Mass Loss as an Index of Seed Deterioration in a Terrestrial Environment

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Abstract: Deterioration of seeds due to weathering may affect the quantity and quality of food available for granivorous wildlife through time. Deterioration rates of seeds during field weathering in terrestrial environments largely are unknown, and the relationship between seed mass loss and loss of specific nutrients during weathering has not been tested. We documented losses of overall mass and masses of 7 nutrients in selected seeds during field weathering and tested the relationships between overall mass loss and loss of individual nutrients and between overall mass loss and seed water and fiber contents. Most seeds lost mass during weathering; seeds of cultivated species lost mass more rapidly than those of wild species. Fat, nitrogen-free extract (NFE), protein, and hemicellulose declined in most seeds with weathering as well. Overall mass loss in seeds was positively correlated with loss of fat, NFE, protein, ash, and water but was not related to seed water or fiber content. Mass loss generally appears to be a valid index of terrestrial seed deterioration. Rapid seed deterioration and/or germination may limit the usefulness of cultivated species in food plantings for granivorous wildlife.

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Production of seeds as food is an important component of habitat management for waterfowl, mourning doves *(Zenaida macroura),* northern bobwhites *(Colinus virginianus),* and other granivorous species. Deterioration of seeds due to weathering and associated decomposition may have considerable impacts on food quantity and quality. Although several studies have indexed deterioration rates of selected seeds important as waterfowl foods under aquatic (flooded) conditions (Neely 1956, McGinn and Glasgow 1965, Shearer et al. 1969, Nelms and Twedt 1996), only 2 studies have indexed seed deterioration under terrestrial conditions (McGinn and Glasgow 1965, Preacher 1978). With 1 exception, all seed deterioration studies in either environment have used mass loss as an index of seed deterioration. McGinn and Glasgow (1965) used seed "soundness," as determined by thumbnail pressure or cutting with a sharp instrument, to index deterioration. Although authors generally have assumed that mass loss reflects loss of important nutrients in seeds (Nelms and Twedt 1996), we are aware of only 1 published study documenting nutritional changes in seeds with

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field weathering (McGinn and Glasgow 1965) and none that has examined the relationship between seed total mass loss and specific nutrient losses.

Available evidence indicates that both seed mass and nutritional composition vary with age and exposure. Studies have shown that seeds exposed to field weathering generally lose mass under both aquatic and terrestrial conditions (Neely 1956, McGinn and Glasgow 1965, Shearer et al. 1969, Preacher 1978, Nelms and Twedt 1996). Additionally, seed storage experiments have indicated that sugar, starch, lipid, and protein levels generally decrease in some seeds with age (Ching and Schoolcraft 1968, Vertucci 1992, Madhava Rao and Kalpana 1994, Locher and Bucheli 1998). These changes are exacerbated by increased temperature and relative humidity (Ching and Schoolcraft 1968, Locher and Bucheli 1998). Evidence of seed nutritional changes under natural conditions is less clear. If percentage composition (by mass) of individual nutrients in seeds is stable during weathering, mass loss of a seed sample reflects proportional loss in mass of each nutrient in the sample. McGinn and Glasgow (1965) concluded that effects of field weathering on relative percentage composition of nutrients in seeds "appeared negligible," and subsequent authors have cited theses stable percentages of nutrients in seeds as evidence that mass and nutrient losses in seeds are likely correlated (Nelms and Twedt 1996). However, the cited study did indicate negative trends in percentage content of some nutrients, notable nitrogen-free extract (NFE; carbohydrate). If percentage composition of some nutrients in seeds changes during weathering, total mass loss of seeds may not be correlated with losses in mass of all nutrients.

Effective habitat management for terrestrially-feeding granivorous wildlife species requires consideration of factors affecting the quantity and quality of food available through time. The usefulness of deterioration studies in assessing impacts of seed deterioration depends on the extent to which the index of deterioration used actually reflects seed nutritional quality. Our primary goals were to document patterns of mass loss among seeds commonly eaten by terrestrial granivores in the southeastern United States and elsewhere and to evaluate mass loss as an index of seed nutritional loss. We also wanted to compare the relative appropriateness of linear and exponential models for representing seed mass loss because previous authors have disagreed in this regard (Neely 1956, Nelms and Twedt 1996). We expected rate of mass loss of seeds to be greatest early in the weathering process and to decline thereafter, so we predicted that an exponential model would be more appropriate than linear model for modeling mass loss. Additionally, we wanted to test the hypothesis that seed losses during weathering are affected by both water and fiber content of seeds. This hypothesis is suggested by evidence that nutrient loss with seed age is species-specific (Madhava Rao and Kalpana 1994) and influenced by seed moisture content (Ching and Schoolcraft 1968) and that wild seeds generally are both higher in fiber content and more resistant to deterioration than are seeds of cultivated species (Dillon 1961, Hayslette and Mirarchi 2001). We predicted a negative relationship between seed mass change and moisture content, and a positive relationship between mass change and fiber content.

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Methods

We studied deterioration of seeds of species commonly cultivated as wildlife foods and seeds of wild species commonly eaten by granivorous wildlife in Alabama at the North Auburn Research Unit of the Alabama Agricultural Experiment Station (AAES) during September–December 1997 and September–January 1998–99. White proso millet, browntop millet, wheat, corn, broadleaf signalgrass *(Brachiaria platyphylla),* common ragweed *(Ambrosia artemisifolia),* and yellow bristlegrass *(Setaria lutescens)* were used during the first year. Sunflower, milo, and common barnyardgrass *(Echinochloa crusgalli)* replaced wheat, corn, and common ragweed the second year. Beginning on 17 September each year, seeds were subjected to deterioration in 3 1.8– × 0.9– × 0.6-m exclosures made of 3.8– × 1.9-cm wooden strips covered in 1.3-cm hardware cloth (top and sides) and 1-mm fiberglass mesh (bottom). We randomly place 3 boxes on bare ground in an open field such that the mesh bottom of each box rested on bare soil. Bottoms of boxes were subdivided into 7 equal-sized compartments with wooden strips. We measured masses of 3 300-cm^3 samples of seeds of each species and placed 1 sample of each species in each box, each within a separate compartment. Seeds were spread evenly in a single layer over the mesh bottom of the compartment.

We removed a 25-g sample of seeds of each species from each of the 3 exclosures at 30-day intervals (17 Oct, 16 Nov, 16 Dec 1997; 17 Oct, 16 Nov, 16 Dec 1998, 15 Jan 1999). Prior to removing samples, we estimated the proportion of seeds of each species germinated in each exclosure in intervals of 0.05. Following removal of samples, we removed as completely as possible all sprouted seeds from exclosures. We air-dried samples 96 hours at room temperature to remove surface moisture, after which we carefully hand-removed all seeds showing signs of germination or other physical damage. Seeds were only dried to remove surface water, not completely desiccated, to simulate their condition when consumed by wildlife. We measured mass (nearest 0.01 g) and volume (nearest 0.5 cm^3) of remaining seeds in each sample, and used mass/cm^3 ratio as a standardized measure of seed mass in analyses, assuming a constant number of seeds/cm^3.

Nutritional analyses of samples were conducted by the Alabama Agricultural Forage Laboratory at Auburn University. Water, crude protein, fat, neutral detergent-insoluble (NDI), acid detergent-insoluble (ADI), and ash fractions were determined following McKnight and Hepp (1998). We used subtraction to determine NFE (100% – protein – fat – NDI), hemicellulose (NDI-ADI), and cellulose-lignin (C-L; ADI-ash). We expressed seed nutritional composition using seed wet mass in all analyses, rather than dry mass, because seeds were only superficially dried prior to measuring mass/volume (to simulate natural seed condition), and we were interested in the contribution of water loss or gain to overall change in seed mass/volume.

For each sample, we multiplied mass/cm^3 by percentage content (by wet mass) of each of 7 nutrients (fat, NFE, protein, hemicellulose, C-L, ash, and water) to obtain mass of each nutrient/cm^3 of sample. We then divided mass/cm^3 of each sample by the original (fresh) mass/cm^3 value for that species in that exclosure to express sample mass as a percentage of original mass; mass/cm^3 of each nutrient in samples were expressed similarly by dividing by the original value. We subtracted 1 from mass values (overall and each nutrient) to obtain % change in overall and nutrient masses over the deterioration interval, and we estimated daily rates of change in these masses separately by species and year using simple linear regression with no intercept (change at 0 days = 0). For comparison, we also modeled overall mass change separately by species and year using exponential ($Y = e^{rt}$) models. We measured associations between changes in overall mass and changes in individual nutrients across species separately by year using Pearson's product-moment correlation. We determined relationships between mass/nutrient changes during weathering and seed water and fiber contents using multiple linear regression; we regressed rates of change in overall and nutrient masses versus original (fresh) water and fiber (hemicellulose + C-L) contents across species separately by year. We used the Statistical Analysis System (SAS Inst. 1990) and $\alpha = 0.05$ for all analyses.

Results

Seed germination during weathering varied among species and/or between years (Table 1). In 1997, >75% of white proso millet and browntop millet seeds germinated in the first 30 days; by day 60, >90% of remaining white proso millet, browntop millet, and wheat had germinated. Extensive germination of white proso millet and wheat precluded further analyses of these 2 species in 1997. Few seeds of corn or any wild food germinated, although 10%–15% of remaining yellow bristlegrass seeds germinated by day 60. Little additional germination of any species was observed after 60 days, so germination was not quantified at 90 days in 1997. Fewer seeds of white proso millet and browntop millet germinated in 1998–99 compared to 1997, but more yellow bristlegrass germinated. In 1998–99, germination was greatest among browntop millet and barnyardgrass (>55% by day 30; Table 1). Few sunflower, milo, or broadleaf signalgrass seeds germinated in 1998–99.

Differences in coefficients of determination between linear and exponential models of overall seed mass change (linear R^2 – exponential R^2) ranged from –0.01 to 0.01 ($\bar{x} = 0.00$) in 1997 and from –0.04 to 0.03 ($\bar{x} = -0.01$) in 1998–99. Based on linear models, mass/cm^3 of all seeds declined over time each year, with the exception of broadleaf signalgrass and common ragweed in 1997 and broadleaf signalgrass in 1998–99 (Table 2). Mass loss rates were greater among cultivated seed ($\geq$0.4%/day) than among wild seeds (<0.3%/day); loss rate was greatest in browntop millet in 1997 and sunflower in 1998–99. Broadleaf signalgrass gained mass each year.

Table 1. Mean[a] proportion[b] of remaining[c] seeds germinating during deterioration of dove foods, eastcentral Alabama, September–December 1997 and September–January 1999.

Year	Food	30 days	60 days	90 days	120 days
1997	White prose millet	0.75–0.80	0.90–0.95		
	Browntop millet	0.75–0.80	0.95–1.00		
	Wheat	0.50–0.55	0.95–1.00		
	Corn	0.00–0.05	0.00–0.05		
	Yellow bristlegrass	0.00–0.05	0.10–0.15		
	Common ragweed	0.00–0.05	0.00–0.05		
	Broadleaf signalgrass	0.00–0.05	0.00–0.05		
1998–99	White proso millet	0.25–0.30	0.10–0.15	0.20–0.25	0.10–0.15
	Sunflower	0.00–0.05	0.00–0.05	0.00–0.05	0.00–0.05
	Brwontop millet	0.55–0.60[d]	0.35–0.40	0.35–0.40	0.30–0.35[d]
	Milo	0.00–0.05	0.00–0.05	0.00–0.05	0.00–0.05
	Yellow bristlegrass	0.30–0.35	0.20–0.25	0.10–0.15	0.05–0.10
	Barnyardgrass	0.55–0.60	0.40–0.45	0.55–0.60	0.45–0.50
	Broadleaf signalgrass	0.05–0.10	0.05–0.10	0.00–0.05	0.05–0.10

a. $N = 3$ unless otherwise noted.

b. Recorded in 0.05 intervals; mean calculated using interval midpoints and expressed as interval.

c. Germinated seeds removed at the end of each interval.

d. $N = 2$.

Trends in fat, NFE, protein, and hemicellulose in seeds generally were similar during field weathering (Table 2). Fat declined in all species each year, with the exception of common ragweed in 1997 (stable) and broadleaf signalgrass in both years (increased). Nitrogen-free extract declined in all species each year except barnyardgrass in 1998–99 (stable) and broadleaf signalgrass in both years (increased). Protein declined in all species except broadleaf signalgrass (stable) each year. Hemicellulose declined in all species each year except common ragweed and broadleaf signalgrass in 1997 (both stable) and white proso millet and milo in 1998–99 (both stable). In 1997, declines in fat, NFE, and protein were greatest in browntop millet, and hemicellulose decline was greatest in corn. In 1998–99, losses of all nutrients except NFE were greatest in sunflower, and NFE loss was greatest in white proso millet. Trends in C-L, ash, and water varied considerably among species and/or between years (Table 2). Cellulose-lignin increased or showed no trend in all species in 1997, but declined in 4 of 7 species in 1998–99. Water, in contrast, declined in 3 of 5 species in 1997, but in only 1 of 7 species in 1998–99. Ash declined in 2 species (both cultivated) each year.

Rate of total mass change was positively correlated with rate of change in mass of all nutrients except hemicellulose, C-L, and water in 1997, and all nutrients except hemicellulose and C-L in 1998–99 (Table 3). Rates of change in total mass and all nutrients were not related to either original water or fiber contents in 1997 ($-1.6 \leq t_2 \leq 2.9$; $P \geq 0.099$) or 1998–99 ($-1.8 \leq t_4 \leq 2.2$; $P \geq 0.089$).

Table 2. Daily rate of change[a] (% original mass/day; *b*) in overall mass and nutrients among seeds subjected to field weathering, eastcentral Alabama, September–January 1997–98 and 1998–99.

Nutrient	Year	Species	b[b]	SE	R^2	P
Total mass	1997	Browntop millet	-1.016	0.075	0.98	<0.001
		Corn	-0.397	0.018	0.98	<0.001
		Yellow bristlegrass	-0.153	0.018	0.87	<0.001
		Common ragweed	-0.037	0.019	0.27	0.072
		Broadleaf signalgrass	0.275	0.029	0.89	<0.001
	1998–99	White proso millet	-0.609	0.085	0.90	<0.001
		Milo	-0.401	0.023	0.96	<0.001
		Browntop millet	-0.439	0.047	0.94	<0.001
		Sunflower	-0.651	0.048	0.95	<0.001
		Yellow bristlegrass	-0.244	0.009	0.99	<0.001
		Barnyardgrass	-0.103	0.042	0.50	0.050
		Broadleaf signalgrass	0.054	0.009	0.74	<0.001
	1997	Browntop millet	-1.336	0.169	0.94	0.001
		Corn	-0.661	0.055	0.93	<0.001
		Yellow bristlegrass	-0.428	0.037	0.92	<0.001
		Common ragweed	-0.088	0.081	0.10	0.300
		Broadleaf signalgrass	0.252	0.048	0.72	<0.001
	1998–99	White proso millet	-0.798	0.118	0.89	<0.001
		Milo	-0.628	0.058	0.90	<0.001
		Browntop millet	-0.736	0.070	0.95	<0.001
		Sunflower	-0.879	0.105	0.88	<0.001
		Yellow bristlegrass	-0.425	0.043	0.89	<0.001
		Barnyardgrass	-0.277	0.014	0.99	<0.001
		Broadleaf signalgrass	0.306	0.073	0.58	0.001
Nitrogen-free extract	1997	Browntop millet	-1.257	0.072	0.99	<0.001
		Corn	-0.208	0.032	0.80	<0.001
		Yellow bristlegrass	-0.308	0.062	0.69	<0.001
		Common ragweed	-0.446	0.082	0.73	<0.001
		Broadleaf signalgrass	0.336	0.067	0.70	<0.001
	1998–99	White proso millet	-0.742	0.124	0.86	0.001
		Milo	-0.495	0.042	0.92	<0.001
		Browntop millet	-0.565	0.074	0.91	<0.001
		Sunflower	-0.400	0.131	0.48	0.012
		Yellow bristlegrass	-0.192	0.053	0.52	0.004
		Barnyardgrass	-0.056	0.036	0.28	0.176
		Broadleaf signalgrass	0.569	0.065	0.85	<0.001
Protein	1997	Browntop millet	-0.892	0.082	0.97	<0.001
		Corn	-0.571	0.058	0.90	<0.001
		Yellow bristlegrass	-0.285	0.030	0.89	<0.001
		Common ragweed	-0.123	0.049	0.37	0.029
		Broadleaf signalgrass	0.112	0.073	0.18	0.154
	1998–99	White proso millet	-0.522	0.035	0.97	<0.001
		Milo	-0.253	0.033	0.82	<0.001
		Browntop millet	-0.377	0.041	0.93	<0.001
		Sunflower	-0.717	0.053	0.95	<0.001
		Yellow bristlegrass	-0.184	0.055	0.48	0.006
		Barnyardgrass	-0.136	0.045	0.61	0.023
		Broadleaf signalgrass	0.033	0.068	0.02	0.634

(table continues)

Nutrient	Year	Species	*b*[b]	SE	R^2	*P*
Hemicellulose	1997	Browntop millet	-0.637	0.005	1.00	<0.001
		Corn	-0.780	0.117	0.80	<0.001
		Yellow bristlegrass	-0.205	0.063	0.49	0.008
		Common ragweed	0.433	0.216	0.27	0.071
		Broadleaf signalgrass	-0.061	0.138	0.02	0.668
	1998–99	White proso millet	-0.199	0.148	0.23	0.228
		Milo	-0.214	0.139	0.16	0.147
		Browntop millet	-0.505	0.081	0.87	<0.001
		Sunflower	-0.693	0.126	0.75	<0.001
		Yellow bristlegrass	-0.558	0.048	0.92	<0.001
		Barnyardgrass	-0.503	0.091	0.84	0.002
		Broadleaf signalgrass	-0.311	0.091	0.48	0.005
Cellulose-lignin	1997	Browntop millet	-0.528	0.244	0.54	0.096
		Corn	0.804	0.265	0.46	0.011
		Yellow bristlegrass	0.050	0.023	0.30	0.054
		Common ragweed	0.156	0.027	0.75	<0.001
		Broadleaf signalgrass	0.377	0.058	0.79	<0.001
	1998–99	White proso millet	0.008	0.129	0.00	0.954
		Milo	-0.013	0.079	0.00	0.869
		Browntop millet	-0.290	0.067	0.76	0.005
		Sunflower	-0.355	0.064	0.76	<0.001
		Barnyardgrass	-0.044	0.077	0.05	0.586
		Broadleaf signalgrass	-0.338	0.045	0.82	<0.001
Ash	1997	Browntop millet	-1.515	0.151	0.96	<0.001
		Corn	-0.541	0.096	0.74	<0.001
		Yellow bristlegrass	-0.004	0.036	0.00	0.916
		Common ragweed	-0.032	0.083	0.01	0.711
		Broadleaf signalgrass	0.326	0.056	0.76	<0.001
	1998–99	White proso millet	-0.472	0.093	0.81	0.002
		Milo	0.123	0.116	0.08	0.310
		Browntop millet	-0.038	0.060	0.06	0.554
		Sunflower	-0.568	0.126	0.67	0.001
		Yellow bristlegrass	0.036	0.041	0.06	0.392
		Barnyardgrass	0.108	0.053	0.41	0.086
		Broadleaf signalgrass	0.186	0.036	0.67	<0.001
Water	1997	Browntop millet	-0.901	0.120	0.93	0.002
		Corn	-0.676	0.073	0.89	<0.001
		Yellow bristlegrass	0.152	0.166	0.07	0.380
		Common ragweed	-0.346	0.124	0.42	0.018
		Broadleaf signalgrass	0.533	0.162	0.50	0.007
	1998–99	White proso millet	0.046	0.147	0.02	0.766
		Milo	-0.053	0.062	0.05	0.410
		Browntop millet	0.068	0.316	0.01	0.838
		Sunflower	-0.359	0.143	0.39	0.031
		Yellow bristlegrass	0.093	0.083	0.10	0.281
		Barnyardgrass	0.337	0.089	0.71	0.009
		Broadleaf signalgrass	0.628	0.101	0.75	<0.001

a. Estimated using simple linear regression.

b. 1997 sample sizes: corn (*N* = 5), all other species (*N* = 12). 1998–99 sample sizes: white proso millet, browntop millet, barnyardgrass (*N*= 7); milo, broadleaf signalgrass (*N*= 14); sunflower (*N* = 11); yellow bristlegrass (*N* = 13).

Table 3. Pearson's product-moment correlations of overall mass loss (% original mass/day) with loss of nutrients among seeds subjected to field deterioration, eastcentral Alabama, September–December 1997 and September–January 1998–99.

Year	*N*	Nutrient	*r*	*P*
1997	5	Fat	0.99	0.001
		Nitrogen-free extract	0.91	0.031
		Protein	0.98	0.003
		Hemicellulose	0.67	0.218
		Cellulose-lignin	0.57	0.313
		Ash	0.99	0.002
		Water	0.87	0.057
1998–99	7	Fat	0.95	0.001
		Nitrogen-free extract	0.88	0.008
		Protein	0.95	<0.001
		Hemicellulose	0.10	0.824
		Cellulose-lignin	-0.12	0.792
		Ash	0.85	0.015
		Water	0.90	0.006

Discussion

Our results confirm earlier findings that most seeds lose mass during field weathering and that seeds of cultivated species deteriorate more rapidly than do those of wild species. Dillon (1961) reported that rapid deterioration and germination limited the value of sorghum and sunflower as yearlong foods for mourning doves, whereas seeds of wild species were more durable. In the only other study using mass loss to index seed deterioration in a terrestrial environment, 8 of the 10 most rapidly-deteriorating seeds were those of cultivated species, and 8 of the 10 species deteriorating least rapidly were wild (Preacher 1978). Our results suggest that less rapid deterioration among wild seeds may not be the result of higher fiber levels in these seeds, although seeds of wild species generally do contain higher levels of fiber than seeds of cultivated species (Hayslette and Mirarchi 2001).

Contrary to our prediction, results indicated that linear models generally are as appropriate as exponential models for representing seed mass loss during weathering. This was surprising, both because we expected mass loss to be greatest during the first 30-day interval and less during each subsequent interval, and because an exponential pattern in mass loss has been reported for seeds in an aquatic environment (Neely 1956). A second aquatic seed deterioration study, however, found that coefficients of determination (R^2) were higher for linear models of mass loss than for curvilinear models (Nelms and Twedt 1996).

Rates of terrestrial seed mass loss documented in our study varied somewhat from those reported earlier (Preacher 1978). Mass loss we observed was greater than previously reported for proso and browntop millets (≥55% vs. 15% and ≥40% vs. 5%, respectively, at 90 days), despite the fact that earlier estimates included germinated seeds as completely deteriorated. Sunflower deterioration was lower in our study than previously reported (20% vs. 65% [excluding germination] at 30 days). Differences in results between our study and Preacher (1978) may have been due to differences in weather, seed variety, or methods. Preacher (1978) documented deterioration rates during November–March. If seed chemical changes during aging are exacerbated by increased temperature and relative humidity (Ching and Schoolcraft 1968, Locher and Bucheli 1998), greater mass loss of millets in our study may have been due to warmer temperatures and higher humidity. Fiberglass envelopes used to hold seeds also may have affected deterioration rates in Preacher's study. Factors responsible for differences in results between studies did not affect all species similarly, however. Deterioration rate of corn in our study (48% at 120 days) was similar to that reported earlier (47%; Preacher 1978).

Results of ours and earlier studies indicate that differences in seed deterioration rates between terrestrial and aquatic situations are species-specific. Terrestrial seed mass loss rates were similar to those reported in aquatic (flooded) environments (Neely 1956, Shearer et al. 1969, Nelms and Twedt 1996) for corn (0.40%/day here vs. 0.36–0.56%/day flooded), milo (0.40%/day vs. 0.32%/day), and bristlegrass (0.15–0.24/day vs. 0.24–36%/day). However, browntop and proso millets lost mass more rapidly in our study (0.44–1.02%/day, 0.61%/day, respectively) than in previous aquatic studies (0.17–0.40%/day, 0.33%/day, respectively), and broadleaf signalgrass appeared to gain mass in our study, but lost 0.39%/day under flooded conditions.

Our results indicate that overall mass loss of seeds generally is due to losses in fat, NFE, protein, ash, and water. Lack of correlation between overall mass loss and loss of hemicellulose and C-L reflects variation in percentage content of nutrients in seeds during weathering. Lack of such variation would have resulted in positive correlations between total mass change rate and rates of change of all individual nutrients. This finding contrasts with conclusions by earlier authors that effects of weathering on percent nutrient contents in seeds were "negligible" (McGinn and Glasgow 1965). However, results of this earlier study did seem to indicate considerable systematic variation in some nutrient percentages with weathering; 5 of 10 species showed a ≥6.7% decline in NFE and a ≥7.1% increase in ash during 120 days of weathering in a terrestrial environment. Despite the apparent variability in nutrient percentages with weathering, the assumption of correlation between mass and nutrient losses in seeds during weathering largely seems validated by our study.

Our study indicates that if germinated seeds are unacceptable as food for wildlife as suggested earlier (Preacher 1978), seed germination may greatly reduce availability of certain foods for granivorous species through time. Germination rates of species tested in both years varied between years, however, suggesting that only limited generalizations can be made with respect to specific species. In general, effects of germination appeared greatest among wheat (a cool season plant), browntop millet, and white proso millet; corn, sunflower and milo availability was little affected by germination. Among wild species we studied, effects of seed germination are likely greatest among barnyardgrass and yellow bristlegrass. Germination has been shown to reduce availability of proso and browntop millets in South Carolina

(Preacher 1978), although only after 90 days in the field. Sunflower seeds germinated and were unavailable after 60 days in South Carolina (Preacher 1978), whereas sunflowers germinated little in our study. Variation in germination rate of some foods in our study between years may have been due to differences in weather or seed viability, whereas differences between our results and those of Preacher (1978) may have been due to these or other site-specific factors such as soil characteristics or to study methods.

Earlier work on deterioration of northern bobwhite foods (Preacher 1978) considered germinated seeds completely deteriorated and unavailable. We removed germinated seeds from samples prior to analysis, so germination did not directly affect estimates of seed deterioration in our study. It is possible, however, that germination may have indirectly affected our estimates of seed deterioration. If seed mass/volume varies with seed viability, gradual elimination of viable seeds from our study through germination and subsequent removal may have reduced the overall viability, and hence mass/volume, of seeds remaining in our study through time. Thus, declines in mass/volume in successive samples may have reflected both mass loss of remaining seeds and removal of more massive viable seeds following germination. We suspect that effects of this latter mechanism were slight, however, because patterns of germination generally did not match patterns in seed mass loss. In particular, corn, milo, and sunflower lost mass rapidly, but few seeds of these species germinated. Regardless, deterioration rates documented in our study should have provided realistic estimates of changing food values of seeds, if germination effectively "removes" seeds as food from the environment.

Management Implications

Rapid deterioration and/or germination may decrease benefits and attractiveness of seeds of cultivated species for granivorous wildlife soon after they become available. Rapid loss of nutrients in sunflower, in particular, may limit its usefulness in food plantings if long-term nutritional benefits to wildlife are desired. In such a situation, planting or otherwise encouraging growth of wild species such as broadleaf signalgrass may be more appropriate because of greater resistance of seeds of these species to germination and deterioration during weathering. Mass loss generally appears to be a valid index of seed nutritional deterioration. Although mass changes do not appear to reflect changes in hemicellulose or C-L in seeds, these seed fractions are largely indigestible to most wildlife (Robbins 1993) and may be of less interest to habitat managers than are other nutrients. Simple linear models seem adequate to model terrestrial seed mass loss. Seed deterioration rates determined in aquatic environments may not be applicable to terrestrial situations. Fiber and water contents of seeds appear to be of little use for predicting resistance to deterioration.

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