Nutritional and Physical Attributes of Seeds of Some Common Sagebrush-steppe Plants: Some Implications for Ecological Theory and Management

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A study was conducted to identify seed attributes which might influence granivore preferences. Physical and chemical characteristics were estimated for seeds of 7 common sagebrush-steppe species *(Artemisia tridentata, Bromus tectorum, Oryzopsis hymenoides, Pascopyrum smithii, Purshia tridentata, Stipa comata* and *Stipa viridula)* and 1 sacrifice food species *(Panicum miliaceum).* Seed weights and caloric contents were determined, as well as % composition contributed by 5 organic, 3 inorganic and 5 synthetically defined fractions (including crude protein, solvent extract, structural and soluble carbohydrates and lignin). Results indicate that % soluble carbohydrate may be a good predictor of granivore seed preference. The generality of this or any other predictor is unknown, since sufficiently detailed seed attribute data are unavailable for most species. For management scenarios involving seeds subject to predation, such data would help effectively translate ecological understanding of granivory into more efficient management practices.

In any land management effort involving direct seeding or depending upon the natural input of seeds, the manager must consider those biotic and abiotic factors which may ultimately affect the successful establishment of the desired vegetation. While abiotic influences such as seedbed characteristics, germination requirements, and soil nutrient levels have been routinely acknowledged and manipulated, biotic interactions affecting the seeds have often been ignored.

One biotic factor which may limit plant establishment is granivory, the consumption of seeds by animals. Since the publication of Janzen's (1971) pivotal review of seed predation by animals, awareness of the potential importance of granivory in the structure and functioning of many ecosystems has expanded and matured. Yet despite the considerable research already conducted, relatively little attention has been devoted to the integration of ecological studies of granivory with vegetation management. Rangelands may be particularly appropriate systems for attempting such an integration, since they occur in relatively xeric habitats, where seeds may be an important food resource ". . .coupling primary production to the infrequent, unpredictable precipitation that limits the productivity of most arid ecosystems" (Brown et al. 1979). Insects (especially ants), birds, and small mammals consume large quantities of seeds on native rangelands (Nelson et al. 1970, Pulliam and Brand 1975, Goebel and Berry 1976, Everett et al. 1978, Whitford 1978) and manipulative field studies have demonstrated that granivores, via their seed selection, can affect the species composition of their plant community (Inouye et al. 1980). It follows, then, that understanding patterns of granivory might contribute significantly to the success of a rangeland management scheme employing seeds.

Our interest in granivory dates from 1981, when we conducted an experiment in which seeds of 6 common indigenous range plant species were offered to granivores at a sagebrush-steppe site near Kemmerer, Wyo., in order to determine granivore seed preferences (Kelrick et al., submitted). One objective of our studies was to examine possible correlations between the observed seed preference hierarchies and some commonly measured attributes of food items—e.g., calories per item, % crude protein, or % available carbohydrate. However, barring our ignorance of some particularly pertinent literature source, it appears that few data on native seeds are available beyond estimates of numbers of seeds per pound. Therefore, we generated the seed data, which include estimates of seed weight, calorimetric content, and % composition of the seeds as contributed by the major classes of organic compounds (proteins, lipids, and carbohydrates) as well as several other relevant organic subclasses and inorganic compounds. We present these data below.

In addition to being of some documentary value, these seed attribute data have promising potential applications. Knowledge of the factors which cause an animal to choose one seed species over another would allow the development of a powerful predictive management tool. If one could elucidate a relationship between seed chemical characteristics and the preferences of various seed predators, then such a predictor would be available for evaluation in a variety of field situations, including managed lands. Thus, quantitative seed data such as those presented below may serve to extend studies of the ecological relationships of granivory into the realm of management practice.

Materials and Methods

Seeds of these plant species were studied: big sagebrush *(Artemisia tridentata),* cheatgrass *(Bromus tectorum),* Indian ricegrass *(Oryzopsis hymenoides),* millet *(Panicum miliaceum),* western wheatgrass *(Pascopyrum [Agropyron] smithii),* bitterbrush *(Purshia tridentata),* needle-and-thread *(Stipa comata),* and green needlegrass *(Stipa viridula).* All seeds were obtained from Native Plants of Utah, Inc. (Salt Lake City, Utah) except those of cheatgrass and some seeds of needle-and-thread, which were collected near Kemmerer, Wyo., at the site described in Parmenter and MacMahon (1983), and those of millet, which were purchased at a local grocery.

The native species examined were selected to satisfy 3 criteria defined by goals of the preference study (Kelrick et al., submitted): (1) the species were present on or near our study site, (2) the set of seeds provided a large range of sizes, and (3) the seeds were available from a commercial supplier. Since we expect that both physical characteristics and nutritional/chemical attributes vary among individual parent plants and parent populations, as well as between years, using purchased seeds collected from areas other than our study site had unknowable effects on granivore seed choice. In acknowledging this uncertainty, we also identify a need to quantify

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such variability in order to more fully understand future manipulations of seed resources.

In this paper, the term "seed" is not employed in the strict botanical sense. Propagules of all 8 plant species studied include a variety of nonovarian tissues, thus they are fruits (Fig. 1). The

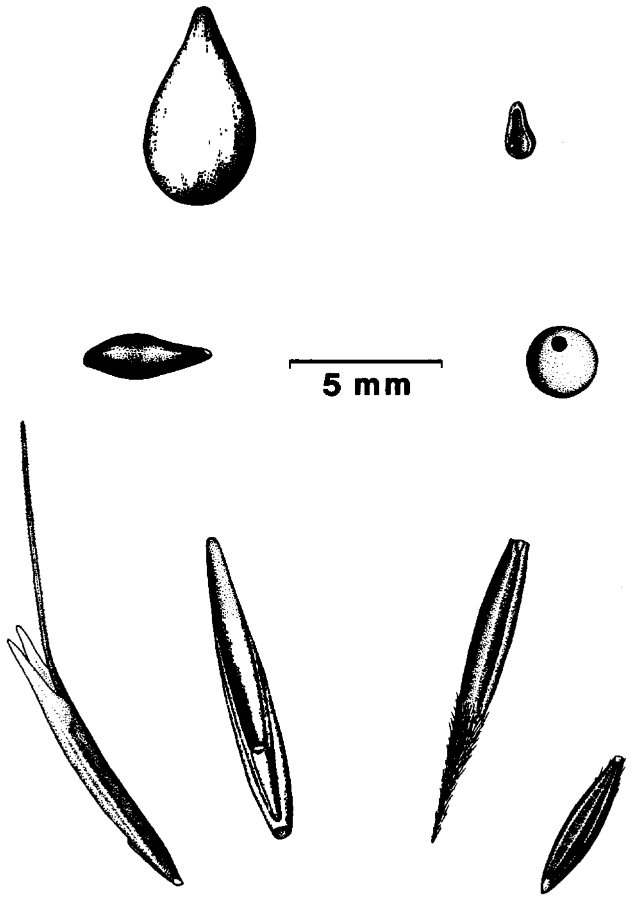

Fig. 1. *Depiction of "seeds" as offered to granivores and as used for analyses described in the text. Species (tissue descriptions) are, l. to r.: top row (shrubs)*—Purshia tridentata *(bare achene),* Artemisia tridentata *(bare achene); middle row (grasses)*—Oryzopsis hymenoides *(caryopsis and indurate palea and lemma),* Panicum miliaceum *(bare caryopsis); bottom row (grasses)*—Bromus tectorum *(caryopsis and palea and lemma, with persistent awn),* Pascopyrum smithii *(caryopsis and palea and lemma),* Stipa comata *(caryopsis and palea and lemma, long awn usually absent or incomplete, sharp callus),* Stipa viridula *(caryopsis and palea and lemma, awn not persistent).*

distinction between fruit and seed is presumably a significant factor influencing granivore preference because the tissue which differentiates the 2 may enhance or detract from the "seed's" desirability as a food item. Seed size and shape may also play a role in granivore recognition and/or selection (e.g., see Harper et al. 1970, Pulliam and Brand 1975). Therefore, clear characterization of the tissues constituting the food items being consumed is important for understanding granivore seed selection.

A literature search provided data on seed weights for all 8 species. In addition, we produced our own estimates by averaging the weights of 5 groups of 100 seeds each for each seed species except sagebrush, for which 10 groups of 100 seeds each were measured to improve the precision of the estimate for these relatively small seeds.

Calorimetric measurements were obtained using a Phillipson microbomb calorimeter, according to guidelines proposed by Paine (1971). The average of 2 consecutive determinations was accepted as the caloric estimate if the individual deviations of the 2 determinations from the mean value were <2% of that value. Determinations of % ash were obtained by averaging the results of 3 replicate oven-dry subsamples ashed at 500°C for 3 hrs.

We encountered published values for only certain of the chemical attributes we wished to know for a subset of the seeds of interest. Values of % of oven-dry weight of protein (N × 6.25) and oil (ether extract) were, respectively: for *Bromus tectorum,* 14.1 and 1.2 (Barclay and Earle 1974); for *Oryzopsis hymenoides,* 11.9 and 2.2; and for *Stipa viridula,* 30.6 and 3.1 (Earle and Jones 1962). Extensive data describing millet seeds (e.g., Ellis 1939, Atlas of nutritional data on U.S. and Canadian feeds 1971) are more generally available than those for native seeds because the former are used as commercial feeds. Our literature search did not provide data sufficient for conducting the planned correlation analyses. Furthermore, since the jargon and techniques used and/or the particular chemical fractions measured may differ among literature sources, the data we found are not necessarily comparable. Even a comparatively well-defined attribute such as % ash can vary in value according to temperature and duration of the combustion process (Paine 1971). The contents of a fraction labeled "lipids" may be much less comparable, varying both biochemically (with the use of different solvents) and nutritionally (e.g., Are phospho- and glycolipids included?). To solve these problems, we sought to produce a methodologically consistent set of nutritional/chemical data for all 8 seed types.

Our seeds were analyzed by the laboratory of the International Feedstuffs Institute, Utah State University, Logan, Utah. Except for the determination of % crude protein (estimated by % kjeldahl N × 6.25), techniques used are described in Fonnesbeck (1976). Duplicate analyses were performed on each of 2 subsamples for each seed type. For 4 seed types, means of % solvent extract were calculated from only 3 of the 4 determinations because 1 measurement in each set was deemed unreliable by laboratory standards.

These particular laboratory analyses provide information on several chemical components which are not routinely measured in studies of seeds. However, Fonnesbeck (1976) suggests that the components measured with this analytical procedure allow a more realistic appraisal of the value of a food item to its consumer than those previously measured; thus, they should facilitate an examination of the appeal of particular seeds to granivores. Some of the components were measured directly in the laboratory, while others are derived by linear combinations of the laboratory values. The list below contains the names, definitions and explanations of the attributes we examined. Those attributes derived by algebraic combination have the appropriate calculation shown in parentheses after the attribute name.

Dry matter—The weight of the sample expressed as a % of the weight of the original sample in the air-dry state, *after* the sample has been in a 105°C oven for ~ 16 hr. Except for the estimate of % free water, all attribute values are expressed on the basis of dry matter, i.e., dry weight = 100%.

Free water— (100% - dry matter) —This water corresponds to the weight loss of the sample during the drying process at 105°C and represents the free water directly available to a granivore upon consumption of a seed, as contrasted with that water which is metabolically derived.

Cell walls—Structural carbohydrates (largely cellulose and hemicellulose), lignin, and acid insoluble ash constituents such as silica comprise this fraction. Ideally, and in this analysis practically, this fraction should be protein-free for an accurate estimate to be obtained. It is largely nonnutritive for most consumers (exceptions are taxa with appropriate gut microflora).

Structural carbohydrates—This cellulose and hemicellulose fraction probably includes some variable quantity of assimilable carbohydrate, depending on the consumer organism.

Lignin—This is a plant secondary cell wall component which is normally considered to be nonnutritive, or even a deterrent to consumption.

Acid insoluble ash—Primarily silica, this is the portion of the total ash (= inorganics) which does not dissolve in a strong acid. It is especially prevalent in the tissues of monocots. Although of no nutritive value, its abrasive properties may deter some granivores and herbivores.

Ash—This represents that % of the dry matter remaining after the sample has been heated to ~600°C for ~8 hr, a mixture of soluble inorganic salts and insoluble compounds like silica.

Crude protein—(Kjeldahl N × 6.25).

Solvent extract—This fraction contains both nutritive and nonnutritive material. Its % contribution routinely exceeds the widely used ether extract value, since the former includes lipids separated from molecules, e.g., lipoproteins, by a dehydrating solvent (methanol).

Soluble ash—(ash - acid insoluble ash) —This represents that portion of the total ash considered to be of nutritive value.

Cell contents—(100% - cell walls).

Soluble carbohydrate—(cell contents - [crude protein + solvent extract + soluble ash]) —This fraction is that portion of the cell contents which is *not* crude protein, solvent extractable lipids or soluble inorganics and which presumably corresponds to carbohydrate which is assimilable by a granivore.

Nonnutritive matter—(lignin + acid insoluble ash) —Both lignin and silica are here considered to be of no nutritional value.

Results

Table 1 presents the seed weight data. Since seed weight is considered one of the least phenotypically plastic attributes of a particular plant species (Harper 1977), one would have predicted good agreement among the various literature values and those we obtained. While this was generally the case, certain species (*Artemisia tridentata, Oryzopsis hymenoides,* and *Stipa viridula)* display considerable variability. This may be due in part to the inconsistency among the sources cited of the entity being weighed. (Again, we stress the need to clarify whether the seed was used, or rather the seed plus some investing structure[s] which in nature form the propagule shed from the parent plant.) Additionally, some species do exhibit the production of a relatively wide range of seed sizes by an individual parent or an entire population (Harper 1977).

Table 1. Literature and authors' values of number of seeds per g. of 8 species.

	No. seeds/g.	
Species	Literature values[1]	This study[2]
Artemisia tridentata	5437 (A), 5679 (B)	4346 (146)
Bromus tectorum	459 (C), 385 (D)	491 (6)
Oryzopsis hymenoides	311 (C), 417 (E), 415 (B) 310 (F), 355 (G)	261 (5)
Panicum miliaceum	181 (C), 180 (F), 185 (G)	172 (4)
Pascopyrum smithii	243 (C), 235 (F), 250 (G)	217 (5)
Purshia tridentata	34 (A), 34 (B)	37 (1)
Stipa comata	254 (C)	178 (3)
Stipa viridula	399 (C), 556 (E), 370 (G)	308 (6)

[1]Letters in parentheses indicate sources: (A) U.S. Forest Service, USDA (1974), (B) Plummer et al. (1968), (C) USDA Yearb. Agric. (1948), (D) Barclay and Earle (1974), (E) Earle and Jones (1962), (F) Ellis et al. (1939), (G) Association of Official Seed Analysts (1981).
[2]Means rounded to nearest whole numbers and the standard error (SE) of groups of 100 seeds (n = 5 for all species except *A. tridentata,* for which n = 10).

Calorimetric values for the 8 species of seeds are listed in Table 2. Values for calories per seed (ash-free) were obtained using this study's estimates of seed weights. Also included in this table are 2 sets of calculated values estimating the daily seed demand exerted by a single granivorous rodent, based on the caloric content of seeds of each species.

The complete set of chemical analyses of seeds from our laboratory determinations is presented in Table 3.

Discussion

A number of ecological insights can be obtained using these data. For example, given an estimate of the daily energy requirement of a particular granivore species, the number of seeds of a particular plant species necessary to provide that amount of energy can be calculated. In Table 2 such calculations are presented using the deermouse *(Peromyscus maniculatus),* a common rangeland granivore. Data are calculated from the daily energy budget of *Peromyscus* as estimated by Parmenter et al. (1984). Numbers of seeds were estimated on the basis of both total seed caloric content and calories generated by the soluble carbohydrate fraction alone. These are conservative estimates, since a deermouse cannot be expected to extract calories as efficiently as a calorimeter. The group of estimates based on the soluble carbohydrate fraction may more realistically reflect the seed demand of a strictly granivorous deermouse, since, at least for some domestic and laboratory animal taxa (sheep, swine, and rats), the % soluble carbohydrate of a food item is highly positively correlated with the digestible energy of that item (Fonnesbeck 1976).

By making the simplistic assumption that granivores choose food items strictly to maximize calories acquired per item, the estimates of seed numbers in Table 2 can serve to formulate predictions of granivore seed preference. Combined with plant species-specific estimates of seed handling times (see Kaufman and Collier

Table 2. Estimates of 1) the caloric content of seeds of 8 species on a per g. seed basis, both unadjusted and adjusted for seed ash content, and on a per seed basis and 2) numbers of seeds of those species providing approximately 7.56 kcal (an estimate of the daily energy requirement of an individual deermouse).

	Calorimetric data				Calculated number of seeds to provide 7.56 (kcal)	
Species	Calories per g. seed[1]	% ash[2]	Calories per ash-free g. seed	Calories per seed (ash-free)[3]	Total caloric content basis	Soluble carbohydrate fraction basis[4]
Artemisia tridentata	4348.8 (.13)	5.3 (.02)	4592.2	1.1	7132	130027
Bromus tectorum	3743.2 (1.57)	4.3 (.12)	3911.4	8.0	949	2175
Oryzopsis hymenoides	4058.0 (.24)	3.6 (.14)	4209.6	16.1	469	1230
Panicum miliaceum	4218.0 (.36)	1.2 (.08)	4269.2	24.8	305	411
Pascopyrum smithii	4288.3 (.75)	6.7 (.04)	4596.2	21.2	357	1279
Purshia tridentata	5598.3 (1.83)	2.3 (.42)	5730.1	154.9	49	134
Stipa comata	4181.1[5]——	5.8 (.46)	4438.5	24.9	304	880
Stipa viridula	4697.1 (.43)	4.6 (.01)	4923.5	16.0	473	1541

[1]Mean (% deviation); n = 2.
[2]Mean (SE); N = 3.
[3]Based on this study's number of seeds per g. (Table 1).
[4]Caloric content of soluble carbohydrate is taken as 4.10 kcal per ash-free g. (Paine 1971).
[5]Based on 1 sample only.

Table 3. Estimates of the contribution (as % of total weight) of various chemical components of the seeds of 8 species (<0.05% = TR).

Species	Dry matter[1,3]	Free water[1]	Cell walls[2,3]	Structural carbohydrates[2,3]	Lignin[2,3]	Acid insoluble ash[2,3]	Ash[2,3]	Crude protein[2,3]	Solvent extract[2,3]	Soluble ash[2]	Cell contents[2]	Soluble carbohydrate[2]	Nonnutritive matter[2]
Artemisia tridentata	93.7	6.3	37.4	12.2	25.1	0.2	5.4	31.1	20.1*	5.2	62.6	6.2	25.3
	(0.13)		(1.66)	(0.41)	(1.24)	(0.10)	(0.05)	(0.73)	(0.42)				
Bromus tectorum	92.1	7.9	43.2	36.3	4.8	2.0	4.8	10.1	2.5	2.8	56.8	41.4	6.8
	(0.12)		(1.93)	(1.57)	(0.23)	(0.28)	(0.08)	(0.19)	(0.10)				
Oryzopsis hymenoides	92.6	7.4	43.1	32.2	8.4	2.5	4.5	13.1	2.8*	2.0	56.9	39.0	10.9
	(0.11)		(0.29)	(0.85)	(0.57)	(0.12)	(0.15)	(0.19)	(0.13)				
Panicum miliaceum	90.5	9.5	2.2	1.8	0.5	TR	1.5	13.8	5.6	1.4	97.8	77.0	0.5
	(0.16)		(0.21)	(0.17)	(0.04)		(0.05)	(0.08)	(0.56)				
Pascopyrum smithii	92.5	7.5	51.2	39.3	7.9	4.1	7.0	11.1	3.6*	2.9	48.8	31.2	12.0
	(0.19)		(0.81)	(0.70)	(0.26)	(0.07)	(0.05)	(0.09)	(0.09)				
Purshia tridentata	91.7	8.3	10.9	6.8	4.1	TR	2.3	14.8	21.4	2.3	89.1	50.6	4.1
	(0.06)		(1.39)	(0.34)	(1.08)		(0.04)	(0.25)	(0.45)				
Stipa comata	92.1	7.9	35.7	26.0	6.4	3.3	6.5	19.3	4.7*	3.2	64.3	37.1	9.7
	(0.14)		(0.72)	(0.55)	(0.27)	(0.11)	(0.15)	(0.19)	(0.85)				
Stipa viridula	92.3	7.7	40.0	27.6	9.3	3.1	4.8	18.3	3.2	1.7	60.0	36.8	12.4
	(0.12)		(0.15)	(0.15)	(0.13)	(0.13)	(0.07)	(0.37)	(0.07)				

[1]Expressed as % of air-dry weight.
[2]Expressed as % of oven-dry weight.
[3]Means, with SE below in parentheses; n = 4 except for asterisked solvent extract values, for which n = 3.

1981), these data also provide a basis for comparing observed granivore seed selection hierarchies with an optimal foraging scheme as suggested by Pyke et al. (1977). Additionally, with population density estimates of granivore taxa, these data might be used to predict the potential granivore impact on the seed resource of a given plant community.

Such theoretical queries have numerous management counterparts. Estimates of granivore seed demand (Table 2) along with estimates of granivore density enable a vegetation manager to account for potential pregermination seed losses due to predation. To accommodate predicted seed losses, seeding rates could be adjusted to exceed potential granivore demand or sacrifice food items could be offered with the introduced seeds of the desired vegetation (Everett et al. 1978). Although foresters have explored this latter tactic (Sullivan and Sullivan 1982), it appears that range managers have not (Everett et al. 1978).

Our attempt to identify a predictor of granivore seed preference from among several of the seed chemical fractions (Table 3) resulted in the choice of soluble carbohydrate. We used Spearman's rank correlation (Conover 1980) to analyze the relationship between granivore seed preference hierarchies among 6 indigenous seed species *(A. tridentata, B. tectorum, O. hymenoides, P. smithii, P. tridentata* and *S. viridula)* and 9 seed attributes (free water, structural carbohydrates, crude protein, solvent extract, cell contents, soluble carbohydrate, nonnutritive matter, total calories/ash-free g and calories/seed [ash-free]). Percent soluble carbohydrate was the seed attribute with the largest value of Spearman's correlation coefficient for the preference hierarchy of all granivores (rodents, birds and ants) combined ($r_s \simeq .829$, $P < .05$; Kelrick et al. [submitted]).

This indication that % soluble carbohydrate could be considered a predictor of seed appeal is supported by several independent data. Comparisons of granivore consumption of millet seed versus seeds of indigenous plants at a variety of arid sites in the southwestern U.S. showed that millet seeds were unequivocally preferred over even the most highly preferred among the indigenous seeds (Parmenter et al. 1984, Kelrick et al. [submitted]). The former are markedly higher in % soluble carbohydrate than the seeds of any of the range species studied herein (Table 3), and although chemical attribute data are presently unavailable for the hot desert seed mixture used by Parmenter et al. (1984), we expect that none of these seeds demonstrate % soluble carbohydrate values exceeding that of millet seeds. The strong positive correlation between % soluble carbohydrate and digestible energy mentioned earlier (Fonnesbeck 1976) also corroborates the results of our correlation analyses. Servello et al. (1983) investigated the digestibility of the natural herbaceous diet of pine voles *(Microtus pinetorum),* and reported a similar positive correlation between the digestible energy of the voles' forage and a "cell solubles" fraction containing ". . .lipids, soluble carbohydrates, most protein and other water-soluble matter" (Van Soest 1967). We believe it reasonable to suspect that % soluble carbohydrate would be the best predictor of digestible energy among the fractions composing "cell solubles", even though the data of Servello et al. (1983) describe the consumption of the plant parts other than seeds. Finally, Everett et al. (1978) have reported that the ubiquitous deermouse, by far the most abundant granivore in our study area (Parmenter and MacMahon 1983), prefers the seeds of *P. tridentata,* which have the highest % soluble carbohydrate among those indigenous seeds we offered to granivores (Table 3).

Having identified a predictor of granivore preference and assumed its validity, it is straightforward to choose seeds which might be appealing sacrifice foods or to predict which seeds of desired vegetation risk the highest predation losses before plant establishment. Field tests are then needed to define the utility of such a predictor. Such a study was conducted by Sullivan and Sullivan (1982) in which sunflower seeds were provided to rodents during a lodgepole pine seeding operation. After 3 weeks, rodents (mainly deermice) consumed ~85% of pine seeds sown in plots where no sunflower seeds were introduced, but when a ratio of 2 sunflower seeds to 1 pine seed was used, pine seed survival was 42–72% after 6 weeks. Based on the reasoning and results described in this paper, we would propose as a naive working hypothesis that sunflower seeds are higher in % soluble carbohydrate than lodgepole pine seeds. Verification of this prediction or the elucidation of some other predictive relationship depends on the availability of adequately detailed seed attribute data like those presented herein. Manipulations such as providing a sacrifice food (Sullivan and Sullivan 1982) show considerable promise for managing certain rangelands of small areal extent such as the revegetation of mined lands. We assert, in addition, that with further knowledge of the factors which cause an animal to choose one particular seed species over another, we could improve our management efficiency.

In conclusion, we submit that the same lack of data which originally inspired our studies precludes assessing the generality of the seed data presented in this paper. Thus, similar analyses of these same species may be necessary to understand patterns of granivory in environments other than the one we studied. Moreover, it seems clear that accurate tissue characterization of seeds studied as well as detailed, species-specific quantitative seed attribute data are valuable for interpreting observed patterns of granivory and developing the predictive capability sought by ecologists and managers alike.

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