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ECOLOGICAL DIFFERENCES OF C_3 AND C_4 PLANT SPECIES FROM CENTRAL UTAH IN HABITATS AND MINERAL COMPOSITION

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ABSTRACT.—Six study sites were established in each of three community life form types (grass, forb, and shrub) containing as dominants or subdominants either C_3 and/or C_4 plants. Soil and vegetation samples were analyzed for total nitrogen, phosphorus, magnesium, calcium, potassium, sodium, zinc, iron, copper, and manganese. Discriminant analysis and analysis of variance statistics were used to evaluate differences in mineral content of soils and plant tissues. C_4 plants in all study sites assimilated higher concentrations of potassium, iron, and calcium than did C_3 plants. Forbs in all sites contained the highest concentrations of minerals, followed by shrubs and grasses.

Studies have shown that 40%–50% of the soluble leaf protein in C_3 species consists of RUBPcase, whereas in C_4 species only about 5%–20% was RUBPcase (Blenkinsop and Dale 1974). Based on this evidence, Brown (1978) suggested that C_4 species should require less nitrogen than do C_3 species. Several studies have supported this hypothesis (Christie 1979, Hallock et al. 1965, Wilson and Haydock 1971, Wilson 1975). It has also been shown that C_4 species require small amounts of sodium for growth (Brownell and Crossland 1972), although these studies were done on species specifically adapted to different environments (saline vs. nonsaline). It was the purpose of this study to investigate the mineral relationships of C_3 and C_4 plant species that grow in natural communities of comparable environmental condition to assess whether ecological differences in mineral uptake do exist.

MATERIALS AND METHODS

Study Area

Thirty-six study sites were established in plant communities bordering Utah Lake, Utah County, Utah, at approximately 40°10′ N, 11°50′ W (Fig. 1). Elevations ranged from 1,368 to 1,408 m above sea level, with a mean of 1,377 m. Six study sites were established in each of six community types. Communities were selected because of the presence of the species *Sporobolus airoides*, *Puccinellia nuttalliana*, *Atriplex patula*, *Kochia scoparia*, *Sarcobatus vermiculatus*, and *Atriplex confertifolia*. These species represent three life forms (grass, forb, and shrub), with each life

Fig. 1. A map of Utah Lake showing the locations of study sites around the lake. Communities shown correspond to P = *Puccinellia*, Sp = *Sporobolus*, A = *Atriplex*, K = *Kochia*, G = Greasewood and Sh = Shadscale.

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TABLE 1. Species along with their mean cover values and life form designation. An asterisk (*) indicates C_4 species, and the letters indicate life form type (i.e., g = grass; f = forb; s = shrub).

1. C_4 grass sites	% cover	2. C_3 grass sites	% cover
Allenrolfia occidentalis - s**	2.5	*Bromus tectorum* - g	2.6
Atriplex patula - f	4.3	*Cardaria draba* - f	1.0
**Distichlis spicata* - g	30.7	*Circium undulatum* - f	1.9
Hordeum jubatum - g	3.9	**Distichlis spicata* - g	7.0
Juncus balticus - g	2.2	*Hutchinsia procumbens* - f	1.6
**Kochia scoparia* - f	1.8	*Iva axillaris* - f	5.8
Lepidium perfoliatium - f	1.1	*Juncus balticus* - g	1.0
Polygonum ramosissimum - f	1.3	**Kochia scoparia* - f	9.4
Puccinellia nuttalliana - g	34.1	*Poa pratensis* - g	2.4
Salicornia rubra - f	4.1	**Sporobolus airoides* - g	55.5
Suaeda depressa - f	11.9	*Suaeda depressa* - f	1.5
3. C_4 forb sites	% cover	4. C_3 forb sites	% cover
Ambrosia artimisiifolia - f	2.1	*Bromus tectorum* - g	8.3
Atriplex patula - f	44.9	*Descurainia sophia* - f	4.2
Bromus tectorum - g	2.2	**Distichlis spicata* - g	1.3
**Distichlis spicata* - g	5.1	*Echinochloa crusgalli* - g	2.6
Echinochloa crusgalli - g	2.4	**Kochia scoparia* - f	60.7
Eleocharis macrostachya - g	1.2	*Lepidium perfoliatum* - f	14.5
Hordeum jubatum - g	5.8	*Puccinellia nuttalliana* - g	1.2
**Kochia scoparia* - f	1.3	*Ranunculus testiculatus* - f	1.3
Lactuca scariola - f	1.4		
Populus alba - s	15.6		
Salix amygdaloides - s	7.9		
Xanthium strumarium - f	4.4		
5. C_3 shrub sites	% cover	6. C_3 shrub sites	% cover
Bromus tectorum - g	33.2	**Atriplex confertifolia* - s	12.1
Cardaria draba - f	3.1	*Bromus tectorum* - g	7.9
Descurainia sophia - f	1.9	*Kochia americana* - f	3.8
Erysimum repandum - f	3.5	*Lepidium perfoliatum* - f	8.2
Lepidium perfoliatum - f	3.4	*Ranunculus testiculatus* - f	57.4
Ranunculus testiculatus - f	16.2	*Sarcobatus vermiculatus* - s	1.3
**Salsola iberica* - f	2.5	*Sitanion hystrix* - g	1.5
Sarcobatus vermiculatus - s	23.5	*Suaeda fruticosa* - f	1.3
Sitanion hystrix - g	1.0	*Tetradymia spinosa* - s	1.0
**Sporobolus airoides* - g	2.6		

form represented by both C_3 and C_4 species (Table 1). Taxonomic references follow Cronquist et al. (1977) for the grasses and Welsh and Moore (1973) for the dicots.

Weather data for Provo, Utah, is representative of the study area. The average annual precipitation is 340 mm, with 60% of the total falling in the winter and spring months. The hottest month of the year is July, averaging 33 C; the coldest month is January, averaging 3 C. Tributary streams from the Uintah and Wasatch mountain ranges directly east of Utah Lake provide the majority of its water. Precipitation in these mountains ranges from 760 to 1,270 mm annually (Swenson et al. 1972).

Field Methods

The study sites were selected to depict representative samples of the six community types in the Utah Lake area (Fig. 1). A 10 x 10 m study plot (0.01 ha) was established at each site. Variation in slope, drainage, erosion, and exposure was kept to a minimum. Plots were delineated by a cord 40.0 m long with loops every 10 m for corners. The corners were secured by steel stakes. Twenty 0.25 m^2 quadrats were placed at regular intervals within the study plot. Density and frequency of all plant species encountered were determined from the quadrat data. Cover values were estimated as suggested by Daubenmire (1959). Only those species showing 1% or more of the total cover are included in the analysis.

Christie (1979) found that the top layer of soil is the region of most active mineral uptake. Therefore, soil samples (an 8 cm core) were taken from the top 20 cm of soil in each study plot from opposite corners and the cen-

ter. Samples were pooled and then analyzed for texture (Bouyoucos 1951), pH, soluble salts, and mineral content. The hydrogen ion concentration was measured with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A paste consisting of a 1:1 g/v soil to water (distilled) mixture was used in determining pH and soluble salts.

Vegetation samples were obtained by taking selected clippings of herbaceous material from the C_3 species (*Sporobolus airoides*, *Kochia scoparia*, and *Atriplex confertifolia*) and the C_4 species (*Puccinellia nuttalliana*, *Atriplex patula*, and *Sarcobatus vermiculatus*) within the study plots. Soil and vegetation samples (new growth leaves) were analyzed for total nitrogen, magnesium, calcium, potassium, sodium (Hesse 1971), zinc, iron, copper, and manganese (Lindsay and Norvell, 1969). Discriminant analysis (Klecka 1975) and analysis of variance (Ott 1977) were used to statistically determine differences in mineral content between C_3 and C_4 species and their habitats.

Discriminant analyses were conducted using the Statistical Package for the Social Sciences (SPSS) computer program (Klecka 1975). This technique distinguishes statistically between two or more groups of stands on the basis of discriminating variables. The groups and variables are selected by the researcher. All variables measured can be used in the analysis (direct method), or a stepwise method can be used to reduce the number of variables to those that provide the best discriminating power among the groups. In this study both the direct and the Wilks stepwise methods were used. The Wilks method uses the overall multivariate F ratio to test for variable differences. It selects the variables independently for entry into the analysis based on the importance of their discriminating power.

The analysis procedure combines the discriminating variables to create discriminant functions designed to provide maximum separation among the groups previously specified (life forms and C_3 and C_4 photosynthetic types). The discriminant program determines the relative percentage of the total variation in the discriminating variables that is accounted for in each function. It also determines the relative importance of each variable used to

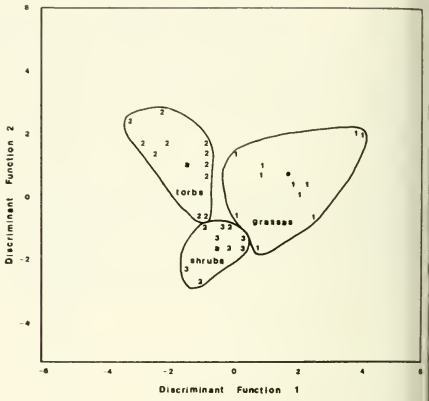

Fig. 2. Discriminant analysis for soil minerals. Of the groups, 83% were classified correctly. Numbers refer to grasses (1), forbs (2), and shrubs (3).

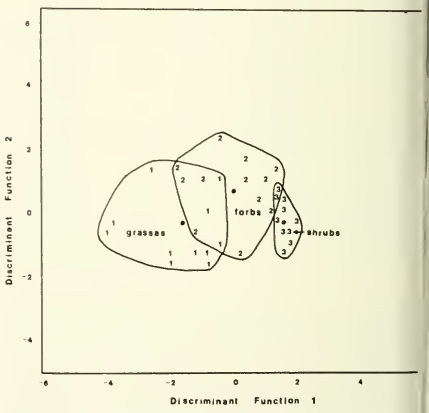

Fig. 3. Discriminant analysis for soil chemistry and texture. Of the groups, 78% were classified correctly. Numbers refer to grasses (1), forbs (2) and shrubs(3).

create the discriminant functions. This information can be used to identify the variables having the greatest influence on the outcome of the analysis.

A graphic representation of the results of discriminant analysis is possible if the discriminant functions are viewed as axes in geometric space. A plot of stands based on the two most important functions locates the stands in

Fig. 4. Discriminant analysis for vegetation (leaf) minerals. Of the groups, 100% were classified correctly. Numbers refer to grasses (1), forbs (2), and shrubs (3).

two-dimensional space in such a way that the relationships among the groups can be visualized. Such a graphic representation is especially important for assessing the amount of separation between one group and another as well as the degree of group overlap.

RESULTS

Results of cover analysis for our study sites are given in Table 1. Only those species showing 1% or more of the total cover are included. In the grass- and forb-dominated communities, *Sporobolus airoides*, and *Kochia scoparia* provided over half the total cover. The shrub communities, however, were dominated in their understory by the invader species *Bromus tectorum* L. and *Ranunculus testiculatus* Cranz. Their presence in the understory is indicative of site disturbance as a result of grazing.

Hydrogen ion concentration showed no significant differences between the communities. All soils were basic, with a pH ranging from 8.1 to 8.7. Soil texture also showed no significant differences between communities, all of them being clay to silty clay loams. Soluble salts were highest in the grass communities and lowest in the shrub communities.

Two-dimensional plots of discriminant analysis of the mineral content of vegetation and soil samples within each life form (grasses, forbs, and shrubs) were made. The percent of grouped cases classified correctly were 83% for the soil materials (Fig. 2) and 78% for soil chemistry and texture (Fig. 3), whereas the mineral content of the vegetation classified the groups 100% correctly (Fig. 4). This indicates that habitat differences in soil mineral chemistry and texture influence the life form type that dominates a site and that differential partitioning of the minerals by the plants occurs to a great extent. The soil, of course, may also be modified by the plants growing in it.

Results of analysis of variance and Newman-Kuel tests for parameters of soil and vegetation mineral content are given in Tables 2 and 3. Analysis of soil mineral content showed significant differences between means for manganese, sodium, and soluble salts. Analysis of vegetation mineral content showed differences between life forms in nitrogen, phosphorus, zinc, manganese, copper, magnesium, potassium, and sodium.

C_3 and C_4 species were 78% correctly classified by minerals for both soil and vegetation samples (Tables 2 and 3). Stem and leaf plots of the discriminant analyses based on soil and vegetation mineral content are given in Figures 5 and 6, respectively.

Results of the analysis of variance between C_3 and C_4 species are shown in Table 4. Iron and manganese are significantly ($p < .05$) higher in concentrations in the soils of C_3-dominated species than of C_4-dominated species. However, concentration of these minerals within the plant tissue is not significantly different. Calcium and potassium showed no significant differences in concentration in soils but were significantly different in the plant tissues of C_3 and C_4 species. Plant:soil ratios were computed for each mineral. Mean differences in iron and sodium assimilation exist between C_3 and C_4 species. Although trends existed for other elements, differences between C_3 and C_4 species were not significant.

DISCUSSION

Brown (1978) suggested that differences in nitrogen use between photosynthetic types (C_3 vs. C_4) would hold for grasses, but he was not sure of the results that might be obtained with respect to other life forms. It appears

TABLE 2. Differences in the mineral concentrations of soils associated with the life forms as determined by analysis of variance and Newman-Keul tests. Means with similar letters following indicate no significant differences for those means. Those with different letters indicate significant differences.

Mineral	Nutrient concentrations in life form soils			Level of significance
	Grasses	Forbs	Shrubs	
	mg/Kg			
Nitrogen	2023a ± 1105	2026a ± 1088	1106a ± 284	NS
Manganese	10.3ab ± 8.87	15.3b ± 8.51	7.1a ± 2.3	.05
Calcium	15287b ± 5195	11231a ± 2804	10368a ± 1497	.05
Magnesium	2002a ± 1168	1260ab ± 1309	748b ± 421	.05
Sodium	3428b ± 2086	1233a ± 1065	474a ± 209	.01
Salt	7470a ± 5712	3251ab ± 2506	639b ± 440	.05

TABLE 3. Differences in the mineral concentrations of plant material (leaves) by life form. Differences determined by analysis of variance and Newman-Keul tests. Means with similar letters following indicate no significant differences for those means. Those with different letters indicate significant differences.

Mineral	Nutrient concentrations in life forms			Level of significance
	Grasses	Forbs	Shrubs	
	mg/Kg			
Nitrogen	9908a ± 3366	22033b ± 3614	16283b ± 4220	.01
Phosphorus	943a ± 507	2471b ± 608	976a ± 244	.01
Zinc	18.8a ± 8.4	33.1b ± 15.4	12.5a ± 3.06	.01
Magnesium	2903a ± 2091	7285b ± 2414	3308a ± 1519	.01
Copper	10.2ab ± 3.1	13.5b ± 3.0	8.3a ± 1.2	.01
Manganese	50.9a ± 28.1	89.6b ± 48.1	72.8ab ± 47.8	.01
Potassium	4264a ± 1916	20183b ± 7911	24175b ± 5472	.01
Sodium	3060a ± 1467	29079b ± 16199	51967b ± 9060	.01

from our data that differences do exist in mineral uptake for the different life forms.

Nitrogen content in the plant tissue of C_3 and C_4 species showed no significant differences. These findings are contrary to the results of Christie (1979) and Hallock et al. (1965) and the hypothesis of Brown (1978). In fact, the C_4 shrub *A. confertifolia* showed less

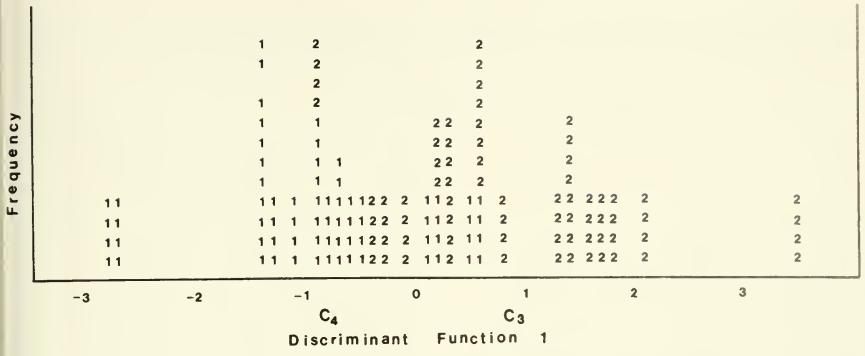

Fig. 5. Histogram of discriminant analysis for soil minerals. 1 = C_4 dominated habitats, 2 = C_3 dominated habitats.

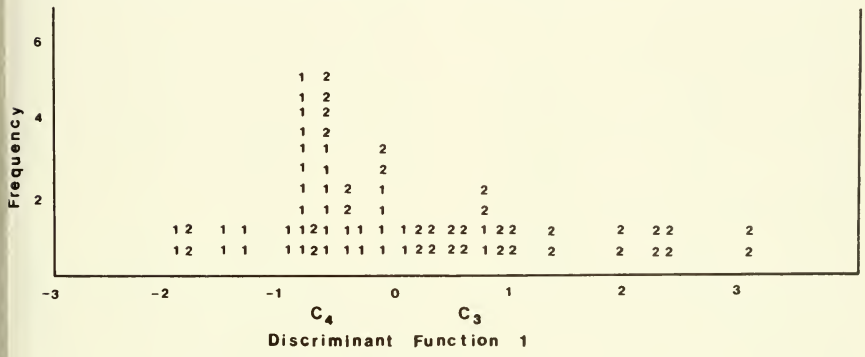

Fig. 6. Histogram of discriminant analysis for vegetation (leaf) minerals. 1 = C_4 – species, 2 = C_3 – species.

nitrogen than the C_3 shrub *S. vermiculatus*. The effect of species being adapted to similar habitats may influence this phenomenon and needs to be further investigated.

The C_3 species of this study were growing in soils significantly higher in iron content than the C_4 species (Table 4), yet no significant differences in iron and manganese concentration of the vegetation was noted. This may be due to some attribute of C_4 plants that allows them to live in soils deficient in iron and still assimilate enough for existence. It could also be due to iron being present in luxury quantities in both habitat soils and the plants assimilating iron without any restrictions. Results of this study also showed calcium to be significantly higher in C_4 vegetation than C_3 vegetation (Table 4). Concentrations of calcium in the soil of both community types is not significantly different, indicating differential uptake of calcium by the species possessing the different photosynthetic pathways. Also the C_4 species in this study assimilated significantly higher quantities of potassium than did C_3 species ($P < .005$). This is in contrast to the results obtained by Hallock et al. (1965).

Sodium may be essential as a micronutrient for C_4 species based upon studies of halophytic C_4 species and nonhalophyte C_3 species (Brownell and Crossland 1972). These workers showed that the C_4 species they studied developed lesions and some species would not flower in the absence of sodium, whereas the C_3 species grew normally. However, our field results indicate that C_4 plants do not necessarily require sodium, but that high

TABLE 4. Summary of mineral concentrations for vegetation and soil data. Means are for vegetation, soil, and plant:soil ratios for C_3 and C_4 plants across all 36 study sites. Significant differences are indicated by the presence of an asterisk (*) next to the means values. One asterisk indicates $p < 0.05$; two asterisks indicate $p < 0.01$.

	mg/Kg					
	Vegetation		Soil		Plant:soil ratio	
	C_3	C_4	C_3	C_4	C_3	C_4
N	16127.0 ± 6910.0	16022.0 ± 5611.0	1667.0 ± 1198.0	1771.0 ± 751.0	15.3 ± 15.2	10.6 ± 4.9
P	1489.0 ± 825.0	1438.0 ± 915.0	47.0 ± 104.9	29.0 ± 32.3	79.7 ± 49.2	79.0 ± 54.0
Zn	22.8 ± 15.1	21.0 ± 11.4	3.5 ± 6.6	1.8 ± 2.0	18.0 ± 11.5	21.3 ± 13.9
Fe	269.0 ± 220.8	349.0 ± 504.0	16.1* ± 14.4	6.5* ± 5.1	28.1 ± 27.0	60.3 ± 63.3
Mn	82.9 ± 37.0	59.4 ± 48.6	14.4 ± 9.3	7.4 ± 3.7	9.5 ± 9.6	8.6 ± 5.7
Cu	10.2 ± 3.6	11.1 ± 3.2	2.5 ± 1.5	1.5 ± .6	5.4 ± 3.1	8.5 ± 3.5
Ca	10089.0* ± 4301.0	13017.0* ± 5875.0	12306.9 ± 3852.7	12644.0 ± 4609.7	0.9 ± 0.4	2.0 ± 1.3
Mg	4390.0 ± 3420.0	4602.0 ± 2162.0	1457.0 ± 1227.5	1217.0 ± 848.2	4.6 ± 4.1	5.4 ± 5.9
K	13433.0** ± 8274.0	18965.0** ± 11589.0	1022.0 ± 952.4	1370.0 ± 889.1	19.6 ± 21.0	16. ± 19.
Na	30778.0 ± 22431.0	25292.0 ± 23463.0	1766.0 ± 1750.7	1658.0 ± 1995.9	76.8 ± 88.1	42. ± 53.
Salt			3921.0 ± 5083.0	3653.0 ± 4025.0		
pH			8.3 ± 0.5	8.3 ± 0.3		
Clay			33.4 ± 13.0	30.8 ± 15.3		
Silt			46.3 ± 16.3	47.6 ± 17.8		
Sand			20.2 ± 11.8	21.7 ± 15.5		

sodium uptake is characteristic of plants adapted to the saline habitat (Table 4).

Salinity would have the same effect on plant-water relations as increasing plant drought: the more salt present in a soil, the wetter the soil must be to dilute the salt and prevent salt hindrance to growth (Donahue et al. 1977). Plants possessing the C_4 photosynthetic pathway typically have a higher water use efficiency than plants possessing the C pathway, which would aid in survival of th plant in semiarid regions (Ludlow 1976). C plants may have a competitive advantage i saline environments due to their high wate use efficiency. Although no significant diffe ences between salt or sodium levels in the tw habitat types and in the C_3 and C_4 plants wer observed, it is important to note that the C

species of this study had slightly higher mean levels of sodium in their tissues and higher plant:soil ratios than the C_4 species. The C_3 species also flowered one to two months earlier in the summer, when moisture conditions in the habitat were more conducive to their growth.

though grasses grew in soils with high concentrations of soluble salts (Table 2), their tissue concentrations of sodium and potassium (Table 3) were much lower than either forbs or shrubs. Although many grasses adapted to saline environments possess salt glands (Liphschitz et al. 1974, Hansen et al. 1976), *Puccinellia nuttalliana* and *Sporobolus airoides* do not and as a result must restrict the amount of sodium and potassium entering their tissues. On the other hand, the shrubs and forbs of this study do possess salt glands or become succulent (Luttge 1971) and thus are able to tolerate higher quantities of sodium and potassium in their tissues.

Both growth form and photosynthetic type showed habitat differences relative to mineral uptake. The detailed physiological basis for these differences must now be further investigated.

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