

# PREDICTING SEED YIELD OF MOIST-SOIL PLANTS

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**Abstract:** Estimates of seed production are important for basic and applied ecological research, calculation of carrying capacity of waterfowl foraging habitats, and evaluation of wetland management. M. K. Laubhan and L. H. Fredrickson predicted seed yield of moist-soil plants using phytomorphological measurements and multiple linear regression (*Journal of Wildlife Management* 56:329–337). We evaluated their general methodology in Mississippi, tested if different morphological measurements would predict seed mass accurately and precisely, and evaluated their significant predictor variables in our models. We measured phytomorphological variables of 6 moist-soil plant species in 1993 and 1994. Significant variation in seed mass was explained by our models ( $P < 0.001$ ,  $R^2_{\text{adj}} = 0.78\text{--}0.97$ ); however, our models never contained the same variables as Laubhan and Fredrickson's models. Models containing significant ( $P \leq 0.01$ ) variables detected by Laubhan and Fredrickson, but developed using our data, had lower predictability and greater collinearity than our models. Although multiple regression models may adequately predict seed yield of moist-soil plants, our results suggested inconsistency in predictor variables, model site-specificity, and need for a simpler predictive approach.

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Moist-soil plants are hydrophytes that grow in response to spring and summer drawdowns and produce seeds and other propagules used as food by waterfowl (Fredrickson and Taylor 1982, Reinecke et al. 1989). Estimates of seed production by moist-soil plants are useful to evaluate effects of wetland management and to estimate carrying capacity of waterfowl foraging habitat in units commonly termed "waterfowl use-days" (Reinecke et al. 1989, Reinecke and Loesch 1996). Traditional methods of estimating seed yield (e.g., vegetation harvest, drying, weighing seeds) are laborious and require field and specialized laboratory equipment (Kelley 1990, Gray 1995:19–20). To increase efficiency, Laubhan and Fredrickson (1992) developed methodology to predict seed yield of 13 common moist-soil plant species in the upper Mississippi Alluvial Valley and the middle Rio Grande Valley, New Mexico, using phytomorphological measurements and multiple linear regression. However, plant morphology and seed production vary spatially and temporally

(Reinecke et al. 1989, Mushet et al. 1992). Thus, our objectives were to evaluate Laubhan and Fredrickson's (1992) method in Mississippi, evaluate different phytomorphological measurements as predictor variables, and develop regression equations for additional plant species.

## STUDY AREA

Our study was conducted in 1993 and 1994 at Noxubee National Wildlife Refuge (NNWR) in eastcentral Mississippi (Wehrle et al. 1995). The specific study site within the refuge was an 80-ha moist-soil management complex composed of 11 impoundments. Moist-soil plants were collected from 4 of the impoundments because a related study was conducted concurrently in these impoundments and plant species therein typified the plant community in the entire management complex (Gray 1995:123–124). Impoundments 2 and 8 (9.6 and 7.1 ha) were study sites in 1993, and impoundments 5a and 7 (1.9 and 5.1 ha) were sites used in 1994.

## METHODS

### Vegetation Sampling and Measurements

Plant species evaluated in 1993 were common barnyardgrass (*Echinochloa crusgalli*), red-root flatsedge (*Cyperus erythrorhizos*), swamp

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smartweed (*Polygonum hydropiperoides*), panic grass (*Panicum agrostoides*), and fall panicum (*Panicum dichotomiflorum*). In 1994, beakrush (*Rhynchospora globularis*) replaced redroot flatsedge because the latter was scarce. These plant species were selected because they produce seeds used by waterfowl (Reinecke et al. 1989), and they were some of the species measured by Laubhan and Fredrickson (1992).

We randomly collected 60 plants/species with visibly mature and intact seed heads (Laubhan and Fredrickson 1992) from the impoundments in October 1993 and 1994. Phytomorphological variables measured included plant height (HT), inflorescence base diameter (ID), inflorescence length (IL), inflorescence number (IN), pedicel number (PN), flower number (FN), flower width (FW), and flower height (FH). Variables HT, ID, IL, and IN also were measured by Laubhan and Fredrickson (1992). Variable PN was not measured for species with spikes (e.g., swamp smartweed). Variables FN, FW, and FH were measured for species with umbels (e.g., redroot flatsedge, beakrush).

We measured plant height (m) in the field from ground level to the tip of the tallest inflorescence. Subsequently, inflorescences were clipped, placed in plastic bags, and refrigerated at 5°C until processed in the lab. We measured raceme (e.g., barnyardgrass), panicle (e.g., panic grasses), and umbel ID in the lab by extending the lowest pair of pedicels horizontally and measuring the combined length (mm) of both pedicels (Figs. 1A–C; Laubhan and Fredrickson 1992). Spike ID was the width (mm) measured at the point where the lowest sessile seed attached to the peduncle (Fig. 1D; Laubhan and Fredrickson 1992). Raceme and panicle IL was the distance (mm) between the lowest pedicel and top of the peduncle (Figs. 1A–B; Laubhan 1992). Umbel IL was the vertical distance (mm) of the center pedicel (Fig. 1C; Laubhan 1992). Spike IL was the distance (mm) between the lowest sessile seed and top of the peduncle (Fig. 1D; Laubhan 1992). The number of inflorescences per plant was IN. Variable IN differed from that measured by Laubhan and Fredrickson (1992): their IN was the total number of inflorescences per 0.0625-m<sup>2</sup> plot. Number of pedicels per plant and flowers per plant were PN and FN (Figs. 1A–C). Width and height of all flowers composing an umbel were FW and FH (Fig. 1C). When individual plants contained multiple inflorescences, we measured morpho-

logical variables for each inflorescence and summed across inflorescences to derive a cumulative value for each variable. Total inflorescence volume (TV) was calculated for each species by substituting IL, ID, or their cumulative values into geometric equations that most closely matched the shape of a species' inflorescence (Figs. 1A–D; Laubhan and Fredrickson 1992).

After measuring all variables, we measured seed production per plant by threshing seeds from inflorescences, removing chaff from samples with forceps and graduated sieves, drying, and weighing. Seeds per plant were oven-dried at 50°C for 24 hr and weighed to the nearest 0.1 g to determine dry mass per plant (Laubhan and Fredrickson 1992).

### Statistical Analysis

We used multiple linear regression to develop prediction equations for each plant species. Dry seed mass (g) per plant (dependent variable [Y]) was regressed against the various phytomorphological variables. We tested assumptions of residual normality and homoscedasticity by using the Shapiro-Wilk test and by examining plotted residuals against predicted values of seed mass (Myers 1990:211–212; Bowerman and O'Connell 1993:185–186). If normality was violated, then outlying residuals (i.e., absolute value of the corresponding Studentized residual >3) were removed until remaining residuals followed a normal distribution (SAS Institute 1987:337; Myers 1990:227). Deletion of outliers may reduce prediction range of the model; however, nonnormally distributed residuals decrease model precision and predictiveness (Myers 1990:91–93). Nevertheless, we only deleted ≤3 outliers from 50–116 samples from 5 of 6 plant species. Weighted least-squares estimation (LSE) was used instead of generalized LSE if residuals were heteroscedastic (SAS Institute 1985:662; Myers 1990:279–280).

We collected phytomorphological data in 1993 and 1994 to potentially incorporate annual variation in seed yield into our models and to increase sample size. Indicator variables (0 and 1) were assigned to 1993 and 1994 samples. The value of an indicator variable is a constant that is added to the intercept of the final model (Myers 1990:137). However, we used the no-intercept method for parameter estimation to be consistent with Laubhan and Fredrickson's (1992) analysis. Therefore, if an indicator variable was retained in our final model, it was the

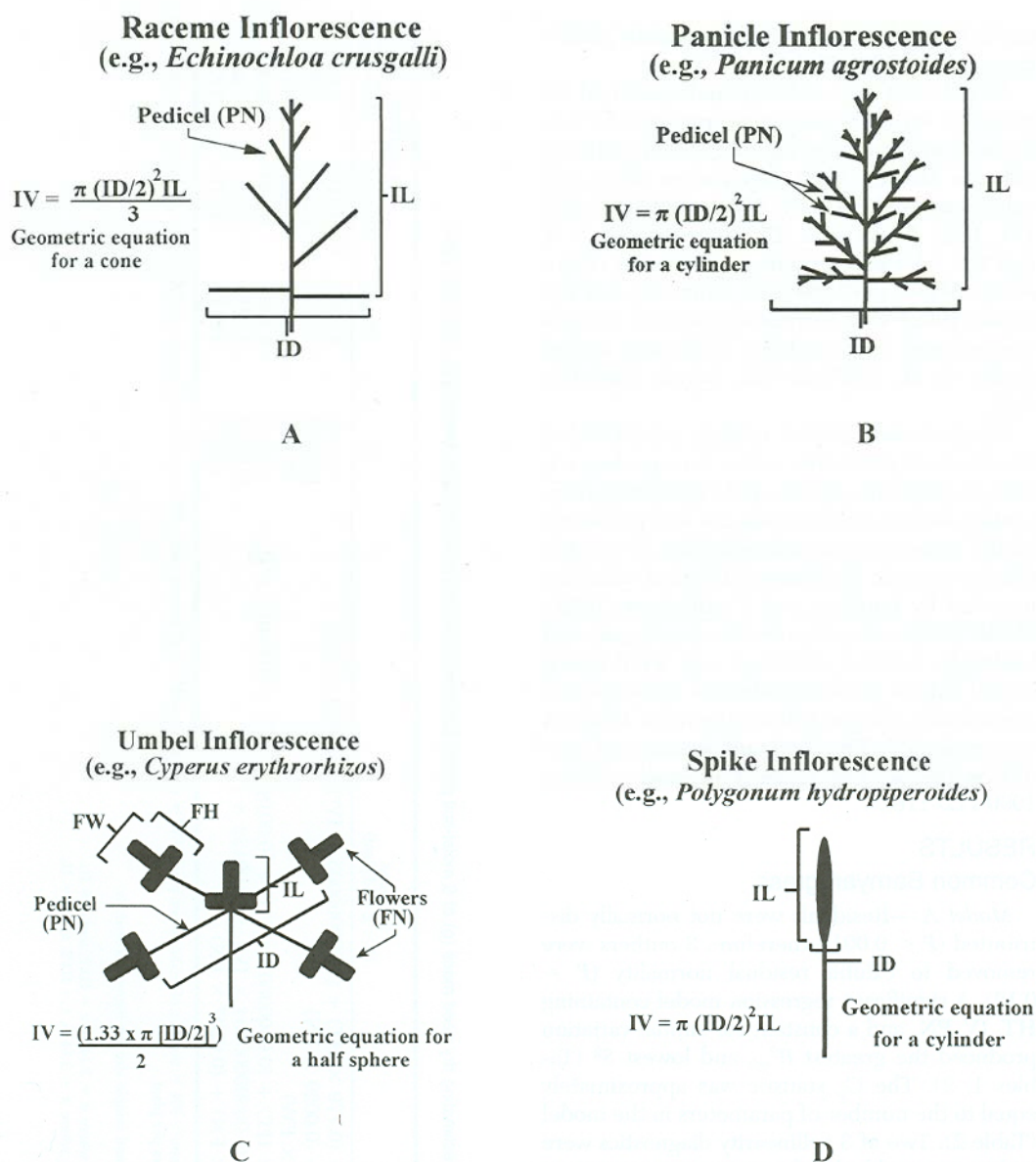


Fig. 1. Measurements taken from (A) raceme, (B) panicle, (C) umbel, and (D) spike inflorescences. Measurements included number of pedicels (PN), inflorescence base diameter (ID), inflorescence length (IL), inflorescence volume (IV), flower width (FW), flower height (FH), and number of flowers (FN). For all geometric equations,  $\pi = 3.1416$ .

only constant in the model and represented annual variation in seed yield (Myers 1990:136).

The all-possible variable selection procedure was used for model development (Myers 1990: 193–197) because other procedures (e.g., stepwise, backward, forward) do not consider all potential models (Myers 1990:185–186). We selected a final model based on the best combination of the following criteria: greatest adjusted coefficient of determination ( $R^2_{adj}$ ),

greatest predicted  $R^2$  ( $R^2_{pred}$ ) (i.e., cross-validation using PRESS residuals), lowest residual mean square ( $S^2$ ), and a Mallows'  $C_p$  statistic ( $C_p$ ). Models were correctly fit (i.e., they did not contain too few [underfit] or too many [overfit] predictor variables) when  $C_p$  was approximately equal to the number of parameters in the final model (Myers 1990:182). Underfit and overfit models may contain biased regression coefficients and collinear predictor variables, result-



ing in inflated variances and inaccurate predictions (Myers 1990:180).

Models that were selected and contained  $\geq 2$  predictor variables also were examined for collinearity via the following diagnostics: variance inflation factors (VIF), eigenvalues (EV), and condition numbers (CN; Myers 1990:166–167, 171, 182). A VIF  $> 10$ , EV approximately = 0, and CN  $> 10$  were criteria suggestive of collinearity (Myers 1990:369–370; Dubovsky and Kaminski 1992). One correlated predictor variable was removed from models if collinearity existed (Judge et al. 1985:912–922; Myers 1990:392, 411).

We presented 2 final models: (1) Model A was the best predictive model for our data relative to selection criteria and collinearity diagnostics, and (2) Model B was the best predictive model using our data and significant ( $P \leq 0.01$ ) species-specific phytomorphological variables reported by Laubhan and Fredrickson (1992). Model B was not presented for panic grass and beakrush, because Laubhan and Fredrickson (1992) did not present models for these species. Additionally, the prediction interval of Model A was presented. Precision and accuracy of prediction beyond this range is unknown (Myers 1990:112–116).

## RESULTS

### Common Barnyardgrass

**Model A.**—Residuals were not normally distributed ( $P < 0.001$ ); therefore, 3 outliers were removed to exhibit residual normality ( $P = 0.12$ ). A significant regression model containing HT, IV, PN, and a constant for annual variation produced the greatest  $R^2_{adj}$  and lowest  $S^2$  (Tables 1, 2). The  $C_p$  statistic was approximately equal to the number of parameters in the model (Table 2). Two of 3 collinearity diagnostics were within acceptable levels, suggesting no serious linear dependencies (Table 2). Cross-validation also indicated good predictive ability ( $R^2_{pred} = 0.952$ ).

**Model B.**—Laubhan and Fredrickson (1992) reported a 2-variable model (HT and IV) for barnyardgrass. Despite significance of the regression ( $F_{2, 112} = 782.7$ ,  $P < 0.001$ ) using our data for HT and IV, Model B was underfit, had a lower  $R^2_{adj}$  than Model A, and a variance nearly twice that of Model A (Table 2).

### Fall Panicum

**Model A.**—Residuals were not normally distributed ( $P = 0.008$ ); therefore, 2 outliers were

Table 1. Regression equations and statistics for estimating dry seed mass (g) of 6 moist-soil plants, Noxubee National Wildlife Refuge, Mississippi, 1993 and 1994.

Plant species	n <sup>a</sup>	Equation <sup>c</sup> (Y = g seed/plant)	P <sup>d</sup>	R <sup>2</sup> <sub>adj</sub>	g seed/plant <sup>b</sup>	
					Minimum	Maximum
Barnyardgrass	113	$-0.496 + (0.779 \times \text{HT}) + (0.0000000005 \times \text{IV}) + (0.019 \times \text{PN})$	610.86	0.956	0.517	5.043
Fall panicum	114	$-0.205 + (0.0029 \times \text{PN})$	1053.68	0.949	0.070	3.558
Redroot flatsedge	51	$(0.00352 \times \text{FW})$	534.43	0.913	0.230	3.150
Swamp smartweed	129	$(0.0298 \times \text{HT}) + (0.00000007 \times \text{IV}) + (0.00183 \times \text{ID}) - (0.00015 \times \text{IL})$	112.38	0.776	0.003	0.360
Panic grass	115	$0.1649 + (0.0000000004 \times \text{IV}) + (0.00122 \times \text{PN})$	1123.72	0.967	0.080	3.420
Beakrush	49	$(0.0067 \times \text{PN}) + (0.0207 \times \text{PN})$	251.80	0.911	0.178	3.626

<sup>a</sup> HT = plant height (m); IV = inflorescence volume (mm<sup>3</sup>); PN = number of pedicels per plant; FW = cumulative width of all flowers (mm); ID = cumulative diameter of all inflorescences (mm); IL = cumulative length of all inflorescences (mm); FN = number of flowers per plant.

<sup>b</sup> Model performance beyond these ranges is unknown.

<sup>c</sup> n = number of individual plants collected per species and sample size for regression analysis.

<sup>d</sup>  $P < 0.001$  for all F-values.

<sup>e</sup> IV based on geometry of a cone, calculated as  $\pi r^2 h/3$ , where  $\pi = 3.1416$ ,  $r = \text{ID}/2$ , and  $h = \text{IL}$ .

<sup>f</sup> IV based on geometry of a cylinder, calculated as  $\pi r^2 h$ , where  $\pi = 3.1416$ ,  $r = \text{ID}/2$ , and  $h = \text{IL}$ .

Table 2. Coefficients of determination ( $R^2_{adj}$ ), variance ( $S^2$ ), Mallows'  $C_p$ , variance inflation factor (VIF), eigenvalues (EV), and condition numbers (CN) used to select models for predicting seed yield of 6 moist-soil plants, Noxubee National Wildlife Refuge, Mississippi, 1993 and 1994.

Plant species	Model <sup>a</sup>	$R^2_{adj}$	$S^2$	$C_p$	VIF	EV	CN
Barnyardgrass	A	0.956	0.179	5.42	12.00	0.056	7.40
	B	0.923	0.338	48.22	1.45	0.440	1.87
Fall panicum	A	0.949	0.069	18.46	3.41	0.159	3.40
	B	0.792	0.241	495.0	34.84	0.014	11.72
Redroot flatsedge	A <sup>b</sup>	0.913	0.019	6.56	NA	NA	NA
	B	0.808	0.385	69.89	34.70	0.017	12.87
Swamp smartweed	A	0.776	0.001	4.24	4.80	0.108	5.18
	B	0.680	0.002	56.12	1.05	0.790	1.24
Panic grass <sup>c</sup>	A	0.967	0.029	3.96	3.90	0.161	3.78
Beakrush <sup>c</sup>	A	0.911	0.150	6.59	5.35	0.098	4.40

<sup>a</sup> A = model selected based on the best combination of selection criteria ( $R^2_{adj}$ ,  $S^2$ ,  $C_p$ ) and collinearity diagnostics (VIF, EV, CN); B = model developed via our data and Laubhan and Fredrickson's (1992) significant ( $P \leq 0.01$ ) predictor variables.

<sup>b</sup> Collinearity diagnostics did not apply (NA), because regression model contained 1 variable.

<sup>c</sup> Model B was not developed, because Laubhan and Fredrickson (1992) did not present a model for this species.

removed to exhibit residual normality ( $P = 0.55$ ). A significant regression ( $F_{2, 112} = 1,053.7$ ,  $P < 0.001$ ) containing IL, PN, and a constant for annual variation yielded  $R^2_{adj} = 0.937$  and  $S^2 = 0.085$ . However, variance inflation factors for IL (VIF = 17.57) and PN (VIF = 20.55) and a condition number (CN = 10.04) suggested multicollinearity. Therefore, the model was reduced to PN and the yearly indicator variable. Variable PN was retained instead of IL because the model with IL had greater  $C_p$  (52.1) and  $S^2$  (0.119) values (Table 2). The  $C_p$  statistic for the final model indicated it was underfit, but it maintained relatively low variance and high  $R^2_{adj}$  (Tables 1, 2). Cross-validation also indicated good predictive ability ( $R^2_{pred} = 0.947$ ).

**Model B.**—A model using our data with Laubhan and Fredrickson's (1992) significant variables (HT and IN) was significant ( $F_{2, 212} = 218.4$ ,  $P < 0.001$ ), but it was underfit, had a lower  $R^2_{adj}$  than Model A, and a variance nearly 5 times that of Model A (Table 2). Additionally, collinearity existed between HT and IN (Table 2).

### Redroot Flatsedge

**Model A.**—Residuals were not normally distributed ( $P < 0.001$ ), but removal of 2 outliers resulted in residual normality ( $P = 0.49$ ). Plotted residuals against predicted values of seed yield indicated heteroscedasticity. Therefore, weighted LSE was used instead of generalized LSE. A significant regression containing FW produced the greatest  $R^2_{adj}$ , lowest  $S^2$ , and an acceptable  $C_p$  (Tables 1, 2). Cross-validation indicated good predictive ability ( $R^2_{pred} = 0.907$ ).

**Model B.**—Laubhan and Fredrickson's (1992) model for redroot flatsedge contained ID, IL, and IN. The model containing these variables and our data was significant ( $F_{3, 49} = 74.1$ ,  $P = 0.001$ ); however, it was underfit, had a lower  $R^2_{adj}$  than Model A, a variance nearly 20 times that of Model A, and collinearity existed among variables (Table 2).

### Swamp Smartweed

**Model A.**—Residuals were not normally distributed ( $P < 0.001$ ), and removal of 2–4 outliers did not result in normally distributed residuals ( $P < 0.001$ ). Therefore, generalized LSE was performed on all smartweed data, recognizing that nonnormally distributed residuals may have prevented optimal model fit and predictiveness. A significant model containing HT, IV, ID, and IL produced the greatest  $R^2_{adj}$ , lowest  $S^2$ , an acceptable  $C_p$  statistic, and no collinearity (Tables 1, 2). However, cross-validation indicated low predictive ability of this model ( $R^2_{pred} = 0.306$ ).

**Model B.**—Laubhan and Fredrickson (1992) reported a 2-variable model (HT and IV) for swamp smartweed. The model developed using our data and these variables was significant ( $F_{2, 127} = 138.3$ ,  $P < 0.001$ ); however, it was underfit, had a lower  $R^2_{adj}$  than Model A, and a variance twice that of Model A (Table 2).

### Panic Grass

**Model A.**—Residuals were not normally distributed ( $P = 0.02$ ); removal of 1 outlier resulted in residual normality ( $P = 0.23$ ). A significant regression model ( $F_{3, 112} = 754.6$ ,  $P < 0.001$ )



containing PN, ID, IV, and a constant for annual variation produced the greatest  $R^2_{adj}$  (0.963), lowest  $S^2$  (0.034), and an acceptable  $C_p$  statistic (5.855). However, collinearity was prevalent. Removing ID produced a significant model, eliminated collinearity, increased  $R^2_{adj}$ , and decreased  $S^2$  (Tables 1, 2). Cross-validation also indicated good predictive ability ( $R^2_{pred} = 0.966$ ).

### Beakrush

**Model A.**—Residuals were not normally distributed ( $P = 0.002$ ); removal of 2 outliers resulted in residual normality ( $P = 0.41$ ). A significant regression model containing PN and FN produced the greatest  $R^2_{adj}$ , lowest  $S^2$ , an acceptable  $C_p$  statistic, and no collinearity (Tables 1, 2). Cross-validation ( $R^2_{pred} = 0.898$ ) also indicated good predictive ability.

## DISCUSSION

### Model A

Our regression models with 1–4 independent variables predicted seed mass of 6 common moist-soil plants with good precision (i.e.,  $R^2_{adj} = 0.91$ – $0.97$  for 5 of 6 plant species). Generally, there was positive relation between seed mass and significant predictor variables, and regression assumptions were met in final models. Furthermore, 5 of 6 models exhibited high predictability (i.e.,  $R^2_{pred} = 0.90$ – $0.97$ ).

The model for swamp smartweed exhibited lowest precision and predictiveness. Reduced performance of this model may have been a consequence of variable seed production ( $CV = 114\%$ ) among sample plants. Variable seed production by smartweeds is common (Olinde et al. 1985). Smartweed may change from sexual (i.e., seed) to asexual (i.e., rhizome) reproduction, and plants within a colony may exhibit both life-history strategies simultaneously in response to environmental factors (e.g., lack of habitat disturbance, prolonged flooding, light intensity; Johannsson 1989, Sultan 1995, Thomas and Cox 1996). Consequently, seed production may decrease or become more variable because plants expend more energy in asexual reproduction (Raven et al. 1992:450–451, 584). Poor model performance also may have been a consequence of nonnormally distributed residuals (Myers 1990:92).

Models for plant species with raceme and panicle inflorescences (e.g., barnyardgrass, panic grass) exhibited greater precision and predic-

tiveness ( $R^2_{adj} \geq 0.95$ ;  $R^2_{pred} \geq 0.95$ ) than models for umbel plants (e.g., beakrush, redroot flatsedge) ( $R^2_{adj} = 0.91$ ;  $R^2_{pred} = 0.90$ – $0.91$ ). Laubhan and Fredrickson (1992) observed similar patterns. They attributed reduced performance in models for umbel plants to variability in number of pedicels per inflorescence, and because they did not measure variables on individual pedicels (e.g., PN, FN, FW, FH). However, we measured these variables, some of which were retained in the final model. We speculate that variation was introduced into our models from variable amounts of chaff in samples. Seeds from umbels, especially redroot flatsedge, were fine and adhered more strongly to inflorescences than seeds of raceme and panicle plants. Consequently, inflorescences fragmented occasionally during threshing, and chaff may have been included with seed samples. Moreover, models for raceme and panicle plants were developed from 2 years of data, and they contained a constant for year effect. Therefore, reduced performance in models for umbels may have been a consequence of smaller sample size and not accounting for potential variation in annual seed production.

Our model for barnyardgrass exhibited high predictability despite relatively poor performance by Laubhan and Fredrickson's (1992) model. They attributed low predictiveness by their model to existence of multiple racemes of varying size per plant. Because of multiple racemes, they chose and measured a "representative" inflorescence from each plant. In contrast, we measured all inflorescences on a plant and summed measurements for each variable across inflorescences to yield a cumulative and perhaps more accurate estimate than from a "representative" inflorescence.

### Model B

Considerable variation in seed mass ( $R^2_{adj} = 0.68$ – $0.92$ ) also was explained by Model B. Although coefficients of determination for our Model As ( $R^2_{adj} = 0.78$ – $0.97$ ) were similar to Laubhan and Fredrickson's (1992) models ( $R^2 = 0.79$ – $0.96$ ), our Model As always exhibited greater  $R^2_{adj}$ , lower  $S^2$  and  $C_p$ , less collinearity, and contained different variables than our Model Bs. We cannot explain differences in performance of our Model Bs relative to Laubhan and Fredrickson's (1992), but we would expect lesser performance from their models using our data from different years and sites. Indeed,



there likely were spatial and temporal differences between their study areas and years and ours that influenced variation in plant morphology and seed production, consequently reducing performance of Model B. Plant morphology and productivity can be influenced by various exogenous factors, including soil and water nutrients, hydroperiod, temperature, photoperiod, herbivory, and competition (Pederson and van der Valk 1984, Mushet et al. 1992, Lehman and Tilman 1997), all of which can vary spatially and temporally (van der Valk 1981, van der Valk et al. 1994). These model differences suggest possible need for development of site- and time-specific models if very precise and accurate estimates of seed production are necessary.

### MANAGEMENT IMPLICATIONS

Laubhan and Fredrickson's (1992) models and our Model As can be used to estimate seed yield of the 6 plant species in this study because predictor variables in both studies explained substantial variation (78–97%) in seed yield. Although our Model As always explained greater variation in seed yield and predicted better than our Model Bs, comparative performance of these models outside our study area is unknown. Indeed, it is possible that Laubhan and Fredrickson's (1992) models could perform better than ours in some locations. Researchers and managers may decide between use of Laubhan and Fredrickson's (1992) and our models by considering geographic, hydrologic, climatic, edaphic, and other environmental similarities between users' areas and study sites where models were developed. Alternatively, mean seed yield per plant species can be estimated on users' areas, and similarity of estimates and predictions from Laubhan and Fredrickson's (1992) and our equations compared qualitatively with theirs. Differences between predicted and area estimates also could be tested with a *t*-test (see Graybill [1976:283–302] and Montgomery and Peck [1982:29–31] for statistical review). Although our study suggests spatial and temporal differences may exist in model predictions, seed-yield estimates from Laubhan and Fredrickson's (1992) and our models likely would suffice for most management purposes. Nevertheless, if very precise and accurate estimates of seed yield are desired, we recommend that individuals choose the most environmentally appropriate model using

the aforementioned techniques, or develop site-specific models. We also encourage researchers to develop models for moist-soil plant species not addressed in these studies. Finally, we note that precise estimates of seed yield by moist-soil plants have been achieved via simple linear regression; researchers and managers may prefer this simplified and efficient approach (Gray et al. 1999).

Our Model As were developed to predict seed yield per plant. Therefore, stem density of plant species also must be estimated when inflorescences are collected. Mean stem density can be multiplied by mean seed yield per plant (from regression predictions) and extrapolated to calculate species-specific seed yield (kg [dry mass]/ha). Finally, areal seed yields can be multiplied by respective estimates of true metabolizable energy (Miller and Reinecke 1984) and divided by the daily energy requirement of waterfowl (e.g., Prince 1979:111) to calculate foraging carrying capacity of moist-soil habitats (Reinecke et al. 1989, Reinecke and Loesch 1996).

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