

Aquatic invertebrate and plant responses following mechanical manipulations of moist-soil habitat

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Abstract Managers mow, disk, and till moist-soil habitats to set back succession and increase inter-persion of emergent vegetation and water for migrant and wintering waterbirds. We evaluated effects of autumn applications of these manipulations on aquatic invertebrates and moist-soil plants during 2 subsequent winters and growing seasons, respectively, at Noxubee National Wildlife Refuge, Mississippi. Greatest seed mass was in tilled and disked plots in 1993 ($P \leq 0.008$) and in tilled plots in 1994 ($P \leq 0.008$). Plant species diversity generally was greatest in tilled plots in both years ($P \leq 0.05$). Mowed and control plots produced greatest aquatic invertebrate mass in winter 1992–93 ($P \leq 0.025$) and diversity in both winters ($P \leq 0.01$). Invertebrate mass and plant standing crop generally did not differ among treatments in winter 1993–94 and both years, respectively. We recommend autumn tilling in small moist-soil habitats to increase plant species diversity and seed yield. For large-scale management, disking may be more practical than tilling and would likely yield similar plant responses. We recommend autumn mowing if moist-soil habitats exist in early seral stages and contain desirable seed-producing plants that are robust and do not readily topple following flooding to create open water areas for waterbirds.

Key words aquatic invertebrates, hydrophytes, Mississippi, moist-soil management, waterfowl habitat, wetland management

Moist-soil habitats are seasonally flooded wetlands dominated by annual and perennial hydrophytes (van der Valk 1981). Managing these wetlands is practiced widely in the United States to provide habitat, especially for waterfowl (Fredrickson and Taylor 1982, Smith et al. 1989). Managed moist-soil habitats typically are impounded by levees with control structures to manipulate hydrology within them (Baldassarre and Bolen 1994:489). Managed moist-soil habitats usually are drained during spring or summer to promote growth of hydrophytes, then flooded during autumn and winter (Reid et al. 1989). Generally,

these wetlands provide rich sources of seeds, tubers, browse, and aquatic invertebrates for a variety of migrating and wintering waterfowl and other wetland-dependent wildlife (Fredrickson and Taylor 1982, Fredrickson and Reid 1986, Duffy and LaBar 1994).

Managers mechanically manipulate moist-soil habitats during spring and summer to set back succession and increase plant productivity and diversity (Fredrickson and Taylor 1982). However, manipulations may be delayed until late summer or autumn because managers may desire to keep areas flooded for breeding waterbirds (Bellrose and

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Holm 1994:500–502, Tacha and Braun 1994) or soils may be too wet to support heavy machinery (Heitmeyer et al. 1989, Kelley 1990). Additionally, managers may perform autumn manipulations to increase interspersed vegetation and open water after flooding to facilitate habitat and resource use by migrant and wintering waterbirds (Gordon et al. 1989, Heitmeyer et al. 1989, de Szalay and Resh 1997). Mowing, disking, and tilling are common manipulations performed in moist-soil habitats during autumn; however, their effects on aquatic invertebrate and moist-soil plant communities have not been widely investigated (de Szalay and Resh 1997). Thus, our objective was to test effects of autumn mowing, disking, and tilling on 1) aquatic invertebrates during winter and 2) moist-soil plants at the end of the subsequent growing season.

Study area

We conducted our study at Noxubee National Wildlife Refuge (NNWR) in east-central Mississippi (Wehrle et al. 1995). The specific study area was an 80-ha moist-soil management complex, consisting of 11 interconnected impoundments. Refuge personnel flooded these impoundments (via gravity flow) between early November and January and maintained inundation until mid-April. Water from an adjacent 17-ha reservoir and from natural precipitation and runoff was used to flood impoundments.

Specific study sites were 4 impoundments. We selected impoundments using the following criteria: 1) presence of continuous, unbroken, emergent vegetation; 2) presence of a plant community dominated by 1–2 perennial or late seral emergent plant species; and 3) availability (i.e., no other ongoing management). We used impoundments 2 and 8 (9.6 and 7.1 ha, respectively) as study sites in 1992–93, and impoundments 5a and 7 (1.9 and 5.1 ha, respectively) in 1993–94. Swamp smartweed (*Polygonum hydropiperoides*) dominated impoundments 2 and 8 and impoundment 7. Beakrush (*Rhynchospora globularis*) and sedge (*Carex lupulina*) were co-dominants in impoundment 5a. Soil in impoundments was primarily Mathiston silt loam (Brent 1973, 1986).

Methods

Experimental design

We designated individual impoundments as experimental blocks because of different pre-treat-

ment vegetation structure or composition. We used 2 different impoundments each year to replicate treatments spatially within the study area. We established 4 square replicate plots (100 m² each) per habitat treatment (i.e., mow, disk, till, and control) in September 1992 and 1993 within each impoundment. Within each 100-m² plot, we randomly located 5 subsampling plots (1 m²) using a grid system and random numbers table. Therefore, we collected aquatic invertebrate and vegetation data from 20 subsample plots/treatment/impoundment (5 subsamples × 4 replicates). However, we collected 15 subsamples from tilled and disked treatments and used these data in analysis of vegetation data in 1993 because water persisted over 1 replicate plot of each treatment during the growing season and appeared to affect plant responses. We averaged subsample data from each 100-m² plot to provide a single datum per replicate plot, and the subsampling error was partitioned in analyses.

Habitat treatments

We randomly assigned habitat treatments to 100-m² plots in October 1992 and 1993. Vegetation was cut to approximately 10–15 cm above ground using a tractor-drawn rotary mower for the mowed treatment and for site-preparation of disked and tilled plots. A disk (55-cm diam) harrow and tractor-drawn rototiller were used after mowing for disked and tilled treatments, respectively. Although disking and tilling were performed following mowing, they are referred to hereafter as disking and tilling. We suspended avian exclusion netting over 100-m² plots in October 1992 and 1993 to prevent depredation of invertebrates and plant propagules by birds and other vertebrates (Severson 1987:28).

Water-level management

Refuge staff flooded impoundments with water from the reservoir and rainfall to a depth of approximately 30–45 cm from mid-late November 1992 and 1993 until mid-April 1993 and 1994. Spring drawdown occurred in ≤3 days (i.e., a fast drawdown; Fredrickson and Taylor 1982) to remove water from plots as simultaneously and uniformly as possible.

Refuge staff also irrigated impoundments using water from the reservoir in both mid-June and early August 1993 and 1994 for 8 consecutive days to minimize apparent drought stress on vegetation. Water depths in impoundments were moni-

tored closely to avoid submersion of plants. Impoundments 2 and 8 could not be irrigated simultaneously in 1993 because they were located at opposite ends of the management complex; hence, time between irrigation of these impoundments was about 2 weeks. Impoundments 5a and 7 were irrigated simultaneously in 1994.

Aquatic invertebrate sampling

We sampled invertebrates between mid-December 1992 and 1993 and mid-March 1993 and 1994. We took 5 subsamples with a sweep net (25 × 45 cm) at random locations within each 100-m² plot/treatment/month. We used a sweep net because this device was most practical for our sampling conditions and it was more effective at collecting a complete representation of existing invertebrates than core or plankton-net samplers (Cheal et al. 1993). We selected 5 new random subsampling sites monthly to prevent sampling the same sites through time. We completed field sampling in 2 days each month. To acquire a quantitative estimate of available invertebrates, we pushed the sweep net along and in contact with the substrate for 2.22 m to sample a 1-m² area (Wehrle et al. 1995). Subsamples were placed in individual plastic bags and refrigerated at 4–5°C until processed to reduce decomposition of invertebrates and associated organic matter. We randomly assigned processing order to all subsamples so any decomposition of invertebrates was distributed equally among treatments.

We removed invertebrates from collected sediment and litter in the lab to determine dry mass by family and treatment. We identified insects using Merritt and Cummins (1984); we used Pennak (1989) and Thorp and Covich (1991) to identify other invertebrates. We placed invertebrates of each family in an aluminum pan and dried them for 24 hours in a forced-air oven at 105°C (Driver 1981, Wehrle et al. 1995). We weighed all invertebrates of a family to the nearest 0.001 g, then we summed masses across families to derive total dry mass/m².

We used dry mass of each family to calculate a Shannon-Weaver index of invertebrate diversity (Ludwig and Reynolds 1988:90-91). We used biomass instead of relative abundance (or density) to compute diversity because biomass can be a more direct indicator of relative importance and energy-nutrient availability in ecological communities (Lyons 1981).

Vegetation sampling

Vegetative variables included above-ground standing crop, plant species diversity, and seed mass. We monitored seed maturation visually during weekly visits to plots, beginning in early September 1993 and 1994. Variables were measured when seed fall initiated (i.e., mid-October 1993, late September 1994).

We estimated above-ground standing crop by clipping plants at ground level from a randomly selected half of each 1-m² plot (van der Valk 1989). We placed clipped vegetation in plastic bags and refrigerated it at 4–5°C to retard decomposition until processed. As with invertebrate samples, processing order was randomly assigned to subsamples, so any decomposition was distributed equally among habitat treatments. Before drying, we identified plants using Radford et al. (1968) and sorted plants by species. We oven-dried subsamples at 60°C to a constant mass (van der Valk 1989). After drying, we weighed plants by species to the nearest 0.1 g and summed masses across species to derive total above-ground standing crop/0.5 m². We calculated the Shannon-Weaver index to estimate plant species diversity/plot. We used above-ground biomass/species as an indicator of relative importance to calculate the diversity index (Lyons 1981).

We discovered that seeds were sometimes dislodged from inflorescences during plant clipping and bagging. Consequently, seed-mass estimates from clip plots could have been negatively biased because of accidental seed loss. Therefore, we collected from both impoundments a random sample of all seed-producing species occurring in plots ($n=60$ individuals/species), threshed and oven-dried (i.e., 50°C for 24 hours) seeds from inflorescences, weighed dried seeds to the nearest 0.1 g, computed a mean seed mass/plant species (from the 60 individuals), multiplied mean seed mass/plant species by its mean stem density/plot, and summed across all species within plots to derive a relative estimate of total seed mass/0.5 m². Seed-producing species occurring in plots and collected for estimates included barnyardgrass (*Echinochloa crusgalli*), red-rooted flatsedge (*Cyperus erythrorhizos*), swamp smart-weed, panic grass (*Panicum agrostoides*), fall panicum (*P. dichotomiflorum*), beakrush, and sedge. Seed threshing, drying, and weighing procedures followed Laubhan and Fredrickson (1992).

Table 1. Aquatic invertebrate familial diversity and total dry mass following autumn tilling, disking, mowing, and no treatment (control) in moist-soil management impoundments (IMP) 2 and 8 and 5a and 7, winters 1992–93 and 1993–94, Noxubee National Wildlife Refuge, Mississippi.

Variable	Winter	Till		Disk		Mow		Control	
		\bar{x}	SE ^a	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Diversity ^b	1992–93	0.16A ^c	0.012	0.21A	0.013	0.29B	0.011	0.42C	0.013
	1993–94	0.16A	0.012	0.26B	0.012	0.28B	0.012	0.41C	0.015
Biomass (g/m ²)	1992–93	0.09A	0.010	0.10A	0.011	0.19B	0.014	0.17B	0.009
	IMP ^d 5a	3.12A	0.502	2.24AB	0.430	1.38B	0.210	0.74B	0.133
	IMP 7	0.10A	0.014	0.17A	0.015	0.13A	0.014	0.18A	0.017

^a $n=8$, 100-m² plots; however, when IMPs were analyzed separately, $n=4$ plots.

^b Shannon–Weaver diversity values were calculated using invertebrate biomass instead of relative abundance (Lyons 1981).

^c Means within rows with the same letter do not differ ($P>0.05$) by Ryan's- F multiple comparison test (SAS Institute 1987:241).

^d Biomass data analyzed separately by IMP because of a treatment-by-IMP interaction ($P=0.001$).

Statistical analyses

We analyzed data by years because impoundments and vegetation within them differed. We used a generalized randomized block (GRB) multivariate analysis of variance (MANOVA) with subsampling error to analyze plant data because 3 dependent variables (i.e., seed mass, species diversity, above-ground standing crop) were fitted to the same effects (i.e., block and treatment; Barker and Barker 1984:15). We also used MANOVA to analyze monthly samples of aquatic invertebrate data (Hand and Taylor 1987:52–53) because MANOVA relies on less restrictive assumptions than repeated measures ANOVA (Milliken and Johnson 1992:432). Additionally, certain MANOVA test statistics (e.g., Pillai-Bartlett [P-B]) are robust to violations of multivariate assumptions (Olson 1974, 1976, 1979). Aquatic invertebrate diversity and mass were analyzed separately with monthly (Dec–Mar) responses as dependent variables and treatments and blocks as independent effects.

When MANOVA was significant ($P\leq 0.05$), we used GRB ANOVA to test main effect hypotheses for each dependent variable (Steel and Torrie 1980:197). We tested univariate assumptions of experimental error normality and homoscedasticity using Shapiro–Wilk and Levene's tests, respectively (SAS Institute 1987:119, Milliken and Johnson 1992:22). When necessary, we transformed data with natural logs to meet assumptions of ANOVA (Steel and Torrie 1980:235). We included a treatment-by-impoundment interaction term in the ANOVA model to test for nonadditivity of fixed treatment and random block effects. Data were analyzed by impoundment and simple main effect hypotheses tested if an interaction ($P\leq 0.05$) was

detected (Cochran 1947). We used Ryan's- F stepwise multiple mean comparison test to compare means when GRB ANOVA was significant ($P\leq 0.05$, Day and Quinn 1989). Comparison-wise error rate (CER) was reported for multiple comparisons to denote significance level (α) at which null hypotheses were tested; SAS does not provide exact P -values for Ryan's- F or $-Q$ test (SAS Institute 1987:240).

Results

Aquatic invertebrates

Winter 1992–93 responses. Familial diversity (MANOVA $F=3.2$; 12, 69 df; $P=0.001$) and dry mass (MANOVA $F=2.89$; 12, 69 df; $P=0.003$) of aquatic invertebrates differed among treatments. Differences in diversity also were detected among treatments in ANOVA ($F=34.38$; 3, 24 df; $P\leq 0.001$; Table 1). Diversity was greatest in control plots and greater in mowed than in disked and tilled plots (CER=0.01). Diversity did not differ between disked and tilled plots.

Invertebrate dry mass also differed among treatments in ANOVA ($F=10.07$; 3, 24 df; $P\leq 0.001$; Table 1). Invertebrate mass was greatest in mowed and control plots (CER=0.025); however, it did not differ between mowed and control or between disked and tilled plots.

Winter 1993–94 responses. Invertebrate familial diversity differed among treatments in MANOVA ($F=3.01$; 12, 69 df; $P=0.002$) and ANOVA ($F=64.92$; 3, 24 df; $P\leq 0.001$; Table 1). Diversity was greatest in control plots (CER=0.01). Diversity was greater in mowed and disked plots than in tilled plots (CER=0.01); however, mowed and disked plots did not differ.

Table 2. Dry seed mass, plant species diversity, and dry above-ground standing crop of moist-soil plants following autumn tilling, disking, mowing, and no treatment (control) in impoundments (IMP) 2 and 8, and 5a and 7, 1993 and 1994, Noxubee National Wildlife Refuge, Mississippi.

Variable	Year	Till		Disk		Mow		Control		
		\bar{x}	CL ^{a,b}	\bar{x}	CL	\bar{x}	CL	\bar{x}	CL	
Seed mass (g/0.5-m ²)	1993	18.7A ^c	15.7–21.6	14.5AB	11.7–17.3	10.8BC	8.3–13.3	8.6C	6.1–11.1	
	1994	60.5A	57.3–63.7	25.6B	22.4–28.8	28.3B	25.3–31.3	10.6C	7.6–13.6	
Diversity ^d IMP ^e 5a IMP 7	1993	0.49A	0.06–0.91	0.29AB	0.11–0.47	0.22AB	0.04–0.40	0.04B	0.004–0.07	
	1994	1.28A	1.03–1.52	0.60B	0.47–0.74	0.57B	0.17–0.97	0.70B	0.40–1.00	
	1994	0.95A	0.58–1.32	0.83A	0.75–0.92	0.68AB	0.33–1.03	0.38B	0.12–0.63	
Standing crop (g/0.5-m ²)	1993	424.6A	262.4–586.7	376.0A	128.6–504.7	292.9A	256.8–329.1	333.6A	219.0–448.2	
	IMP 5a	1994	308.8A	305.5–312.1	268.2A	264.5–271.9	276.7A	273.3–280.0	259.2A	255.5–263.0
	IMP 7	1994	388.9A	285.9–442.0	607.7B	380.7–834.7	703.1B	544.3–861.9	630.3B	440.0–820.3

^a $n=8$, 100-m² plots for all treatments and both years, except $n=7$ for disked and tilled plots in 1993 and $n=4$ when data are presented by IMP.

^b CLs for seed mass and standing crop in IMP 5a were back-transformed from natural log values, but raw data were used to compute CLs in 1993 and 1994 in IMP 7. CLs for species diversity were computed using Lyons' (1981) formula in both years.

^c Means within rows with the same letter do not differ ($P > 0.05$) by Ryan's- F multiple comparison test (SAS Institute 1987:241).

^d Shannon-Weaver diversity values were calculated using plant biomass instead of relative abundance (Lyons 1981).

^e Diversity and standing crop analyzed separately by IMP because of a treatment-by-IMP interaction ($P < 0.01$).

There was a treatment-by-impoundment interaction for invertebrate dry mass (MANOVA $F=3.59$; 12, 69 df; $P=0.001$); therefore, data were analyzed by impoundment. Differences in invertebrate mass existed among treatments within impoundment 5a (ANOVA $F=5.9$; 3, 12 df; $P=0.01$), but not within impoundment 7 (ANOVA $F=1.65$; 3, 12 df; $P=0.23$; Table 1). Invertebrate mass in impoundment 5a was greater in tilled than in mowed and control plots (CER=0.025). We detected no other differences within impoundment 5a.

Vegetation

Autumn 1993 responses. Although the P-B test statistic was not significant (MANOVA $F=1.8$; 9, 66; $P=0.085$), 3 other MANOVA test statistics (i.e., Wilk's λ , Hotelling's T , Roy's Root) revealed differences among treatments ($0.001 \leq P \leq 0.048$). Therefore, we proceeded with univariate analyses of dependent variables.

We detected differences in seed mass among treatments (ANOVA $F=11.01$; 3, 22 df; $P \leq 0.001$; Table 2). Seed mass was greater in tilled plots than in mowed and control plots (CER=0.008), but it did not differ between tilled and disked plots. Additionally, disked plots yielded greater seed mass than control plots (CER=0.008). There were no differences in seed mass between disked and mowed plots or between mowed and control plots.

Plant species diversity differed among treatments (ANOVA $F=5.12$; 3, 22 df; $P=0.008$; Table 2). Diversity was greater in tilled than in control plots (CER=0.025), but there were no differences among other treatment comparisons. Above-ground standing crop did not differ among treatments (ANOVA $F=0.275$; 3, 22 df; $P=0.275$; Table 2).

Autumn 1994 responses. Dry seed mass, plant species diversity, and above-ground standing crop differed among treatments (MANOVA $F=3.27$; 9, 72 df; $P=0.002$); therefore, we performed univariate analyses for each dependent variable.

We detected differences in seed mass among treatments (ANOVA $F=11.56$; 3, 24 df; $P \leq 0.001$; Table 2). Seed mass was greatest in tilled plots (CER=0.008). Seed mass was greater in disked and mowed plots than in control plots (CER=0.008), but it did not differ between disked and mowed plots.

We analyzed plant species diversity by impoundment because of an interaction between impoundment and treatment effects (ANOVA $F=4.69$; 3, 24 df; $P=0.011$). Species diversity differed among treatments (ANOVA $F=13.44$; 3, 12 df; $P=0.001$ and ANOVA $F=7.54$; 3, 12 df; $P=0.004$ for impoundments 5a and 7, respectively; Table 2). Diversity in impoundment 5a was greatest in tilled plots (CER=0.025), but similar among disked, mowed, and control plots. Diversity in impoundment 7 was

greater in tilled and disked plots than in control plots (CER=0.025), but no other differences were detected.

Above-ground standing crop also was analyzed by impoundment because of an interaction between impoundment and treatment effects (ANOVA $F=4.69$; 3, 24 df; $P=0.011$). Standing crop differed among treatments in impoundment 7 (ANOVA $F=6.26$; 3, 12 df; $P=0.008$). In this impoundment, standing crop was greater in disked, mowed, and control plots than in tilled plots (CER=0.025). We detected no differences (ANOVA $F=0.45$; 3, 12 df; $P=0.719$) in standing crop in impoundment 5a (Table 2).

Discussion

Aquatic invertebrates

Mowed and control plots generally produced greater mass and diversity of aquatic invertebrates in winter 1992–93 and both winters, respectively, compared with tilled and disked plots. Increased invertebrate diversity and mass in control and mowed plots may have been partly related to abundant detritus in these plots (Kaminski and Prince 1981). Detritus is an important component of most aquatic food chains because associated microorganisms are important foods for macroinvertebrates (Murkin 1989). Therefore, food-chain breadth and complexity can increase with quantities of detritus and coexisting plant and animal organisms (Murkin 1989). Additionally, aquatic invertebrate communities likely were more diverse in mowed and control plots than in disked and tilled areas because detritus may have enhanced habitat structural complexity, which can increase niche dimensionality and resource partitioning (Pianka 1994:283, 388, 393).

In impoundment 5a during winter 1993–94, aquatic invertebrate mass was greatest in tilled plots. Elevated invertebrate mass in tilled plots resulted from increased occurrence and biomass of crawfish (*Procambarus* spp.), which were comparatively larger (in size) than other invertebrates encountered in this study. Crawfish production may have been enhanced because tilling loosened soil and possibly increased soil aeration, which may have facilitated burrowing, respiration, and foraging by crawfish (LaCaze 1981, Nassar et al. 1991). Additionally, tilling mulched vegetation, mechanically converting coarse-particulate-organic matter (CPOM) to fine-particulate-organic matter (FPOM).

Crawfish seem to prefer FPOM over CPOM because it is easier to ingest and digest (Benke et al. 1988). Finally, detrital and other habitat conditions in tilled plots may have increased prey (e.g., metazoans) for crawfish (Momot 1995).

Vegetation

Tilling generally produced greatest seed mass and species diversity of moist-soil plants. Seed mass was greatest in tilled plots because tilling increased occurrence of annual grasses, which produced more seeds than perennials (Gray 1995:116–117). Tilling likely increased occurrence of grasses and plant species diversity because it scarified soil and its mixing action may have elevated seeds to upper soil horizons (Kelley 1986:40–41, Kirkman and Sharitz 1994), where increased light, soil temperature, moisture, and nutrient availability may have stimulated germination and enhanced photosynthesis (van der Valk and Davis 1978, Galinato and van der Valk 1986). Furthermore, tilling may have reduced litter by incorporating it into the substrate. Litter can inhibit seed germination and seedling growth by reducing light penetration to the substrate and acting as a physical barrier to seedlings (Dieter and Shontz 1978, Smith 1983, van der Valk 1986). Also, litter can be allelopathic and reduce species diversity by inhibiting germination and growth of other plants (Bonasera et al. 1979, van der Valk and Davis 1980).

Above-ground standing crops generally did not differ among treatments. Lack of differences may have been related to Type II error; coefficients of variation for non-significant ANOVA models ranged from 22 to 23% and *post hoc* power ($1-\beta$) for these models was 0.20 at $\alpha=0.05$. Nevertheless, tilling produced the greatest mean above-ground standing crop in 1993 and in impoundment 5a in 1994. Net-primary production in tilled plots may have been enhanced because tilling reduced above-ground litter and its mulching and blending action may have accelerated litter decomposition and nutrient assimilation by plants (van der Valk 1986, Neely and Baker 1989).

In impoundment 7 in 1994, above-ground standing crop in tilled plots was lower than all other treatments. This response may have been influenced partly by hydrology. Tilled plots happened to be randomly located near a borrow ditch within impoundment 7. Plants within these plots experienced deeper water during rainfall and irrigation events than plants in plots farther from the ditch.

Seedlings in tilled plots probably became submersed ≥ 1 time, which may have reduced plant growth and standing crop (Kozlowski 1976, Jackson and Drew 1984, Kozlowski 1984).

Management and research implications

Natural and artificial manipulations of wetlands are useful to revert plant succession to earlier seral stages (Weller 1981:74-79), reduce dense emergent vegetation to increase its interspersion with water (Kaminski and Prince 1981), and control nuisance vegetation (Baldassarre and Bolen 1994:494-503). Typically, manipulations are performed in spring or summer (Fredrickson and Taylor 1982). However, it may be necessary in some regions to perform manipulations in early autumn because of lingering wet conditions or long (continuous) growing seasons (Gordon et al. 1989, Heitmeyer et al. 1989). Manipulations also may be performed twice annually, once in spring to set back succession (Fredrickson and Taylor 1982) and again in autumn to increase interspersion of vegetation and water after flooding (Heitmeyer et al. 1989). Applying management practices twice/year is expensive; therefore, a more economical approach may be autumn manipulations that could revert succession and stimulate production of desirable moist-soil vegetation during the subsequent growing season(s).

Autumn tilling generally produced greatest seed mass, plant species diversity, above-ground standing crop, and occurrence of grass species during the subsequent growing season (Gray 1995:116-117). Therefore, tilling was most effective in converting monotypic or low-diversity stands of perennial or late successional herbaceous vegetation to more diverse plant assemblages. Increased production of seed-bearing grasses following tilling likely would increase foraging carrying capacity of moist-soil habitat for waterfowl (Reinecke et al. 1989). However, sometimes tilling may produce hemp sesbania (*Sesbania exaltata*, Gray 1995:116-117), which is undesirable if dense and expansive stands develop. Nevertheless, summer irrigation can deter establishment of sesbania (Fredrickson and Taylor 1982). Additionally, mowing and appropriate herbicidal treatment of sesbania before inflorescences form can stimulate growth of grasses and sedges underneath the sesbania canopy (R. M. Kaminski, personal observation).

Tilling tended to reduce invertebrate diversity and mass, as would be expected due to temporary reduction in above-ground detritus during the first winter after treatment. Although we did not detect statistical differences in above-ground standing crop of moist-soil plants among treatments, tilling generally produced the greatest mean standing crop during the subsequent growing season. Therefore, we speculate that any reduction in invertebrate mass or diversity in tilled plots would be short-lived and perhaps rejuvenated during the second winter after treatment because of increased quantities of detritus available for invertebrates. Moreover, waterbirds can obtain invertebrates in adjacent, unmanipulated habitat during the first winter after treatment, assuming entire impoundments are not manipulated.

We suggest that autumn tilling may be beneficial if plant communities contain later successional indicator species (e.g., swamp smartweed, rushes [*Juncus* spp.], aster [*Aster* spp.], vines, scrub-shrub wetland). Tilling can set back succession and enhance plant diversity and productivity during the next growing season(s) while increasing vegetation interspersion with water following flooding. Tilling can be accomplished using a tractor-drawn rototiller, but this technique is recommended only for small areas. Alternatively, disking likely will create plant and invertebrate responses similar to those achieved with tilling, and disking is more practical for large-scale management. Disking generally produced the second greatest response in seed mass, plant diversity, and occurrence of grasses. Mowing before tilling or disking may be necessary to facilitate soil scarification. Finally, autumn mowing may be most useful when succession does not need to be reverted and the plant community contains robust annual grasses or sedges that do not topple naturally after flooding. Mowing can create open-water areas for waterbirds while maintaining aquatic invertebrate production and diversity.

Vegetation manipulations may be performed in patches or sinuous strips. A 50:50 ratio of emergent vegetation and open water (i.e., hemi-marsh condition) after flooding may be desirable (Weller 1981, Kaminski and Prince 1981, Murkin et al. 1982, Prather et al. 1994, Murkin et al. 1997). Under previous federal regulations, manipulations of natural vegetation could have been interpreted as "baiting" (United States Fish and Wildlife Service [USFWS] 1994:50 CFR 20.21, Elkins 1996, Manning et al. 1996). However, the USFWS has amended the bait-

ing regulations, and any migratory gamebird may now be hunted over manipulated natural vegetation or planted millet that grows on its own in subsequent years (i.e., naturalized) during legal hunting seasons (Federal Register 1999:29801). Nevertheless, we strongly recommend that wetland managers and hunters carefully study the revised migratory bird hunting regulations regarding baiting and baited areas (Federal Register 1999).

Our data on seed and invertebrate masses by habitat treatment are unique and may be useful to estimate foraging carrying capacity of moist-soil habitats (Reinecke et al. 1989, Reinecke and Loesch 1996). However, our results pertain only to Noxubee National Wildlife Refuge, Mississippi; thus, geographical replication of our study is advised. Coefficients of variation derived from our study can be used to design future experiments. We suggest measuring edaphic, hydrologic, and ambient conditions as covariates to more accurately interpret plant and invertebrate responses to habitat treatments and local environmental factors. Observations of treated plots following our study suggest that autumn tilling and disking produced desirable plant responses for 2 growing seasons after treatment. However, a study examining post-treatment responses for 2-3 consecutive growing seasons is needed to determine frequency of manipulations necessary to sustain plant and invertebrate production and diversity. Effects of autumn and spring prescribed burns on aquatic invertebrate and plant responses in moist-soil habitats also should be examined, as well as the applicability of moist-soil habitat management in northern-prairie and tropical wetlands.

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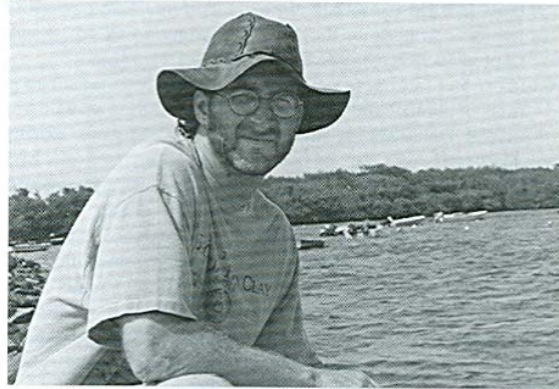
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