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Nutrient balances and maintenance requirements for nitrogen and energy in desert tortoises (*Xerobates agassizii*) consuming forages

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The North American tortoise *Xerobates agassizii* (synonym: *Gopherus agassizii*) consumes herbage and grasses produced from low and variable desert rains. Utilization of *Sphaeralcea ambigua* foliage and the grass *Schismus barbatus* were studied in 8 adult tortoises (2.3 kg body mass). The herbage contained more N but less fiber than the grass. Tortoises ingested and digested more dry matter and energy from herbage than grass. Intakes and retention of N were greater from the herbage than the grass, but amino acid proportions and true N digestibilities were similar between diets. Herbage contained more Ca than grass, especially in relation to P (Ca:P 14.5 *vs.* 1.9), but this was ameliorated by lower absorption of Ca from the herbage. K intakes were greater from the herbage than the grass and associated with the digestive loss of Mg from herbage. Low Na content of both forages resulted in net losses of Na.

Maintenance requirements for dietary N (14.4 mg · $kg^{-0.75}$ · d^{-1}) and for digestible energy (19.9 kJ · $kg^{-0.75}$ · d^{-1}) were lower than estimates for other herbivorous reptiles and consistent with the utilization of desert pastures where quality and abundance may be low and erratic. Modest requirements for these and other nutrients may enable desert tortoises to tolerate temporal deficiencies, but these must ultimately be corrected by a wider dietary selection. Consequently, both diversity and abundance of pasture growth may be critical to long-term nutrient balances of this threatened species.

Key words: Reptile; Protein; Amino acid; Mineral; Calcium; Phosphorus; Sodium; Potassium; Magnesium.

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Introduction

Hot deserts are characterized by low and variable rainfall combined with high evaporation from elevated temperatures and winds (Bradshaw, 1986). These unpredictable conditions produce dramatic changes in both the quality and availability of food for herbivores. Reptiles may be better suited to hot deserts than other vertebrates due to a combination of ectothermy, low water loss, and greater tolerance of physiological fluctuation (Bradshaw, 1992). These attributes may be most pronounced in the tortoises. (Family Testudinidae), a predominantly herbivorous taxa with several species from arid and semi-arid habitats (Zug, 1993).

The North American desert tortoise (*Xerobates agassizii*, synonym: *Gopherus agassizii*) consumes a wide variety of plants (e.g., Burge and Bradley 1976; Hansen, *et al.*, 1976), but herbage and grasses predominate in the diet.

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Since these forages often differ in their nutrient contents, this paper compares the utilization of major organic and mineral nutrients by captive tortoises fed herbage and grass *ad libitum*. Two forages were chosen for their availability and their acceptance by desert tortoises: the leaves of *Sphaeralcea ambigua* (desert mallow) and the aerial parts of the grass *Schismus barbatus*. The apparent nutrient balances of tortoises are compared between forages and combined to estimate requirements for nitrogen (N) and energy at maintenance.

Materials and Methods

Forages were collected in spring from March to May 1992 in the Las Vegas Valley and on Mormon Mesa, Nevada, U.S.A. *Sphaeralcea* leaves were picked from the base of the petiole, whereas the whole aerial portion of *Schismus* was gathered. *Schismus* collections were subsequently cut to 10-cm lengths and mixed together by hand. Collections were chilled in transport and stored at −20°C on return to the laboratory.

Tortoises were maintained in individual outdoor pens for more than 12 months prior to these studies. Any effects of reproductive state, such as a developing egg mass in females, was assumed to be minimal as all animals were held individually for one or more breeding seasons. A pelleted feed formulated as a complete diet (Barboza, 1995) was provided to animals in outdoor pens and during periods of transition between experiments. Experiments were conducted with 8 healthy adults (3 ♂:5♀) in May (*Sphaeralcea*) and July 1992 (*Schismus*). Tortoises were held indoors in metabolism cages 1.67 m long × 0.45 m wide × 0.45 m high. Natural incident lighting was augmented with fluorescent lighting between 6:00 and 18:00 hours. Consistent ambient temperatures were maintained with air conditioning units and electric fans at 31 ± 2°C.

Tortoises were allowed to adjust to metabolism cages and to each diet for 1 month before commencing collections of 13 to 15 days. Feeds were thawed and provided *ad libitum* in the morning and the afternoon of each day. Fresh tap water was also provided *ad libitum* each day. Feed refusals and excreta were collected daily and stored at −20°C. Metabolism cages were fitted with plastic floors and drains to enable complete collections of urine, urinary precipitates, and feces. Tortoises voided large fecal pellets that were separate and distinguishable from their renal wastes. Urine was drained directly into glacial acetic acid to minimize N lost through bacterial activity.

Residues of excreta were removed from cage surfaces and from the shells of tortoises before commencing the collection. These surfaces were washed thoroughly with water and a solution of lithium carbonate (1 g $LiCo_3 \cdot L^{-1}$) to remove urate salts. This procedure was repeated at the end of the collection to recover excreted materials adhering to the animals and their cages. These final cage washes were collected and stored at −20°C for chemical analysis. Daily collections of feed and excreta were combined at the end of the experiment to provide representative samples for chemical analysis.

Dry matter (DM) content was determined by drying to constant mass in a convection oven at 50°C. Dried feeds, feces, and urates were ground through a 2-mm screen for further analyses. Nitrogen content was determined by the Kjeldahl procedure (Helrich, 1990). Dietary fiber was extracted in neutral detergent with the addition of heat-stable amylase and sodium sulphite by the method of Van Soest, *et al.* (1991). Gross energy (GE) was determined by adiabatic bomb calorimetry (Model 1241, Parr, Moline, IL). Samples were combusted in a muffle furnace for 5 hr at 550°C to determine ash content.

Frozen samples of each feed offered were lyophilized and ground for determination of amino acid content. Acid hydrolysates (6 M HCl at 110°C) of these samples were analyzed by high-performance liquid chromatography (Helrich, 1990) at Woodson Tennant Laboratories (Memphis, TN). Amino acid concentrations were expressed on DM basis, with the equivalent N content expressed as a proportion of total N in the diet. Amino acids were also related to the crude protein content of the diet estimated at 6.25 × total N.

Dried feeds and excreta were prepared for mineral analyses by digestion in a mixture of nitric acid (HNO_3) and prechloric acid ($HClO_4$). Phosphorus (P) content was measured with molybdovanadate by the Gomorri method (Helrich, 1990). Calcium (Ca) and magnesium (Mg) were determined by atomic absorption, and sodium (Na) and potassium (K) were measured by atomic emission in a flame spectrophotometer.

The digestible intake of a dietary component was calculated as the difference between the quantities ingested in the feed and voided in the feces. The digestibility of this component was the digestible intake expressed as a percentage of the total intake. Urinary losses of a component were calculated as the sum of losses in the cage wash and in both urinary

fluids and precipitates. The apparent balance for a dietary component was calculated as the difference between the total intake and the combined fecal and urinary losses. Further corrections for extrarenal mineral losses were not necessary because this species lacks salt glands (Dunson, 1976).

Parameters of digestion and balance were compared between diets by analysis of variance. Relationships between parameters were performed by least-squares regression (Wilkinson, 1990). Proportions and percentages were transformed to arcsines for statistical analysis (Zar, 1974). Means are reported with the standard deviation (SD) of the sample.

Results

Sphaeralcea herbage was higher in moisture content (28.2 *vs.* 51.9% DM) than the *Schismus* grass. However, the grass contained more fiber than the herbage as a proportion of either fresh or dry mass (64.6% *vs.* 29.1% DM). Total mineral content as inorganic ash was greater in *Sphaeralcea*, as were the levels of Ca and K in DM (Table 1). Since P contents were similar between the diets, ratios of Ca:P were greater for *Sphaeralcea* than for *Schismus* (14.5 *vs.* 1.9).

Sphaeralcea DM contained higher levels of N than *Schismus* (Table 1). If it is assumed that plant proteins are 16% N (e.g., Robbins, 1993), then crude protein was 23.1% and 11.9% of DM in *Sphaeralcea* and *Schismus*, respectively. The N contents from 18 amino acids were equivalent to 97% and 83% of total N in *Schismus* and *Sphaeralcea*, respectively. A small proportion of total N may be due to the amide groups of asparagine and glutamine because these acids were assayed with aspartate and glutamate, respectively. Although amino acid concentrations on a DM basis reflected the total N content of the forages, the proportions of N and crude protein attributed to each acid were generally similar between forages (Table 2).

Table 1. Composition of *Sphaeralcea* herbage and *Schismus* grass provided to tortoises (DM Basis)

Component	*Sphaeralcea*	*Schismus*
GE (kJ · g^{-1})	16.8	18.1
N (%)	3.7	1.9
Ash (%)	16.1	6.3
Ca (%)	3.20	0.37
P (%)	0.22	0.20
Mg (%)	0.37	0.23
K (%)	2.26	1.50
Na (mg/100g)	47	13

Tortoises maintained similar body mass between diets with small mass gains on *Sphaeralcea* and minor mass losses on *Schismus* (Table 3). Intakes and digestibilities of DM and GE from *Sphaeralcea* were greater than those from *Schismus*. Consequently, digestible intakes of DM and GE in the herbage were much higher than those for the grass diet: 7.1 ± 1.6 g DM · d^{-1} *vs.* 3.5 ± 0.8 g DM · d^{-1}, $P < 0.001$; 129.9 ± 30.9 kJ · d^{-1} *vs.* 58.3 ± 15.4 kJ · d^{-1}, $P < 0.001$.

The high N content and greater DM intakes of *Sphaeralcea* resulted in higher intakes of N than from *Schismus* (Table 3). Since N digestibilities were also greater for *Sphaeralcea*, digestible N intakes of this herbage were much higher than those of *Schismus* grass. Production of urinary wastes were greater on the herbage diet than on the grass (fluid: 22.6 ± 12.6 g · d^{-1} *vs.* 4.6 ± 3.4 g · d^{-1}, $P < 0.01$; precipitates: 480 ± 305 mg DM · d^{-1} *vs.* 66 ± 89 mg DM · d^{-1}, $P < 0.01$). Losses of N in these wastes were approximately 60% of the digestible N intakes for both diets, with 58–69% of the urinary N excreted in precipitates. Balances for N were also greater on *Sphaeralcea* than on *Schismus* and directly related to N intake by the following regression: N balance (mg · d^{-1}) = −8.59 + 0.34 [N intake (mg · d^{-1})]; $R^2 = 0.69$; $P < 0.001$). This relationship predicts maintenance of zero N balance at 25.6 mg N · d^{-1}. N balance was also significantly related to the digestible N intake (Fig. 1). As the intercept for this regression is not significantly different from zero, the digestible intake of N predicted to maintain adult tortoises at N balance is negligible with an upper limit for the 95% confidence interval at 75 mg N · d^{-1}.

These digestible N intakes do not account for endogenous N lost in the feces. Metabolic fecal N is generally estimated as the intercept from the regression of fecal N loss (per unit of DM ingested) on dietary N content (e.g., Hume, 1986, Smith and Green, 1987), but this regression was not significant ($P > 0.1$). However, total fecal N loss was related to N intake of tortoises (Fig. 2) and this relationship predicted an endogenous fecal loss of 27.1 mg N · d^{-1} at zero N intake for both forages. Separate regressions for each forage were significant, but these relationships predicted negligible fecal losses at zero N intake (Fig. 2). Truly digestible N intakes were calculated by adding the combined estimate of endogenous fecal N to the digestible N intakes. The resultant estimates of true N digestibility were similar ($P > 0.1$) between *Sphaeralcea* (88.3 ± 7.9%) and *Schismus* (81.8 ± 8.5%). The truly digestible N intake predicted to maintain zero N bal-

Table 2. Amino acid concentration (g · kg^{-1} DM) and the contribution of each acid to total N (%N) and crude protein (%CP) contents of *Sphaeralcea* herbage and *Schismus* grass provided to tortoises

	Sphaeralcea			*Schismus*		
Component	g · kg^{-1} DM	%N	%CP	g · kg^{-1} DM	%N	%CP
Alanine	12.5	5.3	5.4	9.9	8.2	8.3
Arginine	12.5	10.9	5.4	5.6	9.5	4.7
Aspartate	27.8	7.9	12.0	14.1	7.8	11.9
Cystine	1.8	0.6	0.8	1.4	0.9	1.2
Glutamate	28.2	7.3	12.2	22.7	11.4	19.1
Glycine	12.1	6.1	5.2	5.6	5.5	4.7
Histidine	5.7	4.2	2.5	3.2	4.6	2.7
Isoleucine†	10.3	3.0	4.5	5.6	3.1	4.7
Leucine†	19.6	5.7	8.5	10.9	6.1	9.2
Lysine†	15.3	7.9	6.6	6.2	6.3	5.2
Methionine†	5.0	1.3	2.2	2.8	1.4	2.4
Phenylalanine†	12.8	2.9	5.5	6.6	2.9	5.6
Proline	12.5	4.1	5.4	20.7	13.3	17.4
Serine	10.7	3.9	4.6	6.4	4.5	5.4
Threonine†	12.5	4.0	5.4	6.6	4.1	5.6
Tryptophan†	5.0	1.9	2.2	2.6	1.9	2.2
Tyrosine	6.8	1.4	2.9	3.0	1.2	2.5
Valine†	13.9	4.5	6.0	7.6	4.8	6.4

*Estimated as 6.25 × total N. *Sphaeralcea* and *Schismus* were 23.1% and 11.9% crude protein of DM, respectively.

†Amino acids generally considered essential to omnivores. Arginine, histidine, and glycine/serine may also be required by some species (Scott, 1986).

ance was 23.4 mg · d^{-1} from the following relationship: N balance (mg · $^{-1}$) = −9.26 + 0.40 [Truly digestible N intake (mg · $^{-1}$)], R^2 = 0.72, $P < 0.001$.

The urinary N losses of tortoises were also related to their digestible N intakes (Fig. 3). This regression predicted that the endogenous loss of urinary N is negligible at zero intake of digestible N. This low estimate was confirmed by significant regressions of urinary N loss against total N intake and against truly digestible N intake ($P < 0.001$).

Digestible energy intake was significantly related to N balance in tortoises (Fig. 4). If it is assumed that lean body mass is the principal determinant of whole-body energy expenditure (Blaxter, 1989), then the energy required to maintain lean body mass or zero N balance in an adult nonreproducing animal is an estimate of the maintenance energy requirement (Hume, 1974; Barboza, *et al.*, 1993). This was predicted at a digestible energy intake of 35.5 kJ · d^{-1} with an upper limit for the 95% confidence interval at 55 kJ · d^{-1}.

Mineral intakes reflected both the dietary mineral content and the total feed intake (Table 4). Dietary intakes of Ca were much greater for *Sphaeralcea* than for *Schismus*, but only 11% of the ingested Ca was absorbed from *Sphaeralcea* herbage. Although digestible intakes of Ca tended to be greater from *Sphaeralcea* than from *Schismus* ($P = 0.053$), urinary Ca losses were greater on the herbage diet and resulted in similar Ca balances between diets. These urinary losses were partly due to higher concentrations of Ca in pre-

Table 3. Parameters of apparent digestion and balance in adult tortoises fed *Sphaeralcea* herbage and *Schismus* grass (Mean ± SD)

Parameter (*n*)	*Sphaeralcea* (8)	*Schismus* (8)	Statistic
Body mass (g)	2283 ± 132	2328 ± 115	ns
Mass change (g · d^{-1})	3.9 ± 3.0	−1.6 ± 3.6	**
DM intake (g · d^{-1})	10.3 ± 2.5	5.6 ± 1.3	***
DM digestibility (%)	69.2 ± 4.0	63.0 ± 3.9	*
GE intake (kJ · d^{-1})	173.6 ± 41.8	98.7 ± 24.3	**
GE digestibility (%)	75.4 ± 3.4	59.1 ± 4.0	***
N intake (mg · d^{-1})	381.8 ± 92.1	103.0 ± 26.1	***
N digestibility (%)	80.7 ± 5.9	53.6 ± 5.3	***
Urinary N loss (mg · d^{-1})	184.3 ± 53.7	30.7 ± 25.9	***
N balance (mg · d^{-1})	120.7 ± 49.8	24.9 ± 27.9	***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns = not significant

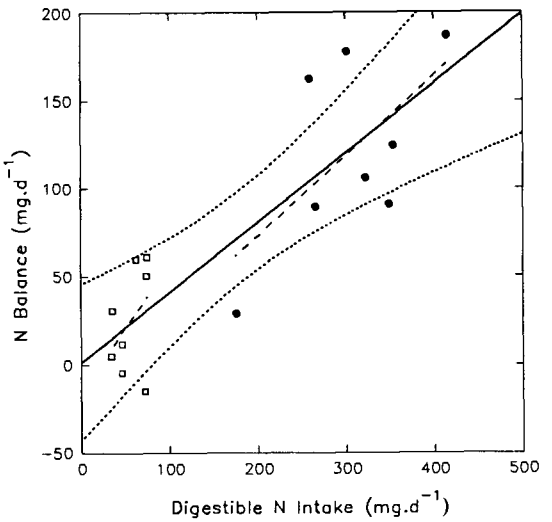

Fig. 1. Regression relationship between N balance (mg · d^{-1}) and digestible N intake (mg · d^{-1}) in adult tortoises fed forages: Y = 1.47 + 0.40X, R^2 = 0.72, $P < 0.001$. Predicted digestible N intake is negligible at zero N balance. Dotted lines indicate 95% confidence limits for the combined regression.
Schismus (grass; open squares): Y = −13.68 + 0.69X, R^2 = 0.17, $P > 0.05$.
Sphaeralcea (herbage; closed circles): Y = −18.36 + 0.46X, R^2 = 0.39, $P > 0.05$.

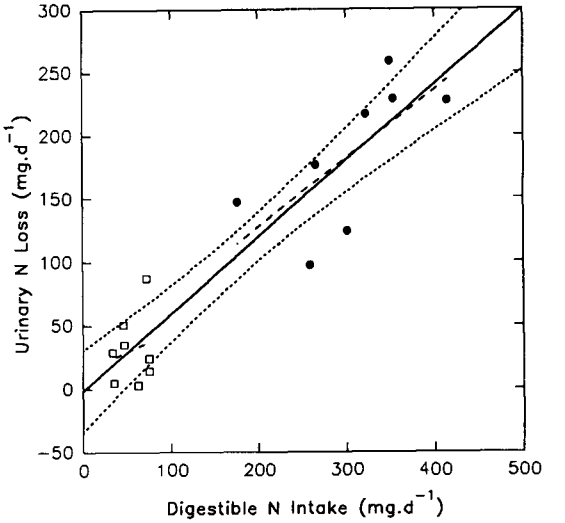

Fig. 3. Regression relationship between urinary N loss (mg · d^{-1}) and digestible N intake (mg · d^{-1}) in adult tortoises fed forages: Y = −1.47 + 0.60X, R^2 = 0.86, $P < 0.001$. Predicted endogenous urinary N loss is negligible at zero digestible intake. Dotted lines indicate 95% confidence limits for the combined regression.
Schismus (grass; open squares): Y = 13.68 + 0.31X, R^2 = 0.04, $P > 0.05$.
Sphaeralcea (herbage; closed circles): Y = 18.36 + 0.54X, R^2 = 0.47, $P > 0.05$.

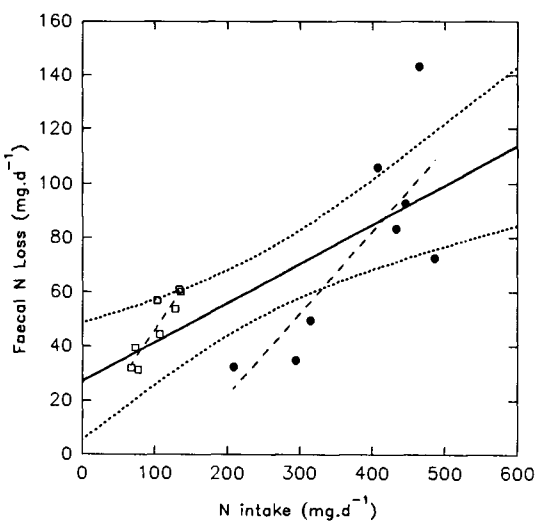

Fig. 2. Regression relationship between faecal N loss (mg · d^{-1}) and N intake (mg · d^{-1}) in adult tortoises fed forages: Y = 27.11 + 0.14X, R^2 = 0.55, $P < 0.01$. Predicted endogenous fecal N loss is 27.11 mg · d^{-1} at zero N intake. Dotted lines indicate 95% confidence limits for the combined regression.
Schismus (grass; open squares): Y = 6.19 + 0.40X, R^2 = 0.83, $P < 0.01$.
Sphaeralcea (herbage; closed circles): Y = −38.52 + 0.30X, R^2 = 0.61, $P < 0.05$.

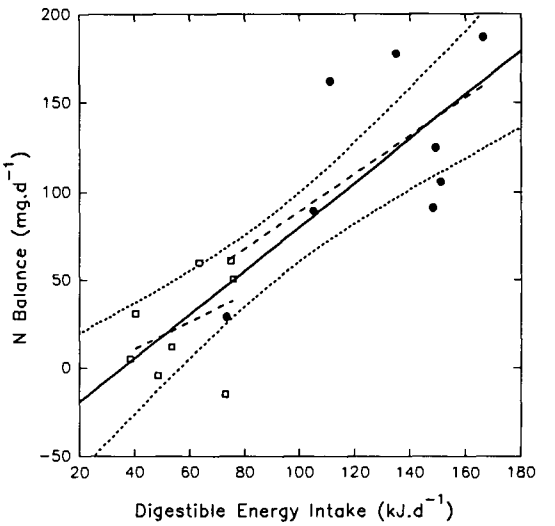

Fig. 4. Regression relationship between N balance (mg · d^{-1}) and digestible energy intake (kJ · d^{-1}) in adult tortoises fed forages: Y = −44.03 + 1.24X, R^2 = 0.71, $P < 0.001$. Predicted energy intake at zero N balance is 35.5 kJ · d^{-1}. Dotted lines indicate 95% confidence limits for the combined regression.
Schismus (grass; open squares): Y = −20.04 + 0.77X, R^2 = 0.16, $P > 0.05$.
Sphaeralcea (herbage; closed circles): Y = −17.00 + 1.06X, R^2 = 0.38, $P > 0.05$.

Table 4. Mineral balances (mg · d^{-1}) in adult tortoises fed *Sphaeralcea* herbage and *Schismus* grass (Mean ± SD)

Parameter (*n*)	*Sphaeralcea* (8)	*Schismus* (8)	Statistic
Ca dietary intake	324.9 ± 82.6	16.7 ± 6.5	***
Ca digestible intake	36.6 ± 32.8	7.7 ± 5.7	ns
Ca urinary loss	19.8 ± 6.6	7.8 ± 1.9	**
Ca balance	16.8 ± 33.3	−0.1 ± 6.8	ns
P dietary intake	22.4 ± 5.5	10.3 ± 2.7	***
P digestible intake	10.5 ± 2.6	4.9 ± 1.7	*
P urinary loss	0.23 ± 0.09	0.10 ± 0.05	**
P balance	10.3 ± 2.5	4.8 ± 1.7	***
Mg dietary intake	37.9 ± 9.3	12.5 ± 3.2	***
Mg digestible intake	−3.0 ± 4.6	5.1 ± 1.7	**
Mg urinary loss	7.5 ± 2.0	3.2 ± 1.4	***
Mg balance	−10.6 ± 5.3	1.9 ± 2.1	***
K dietary intake	232.7 ± 57.4	85.3 ± 20.7	***
K digestible intake	150.0 ± 29.	45.4 ± 13.2	***
K urinary loss	107.7 ± 36.7	23.4 ± 16.2	***
K balance	42.3 ± 25.1	22.0 ± 16.5	ns
Na dietary intake	4.3 ± 1.3	0.7 ± 0.2	***
Na digestible intake	1.5 ± 0.7	−0.4 ± 0.3	***
Na urinary loss†	4.0 ± 2.2	0.9 ± 0.8	**
Na balance†	−2.5 ± 2.5	−1.3 ± 0.8	ns

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns = not significant.
†Values exclude Na present in the cage wash (see text).

cipitates produced on the *Sphaeralcea* diet (1.42 ± 0.24% *vs.* 0.58 ± 0.29% Ca of DM; $P < 0.01$).

Since the P content of diets were similar, P intakes reflected the DM intakes of the forages (Table 4). Digestible intakes of P were greater for *Sphaeralcea* than for *Schismus*, because P availability was also similar between the forages (46%). Small urinary losses of P resulted in greater retention of P on the *Sphaeralcea* herbage.

The poor availability of Mg in *Sphaeralcea* herbage resulted in a digestive loss of Mg (Table 4). Conversely, net retention of Mg was achieved from *Schismus*, even though Mg intakes were lower than those from *Sphaeralcea*. Urinary Mg excretion was greater on *Sphaeralcea* than on *Schismus* and, therefore, exacerbated the Mg loss on the herbage diet. Some of these urinary losses were associated with precipitates that were 0.43 ± 0.13% Mg of DM.

Urinary precipitates were high in K (7.04 ± 1.65% K of DM) on both diets. Thus, urinary K losses were high for both diets and greater for *Sphaeralcea* than for *Schismus* (Table 4). These losses reflected the high digestible intakes of K from *Sphaeralcea*, which were enhanced by a greater availability of K than from the *Schismus* diet.

Conversely, dietary Na intakes were low on both forages. Urinary losses of Na were mainly associated with fluids (*Sphaeralcea* 3.43 ± 1.89 mg · d^{-1}; *Schismus* 0.79 ± 0.71 mg · d^{-1}; $P < 0.01$) rather than the precipitated urates, which were only 0.11 ± 0.06% Na of DM and equivalent to losses of 0.60 ± 0.55 mg · d^{-1} and 0.06 ± 0.10 mg · d^{-1} for *Sphaeralcea* and *Schismus*, respectively ($P < 0.01$). Unlike all other minerals recovered in the cage wash, total Na recovered was significantly related to the volume of fluid used in the wash ($P < 0.001$). Since this suggested that the wash fluid was contaminated with Na, the cage wash was not included in the estimate of urinary Na loss (Table 4: Na in the wash was equivalent to 2.9 ± 0.2 mg · d^{-1} and 6.5 ± 1.2 mg · d^{-1} for *Sphaeralcea* and *Schismus*, respectively). This may underestimate Na loss and, thus, overestimate Na retention, but the error in estimating Na balance would be partly compensated by any ingestion of Na in the drinking water. Although this minor route of Na intake was not assessed, the net losses of Na calculated for both diets are probably only slight overestimates of Na retention.

Discussion

Since most of the N in *Sphaeralcea* and *Schismus* was attributed to amino acids (Table 2), the residual 7–17% of N was probably associated with nucleic acids in the cell contents. The quality of dietary N for tortoises may be assessed from the proportion of amino acids essential for other species, such as domestic poultry (Scott, 1986) and green turtles (*Chelonia mydas*; Wood and Wood, 1977a; 1977b). The proportions of essential amino acids in crude protein of *Sphaeralcea* and *Schismus* generally exceed levels for optimal

growth of these species. However, these forages comprised only 2.2–2.4% methionine with 0.8–1.2% cystine of estimated crude protein (Table 2). Domestic poultry require 1.9–2.1% methionine and 1.6% cystine, whereas hatchling green turtles require 1.5% methionine when cystine is available at 3.1% of crude protein. These requirements for growing animals would exceed those for maintenance of adults because the proportion of essential amino acids and the mass specific N requirement generally decline with age (Scott, 1986; Wood and Wood, 1981). Therefore, the contributions of these sulphur amino acids to the N content of the forages were probably adequate for adult tortoises, but could limit growth of young animals.

The similarity in amino acid proportions between *Sphaeralcea* and *Schismus*, and the similar estimates of true N digestibility for these forages suggest that changes in N balance of tortoises reflected the quantity of N ingested, rather than any limitations in the availability of specific amino acids. The maintenance requirements for N in desert tortoises are lower than those of other herbivorous reptiles. The maintenance requirement of digestible N for the green iguana (*Iguana iguana*) is 150.6 mg $\cdot$ $kg^{-0.80} \cdot d^{-1}$ (Marken Lichtenbelt, 1993), whereas the upper limit of the 95% confidence interval predicted for tortoises was only 40.6 mg digestible N $\cdot$ $kg^{-0.80} \cdot d^{-1}$ (based on the mean body mass of 2305 g). Tortoises may also have lower N requirements than other desert reptiles such as the chuckwalla (*Sauromalus obesus*), which attained zero N balance at digestible intakes of 160 mgN $\cdot$ $kg^{-0.75} \cdot d^{-1}$ when force fed to maintain body mass (Nagy and Shoemaker, 1975). However, this procedure may not accurately reflect N equilibrium because desert tortoises force fed a mixture of spring forages at 62.7 mg N $\cdot$ $kg^{-1} \cdot d^{-1}$ maintained body mass but excreted N at variable rates so that intakes and losses were not significantly different, even though the average N balance was negative (Nagy and Medica, 1986). This intake is greater than the maintenance requirement of 11.1 mg dietary N $\cdot$ $kg^{-1} \cdot d^{-1}$ derived for adult tortoises from the present study.

Measures of N balance in desert tortoises may be increased by infrequent urination and retention of insoluble urates in the urinary bladder (Dantzler and Schmidt-Nielsen, 1966). Although tortoises were acclimated to steady states of intake and excretion prior to these studies, prolonged retention of urinary N may have increased apparent N retention especially at the lower rates of urination on the *Schismus* grass. This may have reduced estimates of endogenous urinary N loss (Fig. 3) and maintenance requirements (Fig. 1). It is likely that the maintenance requirement for N is underestimated by the N balance method (Murphy, 1993) because positive N balances on the *Schismus* diet were accompanied by a small loss in the body mass and (presumably) the N it contains. The N required for maintenance of body mass was estimated as 56 mg N $\cdot$ $kg^{-1} \cdot d^{-1}$ from the regression relationship between body mass change and digestible N intake. This estimate lies within the 95% confidence limits for the regression against N balance in Fig. 1 and further supports the comparatively low requirement for this species. All these estimates of N requirements may also be influenced by differences in energy and other nutrient intakes across dietary N levels. This is an unavoidable consequence of using natural diets in these studies and the error, albeit unknown, is probably small under the controlled conditions.

The maintenance energy requirement derived for adult desert tortoises was 19.9 kJ $\cdot$ $kg^{-0.75} \cdot d^{-1}$ (Fig. 4) at an ambient temperature of 31°C (±2°C). The average resting energy expenditure of desert tortoises is approximately 48% of this maintenance requirement (9.4 kJ $\cdot$ $kg^{-0.75} \cdot d^{-1}$). This approximation was calculated from measures of oxygen consumption at 23°C (6.4–6.9 kJ $\cdot$ $kg^{-0.75} \cdot d^{-1}$) and 35°C (11.6–12.5 kJ $\cdot$ $kg^{-0.75} \cdot d^{-1}$) by Bentley and Schmidt-Nielsen (1966) with energetic equivalents at respiratory quotients of 0.7–1.0 (Robbins, 1993). Resting energy expenditures of desert tortoises are probably lower than other herbivorous reptiles such as the chuckwalla (10.6–11.4 kJ $\cdot$ $kg^{-0.75} \cdot d^{-1}$ at 23°C; Bentley and Schmidt-Nielsen, 1966) and the green iguana (30.1 kJ $\cdot$ $kg^{-1} \cdot d^{-1}$ at 29–37°C; Marken Lichtenbelt, 1993). This suggestion is further supported by average field metabolic rates of free living desert tortoises that are only 35.9 kJ $\cdot$ $kg^{-1} \cdot d^{-1}$ (Nagy and Medica, 1986), while those of green iguanas are 71.7 kJ $\cdot$ $kg^{-1} \cdot d^{-1}$ (Marken Lichtenbelt, *et al.*, 1993).

Energy utilization reflected the relative proportions of fibrous cell walls and cell contents in the forages. As fiber is less digestible than the soluble cell contents of the plant, the digestible energy content of *Sphaeralcea* herbage was greater than that of *Schismus* (12.7 *vs.* 10.7 kJ $\cdot$ g^{-1} DM). This low energy content of *Schismus* combined with low DM intakes provided much smaller intakes of energy than from the *Sphaeralcea* herbage. Intakes of the grass may be constrained by the volume of the digestive tract available for retention of the long stems (Meinberger, *et al.*,

1993), even though the digestive capacity of the tortoise is large (up to 13% of body mass in wild animals; Barboza, 1995). However, the digestive tract fill from these forages also reflects their digestibility. Estimates of total DM in the gut were similar between the forages because the greater intake of the herbage was more digestible than the grass (Barboza, 1995).

Imbalances in minerals may be one of the costs of consuming *Sphaeralcea* and other highly digestible forages. The apparent abundance of Ca may be reduced by dietary oxalates, but intestinal absorption is probably under hormonal control for maintaining Ca homeostasis in concert with that for P (Linder, 1991). Thus, ratios of digestible intakes for Ca:P in *Sphaeralcea* were much lower than that apparent in the diet (3.5:1 *vs.* 14.5:1). The lower levels of Ca and P in *Schismus* were absorbed in similar proportions as Ca:P ratios were 1.9:1 and 1.6:1 for the diet and the digestible intakes, respectively. These ratios of digestible intakes are commensurate with the ratio of Ca:P present in the whole body of heathy desert tortoises (2.4:1; unpublished data).

Since Ca and K were major components of urinary precipitates, the excretion of these minerals may be influenced by urate production and excretion. These salts are dissolved in the renal filtrate but subsequently precipitate in the urinary bladder of the desert tortoise. Although water, ions, and small molecules may subsequently traverse the bladder wall, precipitates are apparently retained and voided intermittently with the fluid contents (Dantzler and Schmidt Nielsen, 1966; Bentley, 1976). The large variation in estimates of urinary Ca and K losses may reflect small perturbations in the excretion of their respective urate salts (Table 4). This mode of Ca and K excretion could obligate N for the formation of uric acid (Minnich, 1972) and also water for the elimination of these salts. These costs could become limiting when tortoises utilize forages high in K or Ca at low intakes of N and water. However, desert tortoises may forestall some of these losses by tolerating elevated levels of K in the blood plasma when forge quality and water availability decline in summer (Minnich, 1982; Nagy and Medica, 1986).

High dietary K may impair the availability and retention of other minerals for tortoises. Net disgestive loss of Mg accompanied high K intakes from *Sphaeralcea,* whereas lower Mg intakes were retained at the lower K intakes from *Schismus*. This suggests an impairment of Mg absorption at high K intakes similar to that reported for ruminant livestock (Suttle, 1987). Elevated levels of dietary K may also impair the retention of Na in ruminants (Suttle, 1987) and may have contributed to the urinary loss of Na from tortoises. As most of this Na was associated with fluids rather than precipitates, higher losses of Na from *Sphaeralcea* were partly due to greater rates of urinary excretion than on the *Schismus* diet. Thus, Na retention in tortoises may also be related to the net exchange of Na across the urinary bladder (Bentley, 1976) and the rate at which these fluids are voided. It is likely that the requirement for Na is relatively low in desert tortoises. The digestible intakes required to compensate for urinary Na lost on *Sphaeralcea* is still only 1.75 mg Na $\cdot$ kg^{-1} $\cdot$ d^{-1} and, thus, considerably lower than the interspecific estimate of dietary Na required for mammals (9 mg $\cdot$ kg^{-1} $\cdot$ d^{-1}; Robbins, 1993).

Net gains in body mass and retention of N suggest that tortoises were able to tolerate the slow loss of Na and Mg on these forages. However, tortoises would eventually require complementary intakes of other foods to restore the loss of these minerals. Therefore, the availability of a selection of forages within the home range of a tortoise may be critical to its nutrient balance in the long term. Consequently, the viability of a diverse seed bed may be essential to the management of pastures for this threatened species.

Lower requirements for energy and N than other herbivorous reptiles may provide a greater tolerance of dietary inadequacy, but would also enable desert tortoises to utilize pastures where production and quality are low and variable. Modest requirements would also facilitate the use of smaller foraging areas than other herbivores (Barboza, 1993), and the rapid deposition of body tissues for reproduction and growth during the brief periods of food abundance. Low metabolic rates and requirements may be a common attribute of tortoises (Bennet and Dawson, 1976) that permit these long-lived reptiles to persist in unpredictable habitats.

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