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Nutritive Quality and Mineral Content of Potential Desert Tortoise Food Plants

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RESEARCH SUMMARY

Grasses, forbs, shrubs, and succulents (cacti) that desert tortoises (*Gopherus agassizii*) might eat were

analyzed over the spring, summer, and fall seasons at two study areas in southwestern Utah (City Creek near St. George and Woodbury-Hardy on the Beaver Dam Slope) and at one site in northwestern Arizona (near Littlefield). Earlier researchers suggested that tortoises were healthier at City Creek than at the other areas, especially Woodbury-Hardy.

Plant materials were analyzed for moisture content, nitrogen (total organic nitrogen; crude protein = 6.25 x total organic nitrogen), phosphorus, potassium, zinc, iron, manganese, copper, calcium, magnesium, sulfur, sodium, ADF (acid detergent fiber), TNC (total nonstructural carbohydrates), and crude fat (ether extract) for a 3-year period (1989-91). Plants from the three areas had similar values for most nutrients and minerals, but Littlefield plants had significantly ($P < 0.05$) higher values for potassium, copper, and fat. Some nutrition and mineral parameters were different for the six plant classes, annual and perennial grasses, annual and perennial forbs, shrubs, and succulents.

In general, when differences existed, annual forbs were higher in mineral and nutrient content than other plant classes. Plants with high moisture content were high for other measured parameters. Various parameters were correlated; potassium and nitrogen were highly correlated with the other variables. Plant mineral values did not generally track soil mineral values. Values of minerals and nutrients for both plants and soils fell in normal ranges for semiarid conditions; however, sodium was low for both soils and plants. Low sodium concentrations may contribute to health problems for desert tortoises. The mineral and nutrient content of cow excrement does not appear to make it a quality food source for desert tortoises as has been recently suggested.

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Nutritive Quality and Mineral Content of Potential Desert Tortoise Food Plants

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INTRODUCTION

The Mojave desert tortoise (*Gopherus agassizii*) population north and west of the Colorado River is protected under provisions of the Endangered Species Act (Federal Register 1990). Desert tortoise subpopulations in southwestern Utah and adjacent Arizona on the Beaver Dam Slope and north of St. George, UT, are at the northeastern limit of the species' distribution (fig. 1; Patterson 1982; Woodbury and Hardy 1948). The three study areas are City Creek, about 4 kilometers north of St. George; Woodbury-Hardy, on the Beaver Dam Slope about 3 kilometers north of the Arizona border; and Littlefield, about 3 kilometers

northeast of Littlefield, AZ, also on the Beaver Dam Slope (fig. 1). The health of tortoises in these subpopulations apparently differs (Bostick 1990; Glenn and others 1990; Grover and DeFalco in press; Jarchow 1987).

The City Creek subpopulation was deemed to be the healthiest, the Woodbury-Hardy subpopulation was deemed least healthy, and the Littlefield subpopulation was deemed intermediate, based on population density and structure, and carapace characteristics. The Woodbury-Hardy subpopulation has a high frequency of animals with bone deformations and thinning plastrons and carapaces (Jarchow 1987).

This study was designed to evaluate the hypothesis that nutritive quality and mineral content of potential desert tortoise food plants differed at the three areas, possibly contributing to the apparent health differences. A second hypothesis was that plant mineral content would be correlated with that of associated soil. Mineral nutrition has been shown to be important in desert tortoise ecophysiology (Nagy and Medica 1986). Information about the nutritive quality and mineral status of the plants should be useful for those concerned with the health and management of a wide range of herbivores.

MATERIALS AND METHODS

Eighteen plant species common to the three study areas form the core of this study (table 1). These species were chosen based on three criteria: (1) annual and perennial plants were included; (2) grasses, forbs, shrubs, and succulents (cacti) were included; and (3) there was evidence that they were, for the most part, desert tortoise food plants (Coombs 1974; Hansen and others 1976; Hohman and Ohmart 1980; Woodbury and Hardy 1948). A few additional species were sampled early or late in the study (for example, *Abronia fragrans*, *Plantago patagonica*, *Schismus barbatus*, and *Sphaeralcea grossulariifolia*) (table 1).

Hansen and others (1976) and Nagy and Medica (1986) have listed desert tortoise food plants from other areas. After our study began, Esque and others (1991) and Esque (1992) documented the primary food plants

Figure 1—Location of plant collection study areas.

Table 1—Species that were analyzed for nutrients and minerals by study area¹

Species	Clity Creek			Woodbury-Hardy			Littlefield		
	1989	1990	1991	1989	1990	1991	1989	1990	1991
Grasses									
<i>Aristida purpurea</i> (purple threeawn)	+	+	+	+	+	+	+	+	+
<i>Bromus rubens</i> (red brome ²)	+	+	+	+	+	+	+	+	+
<i>Erioneuron pilosum</i> (hairy tridens)	+	+	+	+	+	+	+	+	+
<i>Hilaria rigida</i> (big galleta)	+	+	+	+	+	+	+	+	+
<i>Muhlenbergia porteri</i> (bush muhly)	+	+	+	+	+	+	+	+	+
<i>Schismus barbatus</i> (Mediterranean grass ²)	—	—	+	—	—	+	—	—	+
<i>Stipa hymenoides</i> (Indian ricegrass)	+	+	+	+	+	+	+	—	+
Forbs									
<i>Abronia fragrans</i> (fragrant sand-verbena)	+	—	—	—	—	—	—	—	—
<i>Baileya multiradiata</i> (desert bailey)	+	+	+	+	+	+	+	+	+
<i>Eriogonum inflatum</i> (bottlebush or bottlestopper)	+	+	+	+	+	+	+	+	+
<i>Eriodum cicutarium</i> (storksbill ²)	+	+	+	+	+	+	+	+	+
<i>Plantago patagonica</i> (wooly plantain)	—	—	+	—	—	+	—	—	+
<i>Sphaeralcea ambigua</i> (desert globemallow)	+	+	+	+	+	+	+	+	+
<i>Sphaeralcea grossulariifolia</i> (gooseberryleaf globemallow)	—	—	—	+	—	—	—	—	—
Shrubs									
<i>Atriplex canescens</i> (fourwing saltbush)	+	+	+	+	+	+	+	+	+
<i>Ceratoides lanata</i> (winterfat)	+	+	+	+	+	+	+	+	+
<i>Ephedra nevadensis</i> (Nevada ephedra or mormon tea)	+	+	+	+	+	+	+	+	+
<i>Eriogonum fasciculatum</i> (Mojave buckwheat)	+	+	+	+	+	+	—	—	—
<i>Hymenoclea salsola</i> (burrobrush)	+	+	+	+	+	+	+	+	+
<i>Krameria parvifolia</i> (range ratany)	+	+	—	+	+	+	+	+	+
Succulents									
<i>Opuntia basilaris</i> (beavertail pricklypear)	—	—	—	+	+	+	+	+	+
<i>Opuntia erinacea</i> (grizzlybear pricklypear)	+	+	+	+	+	+	+	+	+

¹A plus sign (+) indicates that a sample was taken, a minus sign (—) indicates no sample. The core species are those sampled every year.

²Introduced species.

in the Beaver Dam Slope and St. George areas, including most of the species that we sampled. Plants were collected for analysis in the spring (April, May), summer (June), and fall (October) from 1989 to 1991. The plants in table 1 were all collected in 2-day periods, stored in sealed plastic bags in ice chests for up to 36 hours, weighed, oven-dried for 5 to 10 days (depending on their succulence) at 40 to 60 °C, reweighed, and ground to powder in a Wiley Mill using a 1-millimeter screen. Additional plant samples (appendix A) collected during April 1990 were treated in the same manner; these samples were largely the same species as those of table 1, but included a few additional species.

In general, we collected leaves and associated small twigs as a single collection; in some cases we collected fruits, flowers, and stems separately (appendix B). Leaves and small twigs are the plant parts most likely to be foraged by desert tortoises. Some current-season cow dung was collected, stored, and analyzed in the same manner as the plant material in light of the

recent claim by Bostick (1990) that desert tortoises evolved and flourished as dung feeders.

The nutritive quality and mineral data for plant samples include moisture content, nitrogen (total organic nitrogen; crude protein = 6.25 x total organic nitrogen), phosphorus, potassium, zinc, iron, manganese, copper, calcium, magnesium, sulfur, sodium, acid detergent fiber (ADF), total nonstructural carbohydrates (TNC), and crude fat (ether extract). We use the terms nutritive quality and mineral content realizing the sampled minerals are nutrients for most animals (Robbins 1983). However, the nutritive requirements for desert tortoises are poorly known (Grover and DeFalco in press). Except for moisture content, which was based on total fresh weight, data were collected on a dry weight basis. All analyses, except for moisture content, were performed in the Brigham Young University Plant and Soil Analysis Laboratory. The methods used are found in Horowitz (1980) except for TNC determination, which followed the procedures of

Tiedemann and others (1984). For the few samples with insufficient material for all analyses, fat and occasionally other parameters were not determined. Moisture content could not be determined in a few samples because of drying problems.

Soil samples were also collected and analyzed. Six upland samples and six lowland samples collected from each of the three study areas were analyzed for pH, electrical conductivity (EC), sodium adsorption ratio (SAR), sand, silt, clay, calcium, magnesium, sodium, nitrogen, phosphorus, potassium, zinc, iron, and copper using the methods of Page (1982). The analyses for calcium, magnesium, and sodium were for the water-soluble forms used in the SAR analysis. Soils of the study areas have been classified as Winkel-Rock land, Pintura-Toquerville-Dune land, Cave, and Rock Outcrop-Rock land associations (Mortensen and others 1977). These are shallow, gravelly, fine sandy loams (Winkle-Rock and Cave), deep loamy fine sands and fine sands (Pintura-Toquerville-Dune), and shallow soils over bedrock (Rock Outcrop-Rock). The City Creek site includes Winkel-Rock, Pintura-Toquerville-Dune, and Rock Outcrop-Rock soil associations. The Woodbury-Hardy and Littlefield sites have Cave and Rock Outcrop-Rock soil associations (Mortensen and others 1977). The rocky soil associations in our study areas were sandy.

Statistical analyses, including analysis of variance, Tukey means comparison tests, *t* tests, and correlation coefficients, were performed using SAS (1985). Data are presented proportionally, in percent, for all parameters except zinc, iron, manganese, and copper, which are given in parts per million (ppm). Differences were

considered significant at the $P < 0.05$ level, but actual significance probability values are presented in some cases. All proportional data were arcsine transformed for analyses; they have been converted to real values for presentation here. In comparing cured (quiescent) and green (growing) samples, those with moisture content of 0.23 or greater were considered "green" and those with moisture content less than 0.23 were considered "cured"; 0.23 is the arcsine transfer value of 0.50. This was an arbitrary value that effectively separated green plant tissue (which fell above the value) and cured plant material (which fell below the value). Climatic data are from National Oceanic and Atmospheric Administration (NOAA 1988-91). Botanical nomenclature follows Welsh and others (1987) and Baird (1990).

This study is part of a larger project designed to assay habitat and biological characteristics of desert tortoises at the northern extent of their distribution (Esque and others 1991; McArthur and Sanderson 1992a,b).

RESULTS

The appendixes list the species, times of collection, and seasonal means with significant differences for those species collected intensively for such comparisons.

Table 2 lists mean values of all nutrients and minerals by location. These values are in the normal range for semiarid sites for most parameters (Jones and Hanson 1985; Kincaid 1988; Miller and Ramsey 1988; Rains 1976). However, the level for sodium is abnormally low, the levels for sulfur and iron are low, and the level for phosphorus is in the low end of the

Table 2—Nutrient and mineral values for each study area. Different letters in the same row indicate a significant difference in mean value

Nutrient	Units	City Creek (n = 182)	Woodbury-Hardy (n = 184)	Littlefield (n = 236)
Moisture	Percent ¹	38.08 A	41.50 AB	46.96 B
Nitrogen	Percent	1.58 AB	1.73 B	1.50 A
Phosphorus	Percent	0.13 B	0.10 A	0.14 B
Potassium	Percent	1.29 A	1.39 A	1.71 B
Zinc	ppm	15.13 A	16.30 AB	18.56 B
Iron	ppm	283.41 A	289.34 A	371.12 A
Manganese	ppm	48.64 AB	39.54 A	49.14 B
Copper	ppm	6.00 A	5.79 A	6.76 B
Calcium	Percent	1.18 A	1.43 AB	1.60 B
Magnesium	Percent	0.30 A	0.40 B	0.46 B
Sulfur	Percent	0.29 A	0.36 A	0.40 B
Sodium	Percent	0.010 A	0.010 A	0.012 B
ADF ²	Percent	36.34 A	35.66 A	34.52 A
TNC ³	Percent	7.32 A	7.27 A	8.56 A
Fat ⁴	Percent	7.53 A	7.48 A	8.07 A

¹Based on fresh weight; all other values are based on dry weight.

²Acid detergent fiber.

³Total nonstructural carbohydrates.

⁴Sample numbers for fat were reduced to 153 (City Creek), 152 (Woodbury-Hardy), and 217 (Littlefield).

normal range. Kincaid (1988) points out that sodium is often deficient in plants growing in semiarid environments. Plants in City Creek and Woodbury-Hardy are quite similar in mineral content and nutrients; they differ significantly only in phosphorus and magnesium content. Plants in City Creek were higher in phosphorus and those in Woodbury-Hardy were higher in magnesium. Plants in Littlefield had significantly higher values for potassium, copper, sodium, and fat than both the other areas. Plants in Littlefield had significantly higher values for several of the nutrients and minerals than those for either City Creek or Woodbury-Hardy but not for both: moisture content, zinc, calcium, magnesium, and sulfur were higher than for City Creek; nitrogen, phosphorus, and manganese were higher than for Woodbury-Hardy. When the plant nutrient and mineral contents of the three areas are considered together, they seem similar except for a trend of Littlefield to be high. Values in Littlefield are not significantly lower than any of the values in City Creek or Woodbury-Hardy and have the lowest mean value only for ADF, in which case the lowest value means the highest quality.

The results in table 2 are strongly influenced by the contribution of perennial plants, which were more intensively sampled. Annual plant values are not significantly different among areas except for iron (Littlefield plants were significantly higher than Woodbury-Hardy, but not than City Creek, data not shown) and magnesium (City Creek plants were significantly lower than both (Littlefield and Woodbury-Hardy, data not shown). For perennial plants the differences (table 3) were similar to those for all plants combined (table 2).

Table 4 compares the data for all life forms of plants (annual grasses, perennial grasses, annual forbs, perennial forbs, shrubs, and succulents). Annual grasses are low in water, calcium, and magnesium content and high in nitrogen and copper with respect to the other plant life forms. Perennial grasses are low in nitrogen, phosphorus, potassium, manganese, copper, calcium, magnesium, sulfur, sodium, and fat and high in ADF. Annual forbs are not low in any nutrient or mineral but are high in nitrogen, phosphorus, potassium, iron, and copper. Perennial forbs are low in manganese and high in nitrogen, sulfur, sodium, and fat. Shrubs are low in iron, manganese, and copper and high in nitrogen, potassium, sulfur, sodium, and fat. Succulents are low in nitrogen, iron, copper, sulfur, sodium, and ADF and high in moisture content, potassium, manganese, calcium, and magnesium. These relative values (high, low, similar) are comparative values and should not be interpreted as high or low values outside the context of this study.

When the mineral and nutrient contents are compared within plant life forms by season (table 5), the patterns are usually similar for all plant life forms. Moisture content decreases seasonally from spring to summer and fall except for succulents, which keep their moisture content relatively stable. Nitrogen, phosphorus, potassium, zinc, and fat also decline seasonally following the same general seasonal pattern as moisture content; some of these parameters decline more sharply than others, for example, phosphorus and potassium in perennial forbs, and fat in grasses and perennial forbs. Iron, manganese, copper, calcium,

Table 3—Perennial plants: nutrient and mineral values at each study area. Different letters in the same row indicate a significant difference in mean value

Nutrient	Units	City Creek (n = 158)	Woodbury-Hardy (n = 167)	Littlefield (n = 202)
Moisture	Percent	40.81 A	41.61 A	49.66 B
Nitrogen	Percent	1.55 AB	1.48 A	1.73 B
Phosphorus	Percent	0.13 B	0.10 A	0.13 B
Potassium	Percent	1.29 A	1.36 A	1.73 B
Zinc	ppm	14.77 A	15.84 AB	17.93 B
Iron	ppm	243.15 A	268.92 A	286.61 A
Manganese	ppm	47.51 A	38.61 A	46.17 A
Copper	ppm	5.77 AB	5.63 A	6.53 B
Calcium	Percent	1.18 A	1.43 AB	1.55 B
Magnesium	Percent	0.31 A	0.40 AB	0.49 B
Sulfur	Percent	0.30 A	0.35 AB	0.40 B
Sodium	Percent	0.010 A	0.010 A	0.012 B
ADF ¹	Percent	36.34 A	35.76 A	34.04 A
TNC ²	Percent	7.37 A	7.22 A	8.51 A
Fat ³	Percent	7.17 A	7.48 A	8.07 B

¹Acid detergent fiber.

²Total nonstructural carbohydrates.

³Sample numbers for fat were 132 (City Creek), 137 (Woodbury-Hardy), and 184 (Littlefield).

Table 4—Plant classes: nutrient and mineral values, with significant differences for study areas. Different letters in the same row indicate a significant difference in mean value

		Plant class ¹											
Nutrient	Units	Annual grasses (n = 41)		Perennial grasses (n = 139)		Annual forbs (n = 43)		Perennial forbs (n = 143)		Shrubs (n = 181)		Succulents (n = 66)	
Moisture ²	Percent	20.83	A	27.97	AB	39.72	B	47.41	B	44.66	B	72.93	C
Nitrogen	Percent	1.61	B	1.22	A	1.84	B	1.82	B	1.95	B	1.11	A
Phosphorus	Percent	0.12	ABC	0.09	A	0.19	D	0.15	CD	0.13	BC	0.11	AB
Potassium	Percent	1.19	B	0.75	A	1.52	BCD	1.62	BC	1.85	CD	2.10	D
Zinc	ppm	17.17	B	12.89	A	24.10	C	18.41	BC	16.42	AB	19.23	BC
Iron	ppm	554.16	C	357.94	BC	1,050.23	D	319.50	B	215.60	A	148.09	A
Manganese	ppm	51.51	AB	37.34	A	68.40	B	40.10	A	36.56	A	101.57	C
Copper	ppm	7.51	B	5.74	A	8.15	B	6.75	AB	5.83	A	5.52	A
Calcium	Percent	0.68	A	0.51	A	2.61	C	1.36	B	1.61	B	4.00	D
Magnesium	Percent	0.19	A	0.14	A	0.41	BC	0.38	B	0.47	C	1.20	D
Sulfur	Percent	0.26	AB	0.24	A	0.37	BCD	0.40	CD	0.44	D	0.25	AB
Sodium	Percent	0.009	AB	0.005	A	0.008	AB	0.016	C	0.013	BC	0.0105	A
ADF ³	Percent	37.76	C	44.51	D	34.89	BC	36.64	C	31.45	B	23.87	A
TNC ⁴	Percent	9.33	A	6.40	A	9.61	A	8.09	A	8.12	A	6.89	A
Fat	Percent	7.85	AB	6.57	A	8.32	B	8.12	B	8.52	B	7.64	AB

		Study areas ⁵					
Units		City Creek		Woodbury-Hardy		Littlefield	
Moisture	Percent						
Perennial forbs		41.57	A	42.25	A	55.74	B
Nitrogen	Percent						
Shrubs		1.13	A	1.14	B	1.16	B
Phosphorus	Percent						
Shrubs		0.10	B	0.06	A	0.09	AB
Zinc	ppm						
Shrubs		9	A	13	AB	18	B
Manganese	ppm						
Perennial forbs		48	B	33	A	41	AB
Shrubs		37	AB	41	A	31	A
Succulents		56	A	122	B	125	B
Copper	ppm						
Perennial grasses		4	A	6	AB	7	B
Shrubs		6	AB	3	A	9	B
Magnesium	Percent						
Perennial grasses		0.11	A	0.15	B	0.16	B
Annual forbs		0.28	A	0.48	B	0.44	B
Sulfur	Percent						
Shrubs		0.34	A	0.43	AB	0.54	B

¹Sample numbers for the following analyses were reduced: annual grasses (moisture 39, fat 36), perennial grasses (fat 126), perennial forbs (fat 122), shrubs (moisture 179, fat 162), succulents (TNC and ADF 64, fat 46).

²Based on fresh weight; all other values are based on dry weight.

³Acid detergent fiber.

⁴Total nonstructural carbohydrates.

⁵This portion of the table illustrates the 12 significant differences among sites out of 90 comparisons made.

magnesium, sulfur, and sodium are essentially stable; however, iron increases in forbs and succulents, calcium increases in succulents, magnesium increases in perennial forbs, and sodium decreases in perennial grasses. The TNC trends down seasonally in every case, but significantly so only for perennial forbs. The ADF increases seasonally, significantly so except for annual forbs and succulents.

The five perennial grasses included in our study differ in moisture content, potassium, iron, manganese, calcium, magnesium, sulfur, sodium, and ADF but not in nitrogen, phosphorus, zinc, copper, TNC, and fat (table 6). *Aristida purpurea* is low in potassium, calcium, magnesium, and sulfur and high in iron and ADF. *Erioneuron pilosum* is low in moisture content and potassium and high in iron, manganese,

Table 5—Plant classes: nutrient and mineral values by season. Different letters in the same row within a plant class indicate a significant difference in mean value

Nutrient	Units	Annual grasses			Perennial grasses		
		Spring (n = 17)	Summer (n = 8)	Fall (n = 12)	Spring (n = 52)	Summer (n = 44)	Fall (n = 45)
Moisture	Percent	43.05 B	1.96 A	11.98 A	36.85 B	24.23 A	21.81 A
Nitrogen	Percent	2.14 B	1.31 AB	1.16 A	1.50 B	1.03 A	1.10 A
Phosphorus	Percent	0.22 B	0.09 A	0.04 A	0.11 B	0.09 AB	0.06 A
Potassium	Percent	1.93 B	0.80 AB	0.64 A	1.01 B	0.63 A	0.59 A
Zinc	ppm	22.09 B	13.69 A	12.96 A	16.81 B	10.89 A	10.24 A
Iron	ppm	449.37 A	479.53 A	772.64 A	306.22 A	388.04 A	391.99 A
Manganese	ppm	62.41 A	47.61 A	39.69 A	37.21 AB	32.49 A	42.25 B
Copper	ppm	7.84 A	8.41 A	6.25 A	5.76 A	5.76 A	5.29 A
Calcium	Percent	0.65 A	0.57 A	0.79 A	0.49 A	0.47 A	0.57 A
Magnesium	Percent	0.21 A	0.15 A	0.19 A	0.14 A	0.13 A	0.15 A
Sulfur	Percent	0.33 A	0.22 A	0.24 A	0.24 A	0.26 A	0.29 A
Sodium	Percent	0.009 A	0.011 A	0.007 A	0.006 B	0.005 B	0.004 A
ADF ¹	Percent	33.67 A	39.68 AB	42.38 B	42.40 A	46.39 B	45.13 B
TNC ²	Percent	12.16 A	7.76 A	6.82 A	7.46 A	5.61 A	5.98 A
		(n = 16)	(n = 5)	(n = 11)	(n = 46)	(n = 44)	(n = 36)
Fat	Percent	9.37 B	6.46 AB	6.46 A	7.50 B	6.47 AB	5.58 A
		Annual forbs			Perennial forbs		
		Spring (n = 24)	Summer (n = 9)	Fall (n = 6)	Spring (n = 62)	Summer (n = 42)	Fall (n = 39)
Moisture	Percent	48.99 A	27.19 A	23.72 A	60.63 B	41.847 A	32.66 A
Nitrogen	Percent	2.07 A	1.47 A	1.53 A	2.33 B	1.46 A	1.47 A
Phosphorus	Percent	0.23 B	0.15 AB	0.08 A	0.21 C	0.15 B	0.08 A
Potassium	Percent	2.03 B	1.28 AB	0.88 A	2.22 C	1.40 B	1.06 A
Zinc	ppm	27.04 A	21.16 A	20.25 A	21.16 B	19.36 B	12.96 A
Iron	ppm	728.82 A	1,721.26 B	1,631.27 AB	234.07 A	327.57 AB	475.16 B
Manganese	ppm	72.25 A	67.24 A	60.84 A	40.96 A	32.49 A	46.24 A
Copper	ppm	7.74 A	9.61 A	7.84 A	7.29 A	6.76 A	5.76 A
Calcium	Percent	2.32 A	3.50 A	2.55 A	1.24 A	1.34 A	1.61 A
Magnesium	Percent	0.39 A	0.49 A	0.40 A	0.38 AB	0.33 A	0.45 B
Sulfur	Percent	0.42 A	0.42 A	0.27 A	0.43 A	0.42 A	0.34 A
Sodium	Percent	0.009 A	0.010 A	0.047 A	0.016 A	0.017 A	0.017 A
ADF ¹	Percent	33.37 A	33.24 A	43.66 A	31.37 A	39.98 B	41.70 B
TNC ²	Percent	10.82 A	7.11 A	8.96 A	9.74 B	7.34 AB	6.49 A
		(n = 22)	(n = 9)	(n = 6)	(n = 54)	(n = 37)	(n = 31)
Fat	Percent	9.88 A	6.79 A	5.49 A	8.82 B	8.14 AB	6.95 A
		Shrubs			Succulents		
		Spring (n = 72)	Summer (n = 56)	Fall (n = 51)	Spring (n = 31)	Summer (n = 16)	Fall (n = 18)
Moisture	Percent	52.02 B	40.13 A	39.37 A	73.87 A	69.87 A	74.69 A
Nitrogen	Percent	2.39 B	1.71 A	1.66 A	1.44 B	0.83 A	0.85 A
Phosphorus	Percent	0.18 B	0.12 A	0.10 A	0.15 B	0.08 A	0.07 A
Potassium	Percent	2.14 B	1.78 AB	1.54 A	2.54 B	1.77 A	1.70 A
Zinc	ppm	20.25 C	15.21 B	12.25 A	28.09 B	14.44 A	10.89 A
Iron	ppm	190.43 A	275.53 B	190.43 A	123.20 A	143.99 AB	207.35 B
Manganese	ppm	42.25 A	33.64 A	32.49 A	121.00 A	84.64 A	84.64 A
Copper	ppm	6.25 A	6.25 A	4.84 A	5.29 A	5.29 A	5.76 A
Calcium	Percent	1.47 A	1.70 A	1.67 A	3.34 A	4.24 AB	5.14 B
Magnesium	Percent	0.45 A	0.51 A	0.43 A	1.07 A	1.29 A	1.39 A
Sulfur	Percent	0.44 A	0.44 A	0.44 A	0.36 A	0.36 A	0.36 A
Sodium	Percent	0.011 A	0.015 A	0.014 A	0.005 A	0.006 A	0.005 A
ADF ¹	Percent	28.59 A	33.81 B	32.99 B	23.84 A	23.49 A	24.32 A
TNC ²	Percent	8.65 A	7.17 A	8.44 A	9.24 A	4.72 A	5.34 A
		(n = 64)	(n = 52)	(n = 44)	(n = 19)	(n = 13)	(n = 13)
Fat	Percent	8.99 A	8.08 A	8.38 A	7.89 A	6.90 A	8.06 A

¹Acid detergent fiber.

²Total nonstructural carbohydrates.

Table 6—Perennial grass species: nutrient and mineral values with significant differences for study areas. Different letters in the same row indicate a significant difference in mean value

Nutrient	Units	Perennial grass species				
		<i>Aristida purpurea</i> (n = 28)	<i>Eriogonum pilosum</i> (n = 29)	<i>Hilaria rigida</i> (n = 29)	<i>Muhlenbergia porteri</i> (n = 22)	<i>Stipa hymenoides</i> (n = 22)
Moisture ¹	Percent	24.24 AB	17.55 A	35.76 B	33.91 B	31.06 AB
Nitrogen	Percent	1.12 A	1.25 A	1.18 A	1.23 A	1.25 A
Phosphorus	Percent	0.08 A	0.07 A	0.08 A	0.10 A	0.10 A
Potassium	Percent	0.41 A	0.49 A	0.97 B	0.87 B	1.19 B
Zinc	ppm	13.42 A	15.38 A	10.63 A	13.36 A	10.66 A
Iron	ppm	305.65 B	1,194.52 C	274.34 AB	140.23 A	177.44 AB
Manganese	ppm	32.35 AB	53.53 C	40.16 B	27.55 A	35.04 AB
Copper	ppm	5.81 A	5.93 A	5.26 A	6.12 A	5.47 A
Calcium	Percent	0.35 A	0.76 C	0.50 B	0.43 AB	0.54 B
Magnesium	Percent	0.12 A	0.20 C	0.15 B	0.13 AB	0.13 AB
Sulfur	Percent	0.18 A	0.25 AB	0.26 AB	0.28 AB	0.34 B
Sodium	Percent	0.004 AB	0.006 B	0.008 C	0.004 AB	0.003 A
ADF ²	Percent	46.08 C	46.73 C	42.58 AB	45.65 BC	41.31 A
TNC ³	Percent	6.37 A	6.49 A	6.11 A	6.56 A	6.44 A
		(n = 26)	(n = 24)	(n = 28)	(n = 22)	(n = 21)
Fat	Percent	6.36 A	6.18 A	6.65 A	6.22 A	7.55 A

		Study area ⁴			
		Units	City Creek	Woodbury-Hardy	Littlefield
Zinc	Percent				
<i>Muhlenbergia porteri</i>			11 A	9 A	20 B
Iron	ppm				
<i>Stipa hymenoides</i>			117 A	256 B	158 AB
Manganese	ppm				
<i>Muhlenbergia porteri</i>			21 A	41 B	20 A
Calcium	Percent				
<i>Stipa hymenoides</i>			0.44 A	0.51 A	0.85 B
Magnesium	Percent				
<i>Eriogonum pilosum</i>			0.15 A	0.28 B	0.20 AB
<i>Stipa hymenoides</i>			0.09 A	0.14 AB	0.20 B
Sulfur	Percent				
<i>Stipa hymenoides</i>			0.26 A	0.32 A	0.64 B

¹Based on fresh weight; all other values are dry weight.

²Acid detergent fiber.

³Total nonstructural carbohydrates.

⁴This portion of the table illustrates the 7 significant differences among sites out of 75 comparisons made.

calcium, magnesium, sodium, and ADF. *Hilaria rigida* is high in moisture content, potassium, manganese, calcium, magnesium, and sodium. *Muhlenbergia porteri* is low in iron and manganese and high in moisture content, potassium, and ADF. *Stipa hymenoides* is low in sodium and ADF and high in potassium, calcium, and sulfur.

Cured plants were significantly different than green plants for all measured parameters except manganese and sodium (table 7). With the exception of iron and ADF the mean values were less for cured than for green plants. Cured plants differed by study area only in manganese, calcium, and magnesium with Littlefield

being high in calcium, manganese, and magnesium; Woodbury-Hardy was low in manganese (table 8). Green plants showed more significant differences among the areas (table 8). Moisture content was low at City Creek, potassium and zinc were low at City Creek and high at Littlefield, iron was high at Littlefield, and calcium, magnesium, and sulfur were low at City Creek. When only annuals were considered, all parameters except iron, manganese, sodium, TNC, and fat were significantly different (table 9). Green and cured plants in the common annual grass, *Bromus rubens*, differed in respect to nitrogen, phosphorus, potassium, zinc, magnesium, sulfur, and ADF (table 10).

Table 7—Green versus cured samples: nutrient and mineral values for all plant collections

Nutrient	Units	Green (n = 481 ¹)	Cured (n = 121 ¹)	Significance
Moisture	Percent	53.90	6.00	<0.0001
Nitrogen	Percent	1.80	1.01	<0.0001
Phosphorus	Percent	0.14	0.05	<0.0001
Potassium	Percent	1.70	0.66	<0.0001
Zinc	ppm	18.31	11.46	<0.0001
Iron	ppm	257.68	622.52	<0.0001
Manganese	ppm	45.82	46.44	0.8723
Copper	ppm	6.39	5.59	0.0095
Calcium	Percent	1.52	0.98	<0.0001
Magnesium	Percent	0.44	0.24	<0.0001
Sulfur	Percent	0.38	0.23	<0.0001
Sodium	Percent	0.015	0.008	0.0523
ADF ²	Percent	33.00	44.20	<0.0001
TNC ³	Percent	8.07	6.35	0.0075
Fat	Percent	8.11	6.75	0.0003

¹Except moisture and sulfur, for which green and cured were 482 and 121, respectively; ADF and TNC (479 and 121); and fat (419 and 103).

²Acid detergent fiber.

³Total nonstructural carbohydrates.

Table 8—Green versus cured samples: nutrient and mineral values for each study area. Different letters in the same row within a treatment group (green or cured) indicate a significant difference

Nutrient	Units	Green			Cured			Differences between green and cured ¹
		City Creek (n = 142)	Woodbury- Hardy (n = 137)	Littlefield (n = 202)	City Creek (n = 40)	Woodbury- Hardy (n = 47)	Littlefield (n = 34)	
Moisture	Percent	50.36 A	55.85 B	55.95 B	4.98 A	7.48 A	5.24 A	*
Nitrogen	Percent	1.73 A	1.73 A	1.84 A	1.02 A	0.96 A	1.12 A	*
Phosphorus	Percent	0.16 A	0.14 A	0.14 A	0.06 A	0.04 A	0.06 A	*
Potassium	Percent	1.50 A	1.73 AB	1.86 B	0.64 A	0.52 A	0.81 A	*
Zinc	ppm	16.33 A	18.66 AB	19.52 B	11.24 A	10.33 A	13.39 A	*
Iron	ppm	224.87 A	213.51 A	315.84 B	545.84 A	575.98 A	791.38 A	*
Manganese	ppm	49.76 A	39.56 A	47.54 A	44.78 AB	39.48 A	59.19 B	NS
Copper	ppm	6.20 A	5.94 A	6.85 A	5.32 A	5.38 A	6.23 A	*
Calcium	Percent	1.27 A	1.66 B	1.65 B	0.84 A	0.84 A	1.36 B	*
Magnesium	Percent	0.35 A	0.46 B	0.49 B	0.18 A	0.23 AB	0.28 B	*
Sulfur	Percent	0.31 A	0.41 B	0.43 B	0.22 A	0.23 A	0.23 A	*
Sodium	Percent	0.010 A	0.009 A	0.012 A	0.007 A	0.009 A	0.009 A	NS
ADF ²	Percent	34.23 A	32.35 A	33.10 A	45.67 A	45.57 A	43.08 A	*
TNC ³	Percent	7.69 A	7.96 A	8.45 A	7.01 A	6.31 A	5.98 A	*
Fat	Percent	7.64 A	7.64 A	8.73 A	6.31 A	6.31 A	7.48 A	*

¹* = $P < 0.05$, NS = not significant.

²Acid detergent fiber.

³Total nonstructural carbohydrates.

Table 9—Green versus cured samples: nutrient and mineral values for all annual plants

Nutrient	Units	Green (n = 45)	Cured (n = 31)	Significance
Moisture	Percent	62.24	1.10	<0.0001
Nitrogen	Percent	2.35	1.00	<0.0001
Phosphorus	Percent	0.24	0.08	<0.0001
Potassium	Percent	2.12	0.64	<0.0001
Zinc	ppm	25.64	14.23	<0.0001
Iron	ppm	775.39	809.21	0.843
Manganese	ppm	64.25	53.81	0.143
Copper	ppm	8.44	6.99	0.032
Calcium	Percent	1.78	1.16	0.029
Magnesium	Percent	0.37	0.18	<0.0001
Sulfur	Percent	0.46	0.18	<0.0001
Sodium	Percent	0.008	0.008	0.479
ADF ¹	Percent	32.07	42.59	<0.0001
TNC ²	Percent	10.38	8.23	0.167
Fat	Percent	8.90	6.81	0.057

¹Acid detergent fiber.²Total nonstructural carbohydrates.**Table 10**—*Bromus rubens*: nutrient and mineral values for green versus cured samples

Nutrient	Units	Green (n = 12)	Cured (n = 15)	Significance
Moisture	Percent	59.70	24.14	<0.0001
Nitrogen	Percent	2.63	1.00	<0.0001
Phosphorus	Percent	0.26	0.06	<0.0001
Potassium	Percent	2.35	0.69	<0.0001
Zinc	ppm	24.69	13.72	0.001
Iron	ppm	365.67	646.41	0.085
Manganese	ppm	47.95	47.64	0.974
Copper	ppm	8.68	6.42	0.065
Calcium	Percent	0.74	0.64	0.406
Magnesium	Percent	0.26	0.15	0.025
Sulfur	Percent	0.49	0.16	0.014
Sodium	Percent	0.010	0.010	0.941
ADF ¹	Percent	31.88	42.98	<0.0001
TNC ²	Percent	10.38	6.17	0.201
Fat	Percent	9.13	6.66	0.057

¹Acid detergent fiber.²Total nonstructural carbohydrates.

Figure 2 illustrates the correlation many of the measured parameters had with one another. The most tightly correlated parameters included potassium (13 significant correlations out of 14 possible), nitrogen and ADF (11 each), zinc and manganese (9 each), and phosphorus, copper, and fat (8 each). The least tightly correlated parameters included moisture content (2), TNC (3), and calcium and sodium (5 each). The average number of significant correlations for each parameter was 7.53.

Analysis of soil characteristics detected no significant differences between upper and lower collection sites at the three study areas. When the different study areas were compared (table 11), significant differences among the areas were pH (lower at City Creek), sodium (higher at City Creek, lower at Woodbury-Hardy), SAR (higher at City Creek), and nitrogen (lower at Littlefield). The SAR was very low at all study areas and therefore would not affect pH values to any great extent; ordinarily, it would be inconsistent to have the

	H ₂ O	N	P	K	Zn	Fe	Mn	Cu	Ca	Mg	S	Na	ADF	TNC	Fat
Moisture content		*		*											
Nitrogen			*	*	*	*	*	*			*	*	*		*
Phosphorus				*	*		*	*			*		*		*
Potassium					*	*	*	*	*	*	*	*	*		*
Zinc							*	*		*	*		*		*
Iron							*	*	*				*		*
Manganese								*	*	*			*		
Copper										*				*	
Calcium										*			*		
Magnesium												*	*		
Sulfur													*	*	*
Sodium													*		*
ADF (acid detergent fiber)														*	*
TNC (total nonstructural carbohydrates)															
Fat (ether extract fraction)															

Figure 2—Significant correlations ($P < 0.05$) among minerals and nutrients in plant samples ($n = 602$ except for comparisons with fat where $n = 522$). *Indicates significant correlations.

highest SAR and lowest pH on the same sites in comparisons like ours. Table 12 compares the soil and plant values for elements in the soil and plants at the three study areas.

DISCUSSION

Study areas, weather and water, and plant mineral and nutrient content are all important when considering the data collected. Each of these topics is discussed separately.

Study Areas

Plants of the same species growing on the different areas generally had similar values for City Creek and Woodbury-Hardy; plants at Littlefield often had slightly higher values. In 12 of the 14 cases in which one area had significantly higher values than another, Littlefield had the higher value (table 2). In the other two cases Littlefield shared the significantly higher values with another area: City Creek in the case of phosphorus, and magnesium in the case of

Table 11—Mean values of soil parameters for each study area. Different letters in the same row indicate a significant difference in mean value

Soil parameter	Units	City Creek		Woodbury-Hardy		Littlefield	
Calcium	ppm	121.9	A	132.2	A	150.7	A
Magnesium	ppm	19.3	A	14.2	A	17.2	A
Sodium	ppm	4.64	C	2.24	A	3.31	B
Nitrogen	ppm	453.0	B	475.0	B	183.0	A
Phosphorus	ppm	11.1	A	10.9	A	4.7	A
Potassium	ppm	104.5	A	129.6	A	102.9	A
Zinc	ppm	0.527	A	0.520	A	0.333	A
Copper	ppm	0.663	A	0.500	A	0.453	A
pH		6.8	A	7.5	B	7.5	B
EC ¹	ds/L	0.695	A	0.465	A	0.523	A
SAR ²		0.112	B	0.052	A	0.073	A
Sand	Percent	76.9	A	65.7	A	78.2	A
Silt	Percent	11.8	A	24.7	A	14.1	A
Clay	Percent	11.3	A	9.6	A	7.6	A

¹Electroconductivity.

²Sodium adsorption ratio.

Table 12—Comparison of plant and soil values for various parameters for each study area

Soil parameter	Units	City Creek		Woodbury-Hardy		Littlefield	
		Soil	Plant	Soil	Plant	Soil	Plant
Calcium	ppm	122	11,800	132	14,300	151	15,500
Magnesium	ppm	19	3,100	14	4,000	17	4,900
Sodium	ppm	4.6	100	2.2	100	3.3	120
Nitrogen	ppm	453	15,500	475	14,800	183	17,300
Phosphorus	ppm	11.1	1,300	10.9	1,000	4.7	1,300
Potassium	ppm	104	12,900	130	13,600	103	17,300
Zinc	ppm	0.527	15	0.520	16	0.333	18
Copper	ppm	0.663	6	0.500	6	0.453	7
pH		6.8	—	7.5	—	7.5	—
EC ¹	ds/L	0.695	—	0.465	—	0.523	—
SAR ²		0.112	—	0.052	—	0.073	—

¹Electroconductivity.²Sodium adsorption ratio.

Woodbury-Hardy. The slightly elevated values for Littlefield may relate to slightly better weather conditions (see next section) during the period of study. Soil mineral content is not higher at Littlefield (table 12). In fact, soil characteristics measured in our study are quite similar among the areas; when City Creek is compared to the other areas, it is high in sodium and SAR but low in pH; City Creek and Woodbury-Hardy are high in nitrogen. Our 3-year study could not support the hypothesis that nutrient and mineral content were more favorable for the apparently healthier desert tortoise subpopulation at City Creek.

Weather and Water

The higher nutrient and mineral values for Littlefield may well be associated with a higher moisture content (table 2). Moisture input at our study sites is sporadic, in common with the Mojave environment in general (McArthur and Sanderson 1992a). No data are available to document that the Littlefield area received more moisture than the others; however, more sampling was associated with arroyos there and at Woodbury-Hardy than at City Creek. Sporadic storms could have favored Littlefield over the other areas. Both Woodbury-Hardy and Littlefield are on the Beaver Dam Slope. Figure 3 shows that, during the study period, the Lytle Ranch climatic station on Beaver Dam Wash had a more favorable moisture regime than did the St. George climatic station near City Creek.

Plants with higher moisture content were also higher in nutritive quality and mineral content on a dry-weight basis when all plants were considered (table 7), when annuals were considered (table 9), and when just *Bromus rubens* was considered (table 10). Quality

Figure 3—Average values of precipitation and maximum daily temperature for St. George and the seasonal average values for those parameters for St. George and Lytle Ranch during the study period. Number 1 = October-March 1988-89, 2 = April-September 1989, 3 = October-March 1989-90, 4 = April-September 1990, 5 = October-March 1990-91, 6 = April-September 1991. Data for Lytle Ranch were not collected for period 1.

differences of plants among the study areas were more pronounced when only green plants were considered (table 8). Our data confirm that moisture content is important to plant nutrient and mineral content (Black 1968).

Moisture content was highest in the spring for all plant life forms except succulents (table 5), significantly so for annual and perennial grasses, perennial forbs, and shrubs. On an individual species basis, spring moisture content was significantly higher for 10 of the 20 species of appendix B (omitting from consideration the special flower, fruit, and leaf collections). For individual species and for plant life forms, spring was also the season of highest content for several other nutrients and minerals. For the plant life forms shrubs and succulents, nitrogen, phosphorus, potassium, and zinc were all highest and ADF was lowest in spring (table 5). For individual species (appendix B), spring values were significantly higher than at least one of the other seasons for potassium (10 of 20 species, excluding the special parts collections), nitrogen and phosphorus (9 species), zinc (5 species), sodium (2 species), and manganese, sulfur, and TNC (1 species).

In general, values for all measured parameters decrease from a spring high through summer and fall (increasing ADF represents declining quality). There are, however, exceptions for individual species (appendix B). For *Bromus rubens*, new plants in the fall cause moisture content to rebound. For *Krameria parvifolia*, calcium, magnesium, and sodium are high in the fall. Desert tortoise activity is controlled by moisture and heat so these animals are generally active in foraging and drinking in the spring and fall when food and habitat conditions are best for them (Nagy and Medica 1986; Woodbury and Hardy 1948). They seek shelter underground and become inactive during winter cold and summer heat and drought.

Plant Mineral and Nutrient Parameters

Our discussion is limited to the growing season when desert tortoises may be feeding on the plants we studied. We recognize that these plants have other ecosystem values, such as providing food and habitat for other animals. For discussion of winter values of various plant classes and some individual species, please see Tueller (1979) and Welch (1989) and the references they cite. The values obtained in this study seem to be within the normal range for plants growing in semiarid sites (Krausman and others 1990; Seegmiller and others 1990). As figure 2 illustrates, the elements sampled often covary. Potassium, for example, is significantly correlated with the content of all 10 other elements, manganese with all but sodium and sulfur, nitrogen with all but calcium and magnesium, and copper with all but calcium, sodium, and sulfur.

The very low sodium values for both the soils and plants of our study deserve comment. The soil values for sodium are for water soluble sodium only; even so, the values are low. The sandy nature of our study sites (table 11) no doubt contributed to these low values. The plant sodium values are low but not unprecedented for semiarid sites (Jones and Hanson 1985; Kincaid 1988).

The various mineral and nutrient values were often significantly different among plant classes (table 4). During the sampling seasons of our study it would seem that forage from a mixture of plant life forms would be desirable for foraging animals. Water content is highest in succulents (cacti), also high in perennial and annual forbs and shrubs, and low in annual and perennial grasses. Grasses dry out through the summer and fall. Annual forbs tend to disappear after the spring season unless new cohorts are stimulated by precipitation. Nitrogen (protein) is higher in shrubs, annual and perennial forbs, and annual grasses than it is in perennial grasses and succulents. Phosphorus, zinc, and iron are highest in annual forbs; values are high in perennial forbs as well and in shrubs (phosphorus), succulents (zinc), and annual grasses (iron). Potassium is highest in succulents; values are also high in perennial forbs and shrubs. Manganese and calcium are highest in succulents and annual forbs. Copper is highest in annual forbs and annual grasses. Magnesium is highest in succulents and shrubs. Sulfur is highest in shrubs but is also high in perennial and annual forbs. Sodium is highest in perennial forbs. The ADF is lowest in succulents and highest in perennial grasses. Fat is highest in shrubs and perennial forbs.

Some plants in our study deserve special comment. The introduced annuals, *Bromus rubens*, *Schismus barbatus*, and *Erodium cicutarium*, are by far the most common and readily available herbaceous plants in the study areas (Baird 1990; Esque and others 1991; McArthur and Sanderson 1992a). These plants are also common desert tortoise foods in the study areas under present conditions (Esque and others 1991; Woodbury and Hardy 1948). *Schismus barbatus* is exceptionally high in TNC (13.64 percent) and *E. cicutarium* is high in nitrogen (2.03 percent N = 12.69 percent protein), potassium (1.76 percent), and TNC (8.96 percent) (appendix B). Other species with notably high values for mineral and nutrient parameters include *Plantago patagonica* (calcium and TNC), *Baileya multiradiata* (calcium), *Eriogonum inflatum* (potassium), *Atriplex canescens* (nitrogen, potassium, calcium, and low ADF), *Ceratoides lanata* (nitrogen and potassium), *Hymenoclea salsola* (nitrogen, fat and low ADF), *Eriogonum fasciculatum* and *Krameria parvifolia* (TNC), and *Opuntia basilaris* and *O. erinacea* (water content, potassium, and calcium) (appendix B).

Table 13—The species with the highest and lowest mean values for 13 minerals and nutrients (from appendix B)

Nutrient	High value		Low value		Exceptional value (high or low) from special plant parts	
	Percent		Percent		Percent	
Moisture	74.18	(<i>Opuntia erinacea</i>)	17.55	(<i>Erioneuron pilosum</i>)	—	
Nitrogen	2.63	(<i>Atriplex canescens</i>)	1.12	(<i>Aristida purpurea</i>)	2.93	(<i>Eriogonum inflatum</i> , leaves)
Protein	16.44	(<i>Atriplex canescens</i>)	7.12	(<i>Aristida purpurea</i>)	18.31	(<i>Eriogonum inflatum</i> , leaves)
Phosphorus	0.20	(<i>Erodium cicutarium</i>)	0.07	(<i>Erioneuron pilosum</i>)	0.30	(<i>Sphaeralcea ambigua</i> , flowers)
Potassium	4.19	(<i>Atriplex canescens</i>)	0.42	(<i>Aristida purpurea</i>)		
Zinc	23.28	(<i>Erodium cicutarium</i>)	9.91	(<i>Ephedra nevadensis</i>)	25.32	(<i>Sphaeralcea ambigua</i> , flowers)
Iron	1,561.62	(<i>Plantago patagonica</i>)	116.02	(<i>Ephedra nevadensis</i>)	98.08	(<i>Opuntia erinacea</i> , fruits)
Manganese	95.46	(<i>Opuntia basilaris</i>)	19.02	(<i>Eriogonum fasciculatum</i>)	133.44	(<i>Opuntia erinacea</i> , fruits)
Sulfur	0.98	(<i>Atriplex canescens</i>)	0.17	(<i>Eriogonum fasciculatum</i>)	—	
Sodium	0.043	(<i>Krameria parvifolia</i>)	0.003	(<i>Hymenoclea salsola</i> and <i>Stipa hymenoides</i>)	—	
ADF ¹	46.73	(<i>Erioneuron pilosum</i> and <i>Plantago patagonica</i>)	17.87	(<i>Atriplex canescens</i>)	—	
TNC ²	15.26	(<i>Eriogonum fasciculatum</i>)	5.11	(<i>Ceratoides lanata</i>)	—	
Fat	18.23	(<i>Hymenoclea salsola</i>)	5.24	(<i>Plantago patagonica</i>)	—	

¹Acid detergent fiber.²Total nonstructural carbohydrates.

Table 13 shows the species with the highest and lowest mean values for 13 minerals and nutrients.

Fat and protein (total organic nitrogen) had a significant ($P < 0.05$) positive correlation; protein and ADF, and TNC and ADF were negatively correlated. There were no significant correlations between protein and TNC or fat and ADF (fig. 2; appendix B).

For four species we sampled different plant parts (appendix B). The regular samples for *Eriogonum inflatum* consisted of leaves and small twigs; separate collections were made for flowers and flowering stems, for large flowering stalks, and for small inflorescences and flowers. Leaves and twigs were higher in many measured parameters than the large flowering stalks. Those parameters include moisture content, nitrogen, phosphorus, potassium, iron, manganese, calcium, magnesium, and TNC; ADF was lower. Flowers and flowering stems were lower than the large flowering stalks in potassium, calcium, and (especially during the spring) sodium.

We sampled *Sphaeralcea ambigua* flowers and flowering stems, as well as leaves and twigs. Flowers and flowering stems were higher in nitrogen, phosphorus, potassium, zinc, iron, copper, and calcium than were leaves and twigs. We sampled flowers and fruits of *Ceratoides lanata* as well as leaves. The two kinds of samples differed little, but potassium was up slightly for the samples of flowers and fruit; water content, calcium, and TNC were down slightly. We sampled fruits as well as the pads of *Opuntia basilaris*. The fruits were lower than the pads in respect to moisture content, calcium, and magnesium, but were higher in nitrogen, phosphorus, potassium, and fat.

These samples of separate plant parts suggest some differences, usually not dramatic, for the measured

parameters. Our regular samples were of leaves and closely attached stems—the material most likely to be foraged. One spring during the course of our collections we saw a large desert tortoise with its beak stained purple from the *Krameria* flowers it had eaten. Tortoises, like other herbivores, can be selective in eating plant parts. On another occasion, we noted a tortoise in a patch of *Erodium*. This tortoise voraciously consumed several whole *Erodium* plants. Esque and others (1991) have meticulously documented feeding preferences and habits of tortoises at City Creek and Littlefield. They found that tortoises fed mostly (up to 80 percent) on the plentiful ephemerals, *Bromus*, *Erodium*, and *Schismus*, but that they also consumed a wide array of grasses, forbs, and shrubs. Perhaps desert tortoises fare well on exotic plants as does the Townsend's ground squirrel (*Sperophilus townsendii*) in southwestern Idaho (Yensen and Quinney 1992).

Woodbury and Hardy (1948) and Hansen and others (1976) suggested that the desert tortoise's preferred foods were perennial grasses, especially *Muhlenbergia porteri*. Our analyses do not show a nutritional advantage for perennial grasses; rather annual grasses, annual forbs, and shrubs appear better when nitrogen, phosphorus, and TNC are considered (table 4). Succulents have favorable moisture content, potassium, calcium, magnesium, and ADF. Perennial grasses do have the advantage of consistent production. Among the perennial grasses we studied, nutrient and mineral values were quite similar. However, high values for the following parameters are of note: moisture content (*Hilaria rigida* and *Muhlenbergia porteri*), potassium (*Stipa hymenoides*, *Hilaria rigida*, and *Muhlenbergia porteri*), iron (*Erioneuron pilosum* and *Aristida purpurea*), manganese, magnesium, and sodium

(*Erioneuron pilosum* and *Hilaria rigida*), calcium (*Stipa hymenoides* and *Hilaria rigida*), and sulfur (*Stipa hymenoides*) (table 6). Low values of ADF were found in *Stipa hymenoides* and *Hilaria rigida*.

Harper and Pendleton (1993) recently presented data indicating that cryptobiotic crusts enhance the nutrient and mineral status of plants in desert habitats. They suggested that the associated animals, including desert tortoises, may benefit from the cryptobiotic crust nutrient input. We did not examine this aspect but did note that cryptogams are present at our study sites (McArthur and Sanderson 1992a).

Bostick (1990) suggested that desert tortoises evolved as dung eaters, presenting anecdotal evidence that cow excrement was a useful food for tortoises. Our data included only current-year cow excrement ($n = 11$ from 2 years, three seasons, and two Beaver Dam Slope sites). Cow excrement ranked 21st, last, for several important parameters when compared to the 20 species in appendix B. These were for moisture content (14.00 percent, cow excrement dries out quickly), potassium (0.28 percent), TNC (5.15 percent), and fat (3.87 percent). Cow excrement ranked first in ADF (51.48 percent), a negative food quality characteristic. Cow excrement ranked 12th for nitrogen (1.53 percent = 9.56 percent protein), ahead of perennial grasses and cacti, but behind most other species. Cow excrement generally retained or concentrated high levels of minerals: phosphorus (first, 0.23 percent), zinc (first, 30 ppm), iron (first, 3,400 ppm), manganese (first, 150 ppm), copper (first, 10 ppm), calcium (third, 3.37 percent), sodium (third, 0.037 percent), magnesium (fourth, 0.59 percent), and sulfur (fifth, 0.45 percent). On the whole, our data do not demonstrate that cow excrement is a quality food source. We question Bostick's (1990) thesis that desert tortoises evolved as dung eaters. It is, however, beyond question that tortoises ingest a diverse array of items, including insects, soil, bones, feathers, and excrement (Esque and others 1991; Hansen and others 1976).

The data presented here can be compared with other mineral and nutrient data for plants in semiarid environments and can be extrapolated to determine the adequacy of diets of desert tortoises and other herbivores to the extent requirements for those animals are known (Cook and Harris 1950; Dietz and others 1962; Nagy and Medica 1986; National Academy of Sciences 1975, 1977, 1984).

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APPENDIX A: ADDITIONAL PLANTS COLLECTED FOR NUTRIENT AND MINERAL CONTENT SAMPLING AT CITY CREEK AND LITTLEFIELD

Scientific name

Abronia fragrans
Androstephium breviflorum
Aristida purpurea
Atriplex canescens
Baileya multiradiata
Bromus rubens
Ceratoides lanata
Cryptantha micrantha
Ephedra nevadensis
Erodium cicutarium
Eriogonum fasciculata
Eriogonum inflatum
Erioneuron pilosum
Hilaria rigida

Scientific name

Hymenoclea salsola
Muhlenbergia porteri
Oenothera pallida
Opuntia basilaris
Opuntia erinacea
Oryzopsis hymenoides
Plantago patagonica
Rafinesquia neomexicana
Schismus barbatus
Sphaeralcea ambigua
Stephanomeria exigua
Stipa hymenoides
Streptanthella longirostris

APPENDIX B: PROPORTIONAL VALUES OF POTENTIAL DESERT TORTOISE FOOD PLANTS BY SEASON

Significant differences among seasons indicated by different letters on a line. The abbreviations ADF and TNC stand for acid detergent fiber and total nonstructural carbohydrates.

Nutrient	Spring	Summer	Fall	Average
Annual grasses				
<i>Bromus rubens</i>				
	<i>n</i> = 12	<i>n</i> = 6	<i>n</i> = 9	
Moisture	0.39069 B	0.01761 A	0.18841 AB	0.21267
Nitrogen	0.01989 A	0.01299 A	0.01405 A	0.01627
Phosphorus	0.00221 B	0.00097 AB	0.00058 A	0.00129
Potassium	0.01964 A	0.00817 A	0.00905 A	0.01303
Zinc	0.00002 A	0.00002 A	0.00002 A	0.00002
Iron	0.00041 A	0.00042 A	0.00074 A	0.00051
Manganese	0.00005 A	0.00004 A	0.00004 A	0.00005
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.00620 A	0.00567 A	0.00837 A	0.00676
Magnesium	0.00205 A	0.00141 A	0.00206 A	0.00190
Sulfur	0.00314 A	0.00234 A	0.00292 A	0.00288
Sodium	0.00010 A	0.00009 A	0.00008 A	0.00009
ADF	0.34652 A	0.39744 A	0.41324 A	0.37979
TNC	0.11015 A	0.06789 A	0.05166 A	0.07927
<i>Schismus barbatus</i>				
	<i>n</i> = 11	<i>n</i> = 3	<i>n</i> = 8	
Fat	0.09294 A	0.05968 A	0.06764 A	0.07862
<i>Schismus barbatus</i>				
	<i>n</i> = 5	<i>n</i> = 2	<i>n</i> = 3	
Moisture	0.52749 B	0.02627 A	0.00446 A	0.19637
Nitrogen	0.02538 C	0.01356 B	0.00551 A	0.01569
Phosphorus	0.00207 B	0.00044 A	0.00002 A	0.00080
Potassium	0.01852 C	0.00767 B	0.00115 A	0.00919
Zinc	0.00002 B	0.00001 A	0.00001 A	0.00001
Iron	0.00056 A	0.00070 A	0.00089 A	0.00068
Manganese	0.00008 B	0.00005 AB	0.00004 A	0.00006
Copper	0.00001 B	0.00001 C	0.00000 A	0.00001
Calcium	0.00736 A	0.00584 A	0.00663 A	0.00682
Magnesium	0.00229 A	0.00164 A	0.00132 A	0.00185
Sulfur	0.00358 B	0.00182 AB	0.00116 A	0.00237
Sodium	0.00006 A	0.00017 B	0.00005 A	0.00007
ADF	0.31333 A	0.39470 AB	0.45576 B	0.37127
TNC	0.15114 A	0.11059 A	0.13050 A	0.13641
Fat	0.09552 A	0.07223 A	0.05669 A	0.07616
Perennial grasses				
<i>Aristida purpurea</i>				
	<i>n</i> = 10	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.27857 A	0.25130 A	0.19614 A	0.24242
Nitrogen	0.01467 B	0.01009 A	0.00896 A	0.01124
Phosphorus	0.00125 B	0.00082 AB	0.00045 A	0.00080
Potassium	0.00572 B	0.00378 AB	0.00299 A	0.00414
Zinc	0.00002 A	0.00001 A	0.00001 A	0.00001
Iron	0.00024 A	0.00029 A	0.00040 A	0.00031
Manganese	0.00003 A	0.00003 A	0.00004 A	0.00003
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.00299 A	0.00354 A	0.00398 A	0.00347
Magnesium	0.00102 A	0.00098 A	0.00100 A	0.00116

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
Perennial grasses				
<i>Aristida purpurea</i>				
	<i>n</i> = 10	<i>n</i> = 9	<i>n</i> = 9	
Sulfur	0.00173 A	0.00166 A	0.00219 A	0.00185
Sodium	0.00006 B	0.00004 A	0.00003 A	0.00004
ADF	0.43697 A	0.47651 A	0.47162 A	0.46084
TNC	0.07264 A	0.06002 A	0.05790 A	0.06368
	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 8	
Fat	0.08626 A	0.05997 A	0.04560 A	0.06363
<i>Erioneuron pilosum</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.24905 A	0.11971 A	0.15244 A	0.17553
Nitrogen	0.01365 A	0.01084 A	0.01280 A	0.01249
Phosphorus	0.00077 A	0.00080 A	0.00063 A	0.00073
Potassium	0.00628 A	0.00362 A	0.00477 A	0.00492
Zinc	0.00002 A	0.00002 A	0.00002 A	0.00002
Iron	0.00107 A	0.00134 A	0.00121 A	0.00120
Manganese	0.00005 A	0.00005 A	0.00006 A	0.00005
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.00701 A	0.00762 A	0.00837 A	0.00347
Magnesium	0.00187 A	0.00200 A	0.00229 A	0.00203
Sulfur	0.00212 A	0.00277 A	0.00279 A	0.00252
Sodium	0.00006 A	0.00007 A	0.00005 A	0.00006
ADF	0.45536 A	0.48650 A	0.46294 A	0.46733
TNC	0.07611 A	0.06049 A	0.05659 A	0.06495
	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 6	
Fat	0.07348 A	0.06063 A	0.04762 A	0.06183
<i>Hilaria rigida</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 11	
Moisture	0.46304 B	0.31938 AB	0.27338 A	0.35760
Nitrogen	0.01542 B	0.00905 A	0.01059 AB	0.01179
Phosphorus	0.00111 A	0.00083 A	0.00045 A	0.00080
Potassium	0.01249 A	0.00885 A	0.00736 A	0.00965
Zinc	0.00002 B	0.00001 AB	0.00001 A	0.00001
Iron	0.00024 A	0.00033 A	0.00026 A	0.00028
Manganese	0.00004 A	0.00003 A	0.00004 A	0.00004
Copper	0.00001 A	0.00001 A	0.00000 A	0.00001
Calcium	0.00528 A	0.00459 A	0.00512 A	0.00500
Magnesium	0.00156 A	0.00133 A	0.00173 A	0.00154
Sulfur	0.00260 A	0.00255 A	0.00265 A	0.00260
Sodium	0.00011 A	0.00008 AB	0.00006 A	0.00008
ADF	0.39704 A	0.44452 B	0.44243 B	0.42578
TNC	0.07063 A	0.05278 A	0.05888 A	0.06106
	<i>n</i> = 10	<i>n</i> = 9	<i>n</i> = 9	
Fat	0.07547 A	0.06319 A	0.06044 A	0.06654
<i>Muhlenbergia porteri</i>				
	<i>n</i> = 10	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.46174 B	0.29384 AB	0.25626 A	0.33912
Nitrogen	0.01462 A	0.01149 A	0.01153 A	0.01231
Phosphorus	0.00122 A	0.00092 A	0.00074 A	0.00096
Potassium	0.01294 B	0.00639 A	0.00714 A	0.00874
Zinc	0.00002 A	0.00001 A	0.00001 A	0.00001

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
Perennial grasses				
<i>Muhlenbergia porteri</i>				
	<i>n</i> = 10	<i>n</i> = 9	<i>n</i> = 9	
Iron	0.00011 A	0.00018 A	0.00014 A	0.00014
Manganese	0.00003 A	0.00002 A	0.00003 A	0.00003
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.00401 AB	0.00370 A	0.00539 B	0.00432
Magnesium	0.00122 A	0.00118 A	0.00150 A	0.00130
Sulfur	0.00220 A	0.00276 A	0.00367 A	0.00283
Sodium	0.00004 A	0.00005 A	0.00003 A	0.00004
ADF	0.45148 A	0.47851 A	0.44015 A	0.45646
TNC	0.06880 A	0.06251 A	0.06535 A	0.06564
	<i>n</i> = 8	<i>n</i> = 9	<i>n</i> = 7	
Fat	0.06436 A	0.06145 A	0.06054 A	0.06217
<i>Stipa hymenoides</i>				
	<i>n</i> = 8	<i>n</i> = 7	<i>n</i> = 7	
Moisture	0.38962 A	0.31640 A	0.22116 A	0.31046
Nitrogen	0.01640 A	0.00969 A	0.01141 A	0.01251
Phosphorus	0.00138 A	0.00088 A	0.00061 A	0.00095
Potassium	0.01637 A	0.01074 A	0.00872 A	0.01192
Zinc	0.00002 A	0.00001 A	0.00001 A	0.00001
Iron	0.00014 A	0.00018 A	0.00023 A	0.00018
Manganese	0.00004 A	0.00003 A	0.00003 A	0.00003
Copper	0.00001 A	0.00000 A	0.00000 A	0.00001
Calcium	0.00539 A	0.00475 A	0.00593 A	0.00535
Magnesium	0.00158 A	0.00117 A	0.00108 A	0.00128
Sulfur	0.00336 A	0.00355 A	0.00329 A	0.00341
Sodium	0.00003 A	0.00003 A	0.00002 A	0.00003
ADF	0.37562 A	0.43360 A	0.43618 A	0.41314
TNC	0.08128 A	0.05056 A	0.06078 A	0.06441
	<i>n</i> = 8	<i>n</i> = 7	<i>n</i> = 6	
Fat	0.07706 A	0.08177 A	0.06664 A	0.07552
Annual forbs				
<i>Erodium cicutarium</i>				
	<i>n</i> = 13	<i>n</i> = 8	<i>n</i> = 4	
Moisture	0.58371 A	0.33477 A	0.45267 A	0.48231
Nitrogen	0.02269 A	0.01559 A	0.02296 A	0.02031
Phosphorus	0.00237 A	0.00170 A	0.00143 A	0.00199
Potassium	0.02062 A	0.01402 A	0.01520 A	0.01751
Zinc	0.00002 A	0.00002 A	0.00003 A	0.00002
Iron	0.00094 A	0.00159 A	0.00154 A	0.00122
Manganese	0.00007 A	0.00007 A	0.00007 A	0.00007
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.02666 A	0.03705 A	0.03290 A	0.03080
Magnesium	0.00432 A	0.00518 A	0.00526 A	0.00474
Sulfur	0.00450 A	0.00396 A	0.00358 A	0.00417
Sodium	0.00008 AB	0.00009 B	0.00005 A	0.00008
ADF	0.28830 A	0.31417 A	0.39998 A	0.31389
TNC	0.10476 A	0.06799 A	0.08795 A	0.08960
	<i>n</i> = 12	<i>n</i> = 8	<i>n</i> = 4	
Fat	0.07916 A	0.07068 A	0.05467 A	0.07197

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
Annual forbs				
<i>Plantago patagonica</i>				
	<i>n</i> = 4	<i>n</i> = 1	<i>n</i> = 2	
Moisture	0.69995 B	0.00000 A	0.00251 A	0.30097
Nitrogen	0.01814 B	0.00850 AB	0.00464 A	0.01201
Phosphorus	0.00211 B	0.00060 AB	0.00013 A	0.32041
Potassium	0.01887 C	0.00500 B	0.00120 A	0.00971
Zinc	0.00002 B	0.00001 A	0.00001 A	0.00001
Iron	0.00105 A	0.00298 A	0.00184 A	0.00149
Manganese	0.00006 A	0.00006 A	0.00005 A	0.00006
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.01686 A	0.02091 A	0.01351 A	0.01640
Magnesium	0.00336 A	0.00310 A	0.00195 A	0.00288
Sulfur	0.00736 A	0.00620 A	0.00132 A	0.00499
Sodium	0.00017 A	0.00017 A	0.00005 A	0.00013
ADF	0.44094 A	0.48630 AB	0.51060 B	0.46723
TNC	0.10797 A	0.09859 A	0.09283 A	0.10220
Fat	0.05211 A	0.04699 A	0.05558 A	0.05233
Perennial forbs				
<i>Baileya multiradiata</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.68555 B	0.46483 AB	0.32246 A	0.50490
Nitrogen	0.01903 A	0.01365 A	0.01251 A	0.01520
Phosphorus	0.00195 B	0.00111 AB	0.00095 A	0.00135
Potassium	0.01895 B	0.01238 AB	0.00857 A	0.01335
Zinc	0.00002 A	0.00002 A	0.00002 A	0.00002
Iron	0.00056 A	0.00063 A	0.00150 B	0.00083
Manganese	0.00003 AB	0.00002 A	0.00004 B	0.00003
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.01898 A	0.01947 A	0.02359 A	0.02051
Magnesium	0.00303 A	0.00249 A	0.00358 A	0.00302
Sulfur	0.00405 A	0.00356 A	0.00329 A	0.00366
Sodium	0.00006 A	0.00006 A	0.00004 A	0.00005
ADF	0.34538 A	0.40980 A	0.42825 A	0.39079
TNC	0.10244 A	0.07410 A	0.05926 A	0.07932
	<i>n</i> = 10	<i>n</i> = 6	<i>n</i> = 6	
Fat	0.12232 A	0.10741 A	0.08565 A	0.10778
Smaller inflorescence branches, leaves, and flowers				
<i>Eriogonum inflatum</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.61185 B	0.44104 B	0.19820 A	0.42420
Nitrogen	0.02473 B	0.01678 A	0.01258 A	0.01814
Phosphorus	0.00216 B	0.00131 B	0.00053 A	0.00130
Potassium	0.01803 B	0.01096 A	0.00779 A	0.01229
Zinc	0.00002 B	0.00002 AB	0.00001 A	0.00002
Iron	0.00010 A	0.00017 AB	0.00021 B	0.00015
Manganese	0.00003 A	0.00005 AB	0.00007 B	0.00005
Copper	0.00001 A	0.00001 A	0.00000 A	0.00001
Calcium	0.00413 A	0.00758 B	0.01314 C	0.00757
Magnesium	0.00292 A	0.00412 B	0.00558 C	0.00405
Sulfur	0.00265 A	0.00348 A	0.00229 A	0.00277
Sodium	0.00015 A	0.00029 B	0.00027 B	0.00022
ADF	0.30428 A	0.38504 B	0.43330 B	0.36856
TNC	0.12735 B	0.09847 AB	0.06644 A	0.09800
	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 7	
Fat	0.07468 A	0.07992 A	0.07043 A	0.07531

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
Main fruiting stalk				
<i>Eriogonum inflatum</i>				
	<i>n</i> = 14	<i>n</i> = 9	<i>n</i> = 8	
Moisture	0.56660 B	0.45865 AB	0.24749 A	0.44989
Nitrogen	0.02266 B	0.01260 A	0.01019 A	0.01604
Phosphorus	0.00155 B	0.00178 B	0.00040 A	0.00124
Potassium	0.02799 B	0.01398 A	0.00991 A	0.01838
Zinc	0.00002 A	0.00002 A	0.00001 A	0.00002
Iron	0.00016 A	0.00012 A	0.00026 A	0.00017
Manganese	0.00005 A	0.00003 A	0.00004 A	0.00004
Copper	0.00001 A	0.00001 A	0.00000 A	0.00001
Calcium	0.01005 A	0.00709 A	0.01164 A	0.00991
Magnesium	0.00520 A	0.00327 A	0.00473 A	0.00448
Sulfur	0.00261 A	0.00254 A	0.00212 A	0.00246
Sodium	0.00050 A	0.00033 A	0.00038 A	0.00041
ADF	0.29402 A	0.44511 B	0.54325 B	0.35626
TNC	0.10599 B	0.07531 B	0.05641 A	0.08739
Fat	0.07473 A	0.07374 A	0.06030 A	0.07058
Leaves				
<i>Eriogonum inflatum</i>				
	<i>n</i> = 1	<i>n</i> = 0	<i>n</i> = 4	
Moisture	0.81002 B	—	0.64096 A	0.67735
Nitrogen	0.03111 A	—	0.02876 A	0.02923
Phosphorus	0.00110 A	—	0.00175 A	0.00161
Potassium	0.04589 B	—	0.02189 A	0.02602
Zinc	0.00001 A	—	0.00002 A	0.00002
Iron	0.00035 A	—	0.00056 A	0.00051
Manganese	0.00008 B	—	0.00005 A	0.00006
Copper	0.00001 A	—	0.00001 A	0.00001
Calcium	0.01920 A	—	0.01426 A	0.01520
Magnesium	0.00750 A	—	0.00473 A	0.00523
Sulfur	0.00510 A	—	0.00323 A	0.00357
Sodium	0.00092 A	—	0.00023 A	0.00033
ADF	0.33326 B	—	0.20957 A	0.23280
TNC	0.09452 A	—	0.14419 B	0.13354
Fat	0.04518 A	—	0.05808 A	0.05540
<i>Sphaeralcea ambigua</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.55161 A	0.47222 A	0.41009 A	0.48291
Nitrogen	0.02368 B	0.01283 A	0.01862 AB	0.01846
Phosphorus	0.00173 A	0.00121 A	0.00109 A	0.00135
Potassium	0.02094 B	0.01663 AB	0.01223 A	0.01670
Zinc	0.00002 A	0.00002 A	0.00001 A	0.00002
Iron	0.00024 A	0.00036 A	0.00027 A	0.00029
Manganese	0.00004 A	0.00004 A	0.00003 A	0.00004
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.01936 A	0.01911 A	0.01738 A	0.01865
Magnesium	0.00383 A	0.00282 A	0.00413 A	0.00358
Sulfur	0.00783 A	0.00563 A	0.00658 A	0.00673
Sodium	0.00007 A	0.00010 A	0.00008 A	0.00008
ADF	0.31018 A	0.38339 A	0.37775 A	0.35348
TNC	0.07862 A	0.06704 A	0.04900 A	0.06525
	<i>n</i> = 10	<i>n</i> = 9	<i>n</i> = 7	
Fat	0.09018 A	0.07685 A	0.07161 A	0.08008

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
Flowers				
<i>Sphaeralcea ambigua</i>				
	<i>n</i> = 11	<i>n</i> = 9		
Moisture	0.67595 B	0.14321 A	—	0.45785
Nitrogen	0.02963 B	0.01947 A	—	0.02548
Phosphorus	0.00385 B	0.00201 A	—	0.00308
Potassium	0.02335 B	0.01801 A	—	0.02122
Zinc	0.00003 B	0.00002 A	—	0.00003
Iron	0.00014 A	0.00070 B	—	0.00031
Manganese	0.00003 A	0.00003 A	—	0.00003
Copper	0.00001 A	0.00001 A	—	0.00001
Calcium	0.01192 A	0.01772 B	—	0.01402
Magnesium	0.00297 A	0.00322 A	—	0.00307
Sulfur	0.00656 A	0.00663 A	—	0.00660
Sodium	0.00008 A	0.00020 B	—	0.00012
ADF	0.31705 A	0.37591 A	—	0.33940
TNC	0.07079 A	0.05734 A	—	0.06545
	<i>n</i> = 7	<i>n</i> = 4		
Fat	0.08243 A	0.07621 A	—	0.08002
Shrubs				
<i>Atriplex canescens</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.55410 A	0.52399 A	0.51110 A	0.53148
Nitrogen	0.02812 A	0.02662 A	0.02359 A	0.02621
Phosphorus	0.00192 B	0.00104 A	0.00099 A	0.00132
Potassium	0.04498 A	0.04329 A	0.03683 A	0.04184
Zinc	0.00003 B	0.00002 A	0.00002 A	0.00002
Iron	0.00017 A	0.00023 A	0.00014 A	0.00018
Manganese	0.00005 A	0.00005 A	0.00005 A	0.00005
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.01852 A	0.02494 A	0.02174 A	0.02142
Magnesium	0.01037 A	0.01751 A	0.01183 A	0.01287
Sulfur	0.00810 A	0.01168 B	0.01011 AB	0.00977
Sodium	0.00017 A	0.00018 A	0.00016 A	0.00017
ADF	0.17424 A	0.16821 A	0.19455 A	0.17850
TNC	0.06251 A	0.05545 A	0.06092 A	0.05978
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 7	
Fat	0.06900 A	0.06304 A	0.08431 A	0.07073
Leaves and twigs				
<i>Ceratoides lanata</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.49380 B	0.26257 A	0.29758 A	0.46683
Nitrogen	0.02691 B	0.01642 A	0.01822 A	0.02071
Phosphorus	0.00150 B	0.00076 A	0.00091 A	0.00106
Potassium	0.02770 B	0.01619 A	0.01483 A	0.01972
Zinc	0.00002 A	0.00001 A	0.00001 A	0.00002
Iron	0.00033 A	0.00065 A	0.00036 A	0.00043
Manganese	0.00010 B	0.00007 AB	0.00006 A	0.00008
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.01589 A	0.01574 A	0.01402 A	0.01530
Magnesium	0.00590 A	0.00454 A	0.00417 A	0.00491
Sulfur	0.00423 A	0.00381 A	0.00311 A	0.00374

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
Leaves and twigs				
<i>Ceratoides lanata</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Sodium	0.00013 B	0.00012 B	0.00006 A	0.00010
ADF	0.31148 A	0.39734 B	0.41817 B	0.37059
TNC	0.05554 A	0.04498 A	0.05175 A	0.05100
	<i>n</i> = 9	<i>n</i> = 7	<i>n</i> = 8	
Fat	0.09764 A	0.06804 A	0.06589 A	0.07781
Flowers				
<i>Ceratoides lanata</i>				
	<i>n</i> = 8	<i>n</i> = 5	<i>n</i> = 0	
Moisture	0.51390 B	0.15079 A	—	0.36173
Nitrogen	0.02819 B	0.01544 A	—	0.02284
Phosphorus	0.00195 B	0.00082 A	—	0.00144
Potassium	0.02504 B	0.01983 A	—	0.02296
Zinc	0.00002 B	0.00001 A	—	0.00002
Iron	0.00026 B	0.00065 A	—	0.00039
Manganese	0.00008 A	0.00007 A	—	0.00008
Copper	0.00001 A	0.00001 A	—	0.00001
Calcium	0.01124 A	0.01809 B	—	0.01367
Magnesium	0.00418 A	0.00522 A	—	0.00456
Sulfur	0.00379 A	0.00509 A	—	0.00427
Sodium	0.00009 A	0.00014 B	—	0.00011
ADF	0.32564 A	0.35626 B	—	0.33732
TNC	0.04473 A	0.02389 A	—	0.03597
	<i>n</i> = 5	<i>n</i> = 4	<i>n</i> = 0	
Fat	0.09006 A	0.06834 A	—	0.08008
<i>Hymenoclea salsola</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.62370 B	0.54484 AB	0.49660 A	0.56016
Nitrogen	0.02669 B	0.01607 A	0.01663 A	0.01997
Phosphorus	0.00225 A	0.00203 A	0.00146 A	0.00193
Potassium	0.02504 B	0.01709 A	0.01627 A	0.01967
Zinc	0.00002 A	0.00003 A	0.00002 A	0.00002
Iron	0.00015 A	0.00013 A	0.00012 A	0.00013
Manganese	0.00002 A	0.00002 A	0.00002 A	0.00002
Copper	0.00001 A	0.00001 A	0.00001 A	0.00001
Calcium	0.01503 A	0.01515 A	0.01459 A	0.01493
Magnesium	0.00393 A	0.00386 A	0.00344 A	0.00379
Sulfur	0.00499 A	0.00399 A	0.00551 A	0.00482
Sodium	0.00004 B	0.00003 AB	0.00002 A	0.00003
ADF	0.27027 A	0.33571 B	0.29795 AB	0.29914
TNC	0.09393 A	0.07787 A	0.07883 A	0.08409
	<i>n</i> = 11	<i>n</i> = 8	<i>n</i> = 7	
Fat	0.14964 A	0.18990 AB	0.21455 B	0.17866
<i>Ephedra nevadensis</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.40931 A	0.40194 A	0.36346 A	0.39274
Nitrogen	0.01691 A	0.01569 A	0.01367 A	0.01549
Phosphorus	0.00089 A	0.00102 A	0.00066 A	0.00085
Potassium	0.00529 A	0.00661 A	0.00651 A	0.00607
Zinc	0.00001 A	0.00001 A	0.00001 A	0.00001

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
Flowers				
<i>Ephedra nevadensis</i>				
	<i>n</i> = 11	<i>n</i> = 9	<i>n</i> = 9	
Iron	0.00009 A	0.00015 B	0.00011 AB	0.00011
Manganese	0.00003 A	0.00002 A	0.00003 A	0.00003
Copper	0.00000 A	0.00000 A	0.00000 A	0.00000
Calcium	0.02513 A	0.02485 A	0.02148 A	0.02389
Magnesium	0.00403 A	0.00314 A	0.00316 A	0.00347
Sulfur	0.00414 A	0.00297 A	0.00282 A	0.00334
Sodium	0.00011 A	0.00011 A	0.00017 A	0.00013
ADF	0.38952 A	0.40518 B	0.43588 B	0.40872
TNC	0.08682 A	0.08553 A	0.08248 A	0.08509
	<i>n</i> = 10	<i>n</i> = 9	<i>n</i> = 9	
Fat	0.07537 A	0.07068 A	0.05609 A	0.06295
<i>Eriogonum fasciculatum</i>				
	<i>n</i> = 7	<i>n</i> = 6	<i>n</i> = 6	
Moisture	0.51870 B	0.31947 A	0.27633 A	0.37659
Nitrogen	0.01564 B	0.01227 AB	0.01057 A	0.01289
Phosphorus	0.00131 A	0.00088 A	0.00071 A	0.00097
Potassium	0.01305 B	0.00957 A	0.00676 A	0.00979
Zinc	0.00002 B	0.00002 B	0.00001 A	0.00001
Iron	0.00015 A	0.00025 B	0.00020 AB	0.00019
Manganese	0.00002 A	0.00001 A	0.00002 A	0.00002
Copper	0.00000 A	0.00000 A	0.00000 A	0.00000
Calcium	0.01158 A	0.01190 A	0.01310 A	0.01216
Magnesium	0.00243 A	0.00264 A	0.00261 A	0.00255
Sulfur	0.00164 A	0.00170 A	0.00183 A	0.00171
Sodium	0.00010 A	0.00008 A	0.00007 A	0.00008
ADF	0.26690 A	0.37340 A	0.36972 A	0.33203
TNC	0.17318 A	0.14363 A	0.13738 A	0.15222
	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 5	
Fat	0.07140 A	0.06198 A	0.06183 A	0.06520
<i>Krameria parvifolia</i>				
	<i>n</i> = 8	<i>n</i> = 9	<i>n</i> = 9	
Moisture	0.51590 A	0.49670 A	0.38786 A	0.46463
Nitrogen	0.02359 B	0.01599 A	0.01604 A	0.01819
Phosphorus	0.00253 B	0.00170 AB	0.00106 A	0.00168
Potassium	0.01838 A	0.01942 A	0.01604 A	0.01790
Zinc	0.00002 B	0.00001 AB	0.00001 A	0.00001
Iron	0.00022 A	0.00022 A	0.00027 A	0.00023
Manganese	0.00002 A	0.00002 A	0.00002 A	0.00002
Copper	0.00001 A	0.00001 A	0.00000 A	0.00001
Calcium	0.00868 A	0.01101 AB	0.01481 B	0.01147
Magnesium	0.00248 A	0.00268 A	0.00358 B	0.00291
Sulfur	0.00404 A	0.00344 A	0.00414 A	0.00386
Sodium	0.00017 A	0.00050 B	0.00059 B	0.00041
ADF	0.29184 A	0.37059 A	0.29357 A	0.31919
TNC	0.11260 A	0.09300 A	0.12608 A	0.11008
	<i>n</i> = 7	<i>n</i> = 9	<i>n</i> = 8	
Fat	0.06779 A	0.06198 A	0.06130 A	0.06343

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
Succulents				
Pads				
<i>Opuntia basilaris</i>				
Moisture	<i>n</i> = 8 0.58961 A	<i>n</i> = 6 0.83134 A	<i>n</i> = 6 0.82554 A	0.74068
Nitrogen	<i>n</i> = 7 0.01151 A	<i>n</i> = 6 0.00774 A	<i>n</i> = 6 0.00923 A	0.00953
Phosphorus	0.00097 A	0.00070 A	0.00049 A	0.00072
Potassium	0.02111 A	0.01825 A	0.02091 A	0.02011
Zinc	0.00002 A	0.00001 A	0.00001 A	0.00002
Iron	0.00019 A	0.00025 A	0.00035 A	0.00026
Manganese	0.00014 A	0.00007 A	0.00007 A	0.00009
Copper	0.00000 A	0.00001 A	0.00001 A	0.00001
Calcium	0.04473 A	0.06078 A	0.06915 A	0.05706
Magnesium	0.01326 A	0.01452 A	0.01753 A	0.01496
Sulfur	<i>n</i> = 8 0.00478 A	<i>n</i> = 6 0.00282 A	<i>n</i> = 6 0.00230 A	0.00336
Sodium	<i>n</i> = 7 0.00005 A	<i>n</i> = 6 0.00006 A	<i>n</i> = 6 0.00005 A	0.00006
ADF	<i>n</i> = 7 0.18771 A	<i>n</i> = 5 0.15222 A	<i>n</i> = 6 0.25906 A	0.19996
TNC	<i>n</i> = 6 0.13388 A	<i>n</i> = 5 0.08739 A	<i>n</i> = 6 0.06505 A	0.09393
Fat	<i>n</i> = 5 0.08068 A	<i>n</i> = 5 0.05417 A	<i>n</i> = 6 0.08276 A	0.08221
Pads				
<i>Opuntia erinacea</i>				
Moisture	<i>n</i> = 13 0.72938 A	<i>n</i> = 9 0.74896 A	<i>n</i> = 9 0.75234 A	0.74182
Nitrogen	0.01188 A	0.00887 A	0.00828 A	0.00989
Phosphorus	0.00117 A	0.00081 A	0.00082 A	0.00095
Potassium	0.02006 A	0.01604 A	0.01491 A	0.01732
Zinc	0.00003 A	0.00002 A	0.00001 A	0.00002
Iron	0.00011 A	0.00011 A	0.00013 A	0.00012
Manganese	0.00009 A	0.00009 A	0.00009 A	0.00009
Copper	0.00000 A	0.00000 A	0.00001 A	0.00001
Calcium	0.03630 A	0.03664 A	0.04325 A	0.03835
Magnesium	0.01051 A	0.01372 A	0.01240 A	0.01196
Sulfur	0.00217 A	0.00196 A	0.00226 A	0.00213
Sodium	0.00005 A	0.00007 A	0.00005 A	0.00005
ADF	0.26389 A	0.26389 A	0.23052 A	0.25408
TNC	0.10238 A	0.05264 A	0.05766 A	0.07332
Fat	<i>n</i> = 8 0.07145 A	<i>n</i> = 6 0.07192 A	<i>n</i> = 6 0.07285 A	0.07202

(con.)

APPENDIX B (Con.)

Nutrient	Spring	Summer	Fall	Average
		Succulents		
		Fruits		
		<i>Opuntia erinacea</i>		
	<i>n</i> = 7	<i>n</i> = 3	<i>n</i> = 1	
Moisture	0.83655 B	0.23475 A	0.12239 A	0.61866
Nitrogen	0.01931 B	0.00811 A	0.00631 A	0.01445
Phosphorus	0.00253 B	0.00126 AB	0.00030 A	0.00187
Potassium	0.03366 B	0.02169 A	0.01450 A	0.02819
Zinc	0.00002 A	0.00001 A	0.00001 A	0.00002
Iron	0.00008 A	0.00008 A	0.00027 A	0.00009
Manganese	0.00013 A	0.00013 A	0.00016 A	0.00013
Copper	0.00001 A	0.00000 A	0.00001 A	0.00001
Calcium	0.02224 A	0.02836 A	0.03132 A	0.02463
Magnesium	0.00786 A	0.00781 A	0.00829 A	0.00788
Sulfur	0.00247 A	0.00231 A	0.00220 A	0.00240
Sodium	0.00003 A	0.00003 A	0.00008 A	0.00004
ADF	0.23866 A	0.30116 A	0.26442 A	0.25784
TNC ¹	0.07048	—	—	0.07048
	<i>n</i> = 5	<i>n</i> = 2	<i>n</i> = 1	
Fat	0.08160 A	0.10214 A	0.11842 A	0.11071

¹Technical problems with the summer and fall data led to their omission.

McArthur, E. Durant; Sanderson, Stewart C.; Webb, Bruce L. 1994. Nutritive quality and mineral content of potential desert tortoise food plants. Res. Pap. INT-473. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 26 p.

Minerals and nutrients for desert tortoise food plants from the northeastern Mojave Desert are generally in the normal range for semiarid environments, except that sodium values are low for plants and soil. Annual forbs are often higher in nutritive quality than other plant classes.

KEYWORDS: *Gopherus agassizii*, animal nutrition, mineral nutrition, nutrient content, grasses, forbs, shrubs

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