Moist-Soil Seed Abundance in Managed Wetlands in the Mississippi Alluvial Valley

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ABSTRACT Managed moist-soil units support early succession herbaceous vegetation that produces seeds, tubers, and other plant parts used by waterfowl in the Mississippi Alluvial Valley (MAV), USA. We conducted a stratified multi-stage sample survey on state and federal lands in the MAV of Arkansas, Louisiana, Mississippi, and Missouri during autumns 2002–2004 to generate a contemporary estimate of combined dry mass of seeds and tubers (herein seed abundance) in managed moist-soil units for use by the Lower Mississippi Valley Joint Venture (LMVJV) of the North American Waterfowl Management Plan. We also examined variation in mean seed abundance among moist-soil units in 2003 and 2004 in relation to management intensity (active or passive), soil pH and nutrient levels, proportional occurrence of plant life-forms (e.g., grass, flatsedge, and forb; vine; woody plants), and unit area. Estimates of mean seed abundance were similar in 2002 ($\bar{x} = 537.1$ kg/ha, SE = 100.1) and 2004 ($\bar{x} = 555.2$ kg/ha, SE = 105.2) but 35–40% less in 2003 ($\bar{x} = 396.8$ kg/ha, SE = 116.1). Averaged over years, seed abundance was 496.3 kg/ha (SE = 62.0; CV = 12.5%). Multiple regression analysis indicated seed abundance varied among moist-soil units inversely with proportional occurrence of woody vegetation and unit area and was greater in actively than passively managed units ($R^2_{adj} = 0.37$). Species of early succession grasses occurred more frequently in actively than passively managed units ($P \leq 0.09$), whereas mid- and late-succession plants occurred more often in passively managed units ($P \leq 0.02$). We recommend the LMVJV consider 556 kg/ha as a measure of seed abundance for use in estimating carrying capacity in managed moist-soil units on public lands in the MAV. We recommend active management of moist-soil units to achieve maximum potential seed production and further research to determine recovery rates of seeds of various sizes from core samples and the relationship between seed abundance and unit area. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):707–714; 2008)

DOI: 10.2193/2007-100

KEY WORDS Mississippi Alluvial Valley, moist-soil plants, multi-stage sampling, seed abundance, waterfowl, wetland management.

The Mississippi Alluvial Valley (MAV) is an important region for migrating and wintering waterfowl in North America (Bellrose 1976, Reinecke et al. 1989). Several conservation programs, including the North American Waterfowl Management Plan (NAWMP), North American Bird Conservation Initiative, and Ducks Unlimited Conservation Plan, emphasize the importance of the MAV to waterfowl and other birds (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986, U.S. North American Bird Conservation Initiative Committee 2000, Ducks Unlimited, Inc. 2005). Historically, the MAV contained about 10 million ha of seasonally flooded bottomland–hardwood forest, wherein mallards (*Anas platyrhynchos*), wood ducks (*Aix sponsa*), and other waterfowl obtained resources to fulfill various life-cycle needs (Reinecke et al. 1989, Heitmeyer 2006). Today, agriculture is the dominate land use in the MAV, with only 2.8 million ha of the original bottomland–hardwood ecosystem remaining, of which human activities have mostly degraded or modified (Reinecke et al. 1988, Fredrickson 2005). Although significant gains in habitat area and ecological function are occurring, historic patterns of flooding, productivity, and biodiversity probably cannot be fully restored (King et al. 2005). Consequently, managed habitats such as moist-soil wetlands (i.e., seasonally flooded emergent wetlands dominated by grasses and sedges) and autumn-harvested and winter-flooded croplands are important foraging habitats for waterfowl in the MAV (Fredrickson and Taylor 1982, Reinecke et al. 1989).

The Lower Mississippi Valley Joint Venture (LMVJV) of the NAWMP assumes foraging habitat is the limiting factor for waterfowl during winter (Reinecke et al. 1989, Reinecke and Loesch 1996). The LMVJV uses energy-based estimates of carrying capacity (i.e., duck-energy days [DEDs]) for waterfowl foraging habitats to approximate the number of waterfowl the MAV may support during winter (Reinecke et al. 1989, Loesch et al. 1994). Except for unharvested crops, managed moist-soil wetlands provide the greatest potential DEDs among available foraging habitats (Reinecke and Loesch 1996).

Theories and studies of food choice and foraging behavior of animals are active areas of research (e.g., Stephens and Krebs 1986, Giraldeau and Caraco 2000), and several scientists published recently specific models of the dynamics

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of food exploitation by wintering waterbirds (Miller and Newton 1999, Goss-Custard et al. 2003). The LMVJV and several other joint ventures implementing the NAWMP in migration and wintering areas use food-depletion models to assess habitat carrying capacity and establish conservation goals (e.g., Reinecke and Loesch 1996). These models generally are classed as daily ration models, and carrying capacity is calculated as the difference between total food or energy abundance and a threshold food abundance below which foraging becomes unprofitable divided by the daily food requirement of individuals assumed to be identical and noninterfering (Goss-Custard et al. 2003). Importantly, simulations have shown carrying capacity predicted by these models is especially sensitive to estimates of food abundance (Miller and Eadie 2006). The LMVJV anticipated the need for these data and ranked acquiring them as priority research needs (Loesch et al. 1994).

Management of moist-soil wetlands involves manipulation of soil, hydrology, and vegetation to produce diverse food and cover for wildlife (Fredrickson and Taylor 1982, Fredrickson 1996). Moist-soil plant seeds and tubers resist decomposition when flooded and on average provide true metabolizable energy (TME; approx. 2.5 kcal/g) comparable to rice (3.3 kcal/g) and soybean (2.6 kcal/g; Shearer et al. 1969, Checkett et al. 2002, Kaminski et al. 2003). Additionally, moist-soil wetlands support aquatic invertebrates that supply dietary protein for ducks and provide habitats for other life-cycle functions (Fredrickson and Taylor 1982, Anderson and Smith 1999, Gray et al. 1999).

The LMVJV used an estimate for combined abundance of moist-soil seeds and tubers (hereafter seed abundance) of 450 kg/ha (dry mass) to calculate DEDs for moist-soil wetlands in the MAV (Reinecke and Loesch 1996). The LMVJV considered this preliminary estimate conservative yet representative for the MAV but acknowledged the limited temporal and spatial sampling used to derive this estimate (Loesch et al. 1994). Scientists based previous estimates of moist-soil seed abundance on sampling at smaller spatial scales than currently needed for ecoregional conservation planning (e.g., Reinecke et al. 1989, Haukos and Smith 1993, Naylor 2002, Bowyer et al. 2005). Therefore, we conducted a sample survey to obtain a current, representative, and precise estimate (i.e., CV $\leq$ 15%) of moist-soil seed abundance for managed moist-soil units on public lands in the MAV. We use the term "moist-soil unit" to refer to independently managed moist-soil wetlands on public lands. Additionally, we tested for differences in percent occurrence of plant genera or species in actively and passively managed moist-soil units and attempted to explain variation in mean seed abundance among managed units relative to unit area, management intensity (i.e., active or passive), soil characteristics, and proportional occurrence of plant life-forms.

STUDY AREA

Our study areas were managed moist-soil units on state (wildlife management areas [WMA]) and federal (national wildlife refuges [NWR]) lands in the MAV of Arkansas, Louisiana, Missouri, and Mississippi, USA. We sampled 2 moist-soil units within 3 management areas in each of the 4 states during autumns 2002–2004. All units had water-control structures enabling flooding and drainage. Water supply was derived from rain, runoff, river overflow, and in some cases pumping. Dominant vegetation consisted of plants adapted to moist-soil conditions including grasses (e.g., *Echinochloa* spp., *Leptochloa* spp., *Panicum* spp.), flatsedges (*Carex* spp., *Cyperus* spp.), forbs (*Bidens* spp., *Polygonum* spp., *Xanthium strumarium*), vines (*Campsis radicans, Brunnichia ovata*), and woody plants (*Salix* spp., *Cephalanthus occidentalis*; Kross 2006).

METHODS

We used a stratified multi-stage sample design to estimate moist-soil seed abundance in the MAV (Lohr 1999). We designated states as sample strata to ensure geographic representation of sampling across the MAV, management areas within states (NWR or WMA) as primary sample units, moist-soil units within management areas as secondary sample units, and soil core samples within moist-soil units as tertiary sample units (Stafford et al. 2006*b*). To create the sampling frame of management areas, we queried the MAV Conservation Planning Atlas (CPA; U.S. Fish and Wildlife Service 2002) database and selected all areas managing wetland units for moist-soil vegetation.

The CPA defines moist-soil units as wetlands with levees and water control structures where managers can regulate hydrology independent of other such basins and the primary management objective is producing moist-soil vegetation. Each year during 2002–2004, we used PROC SURVEYSELECT in SAS version 8.02 (SAS Institute, Inc., Cary, NC) to randomly select 3 management areas in each state with equal probabilities and without replacement. Before including management areas in our sample, we interviewed managers to determine the number, vegetative status, and management history of existing moist-soil units. Following interviews, we excluded from the sample and selected a replacement for any management area with <3 units that 1) possessed functioning water management capabilities, 2) were currently managed for herbaceous moist-soil plants rather than crops or other vegetation, and 3) were not tilled or otherwise managed (e.g., permanent wetland) in the current growing season. Consequently, we excluded 4 originally selected management areas over 3 years. We randomly selected 2 moist-soil units from those available within eligible management areas. In 2002, we collected 20 random core samples from each moist-soil unit, whereas in 2003 and 2004, we collected 15 core samples per unit to reduce sample effort yet maintain precision (Penny 2003).

Based on information from managers and descriptions of moist-soil management practices, we categorized each sampled moist-soil unit as actively or passively managed. We designated units with yearly or alternate-year soil disturbance by disking or alternate-year cropping as actively managed, whereas passively managed units were those where the most recent soil disturbance occurred $\geq$3 years before sampling (Penny 2003). Management of actively managed units also generally included gradual spring–summer drawdown, summer irrigation during drought, mowing or herbicide application to control undesirable vegetation (e.g., hemp sesbania [*Sesbania herbacea*], cocklebur [*Xanthium strumarium*]), or fertilization of desirable vegetation. Generally, passively managed units lacked ability to irrigate by pumping and managers applied neither herbicide nor fertilizer.

We sampled moist-soil units during autumns 2002–2004 from mid-October to mid-November when plants in the MAV dehisced most seeds (>90%; Reinecke and Hartke 2005). If any seeds remained attached to panicles at sampling sites, we threshed panicles by hand, causing seeds to fall to the ground before core sampling. We collected soil samples using a core sampler (10-cm depth, 785.4 cm^3; Stafford et al. 2006*a*) and recorded all plant genera or species present within a 0.5-m radius around each sample site. In 2003 and 2004, we inserted a 2-cm-diameter soil probe 16 cm into the ground adjacent to seed sampling sites to collect a soil sample for pH and nutrient analyses. We combined the latter 15 soil samples per management unit into an aggregate sample following methods for soil sampling in croplands (Crouse and McCarty 1999). We stored all samples at $-10°$ C until analyzed.

We immersed frozen moist-soil core samples in a 3% solution of hydrogen peroxide (H_2O_2; Bohm 1979), a mixture of $\leq$250 cm^3 of baking soda and $\leq$1 L of water, or a combination of these for 1–3 hours to oxidize clays and facilitate washing sediments through sieves. In a post hoc experiment, we immersed 10-g samples (wet mass, $n = 10$) of Japanese millet (*Echinochloa crusgalli frumentacea*) in water (control) and solutions of H_2O_2 and water, 250 cm^3 of baking soda and 1 L of water, and H_2O_2, 250 cm^3 of baking soda, and 1 L of water for 3 hours, then oven-dried them to a constant mass. We did not detect a difference in mean dry mass of seed samples among the 4 test groups ($P > 0.20$; H. M. Hagy and R. M. Kaminski, Mississippi State University, unpublished data); hence, we assumed our original solutions of H_2O_2, baking soda, and water did not influence mass of moist-soil seeds in our core samples. We processed core samples by first washing them through a series of graduated sieves (sizes 4 [4.75-mm aperture], 10 [2.0-mm], and 50 [300-μm]) to remove soil from plant litter, seeds, and tubers. After washing soil from samples, we collected all seeds, tubers, and plant debris from sieves and dried each sample at 87° C for 24 hours (Gray et al. 1999).

We recovered tubers and large seeds, such as those from genera *Cyperus*, *Echinochloa*, *Polygonum*, *Sesbania*, and *Setaria*, by visual inspection. We distributed remaining plant and soil material evenly over a grid of 100 equal-sized 1.5-cm^2 cells and randomly selected a subsample of 25 cells (Reinecke and Hartke 2005). We examined the subsample using a 1.25× magnifying lens and light source to remove small seeds, such as those from the genera *Ammannia*, *Cyperus*, *Leptochloa*, and *Panicum*. We dried all seeds and tubers to a constant mass and obtained separate measurements of mass for large seeds and tubers combined and subsamples of small seeds. To determine mass of all seeds and tubers in each sample, we multiplied mass of small seeds by 4 (25% subsample), added combined mass of large seeds and tubers, and converted the total (g/sample, dry mass) to kilograms per hectare.

The Mississippi State University Extension Service (MSU-ES) Soil Testing Laboratory (Mississippi State, MS) analyzed aggregate soil samples for pH, potassium (K [kg/ha]), and phosphorus (P [kg/ha]). We did not measure soil nitrogen (N) because our field-sampling method did not enable accurate estimation of this soil nutrient (Crouse and McCarty 1999).

Statistical Analyses

We used PROC SURVEYMEANS in SAS to compute annual estimates of mean seed abundance for 2002–2004. This procedure employs an unbiased estimator by expanding sample measurements using sample weights derived from probabilities of selecting management areas within strata, moist-soil units within management areas, and core samples within moist-soil units (Lohr 1999). For example, the sample weight of the seed mass for a given soil core was the inverse of the product of the probabilities of selecting a management area within the 4 strata, a moist-soil unit within the management area, and a soil core within the moist-soil unit (Stafford et al. 2006*a*). We also calculated an overall estimate of mean seed abundance among years as an unweighted mean of yearly means for 2002–2004. We estimated variance of the overall mean by summing year-specific variances and dividing by the square of the number of years (i.e., $n = 3^2$; Stafford et al. 2006*a*). We calculated a standard error and 95% confidence interval for the overall estimate using this variance.

We calculated percent occurrence of each genus or species within moist-soil units by dividing the frequency of core-sample locations where a genus or species occurred by the number of samples extracted from the unit (i.e., $n = 15$ or 20) and multiplying the result by 100. Next, we calculated mean (and SE) percent occurrence of each plant genus or species across sampled moist-soil units over years and by management intensity (active, $n = 56$; passive, $n = 16$). Unbalanced sample sizes were not our sampling design but rather a consequence of management applied to sampled moist-soil units. We used a 2-sample t-statistic to test for differences in mean percent occurrence of each plant genus or species between actively and passively managed moist-soil units. We deemed $\alpha \leq 0.10$ significant because the number of passively managed units was small ($n = 16$), and Tacha et al. (1982) considers this Type I error rate reasonable for management studies.

We used multiple linear regression to model variation in seed abundance among management units relative to variables measured in units in 2003 and 2004. We did not collect data on soil characteristics for units sampled in 2002 and did not include data from this year in our regression analysis. We designated mean seed abundance (kg/ha, dry

Table 1. Means, standard errors, and coefficients of variation of combined seed and tuber abundance (kg/ha, dry mass) from a stratified multi-stage sample of moist-soil units on state and federal wildlife management areas in the Mississippi Alluvial Valley (MAV), USA, autumns 2002–2004.

Yr	*n* areas[a]	*n* units[b]	*n* cores[c]	$\bar{x}$	SE	CV (%)
2002	12	24	480	537.1	100.1	18.6
2003	12	24	360	396.8	116.1	29.3
2004	12	24	360	555.2	105.2	18.9
Mean over yr				496.3	62.0	12.5

[a] Public wildlife management areas in the MAV were primary sample units.

[b] Managed moist-soil units within selected management areas were secondary sample units.

[c] Substrate samples (785.4 cm^3) collected within selected moist-soil units were tertiary sample units used to measure seed abundance.

mass) in moist-soil units as the dependent variable; explanatory variables included management intensity (active or passive), proportional occurrence of 4 plant life-forms (grass, flatsedge, or rush; forb; vine; and woody plants), soil pH, selected soil nutrients (P [kg/ha], K [kg/ha]), and unit area (ha). We calculated proportional occurrence of plant life-forms by dividing the number of core sample locations at which each life-form occurred by the number of core samples per unit ($n = 15$). We assessed multicollinearity of explanatory variables using PROC CORR in SAS and removed one of each pair of correlated variables ($|r| \geq 0.30$; Graham 2003) until only independent variables remained (Cody and Smith 1997). Next, we used PROC REG in SAS to calculate and plot residual and predicted values of seed abundance for each moist-soil unit (Cody and Smith 1997). We inspected plots of residuals for funnel-shaped or nonrandom patterns indicating unequal variances among residuals or nonlinear relationships between the dependent and explanatory variables (Gotelli and Ellison 2004). To detect outliers and influential data, we calculated Cook's Distance statistic for the estimate from each unit. We compared models containing all possible subsets of explanatory variables of interest and selected the model with the greatest adjusted coefficient of determination (R^2_{adj}) for inference (Gotelli and Ellison 2004). We also calculated 90% confidence limits of parameter estimates from this model.

RESULTS

Yearly estimates of mean moist-soil seed abundance in the MAV varied from 397 kg/ha to 555 kg/ha (Table 1). The overall estimate of mean seed abundance for 2002–2004 was 496 kg/ha. Within years, coefficients of variation exceeded our a priori goal (CV $\leq$ 15%) for precision (CV = 18.6–29.3%); however, the coefficient of variation for the overall estimate was precise (12.5%; Table 1). Distribution of seed abundance estimates varied among units and years from 71 kg/ha to 2,332 kg/ha and was skewed right (Fig. 1). The greatest frequency of estimates occurred in the interval 300–600 kg/ha, and 16.7% (12 of 72) of estimates exceeded 1,000 kg/ha (Fig. 1).

We identified 48 plant genera or species at soil core sites in sampled moist-soil units. We detected 7 differences in percent occurrence of the genera or species between actively and passively managed units, and the possibility exists that $\geq$1 of the differences may have occurred by chance. Barnyard grasses (*Echinochloa* spp.) and panic grasses (*Panicum* spp.) occurred 44% (SE = 4.7) and 48% (SE = 4.7) more frequently in actively than passively (14%, SE = 4.8, $P \leq 0.01$; 31%, SE = 8.7, $P = 0.09$) managed units (Table 2). Teal grass (*Eragrostis hypnoides*), toothcup (*Ammannia* sp.), water primrose (*Ludwigia* spp.), buckwheat vine (*Brunnichia ovata*), and willow (*Salix* sp.) occurred 7% (SE = 4.6), 21% (SE = 6.4), 15% (SE = 5.3), 8% (SE = 5.1), and 2% (SE = 1.0) more frequently in passively than actively managed units (0.1%, SE = 0.1, $P \leq 0.01$; 7%, SE = 1.7, $P \leq 0.01$; 2%, SE = 0.8, $P \leq 0.01$; 1%, SE = 0.5, $P = 0.02$; 0.2%, SE = 0.2, $P \leq 0.01$; Table 2). We did not detect any other differences in mean percent occurrence of plants between actively and passively managed units ($P \geq 0.10$).

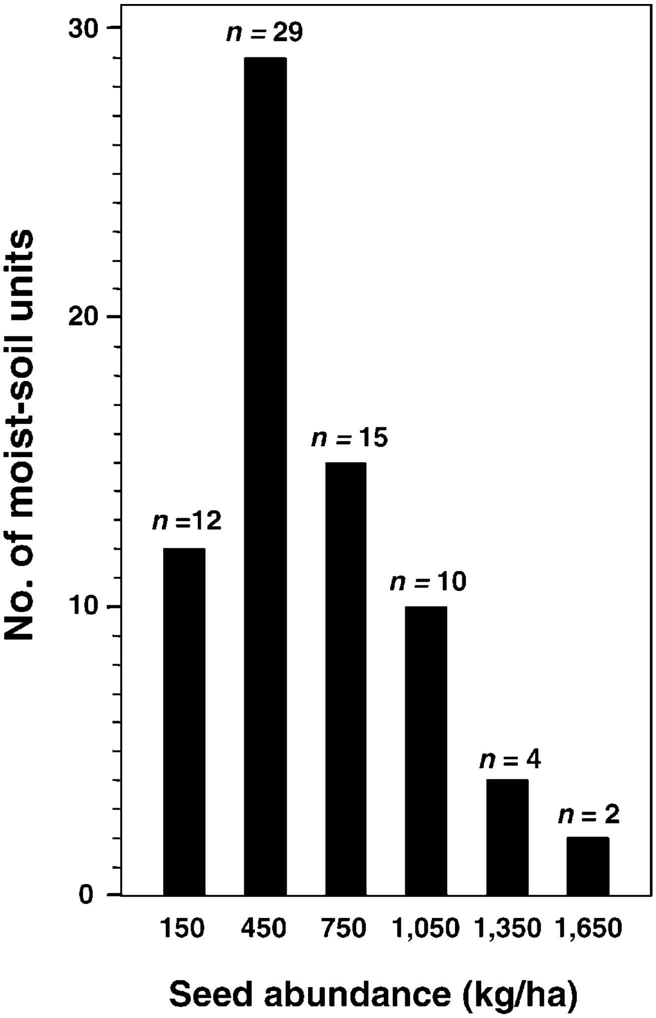

Figure 1. Frequency distribution of estimates of the mean combined abundance of seeds and tubers (kg/ha, dry mass) from a stratified multi-stage sample of moist-soil units ($n = 72$) on state and federal wildlife management areas in the Mississippi Alluvial Valley, USA, autumns 2002–2004.

Table 2. Mean percent occurrence, standard errors, and tests for differences in mean percent occurrence of selected moist-soil plant genera or species between actively ($n = 56$) and passively ($n = 16$) managed moist-soil units on state and federal wildlife management areas in the Mississippi Alluvial Valley, USA, autumns 2002–2004.

Genera or species[a]	Management				Test for difference	
	Active		Passive			
	% occurrence	SE	% occurrence	SE	t_{70}	P
Echinochloa spp.	44.0	4.7	14.1	4.8	−3.26	≤0.01
Panicum spp.	48.0	4.7	31.0	8.7	−1.72	0.09
Eragrostis hypnoides	0.1	0.1	7.1	4.6	2.91	≤0.01
Ammannia sp.	6.9	1.7	21.3	6.4	3.12	≤0.01
Ludwigia spp.	2.3	0.8	15.4	5.3	4.12	≤0.01
Brunnichia ovata	0.7	0.5	7.5	5.1	2.38	0.02
Salix sp.	0.2	0.2	2.1	1.0	3.01	≤0.01

[a] See Kross (2006) for complete list of genera or species, mean percent occurrences, SEs, and t-test results.

Our inspection of plots of residuals indicated the data met the assumptions of equal variances and linear relationships. We lost one soil sample, identified 2 moist-soil units as outliers, and thus performed analyses on data from 45 management units sampled in 2003 or 2004. We determined proportional occurrence of vines was positively correlated with soil K ($r = 0.52$, $P \leq 0.01$) and proportional occurrences of woody vegetation ($r = 0.43$, $P \leq 0.01$) and forbs ($r = 0.30$, $P = 0.04$), whereas proportional occurrence of vines was negatively correlated with proportional occurrence of grasses, flatsedges, or rushes ($r = -0.35$, $P = 0.02$). We also found that soil P was positively correlated with pH ($r = 0.40$, $P \leq 0.01$) and K ($r = 0.57$, $P \leq 0.01$). Because soil P and proportional occurrence of vines correlated with ≥2 other variables, we excluded them from subsequent analyses.

Our best regression model included the variables proportional occurrence of woody vegetation, unit area, and management intensity ($R^2_{adj} = 0.37$). We found proportional occurrence of woody vegetation ($\hat{\beta} = -2{,}563.4$, SE = 769.0; 90% CL: −3,857.5, −1,269.4; $\bar{x} = 0.02$, SE = 0.01) and unit area ($\hat{\beta} = -6.7$, SE = 1.6; 90% CL: −9.4, −3.9; $\bar{x} = 28.3$, SE = 3.2) negatively related to seed abundance, whereas management intensity ($\hat{\beta} = 156.9$, SE = 83.5; 90% CL: 16.3, 297.6; 35 actively managed units; 10 passively managed units) positively related to seed abundance.

DISCUSSION

Moist-Soil Seed Abundance

We addressed the need for reliable estimates of food abundance in primary foraging habitats by providing a precise (CV = 12.5%) estimate of moist-soil seed abundance based on 3 years of temporal variation and a sample frame representing public lands where most moist-soil units occur in the MAV. The original LMVJV estimate of moist-soil seed abundance (450 kg/ha; Reinecke et al. 1989) was a reasonable preliminary value and fell within the 95% confidence interval (426–566 kg/ha) of our overall mean. However, our estimates may be somewhat negatively biased because we could not recover all seeds during sample processing. Reinecke and Hartke (2005) reported recovering all but 12% of barnyard grass seeds from samples containing known numbers of these relatively large seeds. Moreover, we note that large seeds recovered from our samples contributed most (75%; SE = 2%, $n = 72$) of total seed mass. Although our overall estimate of moist-soil seed abundance for the MAV was precise, we conclude it is conservative because of an unknown magnitude of bias from missed small seeds. Nonetheless, our results provide a sound basis for the LMVJV to estimate current seed availability in managed moist-soil wetlands in the MAV and a benchmark for responses to future changes in management practices.

Different methods and spatial scales of sampling, plant species composition, and environments confound comparison of our estimates with previous results. Most previous estimates were site-specific and obtained by harvesting seeds from plant inflorescences (Low and Bellrose 1944, Haukos and Smith 1993, Bowyer et al. 2005). As noted by Reinecke and Hartke (2005), harvesting from inflorescences only represents food available to waterfowl if seeds mature simultaneously within species, sampling is done multiple times to account for different species phenologies, and seeds survive between sampling and waterfowl use. Our method provided a robust estimate of seed available to waterfowl because samples included seeds that survived to time of potential exploitation. Our individual unit means varied from 71 kg/ha to 2,332 kg/ha and generally were consistent with the range of previously reported estimates (Haukos and Smith 1993, Gray et al. 1999, Naylor 2002, Bowyer et al. 2005, Reinecke and Hartke 2005). Although 12 of 72 unit means exceeded 1,000 kg/ha, a high frequency of low estimates (Fig. 1) decreased our overall mean to 496 kg/ha, well below the 1,630 kg/ha suggested by Fredrickson and Taylor (1982) as the potential for actively managed units.

Large-scale surveys such as ours provide important information on food abundance for habitat conservation plans. In California's Central Valley, habitat management objectives initially assumed moist-soil habitats provided >1,300 kg/ha of seed, whereas annual means from a recent large scale survey were 200 kg/ha in 2000 and 585 kg/ha in 2001 (Naylor 2002). In the MAV, habitat objectives initially assumed rice seed available to waterfowl in harvested fields was similar to the 180 kg/ha estimated in the 1980s, whereas comprehensive surveys during 2000–2002 indicated only 80 kg/ha was available (Stafford et al. 2006*a*). Fortunately, conservation plans in the MAV initially adopted a conservative estimate of 450 kg/ha to represent seed available in moist-soil habitats. Thus, our study demonstrated that actual performance exceeded expectations, and moist-soil wetlands can mitigate some of the diminished potential of harvested rice fields to feed waterfowl.

Moist-Soil Management

We found units under active management averaged 157 kg/ha more seeds than passively managed units. Active moist-soil management typically includes soil disking annually or during alternate years, controlling undesirable plants using herbicide or mowing, and irrigating during drought (Low and Bellrose 1944, Fredrickson and Taylor 1982). Naylor (2002) found that annual disking and irrigation had the greatest positive impact on seed production in northern California, and Gray et al. (1999) reported that plots subjected to autumn tilling and disking had greater seed abundance and plant diversity the subsequent year than control plots in Mississippi. Haukos and Smith (1993) increased seed production of 3 plants important to waterfowl by managing water in playa lakes in Texas, and Bowyer et al. (2005) reported an increase in seed production from 25 kg/ha to >475 kg/ha in Illinois wetlands when herbicide or mowing was used to control cocklebur and willow encroachment.

Our analyses indicated barnyard and panic grasses occurred more frequently in actively than passively managed units, which we expected because these species are early successional grasses typically inhabiting recently disturbed and moist soils (Fredrickson and Taylor 1982, Kirkman and Sharitz 1994). Nonetheless, our multiple regression analysis did not detect a positive relationship between seed abundance and proportional occurrence of the plant life-forms represented by grasses, flatsedges, or rushes. However, grasses, flatsedges, or rushes plant life-forms contained a diverse group of species, including some considered undesirable by moist-soil managers (e.g., broomsedge bluestem [*Andropogon virginicus*], little bluestem [*Schizachyrium scoparium*]; Kross 2006) or indicative of advancing plant succession (e.g., tealgrass, broomsedge bluestem, rice cutgrass [*Leersia oryzoides*]; Fredrickson and Taylor 1982). Furthermore, occurrence of grasses, flatsedges or rushes plant life-forms was frequent and varied little among all moist-soil units (0.94, SE = 0.02, $n = 45$). Consequently, we suspect other variables with more variation had relatively increased influence on variation in seed abundance.

Passively managed units were not disked for ≥3 years and our analysis indicated buckwheat vine and willow occurred more frequently in these units. Extensive colonization of moist-soil units by vine and woody species often occurs when succession advances due to infrequent soil disturbance or ineffective water management (Fredrickson and Taylor 1982, Kirkman and Sharitz 1994). Late-successional species decrease growth of desirable seed-producing species by intercepting light and competing for soil nutrients and water (Gray et al. 1999, Bowyer et al. 2005). Our regression modeling indicated occurrence of woody vegetation negatively correlated with seed abundance, which is consistent with Bowyer et al. (2005) who found seed production was lower in areas dominated by willows than in areas dominated by annual plants and where willow and cocklebur were controlled.

Toothcup and teal grass occurred more frequently in passively than actively managed units. Toothcup is an early to mid-successional plant and typically occurs in areas with greater soil moisture and water depth than areas supporting annual grasses and sedges (Fredrickson and Taylor 1982). Teal grass also has a high moisture requirement and often occurs in monotypic patches or as an understory plant beneath taller moist-soil vegetation (Low and Bellrose 1944; R. M. Kaminski, personal observation). We are not aware of specific management techniques that promote teal grass, but our observations indicated it responded to late-summer (Aug or later) drawdowns in the MAV and attracted foraging waterfowl following flooding.

The MSU-ES uses measures of soil pH, K, and P to provide lime and fertilizer recommendations for croplands. Accordingly, we reasoned soil pH and nutrients might affect moist-soil seed abundance similar to crop yield in agricultural systems. However, measured soil nutrients and other characteristics did not correlate with seed abundance. To our knowledge, effects of fertilizing moist-soil plant communities have not been reported. However, most wetland systems contain sufficient soil nutrients to support productive vegetation (Mitsch and Gosselink 2000). Additionally, natural plant communities evolved to survive and reproduce without artificial fertilizer.

Our regression analysis indicated area of moist-soil units was negatively associated with seed abundance. Our model predicted actively managed units of 35–50 ha and passively managed units of 12–25 ha had average seed abundances (approx. 500–600 kg/ha). Reducing unit area below these ranges may increase seed abundance, but may lead to excessive costs of infrastructure and levee construction and limit overall floodable area. Although we cannot infer causation, we speculate that larger units had greater topographic variation that affected abilities to manage soil moisture throughout units. Developing smaller or subdividing larger units may increase efficiency of hydrologic and other active management strategies. Multiple small moist-soil units also provide an opportunity to manage hydrology and habitat selectively in a complex for bird species that have different migration chronologies and habitat requirements (Reinecke et al. 1989, Laubhan et al. 2005).

MANAGEMENT IMPLICATIONS

Using the best available data to account for seeds recovered from soil samples (88%, Reinecke and Hartke 2005), we recommend the LMVJV adopt a value of 556 kg/ha (i.e., 496 kg/ha [this study] + 12%) to calculate carrying capacity of moist-soil units on public lands. Furthermore, because understanding seed recovery rates is critical to using soil samples to estimate food availability, we suggest researchers determine recovery rates of additional moist-soil seeds of various sizes. Researchers also should determine food densities at which waterfowl cease foraging in moist-soil units (i.e., "giving-up" densities). We also recommend active management of moist-soil units to maintain early successional moist-soil plant communities and increase production of seeds and tubers (Fredrickson and Taylor 1982, Gray et al. 1999). We regard ranges in unit area (35–50 ha for actively managed and 12–25 ha for passively managed) as preliminary guidelines and believe future research elucidating the mechanism for the relationship between seed abundance and unit area may allow more explicit recommendations. Finally, we recommend further efforts to explain and predict variation in moist-soil seed and tuber abundance in relation to specific active management practices, plant communities, and local environmental factors.

ACKNOWLEDGMENTS

We acknowledge the following sponsors of our research: Arkansas Game and Fish Commission; Ducks Unlimited, Inc., Institute for Wetland and Waterfowl Research; Federal Aid in Wildlife Restoration (Project W-48, Study 44); the United States Department of Interior Natural Resources Economic Enterprises Research Grant to the Forest and Wildlife Research Center (FWRC) of Mississippi State University; the United States Geological Survey Science Support Program; and the Mississippi Cooperative Fish and Wildlife Research Unit (Research Work Order 75). We thank biologists and managers of the United States Fish and Wildlife Service and the states of Arkansas, Louisiana, Mississippi, and Missouri for helping us conduct research on their management areas. We especially thank the following individuals who contributed substantially to this research: V. Bateman, J. Borza, H. Bracket, B. Buckley, N. Herndon, J. Hitchcock, G. Hopper, J. Jones, M. Kurtz, B. Leopold, J. Mobley, S. Pannala, J. Salas, J. Stafford, and R. Young. Our manuscript has been approved as MSU-FWRC publication WF-229.

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Associate Editor: Hall.