Articles

Seed Abundance for Waterfowl in Wetlands Managed by the Illinois Department of Natural Resources

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Abstract

Managed wetlands on public lands in Illinois, United States, provide foraging habitats for migrating and wintering waterfowl. However, few studies have estimated abundances of waterfowl foods in mid-migration regions of North America, yet such information is needed to inform management and conservation decision-making. During 2005–2007, we used a multistage sampling design to estimate moist-soil plant seed production (kg/ha, dry mass) and energetic carrying capacity at sites managed by the Illinois Department of Natural Resources and modeled variation in seed biomass. Average seed biomass among all sites ranged from 1,030.0 ± 64.1 (SE) kg/ha in 2005 to 501.5 ± 124.1 kg/ha in 2007. Our overall estimate (2005–2007) of moist-soil plant seed biomass was precise (691.3 ± 56.4 kg/ha; CV: 8.2%), equaling 5,128 energetic use-days/ha. This value was similar to or slightly greater than previous estimates from other regions of North America and exceeded the estimate used the Upper Mississippi River and Great Lakes Region Joint Venture for waterfowl conservation planning (514 kg/ha). We formulated eight models to predict abundance of moist-soil plant seeds within sampled wetlands. The best approximating model included the number of desirable plant species within wetlands and study year. The second best model included the categorical effect of management intensity and indicated that, although variable, actively managed wetlands produced about 240 kg/ha more seed than those that were passively managed. As with other regions, wetland management practices that encourage diverse plant communities over monotypes and growth of early successional plants should yield substantial increases in waterfowl food abundances at Illinois Department of Natural Resources sites, especially given that only 27% of our study wetlands were actively managed. Such efforts would also help reduce deficits in energetic carrying capacity identified by the Upper Mississippi River and Great Lakes Region Joint Venture.

Keywords: habitat conservation; Illinois; moist-soil management; public lands; waterfowl

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Introduction

Providing quality foraging habitats for waterfowl in key migration regions may promote good body condition prior to arrival at wintering areas (Fredrickson and Drobney 1979; Reid et al. 1989) and during spring migration (Heitmeyer 1985; LaGrange 1985). In the mid-continent region of the United States, Illinois represents a particularly important ecoregion for migrating and wintering waterfowl. Historically, much of the Illinois and Mississippi River floodplains were dominated by mast-producing bottomland hardwoods (e.g., pin oak *Quercus palustris*), moist-soil areas, emergent marsh, and open-water habitats (Bellrose et al. 1983; Havera 1999a; Stafford et al. 2010). These bottomlands flooded seasonally, providing vast, high-quality foraging habitat for spring- and autumn-migrating waterfowl. However, most of Illinois' natural wetlands were drained for

agriculture during the twentieth century (Havera 1999a). Exacerbating wetland loss, many remaining wetlands have been further degraded or lack productivity due to extensive sedimentation, colonization by invasive plants (e.g., willow *Salix* spp. and cocklebur *Xanthium strumarium*) and animals (e.g., common carp *Cyprinus carpio*), or lack of water control to promote emergent vegetation (Bellrose et al. 1983; Havera 1999a).

Despite landscape-scale modifications, much of Illinois remains critical habitat for migrating waterfowl (Havera 1999a; Soulliere et al. 2007). For example, peak abundance of ducks in the Illinois River valley averaged 362,000 (range: 190,000–546,000) during 1997–2007 (based on aerial inventories; M.M. Horath, Illinois Natural History Survey, unpublished data). Additionally, the Upper Mississippi River and Great Lakes Region Joint Venture (hereafter, JV), which partners with the North American Waterfowl Management Plan to help conserve the continent's waterfowl populations and habitats, relies on the Illinois River valley and other migratory focus areas in Illinois to protect, maintain, enhance, or restore 856,061 ha of wetland habitats for waterfowl. Using values provided in Soulliere et al. (2007), we estimated the JV assumes that wetlands of Illinois will provide food resources to meet the energetic needs of 48.7 million waterfowl use-days during autumn–winter (e.g., based on a mallard-sized duck *Anas platyrhynchos*).

Moist-soil management is a particularly effective strategy to provide forage for migrating and wintering waterfowl (Low and Bellrose 1944; Fredrickson and Taylor 1982; Reinecke et al. 1989; Kaminski et al. 2003). Managed moist-soil habitats are wetlands where hydrology, vegetation, and/or seed banks are manipulated to encourage growth of seed-producing vegetation (Low and Bellrose 1944; Fredrickson and Taylor 1982). Researchers in the Mississippi Alluvial Valley documented considerably more forage in moist-soil habitats than harvested croplands (Reinecke and Loesch 1996; Penny 2003; Reinecke and Hartke 2005), and waterfowl densities may be greater on moist-soil wetlands than harvested and flooded crop fields (Reinecke et al. 1992; Twedt and Nelms 1999). Further, moist-soil plant seeds provide essential amino acids not found in cereal grains (Loesch and Kaminski 1989) and have average true metabolizable energy values similar to agricultural seeds (Checkett et al. 2002; Kaminski et al. 2003).

Because Illinois provides critical habitat for migrating waterfowl, it is not surprising that moist-soil management is commonly used by the Illinois Department of Natural Resources (IDNR) to meet foraging habitat objectives. However, manipulating water levels and seed banks can yield variable results, and managers have limited resources to evaluate the success of their management practices. Further, the combined contribution of IDNR moist-soil areas to foraging carrying capacity for waterfowl is not known. Such information is needed to guide both moist-soil management practices in Illinois and waterfowl habitat conservation efforts relative to goals and objectives outlined by the North American Waterfowl Management Plan and the JV (Soulliere et al. 2007). Therefore, we estimated moist-soil plant seed abundance at IDNR lands during autumns 2005–2007. Our primary objectives were to: 1) estimate moist-soil plant seed abundance and foraging carrying capacity of IDNR moist-soil habitats managed for waterfowl in Illinois, and; 2) model variation in seed abundance with respect to environmental and management-related covariates. Although not a primary objective, we also evaluated the feasibility of using a simple technique to estimate moist-soil plant seed production that was developed in California (Naylor et al. 2005).

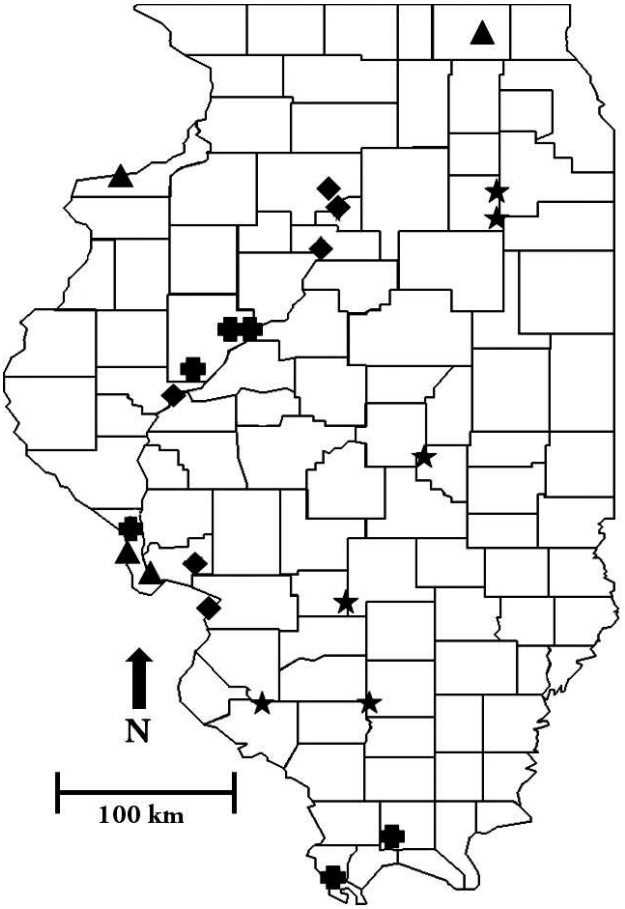

Figure 1. The State of Illinois and locations of Illinois Department of Natural Resources sites (United States) with moist-soil management sampled in 2005 (★), 2006 (♦), 2007 (▲), or multiple years (✚).

Methods

Our study sites consisted of waterfowl areas managed by IDNR and were located throughout the state, from McHenry County in northeastern Illinois to Alexander County in extreme southern Illinois (Figure 1). All sites had infrastructure (e.g., water-control structures and levees) to allow for moist-soil management. Sites ranged in area from 570 to >10,000 ha.

Estimating moist-soil plant seed abundance

We used a multistage sampling design to estimate moist-soil plant seed abundance relative to lands managed by IDNR (Cochran 1977; Seber 1982:64;

Stafford et al. 2006b; Brasher et al. 2007; Kross et al. 2008). To compile our sampling frame, we assembled a comprehensive list of IDNR-managed lands (n = 35 sites) with moist-soil wetlands using literature (Havera 1999b; Willms and Wieda 2002) and interviews of IDNR waterfowl program staff, district wildlife biologists, and site managers. Then, we used PROC SURVEYSELECT in SAS v9.1 to annually select, at random and with replacement, 8–10 waterfowl management areas for sampling (SAS Institute, Inc., Cary, NC). We visited IDNR sites to identify moist-soil units (wetlands) for potential sampling and randomly selected one or two wetlands per site to sample, depending on availability.

We attempted to sample wetlands when most seeds had matured and prior to reflooding of wetland areas. To allocate samples, we measured moist-soil impoundments along their greatest length using ArcMap v9.1 and divided them into six equidistant segments allowing spacing of five transects (i.e., north–south or east–west lines). We designated the impoundment perimeter as the foot of the levee (ideally) or point at which plant species composition transitioned from upland vegetation to hydrophytes. We then allocated three sampling locations along transects by selecting distances between 1 and 100 m from a random numbers table and alternated transect endpoints on opposite sides of the wetland perimeter when possible. Therefore, we sampled vegetation at 15 locations (three samples $\times$ five transects) per wetland. We estimated above- and below-ground seed biomass by extracting a 10-cm-diameter $\times$ 5-cm-depth core in standing vegetation at each sample location (Manley et al. 2004; Stafford et al. 2006a; Kross et al. 2008). Our samples included seeds from standing vegetation, seeds that had already fallen, and some below-ground seeds (i.e., seed bank). We placed core samples in individually labeled bags and froze them until processing. Prior to sorting, we thawed core samples at room temperature and soaked them in a 3% solution of hydrogen peroxide (H_2O_2) for 3–12 h to dissolve clays (Bohm 1979; Kross et al. 2008).

We washed samples with water over a graduated series of 2–3 sieves (mesh sizes 18 [1.00 mm], 35 [500 μm], and 60 [250 μm]) depending on the quantity of vegetation present (Penny 2003; Reinecke and Hartke 2005; Greer et al. 2007). We separated seed heads and seeds from plant debris and dried for 24 h at 87°C (Manley et al. 2004; Stafford et al. 2006a). We threshed dried materials over a second series of five sieves (mesh sizes 14 [1.40 mm], 18 [1.00 mm], 35 [500 μm], 45 [355 μm], and 60 [250 μm]) to further separate seeds from debris (Greer et al. 2007). We classified seeds as large if they were retained by the #35 sieve (e.g., largeseed smartweed *Polygonum pensylvanicum*, millets *Echinochloa* spp., and beggarticks *Bidens* spp.) and small if they remained in the #45 or 60 sieves (e.g., sprangletop *Leptochloa fusca* spp. *fascicularis*, pigweed *Amaranthus* spp., and teal grass *Eragrostis hypnoides*). We separated all large seeds from debris by hand and weighed to the nearest 0.1 mg using an electronic balance. Completely sorting small seeds from samples required extensive processing time; thus, we subsampled a portion (approx. 2.5% by mass) of each small-seed sample to estimate biomass. The percent composition of seeds and debris in the subsample was multiplied by the small-seed sample mass to extrapolate total small-seed abundance in the core. We combined small-seed and large-seed masses to estimate total seed biomass per core.

If small-seed subsampling did not reflect total biomass of small seeds in core samples, our total seed biomass estimates may have been biased; thus, we conducted two trials to investigate this possibility. First, we sorted all small seeds from 10 randomly selected core samples and correlated the proportion of seeds in the total small-seed sample with the proportion in the subsample using PROC CORR, SAS v9.1 (SAS Institute, Inc.). We also recorded the time required to completely sort these 10 samples to evaluate time-costs. Second, we randomly selected 10 samples from each year (n = 30) and sorted two additional 2.5% subsamples from each. Then, we used analysis of variance to compare the proportion of seeds recovered among the three subsamples in PROC MIXED and contrasted subsample means using the PDIFF option of the LSMEANS statement.

We used biomass data from core samples to estimate overall moist-soil plant seed abundance (kg/ha; dry mass) at IDNR sites using the SURVEYMEANS procedure in SAS v9.1 (SAS Institute, Inc.). This procedure allowed us to analyze our data collected under multistage sampling by incorporating weights and selection probabilities from our three sampling stages (Stafford et al. 2006b). The probability of selecting an IDNR site for sampling was the number of sites sampled in a given year divided by the total IDNR sites in our comprehensive list. Similarly, the probability of selecting a wetland was computed as the number of wetlands sampled at each site (one or two) divided by the total number of moist-soil wetlands at that location. Finally, the probability of selecting a soil core from a moist-soil wetland was $15/(\mathrm{AREA}_{ij}/8.107 \times 10^{-7})$, where the number of cores collected in each wetland was 15 and the potential number of cores was the AREA (ha) of wetland j within IDNR site i divided by the area of a core sample (8.107×10^{-7} ha). The weight used in analyses was the inverse of the product of the three probabilities (Stafford et al. 2006b; Brasher et al. 2007; Kross et al. 2008).

We computed an estimate of moist-soil plant seed abundance during the entire study (2005–2007) as the unweighted mean of annual means. The variance of the overall mean was computed as the sum of the annual variances divided by the square of the number of study years (n = 3 [Bowyer et al. 2005; Stafford et al. 2006a; Kross et al. 2008]). Finally, we used seed abundance data to estimate foraging carrying capacity for waterfowl in energetic use-days (EUD), defined as the number of days an area of land could support a medium-sized dabbling duck (*Anas* spp.; sensu Reinecke et al. 1989). Our EUD calculations assumed average true metabolizable energy of moist-soil plant seeds was 2.5 kcal/g (Kaminski et al. 2003). We used data on proportional use of Illinois River valley wetlands by eight dabbling duck species (mallard, American black duck *Anas rubripes*, northern pintail *A. acuta*, blue-winged teal *A. discors*, American green-winged

teal *A. crecca*, American wigeon *A. americana*, gadwall *A. strepera*, northern shoveler *A. clypeata*) during autumns 1993–1996 (Havera 1999) and species-specific estimates of daily energy requirements from Soulliere et al. (2007) to compute the daily energy expenditure as a weighted-average representative of the dabbling-duck guild migrating through central Illinois during autumn (337 kcal/d).

Moist-soil plant seed abundance modeling

We used an information-theoretic approach to investigate factors influencing variation in moist-soil plant seed abundance within IDNR wetlands (Burnham and Anderson 2002). We included the following covariates in candidate models: 1) study year (YEAR), 2) average high temperature during the growing season (1 June–31 August; HIGHTEMP), 3) cumulative precipitation during the growing season (1 June–31 August; PRECIP), 4) total number of desirable (e.g., annual plants producing seeds readily consumed by waterfowl [Bellrose and Anderson 1943; Low and Bellrose 1944; Fredrickson and Taylor 1982]) moist-soil plant species identified at sampling locations within wetlands (DESIRE), 5) total number of woody plant species identified within wetlands during sampling (WOODY), 6) categorical management intensity (MGT; passive or active) and, 7) total number of permanent and hourly IDNR staff divided by total site area in acres (STAFF_AREA). Because it was obvious that our estimates of moist-soil plant seed abundance varied among years, we included YEAR in all models as a control variable. Thus, we developed the following set candidate models:

Year Effect Model:	YEAR
Management Model:	MGT+YEAR
Temperature Model:	HIGHTEMP+YEAR
Precipitation Model:	PRECIP+YEAR
Precipitation Quadratic Model:	PRECIP+PRECIP^2+YEAR
Weather Model:	HIGHTEMP+PRECIP+YEAR
Quality Vegetation Model:	DESIRE+YEAR
Woody Encroachment Model:	WOODY+YEAR
Employee Effort Model:	STAFF_AREA+YEAR
Null Model:	Intercept only

We categorized MGT as passive or active based on field observations during preliminary site visits, subsequent sampling, and interviews with site personnel. We considered a sampled wetland as passively managed if no management other than dewatering occurred within the current or previous year. We considered actively managed wetlands as those influenced by management practices in addition to drawdown, including discing, burning, mowing, herbicide treatment, or rotating moist-soil management with crop plantings. During sampling we recorded the presence of all plant species within 1 m of each sample location and used these data to compile DESIRE and WOODY. We obtained temperature and precipitation data from the weather station nearest each IDNR site via the Midwest Regional Climate Center and used these data to compute HIGHTEMP and PRECIP. Finally, we interviewed IDNR site superintendents to obtain the number of permanent and hourly staff available during the growing season at each site as well as total area managed by these employees. We hypothesized that moist-soil plant seed abundance would be positively related to MGT, DESIRE, HIGHTEMP, and STAFF_AREA, whereas WOODY would negatively associate with seed production. We were uncertain about the possible relationship of PRECIP to seed abundance, but suspected any potential relationship could be complex; that is, PRECIP might increase seed abundance to some point, at which flooding would occur and result in reduced production.

Using the best approximating variance structure (compound symmetry), we fit models in the candidate set using the maximum likelihood estimation method (METHOD = ML) in PROC MIXED, SAS v9.1 (SAS Institute, Inc.). Because we selected sites and wetlands to be sampled with replacement, some IDNR sites were sampled in more than 1 y. To account for potential correlation among seed abundance estimates from the same sites sampled in different years, we included study site as the subject in the REPEATED statement of PROC MIXED. We determined best approximating and competing models by computing Akaike's Information Criterion adjusted for small sample size from -2 log-likelihood scores (AIC_c) and considered models competitive if they were within two AIC_c units of the best model (Burnham and Anderson 2002). We output parameter estimates using the restricted maximum likelihood method in PROC MIXED and considered covariates important if 95% confidence intervals excluded zero.

Evaluation of seed production index

In 2007, we also investigated a simple method of evaluating moist-soil plant seed abundance developed by Naylor et al. (2005) in California. This technique used a scoring system based on the percent coverage and quality (i.e., relative density and size of seed heads; Naylor et al. 2005) of vegetation. Thus, following Naylor et al. (2005), we computed a Seed Production Index (SPI) for each sampled wetland in 2007 and regressed these values with seed biomass estimates from core sampling in PROC REG, SAS v9.1 (SAS Institute, Inc.). We speculated this technique could be a viable method for site managers to efficiently evaluate the quality of their moist-soil units if the SPI explained most variation in seed abundance (i.e., based on core samples).

Results

We sampled moist-soil wetlands at 8–10 sites annually between 5 September and 24 October 2005–2007. Most IDNR sites had at least two moist-soil areas to sample; thus, the number of wetlands sampled ranged from 15 to 18 annually (n = 49 total wetlands; Table 1). Correspondingly, we extracted 225–270 core samples per year (n = 735 total cores; Table 1).

The proportion of small seeds in samples completely sorted correlated well with the proportion of seeds in subsamples from those cores (P = 0.008, r = 0.78). The average time required to completely sort small seeds

Table 1. Number of Illinois Department of Natural Resources (Illinois, United States) sites (*n* sites), moist-soil wetlands (*n* wetlands), core samples (*n* cores), estimated moist-soil plant seed abundance (kg/ha, dry mass) and energetic use days per hectare (EUD), standard error (SE), and coefficient of variation (CV), by seed size category (large [>500 μm] or small [250–500 μm]), 2005–2007. For complete data, see Tables S1–S3 (http://dx.doi.org/10.3996/092010-JFWM-034.S1).

					Seed abundance			EUD	
Year	Seed size	*n* sites	*n* wetlands	*n* cores	$\bar{x}$	SE	CV (%)	$\bar{x}$	SE
2005	Large	8	15	225	375.9	243.1	64.7	2,789	1,803
	Small	8	15	225	654.1	191.3	29.2	4,852	1,419
	Total	8	15	225	1,030.0	64.1	6.2	7,641	476
2006	Large	10	18	270	367.2	70.3	19.2	2,724	522
	Small	10	18	270	178.0	40.6	22.8	1,320	301
	Total	10	18	270	542.4	95.4	17.6	4,024	708
2007	Large	10	16	240	407.8	91.3	22.4	3,025	677
	Small	10	16	240	93.7	37.6	40.1	695	279
	Total	10	16	240	501.5	124.1	24.7	3,720	921
2005–2007	Large	28	49	735	383.6	89.7	23.4	2,846	665
	Small	28	49	735	308.6	66.4	21.5	2,289	493
	Total	28	49	735	691.3	56.4	8.2	5,128	418

from a core sample was 9.3 h; thus, it would have required an estimated 854 person-days (8.0 h/d) to completely sort small seeds from all samples. Analysis of variance indicated no difference among the proportions of small seeds recovered from three replicate subsamples by year ($F_{2,27} \leq 0.28$, $P \geq 0.760$), nor was a difference detected when years were combined ($F_{2,87} = 0.15$, $P = 0.861$).

Moist-soil plant seed abundance

Estimated biomass of moist-soil plant seeds at IDNR sites was greatest in 2005 (1,030.0 kg/ha), and our estimate was precise (CV: 6.2%; Table 1). Estimated seed abundance was considerably less in 2006 and 2007 than in 2005, averaging 542.4 and 501.5 kg/ha (Table 1), respectively. Further, estimates were less precise in 2006 (CV: 17.6%) and 2007 (CV: 24.7%) than in 2005. Seed abundance averaged over years was 691.3 kg/ha (CV: 8.2%; Table 1). In 2005, small seeds (e.g., *Eragrostis* spp., *Amaranthus* spp.) contributed considerably (63.5% of total biomass) to the annual abundance estimate. Conversely, only 32.8% and 18.7% of estimated seed abundance was attributed to small seeds in 2006 and 2007, respectively. Converting abundance estimates to EUD indicated, on average, a hectare of land could have supported 3,720–7,641 EUD annually or 5,128 EUD/ha averaged across the study period, assuming all seeds were available to waterfowl (Table 1).

Models of seed abundance

We considered 2 of 10 models formulated to predict abundance (kg/ha) of moist-soil plant seeds competitive (ΔAIC_c near 2.0); these models cumulatively accounted for 56.4% of model weight (Table 2). In addition to the control variable of YEAR, the best competing model included the fixed effect desirable plant species richness (DESIRE). The parameter estimate for DESIRE indicated an increase of 54.9 kg/ha (95% CI: 3.3, 106.5 kg/ha) for each additional plant species ($\bar{x} = 8.4 \pm 0.4$ [SE] species; range: 1–15 species). The second-best model was 1.8 AIC_c units from the best model and included categorical effects of management intensity (MGT) and YEAR. The parameter estimate for MGT indicated that, after controlling for the influence of study year, drawdown-only management resulted in less seed production ($\hat{\beta}_{MGT(1)} = -239.6$; 95% CI: −632.9, 153.8), although the confidence interval overlapped zero.

Table 2. Candidate models to predict within-wetlands moist-soil plant seed abundance (kg/ha, dry mass) at sites managed by the Illinois Department of Natural Resources, Illinois, United States, 2005–2007, based on second-order Akaike's information criterion (AIC_c), number of estimable parameters (*K*), −2 log-likelihood score (−2 log) and model weight (w_i). For complete data, see Table S4 (http://dx.doi.org/10.3996/092010-JFWM-034.S1).

Model	*K*	−2 log	AIC_c	ΔAIC_c	w_i
DESIRE[a]+YEAR[b]	6	715.0	729.0	0.0	0.401
MGT[c]+YEAR	6	716.8	730.8	1.8	0.163
YEAR	5	719.8	731.2	2.2	0.134
HIGHTEMP[d]+YEAR	6	717.6	731.6	2.6	0.109
WOODY[e]+YEAR	6	718.7	732.7	3.7	0.063
PRECIP[f]+YEAR	6	719.5	733.5	4.5	0.042
PRECIP+HIGHTEMP+YEAR	7	717.0	733.7	4.7	0.038
STAFF_AREA[g]+YEAR	6	719.8	733.8	4.8	0.036
PRECIP+PRECIP^2+YEAR	7	719.4	736.1	7.1	0.011
NULL[h]	3	733.3	739.8	10.8	0.002

[a] Total number of desirable moist-soil plant species identified in a sampled wetland.
[b] Study year.
[c] Management category (1 = passive, 2 = active).
[d] Average high temperature during 1 June–31 August.
[e] Total number of woody plant species identified in a sampled wetland.
[f] Cumulative precipitation during 1 June–31 August.
[g] Number of permanent and hourly staff at a site divided by total site area.
[h] Intercept only.

Seed-production index

Values of the SPI for the 15 wetlands sampled in 2007 ranged from 10 to 67 (Table S5, http://dx.doi.org/10.3996/092010-JFWM-034.S1). There was a significant and positive statistical relationship between the SPI and estimated seed abundance from core samples ($F_{1,13}$ = 24.03, $P < 0.001$). The SPI explained 64.9% of the variation in moist-soil plant seed abundance.

Discussion

Our overall estimate of moist-soil plant seed abundance at IDNR sites during 2005–2007 was precise (CV: 8.2%); thus, we believe it provides a reliable estimate for waterfowl conservation planning in the Upper Mississippi River region. Currently, the JV uses an estimate of moist-soil seed abundance of 514 kg/ha, but then halves this value based on an assumption that only 50% of forage is available to waterfowl (i.e., 257 kg/ha). Our study-period average estimate (691.3 kg/ha) was 34.5% greater than the value used by the JV (gross or halved), which was excluded from our 95% confidence interval (584.7–797.9 kg/ha). Although our overall estimate was spatially and temporally diverse, our study area only encompassed a fraction of the JV region. Thus, our estimates are only relevant to the southern portion of this area. Nonetheless, we suggest it be incorporated in regional energetic-based conservation plans along with existing estimates (e.g., Soulliere et al. 2007).

We sorted seeds as small and large because it would have been impractical for us to completely recover small seeds from samples without subsampling. Reinecke and Hartke (2005) estimated that they recovered 88% of large seeds (i.e., common barnyardgrass) from samples with known seed masses. Although this recovery rate was relatively high, it supports the notion that some seeds are not recovered during core-sample processing (Kross et al. 2008). Thus, our estimates should be considered conservative because we did not quantify potential bias due to seeds missed during sorting. Our estimates could also be potentially biased if subsamples used to estimate small-seed abundance did not reflect small-seed abundance in an entire core. However, our evaluation indicated that the proportions of small seeds in multiple subsamples from one core were statistically consistent. Further, for 10 samples we sorted completely, the proportion of seeds in subsamples predicted well the proportion of seeds in the entire sample. Therefore, we suggest any bias associated with subsampling or incomplete recovery of seeds was minimal and, if present, likely resulted in conservative estimates.

The sampling strategy we employed was intended to yield estimates of seed abundance shortly before migratory waterfowl typically arrive in the region. However, seeds may be lost to a variety of pathways during the migratory period, most notably consumption by nonwaterfowl species and decomposition. Regarding the latter, previous research indicated that seeds of some moist-soil plants lost considerable mass (e.g., 3–43% [Neely 1956; Shearer et al. 1969; Nelms and Twedt 1996]) when flooded for 90 d. Thus, if considerable deterioration or loss of seeds occurred prior to consumption by waterfowl, our estimate of moist-soil plant seed abundance would overestimate availability to waterfowl. Nonetheless, we suggest our estimate is relevant to seed abundance at the onset of migration.

Our 3-y estimate of seed biomass (691.3 kg/ha) was generally greater than published estimates of moist-soil plant seed abundance from other regions of the United States. Bowyer et al. (2005) estimated 790 kg/ha of moist-soil plant seeds during 1999–2001 at Chautauqua National Wildlife Refuge in central Illinois, and estimates varied considerably among years (329–1,231 kg/ha). The only other biomass estimate from Illinois we were aware of indicated 3,155 kg/ha of seeds in millet stands and 653 kg/ha of seeds for 10 other moist-soil plant species (Low and Bellrose 1944).

Studies from other areas of the United States reported considerable, but variable, seed production in moist-soil wetlands. Fredrickson and Taylor (1982) suggested moist-soil plant seed production of 1,629 kg/ha was a reasonable objective for managed wetlands; our estimates were well below this proposed value, as were most other contemporary estimates. Brasher et al. (2007) reported biomass of waterfowl foods in Ohio ranged from 377 to 520 kg/ha during 2001–2004, but these estimates included submersed aquatic vegetation and tubers in addition to moist-soil plant seeds (Brasher et al. 2007). Kross et al. (2008) estimated moist-soil seed abundance at the scale of the Mississippi Alluvial Valley during 2002–2004 and reported seed biomass averaged 496.3 $\pm$ 62.0 (SE) kg/ha (range: 396.8–555.2 kg/ha). Moser et al. (1990) documented 253–1,288 kg/ha of moist-soil plant seeds in Arkansas impoundments during 1988–1990. In contrast to these low estimates, Greer et al. (2007) reported 1,695 kg/ha of plant seeds in managed wetlands of Missouri during 2000–2001. Annual variation in the previous studies was typically attributed to differing management practices (e.g., timing of drawdown, soil disturbance).

Small seeds contributed considerably to overall biomass (44.6%) in our study and were predominant in 2005 samples (63.5%). Other investigations of seed production for waterfowl have separated small from large seeds, but not all reported their respective biomasses. Dugger and Feddersen (2009) estimated abundance of wetland plant seeds in Pool 25 of the Mississippi River (west-central Illinois and east-central Missouri) and reported average biomasses of 2,541 kg/ha in 1999 and 3,336 kg/ha in 2001 were comprised largely of *Cyperus erythrorhizos* (1,264–1,783 kg/ha), *Polygonum lapathifolium* (120–1,148 kg/ha), and *Echinochloa* spp. (144–909 kg/ha). Thus, about half of seed biomass in those years was attributable to the small-seeded *Cyperus* (Dugger and Feddersen 2009). In contrast, Kross et al. (2008) attributed only 25% of total seed mass to small seeds in the Mississippi Alluvial Valley. Similarly, Reinecke and Hartke (2005) reported 83% of seed biomass in west-central Mississippi was due to large seeds. In our experience, many wetland managers evaluate the success of moist-soil management practices in part by the amount of large-seeded annual plants (e.g., millets) produced. However, Havera (1999:534–541) reported

that mallards in our study region readily consumed several small-seeded species, many of which have true-metabolizable energy values as great as or greater than those of large seeds (Kaminski et al. 2003; Dugger et al. 2007) and may also produce tubers (e.g., *Cyperus esculentus*). Thus, our results indicated plants producing small seeds may contribute considerably to total waterfowl forage at IDNR sites.

Models of moist-soil plant seed abundance indicated that biomass increased as the number of desirable plant species increased. Although this result was generally intuitive, our experiences indicate that some wetland managers may consider their practices most successful if they result in monocultures of a few desirable species. In addition to increasing seed yield, increased plant species richness likely provides seeds of varying sizes and nutrient compositions, thereby benefiting multiple species of waterfowl with different bill morphologies and foraging strategies (DuBowy 1988; Guillemain et al. 2002).

Our second-best model included the main effect of MGT (passive = drawdown only, active = drawdown and additional management), which was positively associated with seed production after controlling for year. However, the estimated effect of passive management was variable and, hence, equivocal. Nonetheless, the notion that active management may increase seed production is intuitive and supported by previous studies. For example, Kross et al. (2008) found greater seed production and higher occurrences of early successional grasses in actively managed impoundments in the Mississippi Alluvial Valley. Naylor (2002) reported moist-soil plant seed biomass increased with several categories of increasing management intensity (i.e., timing and rate of drawdown, irrigation, and soil disturbance). Penny (2003) documented greatest biomass of seeds and tubers (= 1,184 $\pm$ 198 kg/ha) in intensively managed moist-soil areas compared to those that were passively managed (= 502 $\pm$ 60 kg/ha). Brasher et al. (2007) reported that autumn energetic carrying capacity of actively managed wetlands in Ohio averaged 1.7 times that of passively managed wetlands, although wetlands of both management types had low food abundances the following spring. Johnson (2007) reported seed biomass during September was 67% greater in managed than unmanaged wetlands in the Great Salt Lake region of Utah. We classified only 13 of our 49 impoundments as actively managed, but the effect-size of MGT indicated these efforts resulted in an average increase in seed abundance of 35% over the study period mean compared with passive management.

We evaluated the SPI developed by Naylor et al. (2005) because we encountered many wetland managers seeking advice on evaluating their moist-soil management practices. To this end, our evaluation of the SPI indicated most variation in seed biomass could be explained by this technique. Our evaluation was only conducted during 1 y; however, the SPI should be evaluated for several years to understand whether the relationship with seed production is consistent throughout a range of environmental conditions. Further, Naylor et al. (2005) based their technique on only six plant genera that produced 90% of the seed in samples from California wetlands, whereas we encountered up to 15 species in our study. Finally, Naylor et al. (2005) found their technique to be repeatable by multiple observers in different wetlands but we did not evaluate repeatability among observers or sites.

Research and Management Implications

Estimated abundance of moist-soil plant seeds at IDNR sites was generally high and exceeded the value used for conservation planning by the JV. Thus, despite annual and site-specific variation in seed production, moist-soil management on Illinois' lands provided relatively abundant waterfowl forage during our study, and we suggest our estimate be incorporated in regional conservation plans. We also note that our findings are part of a growing body of research that provides average estimates of moist-soil plant seed production for waterfowl with generally similar results (e.g., $\pm$200 kg/ha). However, as with our investigation, many such studies have also revealed considerable interannual variation in seed production that could relate to variation in the abundance, distribution, and behavior of waterfowl from year to year. We suggest future studies of food production strive to relate numerical and functional responses of waterfowl to variation in forage abundance and distribution, perhaps through behavioral observations (e.g., Kotler et al. 2007) or experimental manipulations.

Models of seed abundance indicated richness of desirable plant species and presence of active management were indicative of increased seed production. Indeed, actively managed wetlands produced, on average, approximately 235 kg/ha more seed than passively managed sites, but the average effect was highly variable. Nonetheless, the weight of evidence from our results and previous studies supports the notion that disturbance regimes such as discing, mowing, or treating undesirable plants with herbicide can yield substantial increases in seed production. Soulliere et al. (2007) recommended restoring or enhancing 3,400 ha of moist-soil wetland in the JV region to increase carrying capacity based on population deficits of some waterfowl species. Given that only 27% of our wetlands were actively managed, we suggest there is considerable opportunity to increase carrying capacity for waterfowl at IDNR sites and partially address this regional objective. To accomplish this, we recommend an outreach and education program be implemented within the IDNR to promote the principles, practices, and benefits of active moist-soil management.

Finally, it appears that the SPI developed by Naylor et al. (2005) to quickly estimate moist-soil plant seed production in wetlands of California may be useful in Illinois. However, we believe the technique could be improved by modifying the protocol to account for the variety of moist-soil plants found in Illinois wetlands. Further, investigators should verify that the technique can be replicated by different observers, among different wetlands, and over more than 1 y.

Supplemental Material

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Table S1. Data used in computing moist-soil plant seed abundance in 2005, Illinois, United States. Site, name of study site; Area, area of sampled unit in hectares; Impounds, number of impoundments at the study site; Impound, identifier of the sampled impoundment; Trans, transect number; Sample, core sample identifier within transect; Lgseed, mass of large seeds in that sample (mg, dry mass); Smsamp, mass of total small seed sample, including trash (mg, dry mass); Subsamp, mass of small seed subsample selected for sorting (mg, dry mass); Subseed, mass of small seeds within Subsamp (mg, dry mass); Subtrash, mass of material other than seeds in Subsamp (mg, dry mass); Subprop, proportion, by mass, of small seed subsample (mg, dry mass); Smseed, estimated small seed biomass in the sample (mg, dry mass); Allseed, total seed mass (Lgseed + Smseed) (mg, dry mass); Prob2 , probability of selecting a sampled field within a study site; Prob3, probability of extracting a core sample from a study impoundment; Mgt, management category (1 = Passive, 2 = Active).

Table S2. Data used in computing moist-soil plant seed abundance in 2006, Illinois, United States. See Table S1 for abbreviation definitions.

Table S3. Data used in computing moist-soil plant seed abundance in 2007, Illinois, United States. See Table S1 for abbreviation definitions.

Table S4. Modeling data used in computing moist-soil plant seed abundance in 2005, 2006, and 2007, Illinois, United States. Site, name of study site; Year, study year; Impound, impoundment identifier within site; Mean_kg, estimated seed biomass within the impoundment (kg/ha dry mass); Staff, number of permanent staff at the site; Hourly, number of hourly (temp) staff at the site; Mgd_ha, total managed area at the site (in ha); Mgt, management category (1 = Passive, 2 = Active); Precip_sum, sum of precipitation during the growing season (in.); High_temp, average high temperature during the growing season (° F), imperial units were converted to metric in SAS as required; Woody, number of woody plant species documented during sampling; Desire, number of desirable plant species documented during sampling.

Table S5. Data used to determine seed-production index at the specified sites in Illinois, United States. Site, name of study site; kg/ha, average biomass at sampled site in kg/ha; Naylor, seed-production index score based on Naylor et al. (2005).

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