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DIFFERENTIAL RESPONSES TO MAGNESIUM AND CALCIUM BY NATIVE POPULATIONS OF AGROPYRON SPICATUM[1]

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ABSTRACT

Plants of *Agropyron spicatum* (Pursh) Scribn. and Smith. from populations native to serpentine and nonserpentine soils were grown at varying levels of magnesium and calcium in culture solutions. The yields of plants from the two populations were different. At high Mg levels (low Ca) the yield of the serpentine population was significantly higher than that of the nonserpentine population. At low Mg the yield of the serpentine population leveled off at a Mg:Ca ratio of 1:2, while the yield of the nonserpentine population increased up to a Mg:Ca ratio of 1:8 and showed no leveling off. Chemical analyses of tissue showed that the Ca uptake of plants from the serpentine population was significantly higher than that of the nonserpentine population. In addition, the serpentine population maintained a lower Mg concentration in the shoots than the nonserpentine population at comparable Mg substrate levels. The two populations showed differences in Ca and Mg uptake efficiency and Mg/Ca, Ca + Mg/K + Na, and Ca + Mg + K + Na in the shoots. The ecotypic differentiation with respect to Mg and Ca between native populations of serpentine and nonserpentine *A. spicatum* does not appear to be due to any single mechanism but, rather, a combination of several possible mechanisms, i.e., differences in root morphology, uptake mechanisms, translocation of nutrients, and interactions between cations.

ECOTYPIC DIFFERENTIATION of plant species has been described in relation to a number of soil factors. Kruckeberg (1951) found that *Streptanthus glandulosus* Hook., *Gilia capitata* Dougl., and *Achillea borealis* Bong. were differentiated into tolerant and intolerant races with respect to their growth responses on serpentine soil; and Wilkins (1957), and Gregory and Bradshaw (1965) have described populations of *Festuca ovina* L. and *Agrostis tenuis* Sibth. that were tolerant to heavy metals in the soil. Differential response to calcium within the species *Festuca ovina* L., *Trifolium repens* L., and *Cynodon dactylon* (L.) Pers. have been described by Snaydon and Bradshaw (1961, 1969), Snaydon (1962), and Ramakrishnan and Singh (1966).

Grass species as a general group have not been shown to be differentiated into serpentine-tolerant and -intolerant races; Whittaker (1954) suggested that grass species may occupy serpentine soil without being ecotypically differentiated. Walker, Walker, and Ashworth (1955) established the importance of the adverse Ca/Mg ratio common to serpentine substrates, and a differential response to magnesium between species was shown by Madhok and Walker (1969). A differential intraspecific response to magnesium per se has not been shown.

Agropyron spicatum (Pursh) Scribn. and Smith (Gramineae) commonly occurs both on and off serpentine outcrops in central Washington. Kruckeberg (1967), using traditional transplant methods, attempted to determine if this species formed discrete ecotypes in response to serpentine soil; however, it was not possible to elicit a definite differential tolerance. The present study applies nutrient culture techniques to the problem of intraspecific variation of *A. spicatum* from serpentine and nonserpentine substrates.

MATERIALS AND METHODS—*Collection sites*—Plants of serpentine and nonserpentine origin were collected in the Wenatchee Mountains of central Washington. The upper north fork of the Teanaway River in Kittitas County is an area of complex interfingering soil types which offers an ideal study area because of the close proximity of the two soil types, assuring that the general climatic conditions in the two collection sites are approximately the same. Clone material of the serpentine population was collected at an elevation of 1266 m from a soil derived from Serpentinite (N ½ Sec. 11, T22N, R15E), while the nonserpentine population was collected at an elevation of 965 m from soil derived from Swauk Sandstone (S ½ Sec. 19, T22N, R16E).

Soil analyses—Soil samples for analysis were air dried and screened. Duplicate samples were

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TABLE 1. *Analysis of soil chemical properties*

Parent Material	*p*H	Cation Exchange Capacity m Eq/100 g	Exchangeable Cations m Eq/100 g dry soil				Mg/Ca
			Ca	Mg	K	Na	
Serpentinite	6.48 ± 0.12	5.60 ± 0.18	0.40 ± 0.02	3.48 ± 0.09	0.11 ± 0.02	0.09 ± 0.01	8.70
Swauk Sandstone	5.85 ± 0.32	10.81 ± 0.21	3.12 ± 0.04	0.10 ± 0.03	0.55 ± 0.02	0.18 ± 0.01	0.03

used for all determinations. Soil *p*H was determined with a Beckman model 96A *p*H meter by the standard saturation paste method. The cation exchange capacity was determined by the ammonium acetate method; and the exchangeable calcium, magnesium, potassium, and sodium were determined from the leachate.

The exchangeable calcium and magnesium were determined with a Techtron model AAA Atomic Absorption Spectrophotometer, and the exchangeable potassium and sodium were determined with a Beckman DU Flame Spectrophotometer. The soil analyses are presented in Table 1.

Experimental cultures—Plants were cloned and maintained under greenhouse conditions for 5 months before they were used experimentally. The roots were trimmed, leaving two or three leader roots approximately 6 cm in length; and the shoots were trimmed, leaving two stems 3–5 cm in length. Clonal portions were placed in flats containing washed silica sand and allowed a period of 3–4 weeks to become established. In all cases the experimental pairs of plants were of the same clone, and uniformly vigorous plants were selected for all experiments. Preliminary experiments showed that the effects of varying calcium were more readily elucidated than the effects of varying magnesium. For this reason water culture techniques were used for the calcium experiments, while a sand culture system was utilized for magnesium experiments. This system was easier to maintain and more readily accommodated the extensive root systems that developed over a longer growing time.

In those experiments in which magnesium concentration was varied, the clonal portions were

TABLE 2. *Composition of culture solutions used for magnesium and calcium experiments*[a]

Solution Number	Mg (#'s 1–8) or Ca (#'s 9–16) in Solution (mM/liter)	mM/liter						
		$NH_4H_2PO_4$	KNO_3	$Ca(NO_3)_2$	$NaNO_3$	$MgSO_4$	Na_2SO_4	NaCl
1	0.25	0.5	3.0	0.5	3.5	0.25	39.75	0.1
2	0.50	0.5	3.0	0.5	3.5	0.50	39.50	0.1
3	2.50	0.5	3.0	0.5	3.5	2.50	37.50	0.1
4	5.00	0.5	3.0	0.5	3.5	5.00	35.00	0.1
5	10.00	0.5	3.0	0.5	3.5	10.00	30.00	0.1
6	20.00	0.5	3.0	0.5	3.5	20.00	20.00	0.1
7	30.00	0.5	3.0	0.5	3.5	30.00	10.00	0.1
8	40.00	0.5	3.0	0.5	3.5	40.00	0.00	0.1
9	0.005	0.5	3.0	0.005	7.99	0.5	0.5	0.1
10	0.025	0.5	3.0	0.025	7.95	0.5	0.5	0.1
11	0.050	0.5	3.0	0.050	7.90	0.5	0.5	0.1
12	0.250	0.5	3.0	0.250	7.50	0.5	0.5	0.1
13	0.500	0.5	3.0	0.500	7.00	0.5	0.5	0.1
14	1.000	0.5	3.0	1.000	6.00	0.5	0.5	0.1
15	2.000	0.5	3.0	2.000	4.00	0.5	0.5	0.1
16	4.000	0.5	3.0	4.000	0.00	0.5	0.5	0.1

[a] All solutions contained 1 ml each of FeEDTA and A-5 per liter. FeEDTA—26.1 g EDTA dissolved in 268 ml of 1 N NaOH; 24.9 g $FeSO_4 \cdot 7H_2O$ is added to it. The solution is diluted to 1 liter, aerated overnight, and its *p*H adjusted to 5.5 with NaOH. One ml FeEDTA per liter is equal to 5 ppm Fe. A-5 Micronutrient supplement—2.86 g H_3BO_3, 1.81 g $MnCl_2 \cdot 4H_2O$, 0.105 g ZnCl, 0.053 g $CuCl_2 \cdot 2H_2O$, 0.126 g Na_2MoO_4 per liter. One ml A-5 per liter gives 0.5 ppm B, 0.5 ppm Mn, 0.05 ppm Zn, 0.02 ppm Cu, and 0.05 ppm Mo. The *p*H of the culture solution was adjusted to 5.5 with NaOH. The osmotic potential of culture solution numbers 1–8 and 9–16 was –1.10, and –0.38 atm., respectively.

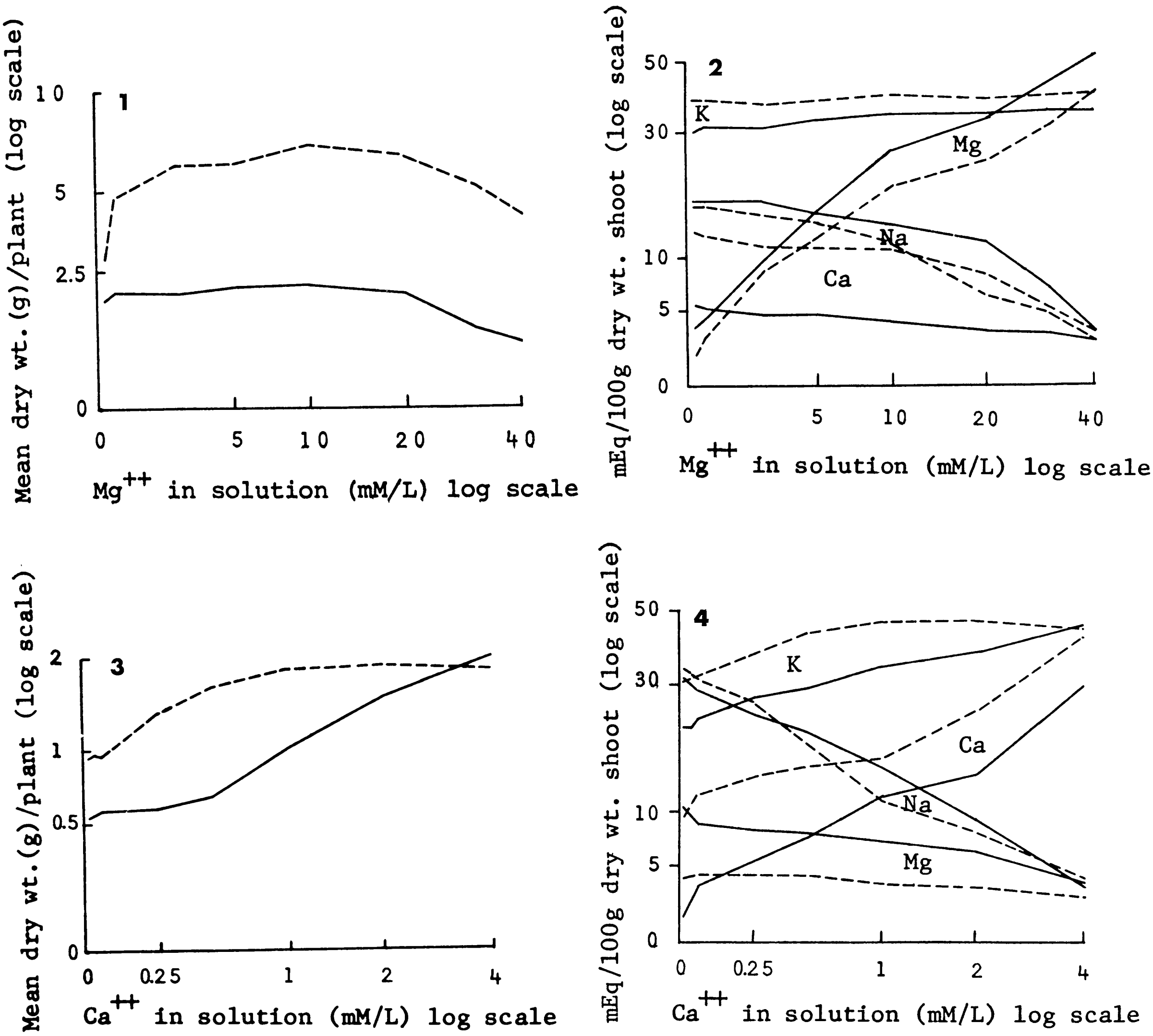

Fig. 1–4. Mean plant yield and cation content in the shoots of serpentine (– – –) and nonserpentine (——) populations of *A. spicatum* grown at varying Mg and Ca levels. **1.** Yield at varying Mg levels. **2.** Cation content in shoots at varying Mg levels. **3.** Yield at varying Ca levels. **4.** Cation content in shoots at varying Ca levels.

transferred directly to a sand culture system. Solutions were pumped by means of a timed air pressure system from 20-liter carboys into 4-gallon crocks containing washed silica sand. The system was adjusted so that the solution would rise within 1.5 cm of the sand surface and remain in that position for 5–10 min before draining back into the carboys. The plants were irrigated four times per day. Three replicate plants were grown for each treatment.

The plants for calcium experiments were transferred to 1.89-liter (two-quart) mason jars which had been painted on the outside with black asphaltum varnish and then wrapped with aluminum foil. Three replicate plants were grown for each treatment.

The solutions used (Table 2) were modified from Hoagland and Arnon #2 (1950). Different magnesium concentrations in culture solutions were obtained by varying $MgSO_4$ and balancing it with Na_2SO_4. Furthermore, the calcium concentration was held constant at 0.5 mM/liter and $NaNO_3$ was used as a reciprocal substitute for $Ca(NO_3)_2$ to maintain the nitrogen level. In experiments where calcium was varied, different levels of calcium were obtained by varying $Ca(NO_3)_2$ and balancing it with $NaNO_3$. The magnesium concentration was held constant at 0.5 mM/liter. All ions, except for the micronutrients and iron, were used at one-half the usual levels. This was done in order to avoid the possible harmful effects of high osmotic potentials

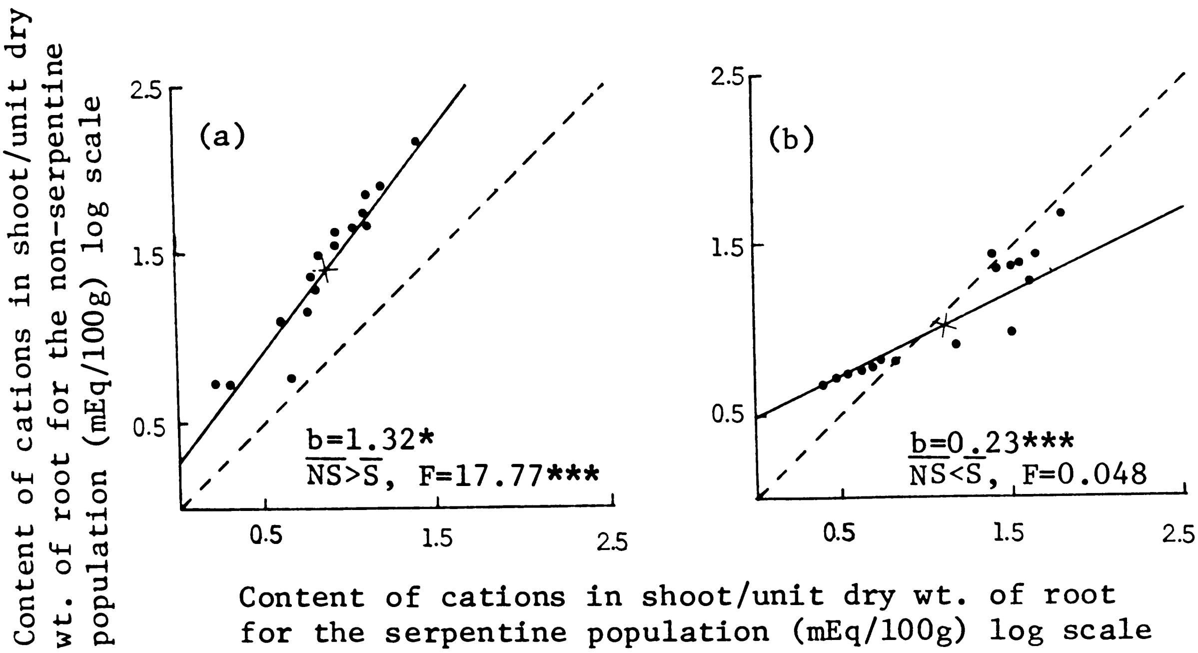

Fig. 5. Comparison of uptake efficiency of serpentine and nonserpentine populations of *A. spicatum*. —— Common regression line; - - - unit slope. * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$ (a) Mg uptake; (b) Ca uptake.

that could result if full strength solutions plus high magnesium concentrations (40 mM/liter) were used.

All experiments were conducted in the greenhouse during the spring and summer months. Plants were grown under natural light during the summer and supplemented with artificial light during early spring. Greenhouse temperatures during spring ranged between 16 and 19 C at night and approximately 21–28 C during the day. Summer temperatures ranged between 18–22 C and 25–35 C for night and day, respectively.

Plants used for the magnesium experiments were harvested after 72 days, while those used for the calcium experiments were harvested after 30 days. At this time the plants had reached maturity or were showing deficiency symptoms. At harvest the plants were divided into roots and shoots and analyzed separately for calcium, magnesium, potassium, and sodium.

The tissue samples were ashed at 300 F for 12 hr, then for 4 hr at 500 F in a muffle furnace, and then taken up in dilute HCl. Normally 2 g of dry tissue were ashed and made up to 100 ml; however, in cases where the samples were less than 1 g in weight, the volume was adjusted in proportion to weight. Tissues were analyzed for calcium, magnesium, potassium, and sodium. Cation content was determined by the same methods described for the determination of exchangeable soil cations.

RESULTS—*Magnesium experiments*—Serpentine and nonserpentine populations were grown in culture solutions 1–8 (Table 2) at 0.25–40.0 mM Mg and a Ca concentration of 0.5 mM/liter. The yields of the two populations are plotted against the Mg level in the culture solutions in Fig. 1. The serpentine population showed a greater response to Mg than did the nonserpentine population; at the two lowest Mg levels the mean yield of the serpentine population was 39% and 68% respectively of their maximum yield, while in contrast the mean yield of the nonserpentine population was 87% and 91%. Plants from the serpentine population showed a substantial yield increase from 0.25–10.0 mM Mg, but decreased at higher Mg concentrations. Magnesium deficiency symptoms were noticeable from 0.25–2.5 mM Mg. In contrast, the nonserpentine population showed only a slight increase in yield from 0.25–10 mM level and decreased at higher Mg treatments. No magnesium deficiency symptoms were noted in the plants of nonserpentine origin; however, calcium deficiency symptoms were noticeable at all Mg levels and became more pronounced with increasing Mg concentration of the culture solutions. At all treatment levels the yield of the serpentine population was significantly higher ($P < 0.01$) than that of the nonserpentine population. Plants from the serpentine population had a higher ($P < 0.025$) mean shoot/root ratio (1.77) than the nonserpentine plants (1.58).

The cation content in the shoots of plants from the two populations is plotted against magnesium concentration in the solutions in Fig. 2. These results show that the shoots of plants from the serpentine population contained more Ca than those from the nonserpentine population. The calcium content of both populations decreased as the Mg concentration in the culture solutions increased, but the average calcium content of the nonserpentine plants was significantly lower ($P < 0.01$) than that of the serpentine plants. In the case of Mg content, this relationship was reversed. The shoots of the nonserpentine plants contained higher concentrations of Mg than the serpentine plants at all treatment levels.

The potassium in the shoot of the serpentine plants generally showed a somewhat higher content than the nonserpentine plants. The sodium content of both populations decreased as the sodium concentration in the culture solutions decreased.

Calcium experiments—Serpentine and nonserpentine plants were grown in culture solutions 9–16 (Table 2) at 0.005–4.0 mM Ca with Mg held constant at 0.5 mM. Figure 3 shows the average yield of plants from both populations plotted against the Ca concentration of the culture solutions. The serpentine plants showed a rapid initial increase up to the 1 mM Ca level. There was a leveling off beyond the 1 mM treatment and a slight decrease from 2–4 mM. The nonserpentine plants, after an initial moderate increase, increased at a more rapid rate from 0.5 to the 4 mM Ca level.

The yield of the serpentine plants was significantly higher than that of the nonserpentine plants up to the 2 mM Ca level ($P < 0.01$), but the yield of the nonserpentine plants surpassed that of the serpentine plants at the 4 mM level. Calcium deficiency symptoms were visible from the 0.005–0.05 mM level in the serpentine plants, while calcium deficiency symptoms in the nonserpentine plants were visible from the 0.005–0.5 mM calcium level. In all instances the deficiency symptoms were more severe in the nonserpentine plants than the serpentine plants at corresponding calcium levels. There were slight magnesium deficiency symptoms in the serpentine plants at the 4 mM Ca level, but none were noted in any of the plants from the nonserpentine population. Plants from the nonserpentine population had a higher mean shoot/root ratio (2.10) than the serpentine plants (1.92), but this difference was not significant.

The level of cations in the shoots of both populations are shown in Fig. 4. The Ca content of serpentine plants was consistently higher than that of the nonserpentine plants. The Ca content of both populations increased sharply up to the 0.05 mM level, then increased up to the 4 mM level, remaining almost parallel in the two groups. The Mg content of the nonserpentine plants was the reverse of the Ca content, decreasing sharply from 0.005–0.5 mM, with a more moderate yet consistent decrease to the 4.0 mM treatment. The Mg content of the serpentine plants remained almost constant from the 0.005 to the 0.5 mM level, at which point there was a moderate decrease to the 4.0 mM level. At all calcium levels in the culture solution the shoots of the serpentine plants showed a higher calcium content than the nonserpentine plants ($P < 0.01$).

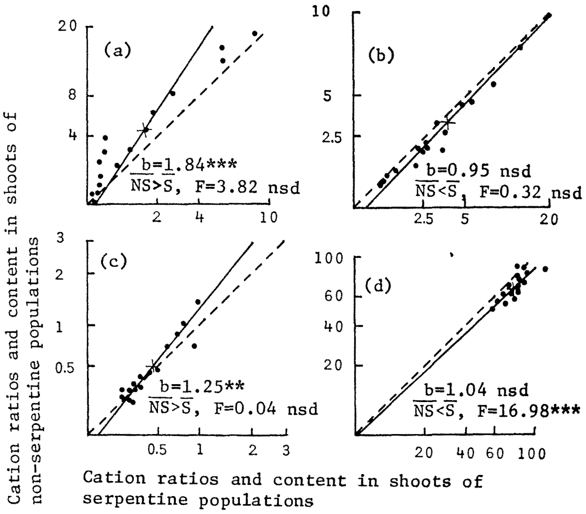

Fig. 6. Comparison of cation ratios and content in shoots of plants from serpentine and nonserpentine populations of *A. spicatum* grown at varying Mg and Ca levels. —— Common regression line; – – – unit slope. (a) Mg/Ca; (b) K/Na; (c) Ca + Mg/K + Na; (d) Mg + Ca + K + Na.

The potassium content in the shoots of both populations increased as the Ca concentration in the culture solution increased; however, the potassium content was consistently higher in the serpentine population. As was the case in the Mg experiments, the sodium content in both populations decreased as the sodium in the cuture solution decreased. The total amount of major cations increased somewhat in both populations at the higher Ca concentrations.

Data for both experiments are presented jointly in Fig. 5 and 6. The mean value for the serpentine population at each magnesium and calcium level is plotted against the mean value of the nonserpentine population at a comparable level on a logarthimic basis. Three parameters are considered: (1) uptake of Ca and Mg per unit dry weight of root (uptake efficiency), (2) cation ratios in the shoots, and (3) total major cation uptake by the shoots. If both populations had an identical uptake efficiency or cationic ratio, the values would lie on a line of unit slope through the origin. The difference between populations is measured by the slope of the common regression line (b) and by the F-ratio of the mean square between populations over the mean square within populations (1, 31 df).

Data for Mg uptake (Fig. 5a) show that the nonserpentine population had a significantly higher uptake efficiency than the serpentine population ($P < 0.001$). The regression coefficient differed significantly from unity, indicating that the nonserpentine population had a higher uptake efficiency for Mg at high uptake levels. The difference in uptake efficiency for Ca (Fig. 5b) was not significant, but the regression coefficient differed significantly from unity ($P < 0.001$). The nonserpentine population had a higher uptake efficiency for Ca at low Ca uptake levels, while the serpentine population had a higher uptake efficiency at high uptake levels.

There were no significant differences in Mg/Ca, K/Na, and Ca + Mg/K + Na ratios (Fig. 6a, 6b, 6c); however, the regression coefficienct for Mg/Ca and Ca + Mg/K + Na differed significantly from unity. The serpentine population had a significantly higher total cation uptake (Ca + Mg + K + Na) than the nonserpentine population, but the regression coefficient did not differ significantly from unity (Fig. 6d).

DISCUSSION—The yield of plants at varying Mg concentrations (Fig. 1) shows a clear differentiation between populations of *A. spicatum* from serpentine and nonserpentine soils, and a relationship between Mg response and soil Mg (Table 1) is apparent. As indicated by the Ca content in the shoots (Fig. 2), this differentiation seems to be due, in part, to a greater uptake of Ca at low levels by plants from the serpentine population. In addition, the serpentine plants maintain a lower level of Mg in the shoots at higher substrate concentrations of Mg than the nonserpentine plants (Fig. 2, 5a). It appears that a higher external Mg concentration is necessary to maintain a sufficient internal Mg supply in the shoots of serpentine plants as compared to nonserpentine plants. Results of the calcium experiments (Fig. 3, 4) tend to corroborate the differential uptake of calcium noted in the magnesium experiments. The yield of plants from the serpentine population appears to be limited by low Ca up to the 0.5 mM level, but above this level Mg seems to be the limiting factor. Yield of the nonserpentine plants increased as the Ca concentration in the culture solution increased, indicating that Mg was not limiting, at least up to a Mg:Ca ratio of 1:8.

The differences between populations in response to varying cations could be brought about by: (1) root morphology, (2) uptake mechanisms, (3) translocation, and (4) an interaction between cations. The evidence presented here does not allow a full analysis of these possible mechanisms; however, some tentative conclusions can be drawn.

It has been shown that varieties of crop plants show a differential response to nutrients because of a difference in root size (Epstein and Jefferies, 1964). In the magnesium experiment the shoot/root ratio was significantly higher in the serpentine population than in the nonserpentine population. In the case of the calcium experiment the shoot/root ratio was reversed, although the difference was not significant. In both experiments the total cation content of the shoots of the serpentine population was significantly higher than that of the nonserpentine population. This alone does not appear to account for the observed differences since: (1) there were large differences in uptake of nutrients per unit weight of root (Fig. 5); (2) there were differences in shoot cationic ratios between populations (Fig. 6); and (3) the response to Mg/Ca ratios was reversed in the two populations, i.e., the nonserpentine population was less tolerant of high Mg/Ca ratios while the serpentine population appeared to be less tolerant of low Mg/Ca ratios.

From the data presented here it is not altogether possible to separate cationic uptake from translocation. In both experiments the serpentine population consistently maintained a higher Ca content in the shoots and the entire plant than the nonserpentine population. The nonserpentine population had a consistently higher Mg content in the shoots than the serpentine population; however, there was no consistent difference in Mg content of the entire plant. In the Mg experiments, the roots of the serpentine population had higher Mg content than the roots of the nonserpentine population ($P < 0.100$), but in the Ca experiments the reverse was true ($P < 0.001$). It appears that the populations differ in selective uptake of Ca and Mg. However, there is evidence that translocation of Mg at high substrate concentrations in the serpentine population may play a role in this differentiation.

Walker et al. (1955) showed that *Helianthus bolanderi* Gray subspecies *exilis* Heiser, a serpentine endemic, absorbed higher concentrations of Ca than the common cultivated sunflower *H. annus* L. Furthermore, Madhok and Walker (1969) indicated a probable depression of Mg uptake by Ca in *H. bolanderi exilis.* The data presented here (Fig. 2, 4) suggest a possible depression of Ca content in the shoots by high Mg substrate concentrations and a possible depression of Mg content by Ca, particularly in plants from the serpentine population.

From the data presented here, it does not appear that a single mechanism is responsible for the noted differentiation between populations of *A. spicatum* from serpentine and nonserpentine soils. Rather, it seems that several possible mechanisms, i.e., root morphology, cationic uptake, translocation of nutrients, and interactions between nutrient cations may have responded to the selective pressure imposed by the serpentine substrate.

The results of this study have shown serpentine and nonserpentine populations of *A. spicatum* to be differentiated with respect to Mg and Ca substrate levels. This differential response is presumed to be under genetic control; populations of *A. spicatum* are probably genotypically differentiated and can be considered to be ecotypic varients in the sense of Clausen, Keck, and Hiesey (1945) and Kruckeberg (1951). However, one must not overlook the possibility that soil properties other than the levels of Mg and Ca may affect plant growth on serpentine soils and thus may be part of the ecotypic response (Krause, 1958; Proctor, 1971).

Physiologically distinct populations within a well-defined, taxonomic species have been shown by a number of authors over a wide range of edaphic conditions. This is particularly true of ubiquitous species. These differences should be recognized and allowances in interpretation made in studies dealing with natural populations of wide-ranging plant species.

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