NONSTRUCTURAL CARBOHYDRATE AND ELEMENT POOLS IN GLOBEMALLOW (*SPHAERALCEA*): DEFOLIATION EFFECTS AND SEASONAL TRENDS

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ABSTRACT.—Globemallows (*Sphaeralcea* spp.) are arid land forbs suitable for seeding with crested wheatgrass (*Agropyron cristatum* [L.] Gaertner). However, little is known about the quantitative role of total nonstructural carbohydrates (TNC) in relation to globemallow tolerance of grazing, or about seasonal dynamics of mineral elements. The objectives of this study were to compare TNC and element pools (concentration × biomass) in the roots, crowns, and shoots of clipped versus unclipped *S. munroana* (Dougl.) Spach. Seedlings of *S. munroana* were transplanted to a northern Utah field site in 1985. Interplanted crested wheatgrass provided a uniform competitive background. One-half of the globemallows were clipped to 5 cm on 10 May 1986 when stems were elongating and root and crown TNC pools were low. The remaining globemallows were not clipped. Root, crown, and shoot pools of TNC and elements (N, P, K, Ca, and Mg) were determined on 1 May, 20 May, 7 June, 11 July, 22 September, and 5 November 1986, and 29 May 1987. Defoliation did not affect shoot weights during a 1-year period. Experiment-long TNC and element pools also were not affected by clipping. Results indicate that *S. munroana* shoot recovery from a single spring grazing during a 1-year period would not be impaired by low root and crown TNC pools, and that TNC stored in the roots and crowns would account for only 7% of the regrowth produced. Furthermore, TNC and element pools of roots and crowns were generally constant from May to September but increased from September to November. TNC and element pools in shoots increased from May to September and then generally declined by November. TNC pools of roots and crowns declined during winter.

Key words: Sphaeralcea munroana, *clipping effects, herbivory, animal nutrition.*

Globemallows (Malvaceae: *Sphaeralcea*) are perennial forbs native to the western USA and are of interest for rangeland seeding (Horton 1989, Pendery and Rumbaugh 1990). Several studies have shown that globemallows are grazed by livestock and wildlife (Hyder et al. 1975, Howard et al. 1990, Rumbaugh et al. 1993a). Understanding factors related to globemallow tolerance to grazing would enhance our ability to manage these species.

Total nonstructural carbohydrates (TNC) in roots and crowns have been considered an important energy source for the regrowth of grass and forb shoots following defoliation (Brown et al. 1972, Holechek et al. 1989). However, research by Caldwell et al. (1981) and Richards and Caldwell (1985) showed that root and crown TNC concentrations or pools (concentration × biomass) were not strongly correlated with the regrowth of defoliated *Agropyron* bunchgrasses. Recent work with alfalfa has also questioned the role of root TNC in shoot regrowth (Fankhauser and Volenec 1989, Hendershot and Volenec 1989).

Studies in Colorado investigated herbivory tolerance of *S. coccinea* (Nutt.) Rydb. in relation to root and crown TNC concentrations (Trlica et al. 1977, Menke and Trlica 1983). Herbivory tolerance of globemallow has not been investigated in relation to TNC pools. Furthermore, mechanistic studies such as the etiolated regrowth technique (Richards and Caldwell 1985) have not been done to evaluate the degree to which stored TNC contribute to the regrowth of globemallows following defoliation. While TNC have been the focus of many herbivory tolerance studies, elements may also be associated with herbivory tolerance (Chapin 1980a, 1980b, Chapin et al. 1980, Caldwell et al. 1981).

Seasonal trends of TNC concentrations in *S. coccinea* were studied by Menke and Trlica (1981). Rumbaugh et al. (1993b) reported element concentrations in globemallow taxa in

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the spring and fall. However, seasonal trends of element and TNC pools in globemallow have not been reported.

The first objective of this study was to determine if pools of TNC and elements (N, P, K, Ca, Mg) in the roots, crowns, and shoots of clipped versus unclipped *S. munroana* differed on seven dates over a 1-year period. The second objective was to determine the amount of regrowth produced in light versus dark by *S. munroana* clipped during the stems elongating or the seed shattering phenological stages.

MATERIALS AND METHODS

Study Site and Experimental Planting

These studies were conducted 3 km south of Logan, Utah (41°45'N, 111°48'W, 1389 m) in 1986 and spring 1987. Mean annual precipitation and temperature based on 28 years of records from a recording station 2 km from the study site were 471 mm and 7.4°C, respectively. Total precipitation and average temperature were 718 mm and 8.3°C in 1986, and 426 mm and 7.7°C in 1987. Soil at the site is a Nibley silt clay loam (Aquic Argiustoll).

Seeds of *S. munroana* were purchased commercially. The collection site was near Vernal, Utah, in pinyon-juniper (*Pinus-Juniperus*) vegetation on a sandy soil. Globemallow seeds were germinated and the seedlings transplanted into containers (164 cm^3) containing a rooting medium of 4 parts sand: 2 parts peat moss: 1 part vermiculite. Plants were grown with no fertilization in the greenhouse during the winter of 1985. Crested wheatgrass seeds also were purchased commercially, and the plants were grown in the greenhouse as described above.

Crested wheatgrass and globemallow plants were transplanted to the field on 1 May 1985. They were planted in a checkerboard pattern with 0.5-m spacing between plants. Therefore, each plot was 1 × 1 m, with four crested wheatgrasses competitors surrounding each *S. munroana.* The planting was 33 × 7 m overall.

TNC and Element Study

This study had a completely randomized experimental design with two treatments (clipped versus unclipped plants) and seven sampling dates. Twelve previously unclipped *S. munroana* plants were sampled for TNC and elements on 1 May 1986 when most plants were in the leaves elongating phenological stage (phenological terminology follows Menke and Trlica [1981]). Seventy-two other globemallow plants were assigned to be clipped or unclipped. Clipping was done at a 5-cm height on 10 May 1986 when stems were elongating.

Six clipped and six unclipped globemallow plants were then sampled on 20 May, 7 June, 11 July, 22 September, and 5 November 1986, and 29 May 1987. The most common phenological stages on these dates were stems elongating, flower buds developing, fruit developing, leaves brown, fall quiescence, and flower buds developing, respectively. These stages represented most of the phenological conditions occurring during a growing season. Furthermore, root and crown TNC concentrations in *S. coccinea* are lowest during the stems elongating phenological stage (Menke and Trlica 1981). Assuming similar patterns for TNC pools in *S. munroana,* we expected clipping at this stage to have its greatest impact on the reestablishment of shoots, if the quantity (pool) of soluble carbon in roots and crowns is important for recovery. Crested wheatgrass plants also were clipped to 5 cm on 10 May 1986 because crested wheatgrass stands often are grazed in the spring (Horton 1989).

Plants of *S. munroana* were sampled between 0800 and 1200 h to minimize the effects of diurnal fluctuations in TNC (Chatterton et al. 1972). Sampled plants were divided into roots, crowns, and shoots. Crowns included about 1.5 cm of root and stem. Following excavation of soil monoliths (30 × 30 × 30 cm), the shallow braided tap roots were carefully separated from the soil with hand tools. This method sampled only a portion of the root system because roots extended to a greater depth and radius than the soil monolith; however, it was a practical attempt to extract roots given limited resources. Likewise, small fine roots within the soil monolith were probably only partially sampled. These shortcomings mean that root pools were underestimated. Plant parts were washed in a series of three water-filled plastic tubs in the field and placed in a portable freezer (–7°C). Samples were transferred to another freezer (–18°C) at

the end of the day, where they were stored prior to chemical analyses.

Fifty-milligram subsamples of ground, lyophilized plant tissue were analyzed for TNC, as described by Chatterton et al. (1987). A commercial amylase preparation was used to digest starch in the tissue (0.1% Clarase 40,000 for 24 h at 38°C). TNC were determined colorimetrically and included starch and soluble carbohydrates. Plant weights were evaluated on a structural dry-weight basis, which is the plant part dry weight minus TNC. This method avoids errors associated with simultaneous changes in carbohydrate content and dry weight (Chatterton et al. 1987).

Additional 0.5-g subsamples of the plant tissue were digested in 3:1 nitric:perchloric acid, diluted (1:100) with water, and analyzed colorimetrically for P using the vanadomolybdate procedure (Greweling 1976). A second aliquot was further diluted (1:10) with 1 g La L^{-1} as $LaCl_2$ and analyzed for Ca and Mg by atomic absorption spectrometry, and for K by flame emission spectrometry (Greweling 1976). Total N was determined by the Kjeldahl procedure (Bremner 1965). The 29 May 1987 samples were inadvertently discarded before elemental analyses were done.

Etiolated Regrowth Study

This study was a 2 × 2 factorial in a completely randomized experimental design. Twenty globemallow plants were clipped on 11 May 1986 when the stems were elongating. Ten of these plants were covered with plastic buckets painted black on the inside and white on the outside. The other 10 plants were not covered and regrew under ambient light conditions. Twenty other globemallow plants were clipped on 21 July 1986 during seed shattering when growth was much slower, and when we expected TNC pools in the roots and crowns to be higher than in the spring. Again 10 plants were covered with buckets and the other 10 were not covered. All plants were harvested when etiolated regrowth was not apparent for 1 week, which was on 31 May and 25 August for plants clipped in the stems elongating and seed shattering stages, respectively. Harvested material was dried (60°C) and weighed. Because plants of *S. munroana* were selected from the experimental planting border in this study, they had three crested wheatgrass competitors, not four as in the previous study.

Statistical Analyses

Data were reduced and analyzed by analysis of variance with SAS (SAS Institute, Inc. 1985). Clipping was considered a fixed factor, and date of sampling was considered a random factor in the TNC and element study. Phenological stage and regrowth environment (light or dark) were considered fixed factors in the etiolated regrowth study. Single degree of freedom contrasts and protected least significant difference tests were used to determine

TABLE 1. Average effects of clipping on 10 May 1986 versus not clipping on seven response variable pools measured for globemallow roots, crowns, and shoots. Clipped versus unclipped plant means did not differ significantly for any response variable ($P > .05$; $n = 36$ for TNC and weight responses, otherwise $n = 30$). Whole-plant pools (the sum of root, crown, and shoot pools) also did not differ significantly due to clipping for any response variable.

Clipping treatment	TNC[a]			Weight			N		
	Root	Crown	Shoot	Root	Crown	Shoot	Root	Crown	Shoot
	mg			g SDW[b]			mg		
Clipped	1000	372	2163	10	8	28	64	51	232
Unclipped	995	479	2148	11	8	28	106	72	330

	P			K			Ca			Mg		
	Root	Crown	Shoot	Root	Crown	Shoot	Root	Crown	Shoot	Root	Crown	Shoot
	mg											
Clipped	13	9	46	142	83	445	176	115	414	35	25	117
Unclipped	17	10	51	145	95	473	191	116	433	34	25	109

[a]TNC = total nonstructural carbohydrate.
[b]SDW = structural dry weight (see Materials and Methods).

which means differed significantly. Differences were considered significant for all test statistics when $P \leq .05$.

RESULTS

Interactions between clipping treatment and sampling date were not statistically significant for TNC or element data. Moreover, clipping did not significantly affect experiment-long mean TNC, N, P, K, Ca, or Mg pools (Table 1). When averaged over all sampling dates, plant part weights (roots, crowns, shoots, or whole plants) also were not significantly affected by clipping.

The phenological stage by regrowth environment interaction was not significant in the statistical analyses of the etiolated regrowth data. However, *S. munroana* plants regrowing in the light produced significantly more shoot regrowth than plants regrowing in the dark (Fig. 1). The amount of regrowth did not differ significantly between the stems elongating and seed shattering stages.

Root TNC pools increased significantly between 7 June and 22 September, and between 22 September and 5 November (Fig. 2). Root TNC pools declined significantly during winter. Crown TNC pools were statistically constant until 22 September, increased significantly between 22 September and 5 November, and then declined significantly during winter. Shoot TNC pools tended to increase during the growing season, although this trend was not significant until 22 September. Unlike crowns and roots, shoot TNC pools declined significantly between 22 September and 5 November. Whole-plant TNC pools increased significantly between 1 May and 22 September, remained at a high level through 5 November, and then declined

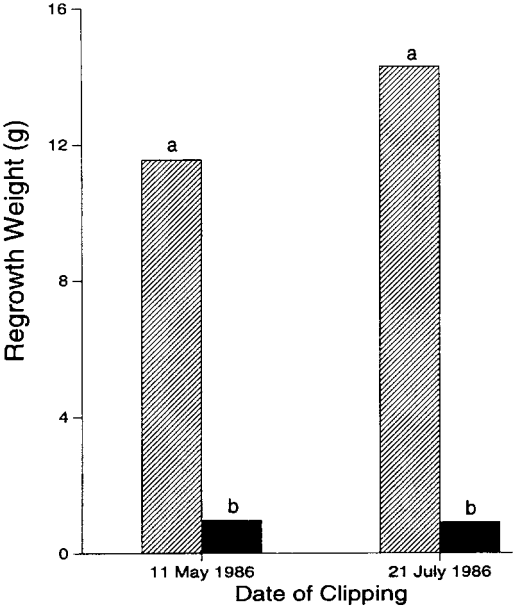

Fig. 1. Mean regrowth biomass of plants initially clipped 11 May and 21 July 1986 and regrown in sunlight (crosshatched bars) or in the dark (black bars) for 20 and 27 days, respectively. Plants were in the stems elongating and seed shattering phenological stages on 11 May and 21 July, respectively. Means with different letters differed significantly ($P \leq .05$, $n = 10$).

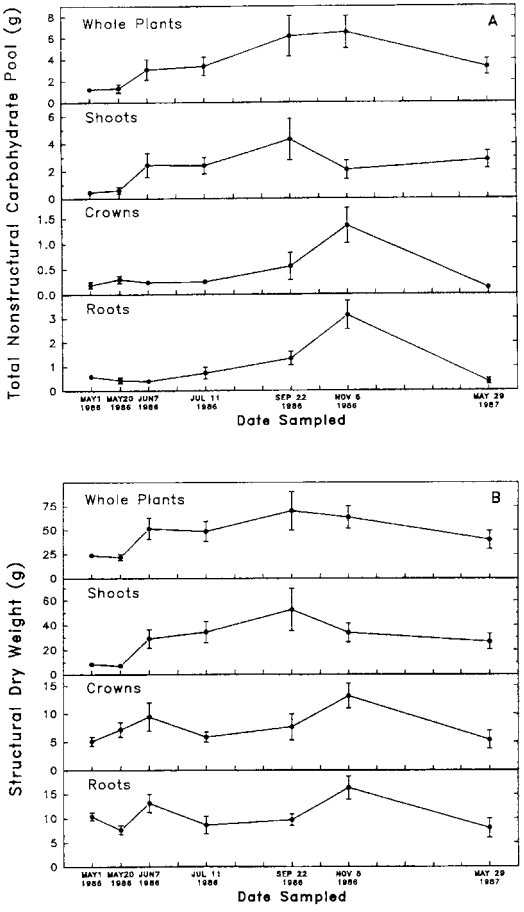

Fig. 2. Total nonstructural carbohydrate pools (A) and structural dry weights (B) of globemallow roots, crowns, shoots, and whole plants on seven sampling dates. Means (± 1 standard error) are the average of clipped and unclipped plants ($n = 12$). Structural dry weight was calculated by subtracting the total nonstructural carbohydrate pool from the plant part dry weight.

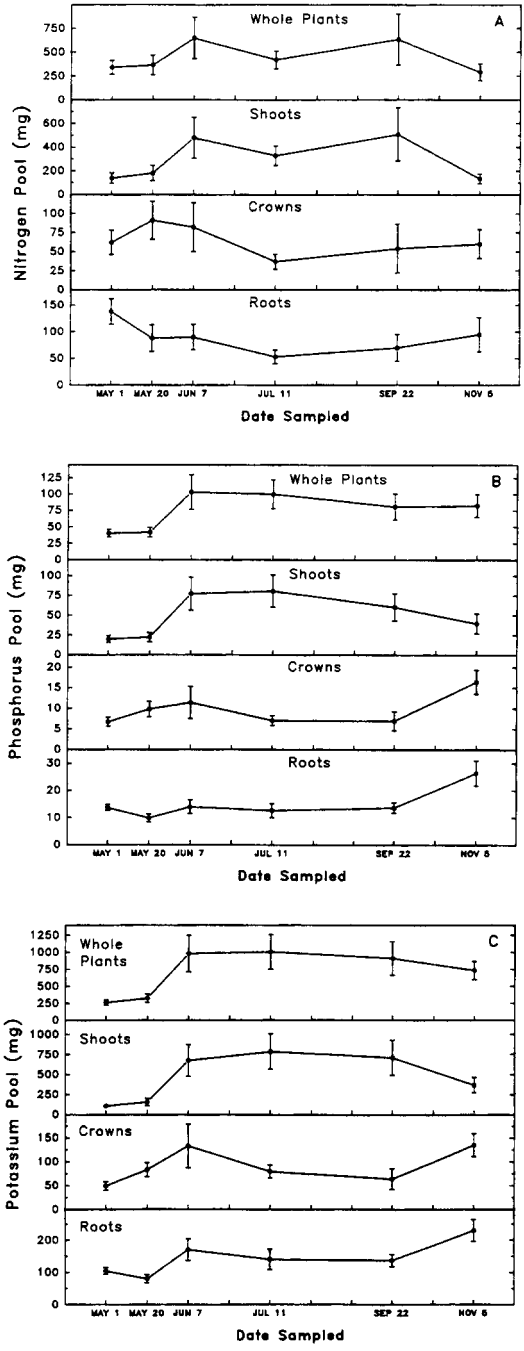

Fig. 3. Nitrogen (A), phosphorus (B), and potassium (C) pools in globemallow roots, crowns, shoots, and whole plants on six sampling dates in 1986. Means (±1 standard error) are the average of clipped and unclipped plants (n = 12).

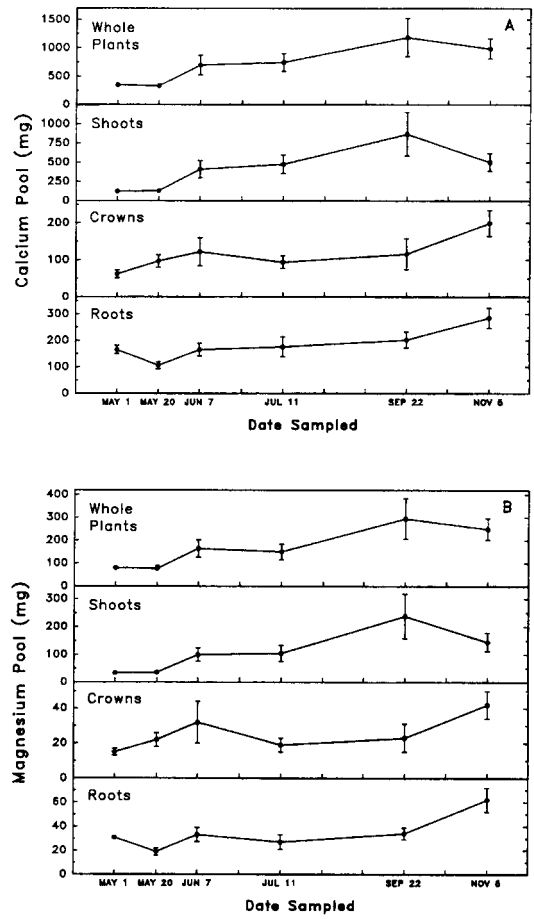

Fig. 4. Calcium (A) and magnesium (B) pools in globemallow roots, crowns, shoots, and whole plants on six sampling dates in 1986. Means (±1 standard error) are the average of clipped and unclipped plants (n = 12).

significantly during winter. Shoots contained the largest proportion of the TNC pool from 7 June to 22 September. Crowns and roots together were a relatively large soluble carbon pool on 1 May, 20 May, and 5 November.

Significant differences in element pools also were found on different dates (Figs. 3, 4). Root and crown pools were statistically constant between 1 May and 22 September, with the exception of root N pools. Root and crown P, K, Ca, and Mg pools increased significantly between 22 September and 5 November. Shoot element pools increased significantly between 1 May and 22 September. Shoot pools tended to decline from their seasonal highs by 5 November (significantly for N and P, nonsignificantly for K, Ca, and Mg).

DISCUSSION

Clipping Effects

The experimental planting and clipping treatment in our study simulated a crested wheatgrass stand interseeded with forbs in which all species are heavily grazed once annually, as in some rotational grazing systems. Our results indicated that a single grazing during the stems elongating phenological stage would not significantly affect average shoot weights of *S. munroana* during a 1-year period (Table 1). If low root and crown TNC pools in early May (Fig. 2) impair shoot recovery following a single spring grazing event, differences in clipped versus unclipped plant shoot weights should have occurred. While stored TNC were not important for long-term regrowth in this study, stored TNC may have contributed to short-term (1–7 days) recovery (Smith and Silva 1969, Richards and Caldwell 1985). Also, results might have differed had clipping been done at other phenological stages; however, this study was not designed to examine those questions.

Our results also showed that TNC in roots and crowns accounted for only 7% of the biomass in regrowing shoots following clipping during the stems elongating and seed shattering phenological stages (Fig. 1). We assume the remainder of the regrowth was derived from TNC produced by current photosynthesis. While root and crown TNC pools were not quantitatively large contributors to shoot regrowth, Richards and Caldwell (1985) pointed out that the efficiency with which a species allocates available carbon to aboveground meristems and utilizes the carbon for new foliage may be a key physiological feature determining the species' ability to tolerate defoliation by large grazing animals. We did not address meristematic limitations or the efficiency of TNC allocation to shoot regrowth in *S. munroana.*

While a 5-cm clipping height is frequently used in clipping studies (e.g., Richards and Caldwell 1985), it may be more severe than most grazing. Spring grazing by sheep in Utah caused most forbs to be defoliated once or twice and reduced the leaf area index by 55% (Hodgkinson 1980). Rumbaugh et al. (1993a) reported 75% utilization of globemallows grazed by sheep in small experimental pastures during the spring. We estimate our clipping treatment reduced leaf area about 90%. Moreover, if the plant community or herbivory pattern were more complex, interspecific and intraspecific differences in carbon accumulation and translocation efficiency could occur, which might affect responses to grazing and the competitive balance among species.

Trlica et al. (1977) found that *S. coccinea* plants clipped once during early or rapid growth had root and crown TNC concentrations that did not differ significantly from unclipped plants after 14 or 26 months. Menke and Trlica (1983) reported that *S. coccinea* plants clipped once at any of five phenological stages did not have significantly different root and crown TNC concentrations relative to control plants. They also found that TNC concentrations were reduced only when repeated clippings were applied.

Seasonal Trends

Root and crown TNC pools in *S. munroana* were relatively low through much of the growing season but exhibited a sharp increase in the fall (Fig. 2), which is similar to the trends for TNC concentrations for *S. coccinea* reported by Menke and Trlica (1981). However, Menke and Trlica (1981) predicted that species with "flat" or "extended" root and crown TNC cycles would be sensitive to defoliation unless they are rhizomatous, like *S. coccinea. S. munroana,* which had flat root and crown TNC cycles (Fig. 2), but which is not rhizomatous, was not significantly affected by a single severe defoliation (Table 1). The significant decline in shoot TNC pools between 22 September and 5 November, and the concomitant increase in root and shoot pools, probably reflected senescence and translocation of TNC to the roots and crowns for wintertime respiration.

Large increases in shoot element pools from mid-spring through summer (1 May–22 September), coincident with statistically constant root plus crown pools, indicated that elements were being absorbed from the soil or from portions of the root system not sampled (Figs. 3, 4). Increases in root plus crown pools during the fall (22 September–5 November) could have been met by translocation from senescing shoots, which had decreasing element pools during the fall. Chapin (1980b) and Chapin et al. (1980) reported that perennial

TABLE 2. Concentrations of total nonstructural carbohydrates (TNC) and five elements in globemallow shoots on seven sampling dates in Cache Valley, Utah. Means (±1 standard error) are the average of clipped and unclipped plants (n = 12).

Constituent	Sampling date						
	1 May 1986	20 May 1986	1 June 1986	11 July 1986	22 Sept. 1986	5 Nov. 1986	29 May 1987
	mg g^{-1}[a]						
TNC	52.5 ± 6.3	62.5 ± 11.0	72.8 ± 7.6	74.4 ± 7.2	84.2 ± 5.4	58.5 ± 5.8	115.7 ± 8.5
N	19.1 ± 3.6	15.2 ± 3.3	16.5 ± 3.5	11.6 ± 2.1	7.8 ± 2.1	6.4 ± 2.0	—
P	2.6 ± 0.3	2.3 ± 0.2	2.6 ± 0.1	2.2 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	—
K	11.4 ± 0.9	15.5 ± 1.3	21.2 ± 0.8	20.1 ± 0.5	13.0 ± 0.7	10.3 ± 0.6	—
Ca	14.1 ± 0.6	13.9 ± 0.9	13.5 ± 0.7	12.8 ± 0.5	17.0 ± 1.1	14.8 ± 0.8	—
Mg	4.1 ± 0.2	3.9 ± 0.2	3.4 ± 0.2	2.7 ± 0.1	4.1 ± 0.1	4.3 ± 0.3	—

[a]TNC concentrations are on a structural dry weight basis (see Materials and Methods).

plants of infertile habitats support spring growth more by drawing on stored nutrients than by concurrent absorption from the soil. Depleted nutrient reserves are gradually replenished during the summer by absorption from the soil and during the autumn by translocation from senescing leaves.

Element levels expressed as concentrations are useful for consideration of the nutritional value of *S. munroana* shoots to herbivores (Table 2). For cow-calf livestock operations these nutrient concentrations are likely low to adequate (Church 1988). Rumbaugh et al. (1993b) found that swards of crested wheatgrass and globemallow were nutritionally adequate for livestock in spring and fall. The accession of *S. munroana* used in this study was also studied by Rumbaugh et al. (1993b), and they found somewhat higher N, P, K, Ca, and Mg concentrations in this accession at their Idaho study site than we did at our Utah study site.

Shoot N, P, and K concentrations were highest in the spring and lowest in the fall (Table 2). Shoot TNC concentrations tended to be higher in the summer and fall than in the spring. Chapin et al. (1986) found that tundra herbivores selected plants with high N, P, and K concentrations during early growth but generally did not select plants high in leaf TNC. They interpreted this as indicating nutrients were more important than energy in summer forage selection. Rumbaugh et al. (1993a) found that consumption of globemallows (including the accession of *S. munroana* used in this study) by sheep was significantly higher in the spring than in the fall, and Rumbaugh et al. (1993b) reported that utilization appeared to be positively influenced by leaf N concentrations and stem Ca:P ratio.

Chapin et al. (1986) found that N, P, and K concentrations were positively correlated with each other in leaves. They found that TNC concentrations were weakly and negatively correlated with N, P, and K concentrations. We found significant positive correlations among N, P, and K concentrations in shoots (Table 3). Concentrations of N and P were not significantly correlated with TNC concentration; however, K had a significant positive correlation with TNC.

SUMMARY AND CONCLUSIONS

A single, severe spring clipping when root and crown TNC pools were low did not significantly affect the average shoot weight of *S. munroana* through a 1-year period. Experiment-long TNC, N, P, K, Ca, and Mg pools in the roots, crowns, shoots, and whole plants of *S. munroana* also were not significantly affected by clipping. The etiolated regrowth experiment showed that TNC in roots and crowns accounted for only 7% of the shoot biomass in globemallow regrowing after clipping. These results indicate that *S. munroana* shoot recovery from a single spring grazing through a 1-year period would not be impaired by low root and crown TNC pools, and that TNC in

TABLE 3. Pearson correlation coefficients (r) among globemallow shoot weight, total nonstructural carbohydrate (TNC) concentration, and five element concentrations.

	TNC	N	P	K	Ca	Mg
Wt.	.18	–.23	–.34**	.02	–.17	–.11
TNC	—	.10	–.09	.25*	.14	–.20
N		—	.60**	.29*	.16	.09
P			—	.49**	–.09	–.03
K				—	–.08	–.44**
Ca					—	.42**
Mg						—

*$P \leq .05$.
**$P \geq .01$.

the roots and crowns would not make a quantitatively large contribution to regrowth. TNC and element pools of roots and crowns were generally constant from May to September but increased from September to November. TNC and element pools in shoots increased from May to September and then generally declined by November. TNC pools of roots and crowns declined during winter.

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