves and seeds were dried (85 °C) to constant weight and 1·0 g of each material was digested with 20 ml HNO$_3$ for destruction of organic matter, excess acid evaporated to 2 ml and the digest made up to 25 ml with H$_2$O. Mineral element concentrations (K, Mg, Ca, Mn, Fe, Cu, Zn, B, P and S) in leaf and seed samples were determined by ICP-ES. Concentrations of three additional elements were determined only in the seed samples: Rb by flame AAS using 1000 mg l^{-1} of K$^+$ (as KCl) in standards and sample solutions to obtain a uniform excitation state of the Rb atoms; Co and Mo by AAS–carbon rod technique to attain sufficient sensitivity. All analyses were performed in duplicate. Five blanks, with only HNO$_3$, were treated as the samples and 'background' concentrations (mainly some B released from the Pyrex glassware) were subtracted from the sample readings.

All concentration data, calculated as μmol g^{-1} d. wt, are communicated as means of the leaf or seed material as a whole, or as mean molar ratios (limestone:silicate soil) of these concentrations, calculated from the individual samples. The probability of differences between means or mean ratios, the 95 % confidence limits of means, and two-tailed *t*-tests were calculated using a StatView Programme for Macintosh. All calculations on ratios were performed on log-transformed data to approach a normal distribution of the sets.

RESULTS

Seeds

The mean concentrations of mineral elements in seeds of the species studied differed to some extent between calcareous and silicate soils (Table 2). The concentrations of Rb and Co in seeds of plants originating from limestone soils were, on average, only about half those characterizing plants from silicate soils. The concentrations of Mn, Mg, Zn and P also tended to be lower, or slightly lower, in seeds of the limestone-soil plants, although differences were not consistently significant.

On the contrary, mean seed concentrations of Ca were higher in limestone-soil plants, although they only exceeded those of the silicate-soil plants by 20–25 % (Table 2). Mo also tended to be slightly higher in seeds of the limestone plants, but variability among species precluded any conclusions about significance. Mean seed concentrations of K, Fe, B and S did not differ at all between soils, and mean Cu

TABLE 2. *Mean concentrations, μmol g^{-1} d. wt, in leaves and seeds of 35 species from calcareous and silicate soils*

	Leaf		Seed	
	Calcareous	Silicate	Calcareous	Silicate
Potassium	614^{a}	637^{a}	229^{b}	228^{b}
Rubidium	—	—	0·14^{a}	0·32^{b}
Magnesium	106^{a}	110^{a}	95^{a}	104^{a}
Calcium	374^{a}	208^{b}	246^{c}	199^{b}
Manganese	1·7^{a}	5·7^{b}	0·9^{c}	1·4^{ac}
Iron	1·2^{a}	2·1^{b}	1·3^{a}	1·3^{a}
Cobalt	—	—	0·0021^{a}	0·0045^{b}
Copper	0·15^{a}	0·18^{b}	0·17^{ab}	0·19^{b}
Zinc	1·08^{a}	1·17^{a}	0·53^{b}	0·65^{c}
Molybdenum	—	—	0·016^{a}	0·013^{a}
Boron	3·4^{a}	4·3^{b}	3·4^{a}	3·3^{a}
Phosphorus	84^{a}	88^{a}	134^{b}	152^{c}
Sulphur	93^{a}	85^{a}	77^{b}	76^{b}

Means of the same element with different superscripts differ ($P < 0·05$) according to two-tailed *t*-test.

TABLE 3. *Seed-to-leaf enrichment ratios (concentration in seeds : concentration in leaves) in 35 plant species from limestone (calcareous) and silicate soils*

	Calcareous soils	Silicate soils
Potassium	0·37^{a}	0·36^{a}
Magnesium	0·90^{a}	0·95^{a}
Calcium	0·66^{a}	0·96^{b}
Manganese	0·53^{a}	0·25^{b}
Iron	1·08^{a}	0·62^{b}
Copper	1·13^{a}	1·06^{a}
Zinc	0·49^{a}	0·55^{a}
Boron	1·00^{a}	0·77^{b}
Phosphorus	1·60^{a}	1·72^{a}
Sulphur	0·83^{a}	0·89^{a}

Mean ratios of an element differ significantly ($P < 0·05$) if indicated by different superscripts.

concentrations tended to be only slightly lower in seeds of plants from the calcareous soils.

Leaves

Mean concentrations of Mn in leaves of the limestone-soil plants were only about one third of the leaf concentrations in silicate-soil plants (Table 2). The mean concentrations of Cu, B and particularly Fe were also significantly lower in leaves of the limestone-soil plants, whereas those of Ca were much higher. Leaf concentrations of K, Mg, Zn, P and S did not differ ($P > 0·05$) between soil types.

Seed/leaf concentration ratios

Several elements had lower concentrations of mineral nutrients in seeds, compared to leaves, from both types of soil (Table 3). This was particularly true for K, Mn and Zn, whose mean seed concentrations were only a third to a half those of mean leaf concentrations. Consistently lower seed concentrations were also recorded for S, as well as for Ca (but only on limestone soils) and for Fe and B (only on silicate soils). There were no mean differences between Mg and Cu concentrations in either soil type. In contrast, the mean concentration of P was significantly higher in seeds than in leaves of plants originating from both types of soil.

DISCUSSION

Our results partly support the hypothesis that elements which are less readily available to plants on limestone (calcareous) soils are enriched in seeds compared to leaves, probably making the seeds an important nutrient resource soon after germination. Although plants from the limestone soils were not able to raise their leaf concentrations of Fe and Mn to the same level as the silicate soil plants, they concentrated these elements, especially Fe, in their seeds to the same extent as plants from silicate soils. Seed-to-leaf enrichment ratios for Mn and B, both elements which might be less available under calcareous soil conditions, were also higher in plants from limestone soils (Table 3).

The availability of B in soil is dependent on several factors including organic matter content and soil acidity (Adhikari *et al*., 1993; Lehto and Malkonen, 1994). At pH > 7·4, as well as in highly acidic soils, uptake of B may be reduced (Dionne and Pesant, 1978; Peterson and Newman, 1976), although this is not always the case (Gupta and Macleod, 1977; Adams, Hamzah and Swift, 1991). In our study, calcareous soil conditions had no apparent negative influence on transport of B to seeds, but leaf B concentration was lower in plants from these soils.

Less available forms of phosphorus are present in the limestone soils of northern Europe (Tyler, 1992), and P was the only element which was really concentrated in seeds compared to leaves. However, plants from the limestone and silicate soils did not differ in this respect (Table 3). Hocking and Steer (1983) reported higher concentrations of P in vegetative parts of mature *Helianthus annuus* than in seeds. A higher P content was found in seeds of plants growing in non-calcareous than in calcareous soil (Esler *et al*., 1989), whereas P-fertilizer studies on rape did not demonstrate any influence of soil type on plant uptake of P (Bailey and Grant, 1990).

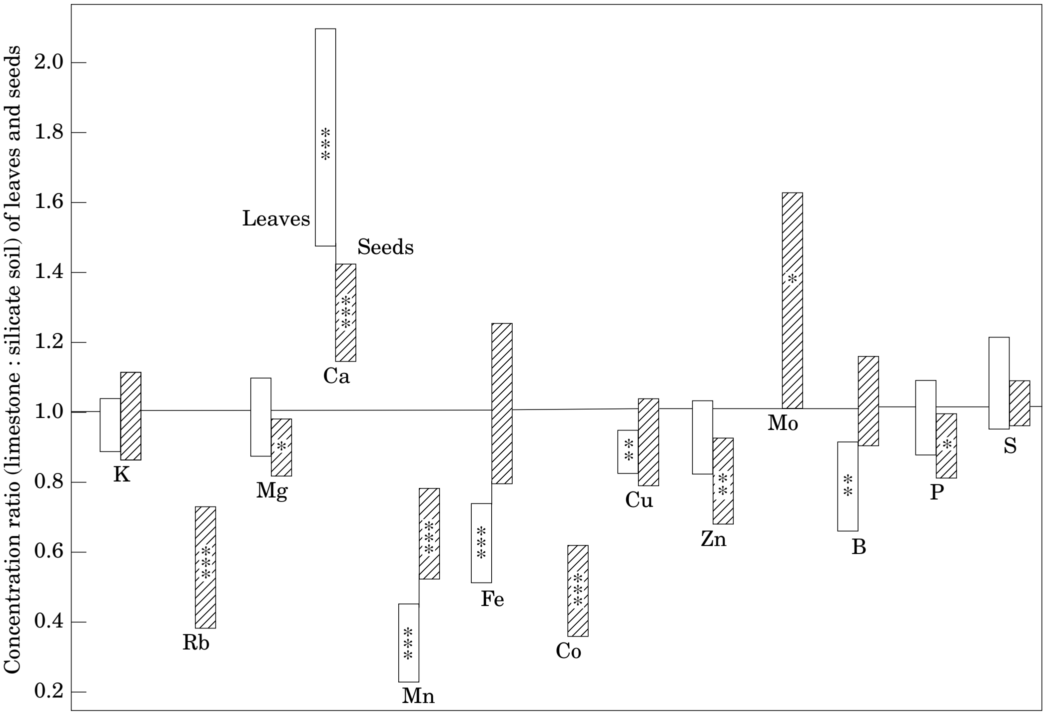

FIG. 1. 95 % confidence ranges of the mean ratios (limestone:silicate soil) of element concentrations in leaves (☐) and seeds (▨) of the 35 species studied. Significance for a mean ratio different from 1 according to two-tailed *t*-test is indicated in the bars as: $^{*}P < 0{\cdot}05$, $^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$.

Potassium was found at much lower concentrations in seeds compared to leaves, irrespective of soil type (Table 3). This element is largely taken up selectively and actively by plants (Mengel and Kirkby, 1982) and a considerable net uptake takes place shortly after germination (Ockenden and Lott, 1988). Several other elements studied, e.g. Mg and Cu, had similar concentrations in seeds and leaves, and there were little or no differences between silicate and limestone soils (Fig. 1). The findings of Fageria, Zimmermann and Baligar (1995) that lime seems to increase Mg uptake by plants was not supported in our study. These authors also reported a lime-dependent lower uptake of Cu, which is consistent with our findings of slightly lower leaf concentrations of Cu in plants from limestone soils. Our study revealed slightly higher S concentrations in leaves than in seeds for both soil types. However, Fenner (1986*b*) reported higher S concentrations in seeds than in shoots of plants grown in nutrient solution.

Plants from calcareous soils appear able to avoid high Ca concentrations in their seeds but not their leaves, a situation which results in a low seed-to-leaf ratio in these soils (Table 3). In a comparative study of the concentrations of ten nutrients in 83 (mostly herbaceous) species from central England, only Ca (positively) and Mn (negatively) were consistently correlated with soil pH (Thompson *et al.*, 1997). A high pH or Mg content of the soil may decrease Zn availability (Grant and Bailey, 1989). However, Coventry *et al.* (1987) found no influence of liming on Zn uptake in wheat plants. In our study, Zn transport to the seeds did not seem to be influenced by soil type, as the seed-to-leaf concentration ratio of this element was the same for the silicate and limestone soils. The Zn content of seeds was considered sufficient, in most cases, to support seedling development in *Zea mays* L. (Peaslee and Leggett, 1980).

Molybdenum, present in soils mainly as the oxoanion, molybdate, is an important element in N_2 fixation by plants of the Papilionaceae. Comparatively high concentrations of Mo were measured in seeds from this family, resulting in high variability of the primary data for this element. However, seed concentrations of Mo tended to be higher ($P = 0{\cdot}05$) in plants from limestone soils, which is consistent with soil chemical theory and empirical experience of Mo availability in relation to soil properties.

It may be concluded that our hypothesis that elements which are deficient or less available in limestone soils tend to be accumulated preferentially in seeds to serve as a starting source for seedling growth, was fully supported by the results for Fe and partly supported for Mn and B. A generally high seed-to-leaf enrichment ratio, irrespective of soil type, was also shown for P.

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