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From the Field

Temporally Robust Models for Predicting Seed Yield of Moist-Soil Plants

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ABSTRACT Rapid assessment of food production and subsequent availability is fundamental to evaluating wetland management practices and general habitat quality for waterfowl. Traditional methods of estimating food biomass (e.g., plot and core sampling) require considerable time, expertise, and cost. Rapid assessment models using plant measurements or scanned seed-head area have recently been adapted to predict seed production in moist-soil wetlands. We evaluated existing models of seed production and estimated benthic seed density with data collected during autumn 2011 in western Tennessee, USA, to improve prediction capability of seed availability for waterfowl. Generally, all models explained significant variation ($r^2 = 0.85$–0.98) and accurately predicted seed production in moist-soil plants ($r^2 = 0.84$–0.97). Belowground proportions of seed biomass and duck energy days differed across species relative to previously reported biomass estimates in moist-soil wetlands ($\bar{x} = 0.4$–9.1%); thus, production estimates from models should be adjusted on a species-specific basis and the effect of belowground seeds on overall energetic carrying capacity estimates will vary with species composition of wetlands. We recommend use of updated most-soil rapid-assessment models incorporating seed bank estimates to predict waterfowl food availability and evaluate management practices.

KEY WORDS carrying capacity, dabbling duck, Tennessee National Wildlife Refuge, waterfowl, wetlands.

Habitat conservation for North American waterfowl is based on the premise that food is limiting during the nonbreeding period and may affect trends in populations (Heitmeyer and Fredrickson 1981, Newton 2006, NAWMP 2012). Thus, managers use food availability in lieu of other functional uses of habitat by waterfowl (e.g., value as thermal cover, refugia from predators, pair-bond isolation) as a surrogate for habitat quality (Brasher et al. 2007, Hagy and Kaminski 2012). Conservation planners and habitat managers estimate food resources in wetlands located along migration routes and at wintering sites to estimate energetic carrying capacity and evaluate wetland management practices for waterfowl (Gray et al. 2013, Williams et al. 2014). Energetic carrying capacity is often measured using duck energy days (DEDs; Reinecke and Loesch 1996), a measure of available energy expressed in the currency of the energetic requirements of one duck for 1 day. Food resources in wetlands include seeds, plant material, and aquatic invertebrates (Fredrickson and Taylor 1982, Baldassarre and Bolen 2006). Available seed biomass often drives DED calculations because dabbling ducks primarily consume this food resource during migration and winter (Delnicki and Reinecke 1986, Anderson and Smith 1999, Heitmeyer 2006). Traditional methods of estimating seed and tuber biomass, often a surrogate of energetic carrying capacity, include measuring vegetation characteristics to predict seed yield (Laubhan and Fredrickson 1992, Gray et al. 1999*a*) or taking benthic core samples before waterfowl access wetlands (Kross et al. 2008*b*, Hagy and Kaminski 2012), but these procedures are time-consuming and costly (Gray et al. 1999*a*, Stafford et al. 2010). Thus, managers require rapid assessment methods to more efficiently evaluate habitat quality for migrating and wintering waterfowl (Laubhan and Fredrickson 1992).

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Several methods have been used to rapidly estimate seed production and availability for waterfowl. Initial studies developed multiple linear-regression models using multiple plant morphological measurements (e.g., plant height and inflorescence diameter; Laubhan and Fredrickson 1992, Gray et al. 1999*b*, Sherfy and Kirkpatrick 1999), but plant measurements were tedious and time-consuming to obtain and model predictions were biased when used outside the region where they were developed (Gray et al. 1999*a*,*b*). Naylor et al. (2005) developed a simplified visual foraging habitat quality index for moist-soil wetlands in California, USA. However, performance outside of that region was reduced similar to previous models (Laubhan and Fredrickson 1992, Gray et al. 1999*b*, Stafford et al. 2011). Gray et al. (2009) improved morphological models by streamlining the measurement process using desktop or portable scanners. Prediction models produced by Gray et al. (2009) depended on scanned seed-head area instead of time-consuming morphological measurements and retained robust predictive power ($r^2 > 0.91$). However, updated morphological models predict seed production rather than seed availability. Seed availability can be affected by decomposition, granivory, germination, and other factors prior to waterfowl accessing foods, including presence of an unknown biomass of seeds in the substrate remaining from previous growing seasons (Neely 1956; McGinn and Glasgow 1963; Nelms and Twedt 1996; Kross et al. 2008*a*; Foster et al. 2010*a*,*b*). Additionally, current models have not been evaluated for annual changes in seed production using data collected across multiple years (Gray et al. 2009).

We evaluated effects of temporal variation and belowground seed density on seed production estimates from models developed by Gray et al. (2009). We examined 1) previously published seed-yield models from moist-soil plants to assess effects of temporal variation in seed production on estimates; and 2) belowground biomass to adjust production estimates for foods actually available at the time of sampling. We predicted previously published models would be robust over time and belowground food resources would be significant and require model adjustment due to sources of variation among plant species.

STUDY AREA

We conducted our study during September 2011 on the Duck River Unit (DRU) of Tennessee National Wildlife Refuge (TNWR; 10,820 ha) and Cross Creeks National Wildlife Refuge (CCNWR: 3,586 ha) in western Tennessee, USA. We utilized similar data collected for a previous study during September 2005–2006 on the DRU (Gray et al. 2009). The TNWR and CCNWR contained diverse habitat complexes and provided sanctuary to as many as 200,000 wintering waterfowl (Sanders et al. 1995, USFWS 2010). The DRU and CCNWR consisted of riverine wetlands and seasonally flooded impoundments. Impoundments were flooded via precipitation, pumping from the Tennessee River (DRU), and gravity drain through multiple water-control structures throughout the main body of the refuge. Refuge biologists used intensive management practices typical for the Southeast, including April–June drawdowns and periodic disking to set back succession (Strader and Stinson 2005, USFWS 2010).

METHODS

During September 2011, we located stands of moist-soil vegetation within DRU and CCNWR impoundments and collected mature seed heads of redroot flatsedge (*Cyperus erythrorhizos*), barnyardgrass (*Echinochloa crus-galli*), Walter's millet (*E. walteri*), red sprangletop (*Leptochloa panicea* subsp. *brachiata*), rice cutgrass (*Leersia oryzoides*), fall panicum (*Panicum dichotomiflorum*), and curlytop knotweed (*Polygonum lapathifolium*; Schummer et al. 2012). We placed a transect randomly within stands containing desired species of vegetation and selected a random distance along the transect (0–10 m) to the first sample location. We then collected plant seed heads and core samples at fixed intervals predetermined to span the experimental plot. We collected one core sample (10 cm in depth and diam) adjacent to each sampled plant to adjust models for belowground food resources and link production estimates to food availability estimates for waterfowl. We swept away surface debris prior to sampling and assumed that core samples obtained adjacent to each sampled plant were representative of benthic seeds associated with that species from previous growing seasons. We were unable to locate rice cutgrass on the DRU and CCNWR and collected samples of that species from Seven Islands Wildlife Refuge in Sevier County, Tennessee.

Following the procedures of Gray et al. (2009), we placed each seed head and associated core sample in separate, appropriately labeled Ziploc® bags (S. C. Johnson & Son, Racine, WI, USA) and transported them to the University of Tennessee—Knoxville for processing. In the laboratory, we spread racemes and umbels so that overlapping was minimized and dried seed heads in a plant press for approximately 1 month. Following drying and pressing, we scanned seed heads with a desktop scanner, threshed seeds from heads, dried seeds to constant mass in a drying oven at $\geq 70^\circ$ C for ≥ 24 hr, and weighed seeds to the nearest 0.1 mg. We washed core samples through a large (1.4 mm) and small (300 μm) sieve to separate seeds from soil and removed seeds of target species (i.e., seeds of the adjacent plant species) from both sieves by hand. We quartered (by mass) small sieve portions to increase processing efficiency (Stafford et al. 2010, Hagy et al. 2011). Seeds and tubers recovered from core samples were dried and weighed as previously described. We converted biomass estimates (threshed seeds and core samples; kg/ha) to duck energy days (DED) using published true metabolizable energy values (Hoffman and Bookhout 1985, Sherfy and Kirkpatrick 1999, Checkett et al. 2002) and the mean daily energetic requirements of dabbling duck species occurring in the Mississippi Alluvial Valley (MAV; 294.4 kcal/duck/day; Gray et al. 2013).

We tested the prediction accuracy of existing models by comparing actual seed yield (g) with predicted seed yield from models of scanned seed-head area (Gray et al. 2009). We used simple linear regression and cross-validation to evaluate models presented by Gray et al. (2009). To cross-validate existing models, we inputted scanned seed-head area into existing models and regressed the resulting value against threshed seed mass in SAS 9.3 (PROC REG in SAS v9.2; SAS 2012). Additionally, we built 2 sets of linear models for each species using 1) data from 2011; and 2) combined data from 2005 to 2006 and 2011. We examined plots of residual values to ensure homoscedacity across years. We used weighted least-squares regression for combined models of barnyardgrass and rice cutgrass, because plots of residuals revealed nonconstant variance (Gray et al. 2009). We

Table 1. Mean scanned seed-head area ($\bar{x}$), percent difference between years ($\Delta\bar{x}$), sample size (n), and results from a simple linear regression of predicted and observed seed biomass estimates (i.e., cross-validation) with variance explained (r^2) and the difference in variance explained between years (Δr^2) of 7 moist-soil plant species collected at Tennessee and Cross Creeks National Wildlife Refuges and Seven Islands Wildlife Refuge, Tennessee, USA, during September 2005–2006 and 2011.

	2005–2006[a]		2011[a]							
Species	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\Delta\bar{x}$ **(%)**	n	F	P	r^2	Δr^2
Redroot flatsedge	186.6A	9.3	82.2B	4.4	−127	79	915.3	<0.001	0.92	−0.05
Barnyardgrass	48.1A	1.9	65.2B	3.2	26	78	352.2	<0.001	0.82	−0.15
Walter's millet	111.4A	4.5	93.5B	5.3	−19	40	743.7	<0.001	0.95	−0.02
Red sprangletop	66.4A	2.6	43.0B	3.1	−54	75	512.3	<0.001	0.87	−0.09
Rice cutgrass	18.6A	0.7	17.3A	0.6	−8	38	402.3	<0.001	0.92	−0.07
Fall panicum	24.2A	1.7	39.8B	3.9	39	73	347.1	<0.001	0.83	−0.07
Curlytop knotweed	31.5A	2.6	54.8B	4.1	43	77	1,879.6	<0.001	0.96	−0.01

[a] Means within rows followed by unlike letters represent significant differences ($P < 0.05$) using a Student's t-test.

evaluated models using explained variance (r^2, r^2pred), with r^2pred calculated by subtracting the quotient of the total sums of squares and the predicted residual sums of squares from 1. If plots indicated heterogeneity of variances among years, we used a Welch option to account for differences. We used individual t-tests for each species to determine whether mean seed-head area differed from 2005 to 2006 (Gray et al. 2009) and 2011 (Table 1).

We averaged benthic seed biomass across samples and generated a constant, additive adjustment for each species, which could be incorporated into biomass or DED estimates. Variation in true metabolizable energy values among species may result in DED differences where biomass differences do not occur. Thus, we tested for differences in belowground seed biomass and DEDs among species using a one-way analysis of variance (ANOVA) and used Tukey's Honestly Significant Difference test to determine pairwise differences when the ANOVA was significant ($\alpha = 0.05$; Zar 2009).

RESULTS

Models presented in Gray et al. (2009) adequately predicted seed mass from heads collected at TNWR and CCNWR in 2011 ($F_{1,35} > 347.1$, $P < 0.001$), although variance explained was slightly less than across original samples ($r^2 = 0.82$–0.96). Barnyardgrass ($\Delta r^2 = -0.15$) and red sprangletop ($\Delta r^2 = -0.09$) model predictions had notably reduced r^2-values (Table 1). Seed head area was less for redroot flatsedge (−127%), Walter's millet (−19%), and red sprangletop (−54%), but greater for barnyardgrass (26%), fall panicum (39%), and curlytop knotweed (43%) in 2011 samples than those collected in 2005–2006 ($P < 0.01$; Gray et al. 2009). Regression models using 2011 samples generally explained similar proportions of variation as did those presented in Gray et al. (2009; $r^2 = 0.85$–0.97), but models resultant from combining 2005–2006 and 2011 data had slightly less predictive ability for some species ($r^2 = 0.82$–0.97; Table 2).

Mean benthic seed mass from autumn samples differed among plant species ($F_{6,123} = 6.6$, $P < 0.01$) and was greatest in samples collected adjacent to Walter's millet (36.7 kg/ha), rice cutgrass (45.0 kg/ha), and red sprangletop (27.1 kg/ha; Table 3). Notably, barnyardgrass and curlytop knotweed had the lowest benthic seed masses (1.8 and 7.3 kg/ha, respectively), despite being 2 of the largest of the 7 seeds examined (Schummer et al. 2012). Similarly DED estimates differed among plant species ($F_{6,123} = 20.3$, $P < 0.01$) and species-specific adjustments were greatest for Walter's millet (326.7 DED/ha), rice cutgrass (445.3 DED/ha), and red sprangletop (242.6 DED/ha). Adjustments varied widely, however, ranging from 12.9 DED/ha (redroot flatsedge) to 445.3 DED/ha (rice cutgrass; Table 3).

DISCUSSION

All models explained substantial variation in seed production of moist-soil plants and had high predictive ability, providing further support for scanned seed-head area of moist-soil plants as an appropriate indicator of seed production (see Gray et al. 1999*a*, 2009; Anderson 2006). Intuitively, models performed better when used with data from which they were generated. However, variance explained was only slightly reduced when using models previously presented by Gray et al. (2009) or new models using data from 2005 to 2006 and 2011 combined. Despite different seed-head area across years for most species, models presented by Gray et al. (2009) accurately predicted seed biomass (Table 1). Thus, temporal variation in our study area seemed to have little effect on explanatory power of models and we suggest that rapid-assessment models of moist-soil plant-seed production are robust to temporal variation in plant morphology.

Seed-head sampling for rapid-assessment models occurs prior to plant senescence in late summer or early autumn, which may be several months before the arrival of most migrating waterfowl. During this time between assessment and waterfowl arrival, seed loss may be significant and model adjustments that account for these losses are not currently available for moist-soil plants. Stafford et al. (2006) and Kross et al. (2008*a*) reported significant declines (71% and 78%, respectively) in waste rice during this "pre-arrival" period in the Mississippi Alluvial Valley and Foster et al. (2010*b*) reported losses exceeding 75% for agricultural grains during September–January in Tennessee. Other studies have documented decomposition of moist-soil seeds in wetlands (e.g., Neely 1956, McGinn and Glasgow 1963, Nelms and Twedt 1996, Anderson and Smith 2002, Foster et al. 2010*a*), but previous studies failed to account for seed loss due to

Table 2. Models for predicting seed production of 7 common moist-soil plants collected at Tennessee and Cross Creeks National Wildlife Refuges and Seven Islands Wildlife Refuge, Tennessee, USA, during September 2005–2006 and 2011 using scanned seed-head area (AREA, cm^2), sample size (n), and results from simple linear regression with variance explained (r^2).

Species	Class[a]	n	Model[b]	F	P	r^2	r^2_{pred}
Redroot flatsedge	2005–2006	59	Y = (0.018 × AREA) + 0.209	1,070.1	<0.001	0.97	0.97
	2011	78	Y = (0.022 × AREA) − 0.001	689.2	<0.001	0.95	0.94
	Combined	136	Y = (0.019 × AREA) − 0.001	2,036.3	<0.001	0.97	0.97
Barnyardgrass	2005–2006	60	Y = (0.026 × AREA) − 0.023	982.2	<0.001	0.97	0.97
	2011	76	Y = (0.013 × AREA) + 0.002	268.7	<0.001	0.88	0.85
	Combined	136	Y = (0.015 × AREA) + 0.001	473.7	<0.001	0.88	0.85
Walter's millet	2005–2006	60	Y = (0.010 × AREA) + 0.256	1,178.2	<0.001	0.98	0.97
	2011	37	Y = (0.019 × AREA) − 0.001	579.2	<0.001	0.97	0.97
	Combined	95	Y = (0.012 × AREA) + 0.001	572.2	<0.001	0.92	0.91
Red sprangletop	2005–2006	59	Y = (0.008 × AREA) + 0.301	682.2	<0.001	0.96	0.96
	2011	74	Y = (0.009 × AREA) + 0.001	355.9	<0.001	0.91	0.89
	Combined	133	Y = (0.012 × AREA) − 0.001	719.2	<0.001	0.92	0.91
Rice cutgrass	2005–2006	59	Y = (0.009 × AREA) + 0.009	2,664.8	<0.001	0.99	0.99
	2011	36	Y = (0.007 × AREA) + 0.001	386.8	<0.001	0.96	0.95
	Combined	95	Y = (0.007 × AREA) + 0.001	1,297.4	<0.001	0.97	0.96
Fall panicum	2005–2006	58	Y = (0.023 × AREA) − 0.281	326.2	<0.001	0.92	0.90
	2011	73	Y = (0.010 × AREA) + 0.001	528.9	<0.001	0.94	0.93
	Combined	130	Y = (0.009 × AREA) + 0.001	375.3	<0.001	0.85	0.82
Curlytop knotweed	2005–2006	62	Y = (0.045 × AREA) − 0.059	1,067.5	<0.001	0.97	0.97
	2011	74	Y = (0.044 × AREA) − 0.001	1,262.8	<0.001	0.97	0.97
	Combined	136	Y = (0.044 × AREA) − 0.001	2,066.1	<0.001	0.97	0.97

[a] 2005–2006 models (Gray et al. 2009).
[b] We created all models using simple linear regression, with the exception of the combined models for rice cutgrass and barnyardgrass. We generated these equations with weighted least-squares regression because of nonconstant variance.

granivory or only estimated loss after the arrival of waterfowl in autumn and winter. Thus, information is not available to determine loss or decomposition of moist-soil seeds between early autumn when rapid assessment sampling must occur and late autumn when most waterfowl arrive in migration and wintering areas. Future research should explore these losses and relationships between visual (Naylor et al. 2005) and rapid quantitative (Gray et al. 2009) seed production estimates, estimates of seed availability during late autumn and winter, and concurrent waterfowl use to further verify the use of these methods as indices of foraging habitat quality for waterfowl.

Current rapid-assessment models using scanned seed-head area appear to be good predictors of seed production and available food resources for migrating and wintering waterfowl, even without having been adjusted for belowground seed resources. Benthic core samples collected adjacent to plants used for rapid seed-production estimates contained seed biomass that varied by species and benthic resources have variable effects on overall carrying capacity estimates, depending on species composition of wetlands. Further, benthic seed biomass was low relative to overall seed density estimates provided by Kross et al. (2008*b*) for managed moist-soil wetlands in the Mississippi Alluvial Valley (MAV; 496 kg/ha). For instance, benthic seed masses adjacent to Walter's millet (7.6%), rice cutgrass (9.1%), red sprangletop (5.4%), redroot flatsedge (0.5%), barnyardgrass (0.4%), fall panicum (1.7%), and curlytop knotweed (1.5%) comprised a small proportion of seed density relative to estimates from Kross et al. (2008*b*), and adjusting estimates for benthic resources would not have large effects on food availability estimates unless densities were near a foraging threshold (Hagy and Kaminski 2015). Our models validate existing methods used to rapidly estimate seed production in and energetic carrying capacity of moist-soil wetlands. More importantly, our results suggest that benthic seeds from previous years contribute little to food biomass estimates, emphasizing the importance of annual moist-soil plant production to migrating and wintering waterfowl.

Table 3. Mean ($\bar{x}$) and standard error (SE) of belowground seed density (kg/ha[dry]) of each seed species, number of core samples processed (n), and duck energy days (DED) from core samples adjacent to 7 moist-soil plant species collected at Tennessee and Cross Creeks National Wildlife Refuges and Seven Islands Wildlife Refuge, Tennessee, USA, during September 2011.

		kg/ha[a]		DED[a]	
Species	n	$\bar{x}$	SE	$\bar{x}$	SE
Redroot flatsedge	11	2.3A	1.0	12.9A	5.9
Barnyardgrass	10	1.8A	0.8	16.0A	6.8
Walter's millet	26	36.7B	8.6	326.7B	76.6
Rice cutgrass	10	45.0B	16.1	445.3B	159.2
Red sprangletop	13	27.1B	6.1	242.6B	54.7
Fall panicum	33	8.8A	2.6	73.3A	21.7
Curlytop knotweed	27	7.3A	2.6	30.0A	10.8

[a] Means within columns followed by unlike letters are different by analysis of variance and Tukey's Honestly Significant Difference test.

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