CHAPTER 3

DISCING EFFECTS ON SEED PRODUCTION AND DISTRIBUTION OF MOIST-SOIL VEGETATION

INTRODUCTION

Migration of waterfowl is primarily influenced by seasonal abundance of food (Bellrose 1980). The highest densities of breeding waterfowl in North America occur in the Prairie Pothole region, where temporarily and seasonally saturated wetlands provide abundant plant and animal foods (Bellrose 1980). Nonbreeding waterfowl also concentrate in areas of seasonally abundant food, frequently including waste grain as a significant component of the diet. Among Atlantic Flyway wintering areas, Chesapeake Bay and the mid-Atlantic coastal sounds historically supported a high density and diversity of wintering waterfowl (Hindman and Stotts 1989).

Waterfowl management efforts were traditionally focused on increasing production on the breeding grounds. Much effort has been devoted to study of breeding birds, including physiology and nutrition (see reviews by Alisauskas and Ankney 1992, Krapu and Reinecke 1992). Although general habitat management guidelines for migrating and wintering birds have been proposed (Smith et al. 1989), there is comparatively little physiological information upon which to base management recommendations (Baldassarre and Bolen 1994). Physiological and nutritional studies of nonbreeding waterfowl have focused primarily on food habits (Delnicki and Reinecke 1986, Miller 1987, Euliss et al. 1991, Thompson et al. 1992), condition and weight dynamics (Joyner et al. 1984, Whyte and Bolen 1984*a*, 1984*b*, Miller 1986, Heitmeyer 1988, Tietje and Teer 1988, Morton et al. 1990), and stress responses to extreme weather (Bennett and Bolen 1978, Jorde et al. 1984). Given the significance of late winter condition to reproductive success for many Anatids (Alisauskas and Ankney 1992), nutrition should be a significant concern in management of important wintering areas.

Body Condition and Nutrition of Wintering Waterfowl

Mid-winter movement of birds between wintering areas is influenced by weather conditions and the availability of food (Bennett and Bolen 1978, Jorde et al. 1984). Waste grain is a primary source of early winter forage for some dabbling ducks, although its availability can be limited by severe weather and late winter depletion (Baldassarre et al. 1983, Whyte and Bolen 1984*b*). Bennett and Bolen (1978) concluded that female green-winged teal (*Anas crecca*) in Texas responded to extreme winter conditions (especially wind) by moving south to more favorable weather conditions. Access to a stable supply of nutritious forage could reduce winter movements and associated energy expenditure, allowing storage of reserves for the northward migration and breeding season. Breeding and nonbreeding gadwalls (*A. strepera;* Ankney and Alisauskas 1991) and ruddy ducks (*Oxyura jamaicensis;* Alisauskas and Ankney 1994) can be distinguished by lipid reserves, suggesting that nutritional status on the wintering grounds is a potential determinant of reproductive success (Heitmeyer and Fredrickson 1981, Krapu 1981), particularly for species for which endogenous nutrients obtained on the wintering grounds are the primary source of reproductive energy.

Weather and food availability play a direct role in determining condition of wintering birds. Severe winter conditions can reduce availability of food and increase physiological demands on birds, resulting in low body mass, depleted reserves and mortality during severe winters (Thornburg et al. 1988, Tietje and Teer 1988, Bergan and Smith 1993). Whyte and Bolen (1984*b*) found that lipid reserves of mallards (*Anas platyrhynchos*) in Texas were reduced after mid-winter snowstorms, but were stable or increasing after periods of low temperature and heavy snow in early winter. They postulated that mallards did not exhibit stress responses in early winter due to an abundant supply of high-carbohydrate food (waste corn) that became depleted by mid-winter. Lipid reserves of green-winged teal wintering in coastal marsh habitats are higher than lipid reserves of birds wintering in agricultural habitats (Rave and Baldassarre 1991), suggesting that diet quality directly influences anabolic processes. Late winter weight loss in Canada geese (*Branta canadensis*) reflects food availability and ambient conditions, rather than being an endogenous adaptation to reduce body weight prior to spring migration (Joyner et al. 1984). Birds in the northern portion of wintering ranges would be expected to exhibit poor body condition and might be predisposed to stress-induced mortality (Bennett and Bolen 1978).

Several studies have shown physiological and demographic consequences of winter diet restriction in ducks. Richardson and Kaminski (1992) found that prebasic molt in captive female mallards was delayed under conditions of poor diet quality. Captive wood ducks (*Aix sponsa*) fed restricted diets during winter weighed less, had increased mortality and decreased pair formation compared to a control group (Demarest et al. 1997). Game-farm mallards on restricted winter diets nested 3 weeks later than control birds, although no significant delay in nest initiation occurred in wild-strain birds (Dubovsky and Kaminski 1994). Demarest et al. (1997) suggest that food restriction of 15-20% below ad libitum levels may represent a threshold above which survival and reproduction are compromised. However, captive mallards lost 3-7% of body weight during winter despite being fed a nutritious ad libitum diet, suggesting that there is an endogenous component to overwinter body mass change (Loesch et al. 1992).

Molt and migration result in increased demands for energy (Hohman et al. 1992) and protein (Heitmeyer 1988). The lipid reserves of dusky Canada geese (*B. c. occidentalis*) were depleted by 52% during spring migration, a higher rate of endogenous energy expenditure than during any period of the reproductive season (Bromley and Jarvis 1993). Mallards have relatively high energy demands during fall because prealternate molt corresponds with the southward migration, although these events occur early in the fall when high-energy foods are abundant (Heitmeyer 1988). Energetic costs of wing and body molt can limit the capability to store lipids in preparation for fall migration and winter, influencing the timing of migration and increasing demand for high quality forage on the wintering grounds (Hohman et al. 1992). Therefore, productive costs of the nonbreeding season should be an important factor in managing winter waterfowl habitats.

Wetland Management in Waterfowl Wintering Areas

Seeds, tubers, and associated invertebrate fauna of submerged aquatic vegetation (SAV), a formerly abundant resource in Chesapeake Bay, historically provided the primary source of forage for many wintering waterfowl (Hindman and Stotts 1989). Dramatic declines in SAV abundance have led to reduced populations (Krementz 1991) and reliance on suboptimal diets (Perry et al. 1981, 1986) by some waterfowl wintering in Chesapeake Bay. Goose and dabbling duck diets have changed to include high proportions of grain and moist-soil plant seeds (Hindman and Stotts 1989).

Habitat management efforts in wintering areas have recognized food abundance and availability as primary goals (Chabreck 1979). Because of the importance of SAV as waterfowl food, management practices have been proposed to encourage growth of submerged aquatics in coastal impoundments. However, management for highly desirable species such as widgeongrass (*Ruppia maritima*) requires flooding during the growing season (Swiderek et al. 1988, Hindman and Stotts 1989). While this approach may produce an abundant source of waterfowl food, it is incompatible with the water depth requirements of spring migrant shorebirds (Weber and Haig 1996). In contrast, moist-soil management can provide for the habitat needs of migrant shorebirds, while encouraging germination of seed-producing plants that may be consumed by waterfowl (Fredrickson and Taylor 1982).

Implementing moist-soil management typically involves manipulation of seasonal water levels to produce desirable habitat conditions and encourage production of wildlife foods. Hydrological regimes typically include spring drawdowns to provide exposed substrate for germination and growth of seed-producing herbaceous plants, and shallow fall floods to provide foraging habitat for waterfowl (Fredrickson and Taylor 1982, Reid et al. 1989). Seasonal fluctuation of water levels also can enhance production of aquatic macroinvertebrates (Nelson and Kadlec 1984, Neckles et al. 1990) and create an interspersion of vegetation and open water that favors waterfowl use (Murkin et al. 1997).

Although the value of moist-soil plant seeds to waterfowl is recognized, few published studies have addressed the effect of moist-soil impoundment management practices on seed production. Harrison and Chabreck (1988) showed that frequency of occurrence and seed production of moist-soil plants were higher in artificial openings than in untreated sites in Louisiana red maple swamps. Gray (1995) found that discing of moist-soil impoundments in Mississippi increased seed production about 2.5 times, although mowing did not result in detectable increases in seed production. Burning of emergent vegetation in diked brackish marshes in California increased percent cover of 3 waterfowl food plants, although mowing had no effect on these taxa (de Szalay and Resh 1997). Kelley (1990) and Reid et al. (1989) recommend shallow discing of moist-soil impoundments to increase production of seed-producing plants, but do not provide data on plant responses to this treatment.

Several studies also have shown that appropriate hydrological conditions can enhance production of desirable plant species. Mushet et al. (1992) found that sprangletop (*Leptochloa fasicularis*) yielded approximately 0.01 g of seed per plant when irrigated during May and June, whereas plants in unirrigated wetlands produced almost no seed. Irrigation treatments did not affect seed production of swamp timothy (*Heleochloa schoenoides*), pricklegrass (*Crypsis niliaca*), or barnyard grass (*Echinochloa crusgalli*), although all 4 species grew taller and all but barnyard grass grew heavier in irrigated wetlands. Seed biomass and aboveground standing crop of willow smartweed (*Persicaria lapathifolia*), pink smartweed (*P. pensylvanica*) and barnyard grass were higher in managed than in unmanaged playa wetlands in Texas (Haukos and Smith 1993), suggesting that waterfowl food production can be increased by creating hydrological conditions that favor desirable plant species.

Diet and Habitat Use of Wintering Waterfowl

Although moist-soil impoundments may represent a relatively small proportion of wetland acreage on a regional scale, they constitute an important source of waterfowl foraging habitat and can provide sufficient habitat heterogeneity to support several foraging guilds (Reid et al. 1989). Dabbling duck use of mid-Atlantic coastal impoundments during migration and wintering periods varies according to migration chronology and habitat conditions (Hindman and Stotts 1989, Gordon et al. 1998). Seeds of moist-soil plants are common diet items of wintering waterfowl in the southeastern United States (Chabreck et al. 1989), and may be an important proximate factor contributing to habitat selection (Jorde et al. 1983, Miller 1987).

Plant material accounted for 2% of blue-winged teal (*Anas discors*) and northern shoveler (*A. clypeata*) diets during early winter in Mexico, and increased to 97% and 77% in late winter for teal and shovelers, respectively (Thompson et al. 1992). However, Combs and Fredrickson (1996) did not detect seasonal changes in aggregate percent dry mass of moist-soil plant seeds in mallard diets in Missouri; mean consumption of seeds ranged from 20% to 61% among years.

Northern pintail (*A. acuta*) and green-winged teal diets during winter in California contained 74% and 62% aggregate percent volume of plant matter, respectively, and generally reflected relative abundance of moist-soil plants among habitat types (Euliss and Harris 1987). Euliss et al. (1991) concluded that, despite their differences in bill and body morphology, habitat use, and mode of foraging, northern pintails, ruddy ducks, and northern shovelers are opportunistic foragers that shift their diets seasonally to the most abundant available foods.

Waterfowl respond to structural habitat characteristics that suggest discing may favor use by wintering birds. Mallards used relatively open areas within green-tree reservoir habitats in Mississippi (Kaminski et al. 1993). Kaminski and Prince (1981) and Murkin et al. (1982) showed that waterfowl use of the Delta Marsh was higher where a cover:water ratio of 50:50 had been created by mowing or rototilling. Duck densities also increased in response to openings in prairie wetlands created by herbicide application (Solberg and Higgins 1993, Linz et al. 1996). Five of 6 species of postbreeding dabbling ducks on the Delta Marsh selected less vegetated, deeper water habitat in fall relative to spring and summer (Murkin et al. 1997). Comparative studies have also shown that waterfowl use of managed wetlands can be higher than of adjacent unmanaged wetlands. Haukos and Smith (1993) observed higher densities of mallards, pintails and green-winged teal in managed than in unmanaged playa wetlands in Texas. Six species of dabbling ducks in coastal South Carolina used managed impoundments with greater than expected frequency of occurrence relative to unmanaged tidal marshes (Gordon et al. 1998). Both studies concluded that greater food production in managed wetlands was an important factor in determining disproportionate waterfowl use patterns. The potential physiological consequences of winter habitat selection were shown by Tietje and Teer (1988), who found that northern shovelers wintering in freshwater habitats consumed greater quantities of vegetation and seeds and had higher body, omental fat and sternal muscle weights than birds in saline habitats. Because winter condition can subsequently affect reproductive success (Alisauskas and Ankney 1992), potential nutritional consequences of habitat management are an important consideration.

OBJECTIVES

The primary objective of this study was to assess the effect of moist-soil impoundment discing on seed production and distribution of moist-soil plants. Specific objectives were to determine the effect of impoundment discing on

- Total seed production by moist-soil plants.
- Seed production by individual dominant plant species.
- Distribution (measured as percent cover) of dominant plant species.
- Vegetation height.

METHODS

Study Area and Sampling Approach

The study was conducted at Back Bay National Wildlife Refuge (NWR), Virginia Beach, Virginia. The refuge is located at the northern end of the Outer Banks barrier island, near the juncture of the barrier island and the mainland. Its mid-Atlantic location and proximity to major habitat features of significance to waterfowl (Chesapeake Bay, Back Bay) and shorebirds (coastal beaches, Delaware Bay) make the refuge an ideal location for examining integrated impoundment management. Dominant habitat features include moist-soil impoundments, coastal scrub and forest, nontidal marsh, and an extensive beach and dune system. Back Bay, a nontidal freshwater sound, borders the refuge to the west and is the primary source of impoundment water. Impoundments are flooded by pumping fresh water from Back Bay into a central storage pool, from which individual impoundments can be flooded by gravity. Dominant plant species in impoundments are generally reflective of freshwater influence (e.g., *Panicum virgatum, P. dichotomiflorum, Echinochloa crusgalli, Eleocharis* spp.), although several salt-tolerant species (*Spartina patens, Distichlis spicata*) also are common. Scattered upland hummocks and ridges throughout the impoundments contain remnant coastal scrub and forest species (e.g., *Quercus virginiana*, *Myrica cerifera*).

Two impoundments, Pool A (537 ha) and Pool C (475 ha) (Fig. 3.1) were selected for this study. Both impoundments are surrounded by containment dikes and are drained by water control structures near their respective southwestern corners. Substrate topography slopes gradually downward from east to west, such that the eastern portion of both impoundments is initially exposed during drawdown. Under complete drawdown conditions, substrate in the eastern portion of the impoundments is frequently dry, while that in the western portion remains shallowly flooded. The ability to create exposed substrate through drawdown in the eastern portions facilitates management for both moist-soil plants and migrant shorebirds. A typical management approach includes drawdown initiation in early spring, with the goal of initial substrate exposure upon the first arrival of migrant shorebirds (generally between 1 and 15 May). Drawdown continues through the shorebird migration period to provide new arrivals with access to recently exposed substrate. Impoundment flooding is initiated during early fall with the goal of providing shallowly flooded stands of emergent vegetation for migrant waterfowl. Flooded conditions are maintained during winter to provide foraging habitat for wintering waterfowl and wading birds.

During summer 1995, refuge biologists identified discing as a high priority management action for the eastern portions of Pools A and C due to increasing dominance by perennial species. Discing was conducted during November 1995 by drawing a coarse-bladed disc through treatment areas. Depth of discing was not strictly controlled, but was approximately 15 cm. Disced and undisced areas were interspersed along the north-south axis of each impoundment (see Chapter 2 for details on assignment of treatments). Study plot locations were randomly located in the available disced and undisced habitat. Each impoundment contained 8 plots, equally allocated between treatments (disced vs. control). Within randomly selected locations, the 30 m x 75 m plots were randomly positioned such that they were >5 m from habitat edges (e.g., upland ridges, drainage ditches), and 10 - 20 m from the toe of impoundment dikes. Two control plots included small (<150 m^2) upland islands within the plots. All sampling locations were constrained to be >2 m from the edge of these islands. Plots were oriented with the 75m dimension on an east-west axis, and divided into 5 30 m x 15 m subplots to stratify sampling across the water depth gradient (Fig. 3.2). Plot and subplot corners were permanently marked with orange wooden stakes during March 1996.

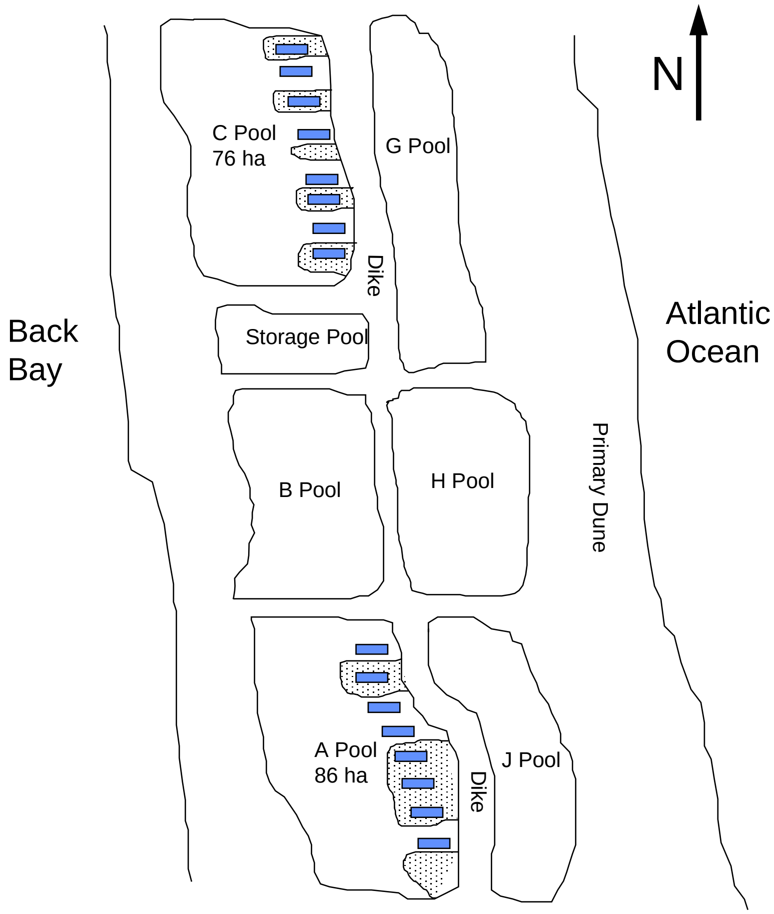

Fig. 3.1. Approximate locations of disced areas (stippled) and 30-m x 75-m study plots (rectangles) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

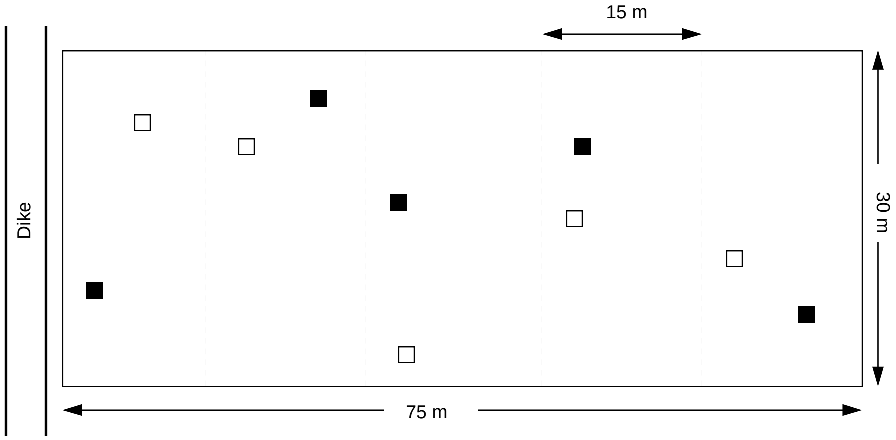

Fig. 3.2. Dimensions and configuration of sampling plots in moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Squares represent exclosures and open sampling stations used for invertebrate sampling (see Chapter 2).

Sampling methods were designed to provide estimates of plant community composition, structure and seed production in response to discing. Sampling was conducted during early fall to correspond with the arrival of early migrant waterfowl, while ensuring that senescence of herbaceous annuals was minimal. All data were collected at random locations constrained to be >1m from permanent invertebrate sampling stations (see Chapter 2).

Plant Community Composition

During September 1996 and 1997, a 1- x 1-m quadrat was placed at a random location within each subplot (i.e., 5 subsamples per plot). Total absolute percent cover was visually estimated for two vegetation layers (emergent plants and submerged aquatics). Submerged aquatics included several species (*Bidens cernua*, *Hydrocotyle spp*., and *Centella spp.*) that also occurred on unflooded substrate. Where these species were not submerged, they were considered components of the emergent plant layer. Within vegetation layers, relative cover of dominant species was recorded. Estimates of percent cover were recorded in 5% increments.

Seed Biomass

To account for phenological variation among species, seed production was estimated twice each year. The first estimate was in conjunction with plant community composition sampling during September, and the second estimate was conducted during October. Seed production was estimated in randomly located 0.0625-m^2 sampling frames, following the method of Laubhan and Fredrickson (1992). During September sampling, the seed production sampling frame was placed at a random location within the randomly-located 1- x 1-m quadrats used for collection of plant community composition data. During October sampling, the frame was located at a random location within each subplot. To avoid double sampling, October locations were constrained to be >1m from September locations.

Laubhan and Fredrickson (1992) recommend counting the total number of seed heads per species within the sampling frame. Stems of some plant species on the study area, such as salt meadow hay (*Spartina patens*) and 3-square bulrush (*Scirpus americanus*), were not always completely upright. Sample frames placed in these locations often had no seed heads in the frame, although several seed-producing plants were rooted in the frame. To remove bias associated with stem orientation, number of rooted plants per frame with viable seed heads was recorded for each species. Morphological dimensions of a representative specimen of each species were measured to generate seed biomass estimates using the linear regression equations of Laubhan and Fredrickson (1992). Regression equations for prediction of seed biomass were not available for several plant species. For the most common of these species, regression equations were generated from plant specimens (n = 14 - 35) collected at Back Bay and Prime Hook National Wildlife Refuges (Appendix C). Morphological dimensions (width and height) of inflorescences were measured using calipers or a plastic ruler. Inflorescences were collected in paper bags, and seed was manually separated from chaff, air-dried and weighed (± 0.0001 g). Regression equations were not developed for less common species (e.g., *Juncus* sp.). When these species were encountered during sampling, a representative specimen was collected, dried and weighed. For all species, biomass estimates were generated from a single specimen within each randomly located sampling frame, although the method of estimation (published regression equation, developed regression equation, direct biomass determination) differed among species. Seed production per unit area was determined by multiplying biomass per plant by stem density (stems / m^2).

Weighing of seed from collected plants was conducted after plants had air dried in paper bags. Seed was manually stripped from inflorescences and weighed to the nearest 0.0001g. Complete separation of seeds from chaff (achenes, awns, etc.) was not possible for all species, and some specimens had lost a portion of their seed prior to collection. Although these factors introduce error into seed production estimates, collection and separation methods were consistent between treatment and control areas. The estimates produced are thus not likely to be biased relative to detection of treatment effects on seed production.

Vegetation Height

Vegetation height was evaluated following the method of Robel et al. (1970). This method was designed for estimation of grassland plant biomass through a measure of vertical obstruction. Application of the method in this study was predicated on the assumption that a similar relationship between vertical obstruction and biomass exists for herbaceous wetland plants. Vertical obstruction was measured using a 1-m length of 1.28-cm diameter PVC pipe. The pipe was marked at 5-cm increments, with alternating segments painted red to provide visual contrast, and was attached to the sampling frame used for seed production estimation. Four estimates of vertical obstruction were recorded at each location for seed production estimation. Estimates were recorded at the four cardinal directions from a distance of 4m with the observer's eye 1m above the marsh substrate (Robel et al. 1970). Vertical obstruction was recorded as the lowest 5-cm segment partially visible above the vegetation. Vegetation height was estimated by multiplying the mean of the four vertical obstruction readings at each location by 5 cm.

Data Analysis

Linear regression equations were developed to predict seed yield of 5 moist-soil plant species (see Appendix C). Some species (e.g., *Scirpus olneyi*) frequently had several inflorescences per plant. For these species, each plant was considered an independent sampling unit, where seed biomass was the sum of biomass for all inflorescences. Many equations developed by Laubhan and Fredrickson (1992) included inflorescence volume as an important predictor of seed biomass. For species with multiple inflorescences, volume was determined for each inflorescence and total inflorescence volume for the plant was calculated as the sum of volumes for individual inflorescences. Predictive equations were generated using stepwise linear regression (PROC REG, SAS Institute 1990*b*) with a zero intercept constraint (Laubhan and Fredrickson 1992). Total seed biomass was the dependent variable, and potential independent variables included direct measures of inflorescence dimensions as well as several estimates of inflorescence volume based on approximation to geometric forms (e.g., cone or cylinder).

The main effects of interest in analysis of seed production data were year (1996 vs. 1997) and treatment (discing vs. control). Study plots (n = 16) were considered independent sampling units, with subplots (n = 5 per plot) as subsamples and pools (n = 2) as the blocking factor. Vegetation density, stem density, and seed production data were collected twice each field season. Sampling periods within years (September vs. October) were considered subsamples for these analyses. The mean of each response variable was generated for each plant species within plots and years. For sampling locations in which a given plant species did not occur, zero values were included for stem density and seed production (Laubhan 1992). Total seed production and stem density within plots and years were calculated by summing means for all species.

Main effects and interactions between effects and the blocking factor (Pool) were analyzed using mixed linear models (PROC MIXED; Littell et al. 1996). This approach uses a likelihood-based procedure to estimate variance components for random effects, and is preferable to general linear models (e.g., PROC GLM; SAS Institute 1990*b*) that do not fully account for random effects (Littell et al. 1996). Mixed models are appropriate for field studies that include both fixed and random effects (Bennington and Thayne 1994). Models generated for this study included Plot (nested within Pool x Treatment) as a random effect, with Treatment and Time as fixed effects. Separate models were generated with total seed production and total stem density as dependent variables. Both models included Vegetation Height as a covariate. Lack of a treatment effect on the covariate is a fundamental assumption of analysis of covariance (Littell et al. 1996). This assumption was verified in a model testing Treatment, Time and Pool effects on Vegetation Height. The Treatment effect in this model was nonsignificant ($P = 0.1185$), as were all interactions with Treatment ($P > 0.463$) (see Results).

Where significant overall treatment effects on stem density or seed production occurred, separate models were generated by plant species using the same model structure analyzed for total stem density and seed production. As these models did not constitute multiple comparisons among levels of an independent variable, Bonferroni adjustment of error rates was not conducted. Seed production, stem density and vegetation height data were $\log_{10}(x + 1)$ transformed, and percent cover data were arcsine ($x^{0.5}$) transformed prior to statistical analysis (Sokal and Rohlf 1995). As additivity of seed production and stem densities among species was desirable, means and standard errors were not back-transformed from least squares means. Means were generated as the arithmetic mean across levels of significant main effects, using PROC MEANS (SAS Institute 1990*a*), and are presented ± 1 SE. As the consequences of Type I error were deemed minimal for this study, statistical significance was accepted at $\alpha = 0.10$.

RESULTS

Predictive Equations

Linear regression equations explained 91 to 98% of the variation in seed biomass for the 5 species investigated (Table 3.1; see Appendix C). An estimate of inflorescence volume was retained as a significant predictive variable in models for *Dichromena colorata*, *Scirpus americanus*, and *S. olneyi*, whereas the model for *Panicum virgatum* included inflorescence width as the only significant predictive variable. The model for *Spartina patens* included a linear combination of 3 inflorescence dimensions. As the precision of these models was comparable to that reported by Laubhan and Fredrickson (1992), their use should not introduce bias into seed production estimates.

Seed Production

Total seed production was higher ($F = 4.26$, $P = 0.0614$) in disced (1052 ± 468 kg/ha) than in control (529 ± 226 kg/ha) plots (Fig. 3.3), but did not differ among years ($F = 2.37$, $P = 0.128$) or pools ($F = 1.14$, $P = 0.307$). No interaction terms were significant in the total seed production model (Table 3.2). Despite this treatment effect, seed production of individual species differed between disced and control plots only for *Cyperus iria*, *Echinochloa crus-galli*, *Fimbristylis annua,* and *Panicum dichotomiflorum* (Table 3.3). All 4 of these species produced greater seed biomass in disced plots, although the magnitude of the treatment effect varied among years only for *Fimbristylis annua* (i.e., significant Year x Treatment interaction; Table 3.3). Year x treatment interactions were also significant for *Dichromena colorata*, *Distichlis spicata* and *Scirpus olneyi* (Table 3.3).

Total stem density of seed-producing plants did not differ ($F = 1.80$, $P = 0.205$) between disced (191 ± 36 stems/m^2) and control (157 ± 37 stems/m^2) plots, nor among years ($F = 0.95$, $P = 0.332$) or pools ($F = 0.30$, $P = 0.593$). However, both the Year x Treatment ($F = 3.77$, $P = 0.056$; Fig. 3.4) and Year x Treatment x Pool ($F = 7.43$, $P = 0.008$; Fig. 3.5) interaction terms were significant in the total stem density model (Table 3.4). Stem density differed between disced and control plots in C-Pool plots during both years ($F = 3.76$, $P = 0.056$; Fig. 3.5). Stem density in A-Pool increased from 1996 to 1997 in disced plots ($F = 3.30$, $P = 0.086$) and decreased from 1996

Table 3.1. Regression equations developed for predicting seed biomass of 5 moist-soil plant species collected at Back Bay and Prime Hook National Wildlife Refuges. Seed biomass (g / plant) is the response variable for all equations. A predictive equation was developed for a 6th species (*Eleocharis quadrangulata*) (see Appendix C), but this species did not occur in any seed production sampling quadrats.

Species	**Regression Equation**	**n**	**r^2**	***F***	***P***
Dichromena colorata	$0.0002619 * \pi * (\text{WIDTH}^{a} * 0.5)^{2}$	28	0.92	298.97	<0.0001
Panicum virgatum	$0.01832 * (\text{WIDTH}^{a})$	30	0.91	292.87	<0.0001
Scirpus americanus	$0.4212 * \Sigma^{b} (\pi * (\text{WIDTH}^{c} * 0.5)^{2} * \text{HEIGHT}^{c})$	35	0.92	421.38	<0.0001
Scirpus olneyi	$0.0004808 * \Sigma (\pi * (\text{WIDTH}^{c} * 0.5)^{2} * \text{HEIGHT}^{c})$	14	0.98	565.32	<0.0001
Spartina patens	$0.008006 * ((5.2873 * \text{HEIGHT1}^{d}) + (0.06246 * \text{HEIGHT3}) - (1.5220 * \text{WIDTH3}))$	30	0.95	549.48	<0.0001

[a] WIDTH = Inflorescence width (cm).

[b] Denotes sum of paranthetic quantity for all inflorescences on each plant.

[c] WIDTH = Infloresence width at widest point (mm), HEIGHT = Inflorescence height at longest point (mm).

[d] HEIGHT1 = Height of lowest inflorescence (mm), HEIGHT3 = Height of third inflorescence from bottom (mm), WIDTH 3 = Width of third inflorescence from bottom (mm).

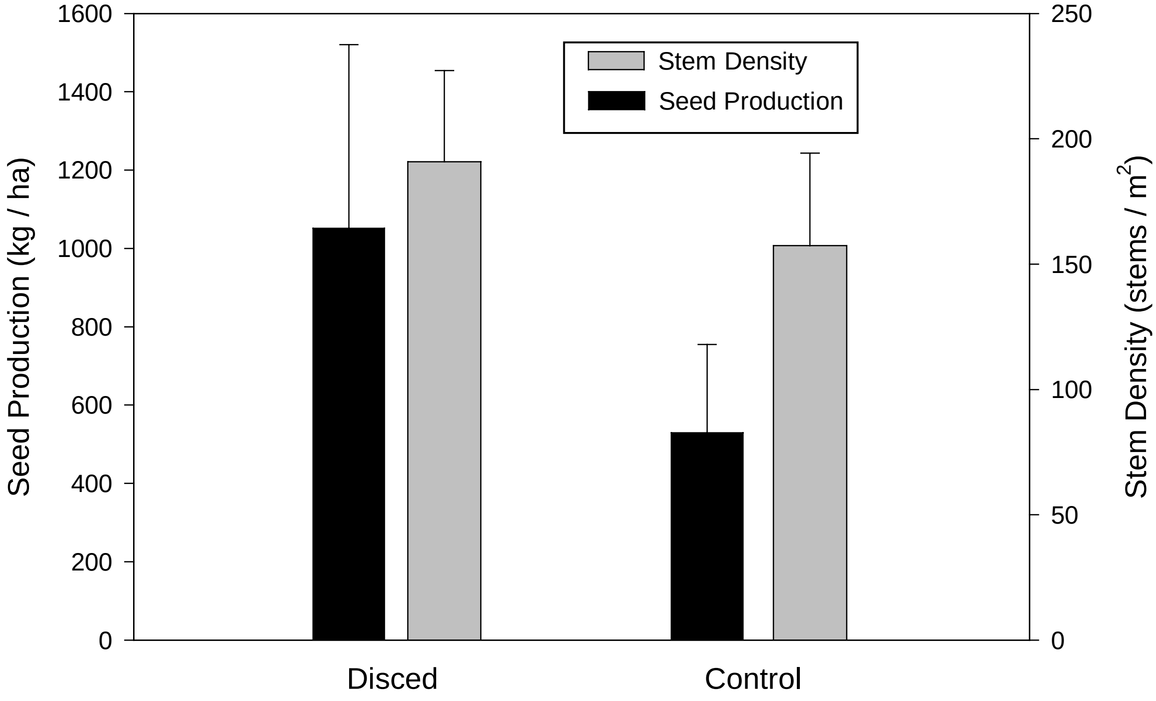

Figure 3.3. Mean (+ SE) moist-soil plant seed production (black bars) and stem density (gray bars) in disced and control study plots at Back Bay National Wildlife Refuge, Virginia Beach, Virginia, 1996-97.

Table 3.2. Results of the repeated measures mixed model ANOVA for total moist-soil plant seed production at Back Bay National Wildlife Refuge, Virginia Beach, Virginia, 1996-97. Analysis was conducted on log-transformed variables using PROC MIXED (Littell et al. 1996).

Source	***df***	***F***	***P***
Between Plots			
Pool	1,12	1.14	0.307
Treatment	1,12	4.26	0.062
Pool x Treatment	1,12	0.40	0.538
Within Plots			
Year	1,75	2.37	0.128
Year x Pool	1,75	0.04	0.836
Year x Treatment	1,75	1.08	0.301
Year x Pool x Treatment	1,75	1.98	0.163
Covariate			
Plant Height	1,75	31.91	0.0001

Table 3.3. Mean seed production (kg / ha) for 30 species of moist-soil plants in disced (*n* = 8) and control (*n* = 8) study plots at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. *F*- and *P*-values are from mixed model analysis of variance for each species. Mixed models included Year, Treatment and Pool as main effects, as well as all 2- and 3- way interactions. *P*-values with asterisks were considered statistically significant (*P* < 0.10). Complete ANOVA tables for each species are provided in Appendix E.

	1996				**1997**						**Year x**	
	Control		**Disced**		**Control**		**Disced**		**Treatment**		**Treatment**	
Species	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	***F***	***P***	***F***	***P***
Bidens cernua	6.21	4.34	3.75	1.72	38.91	21.92	31.95	20.94	0.02	0.875	0.14	0.708
Carex albulotescens	1.48	1.48	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.568	0.94	0.335
Carex tribuloides	0.00	0.00	0.15	0.15	0.00	0.00	0.00	0.00	1.57	0.212	1.05	0.306
Cyperus erythrorhizos	635.43	357.63	1386.58	775.32	0.00	0.00	0.62	0.62	2.31	0.130	0.12	0.728
Cyperus esculentus	4.00	2.38	13.82	8.06	7.92	6.50	2.50	2.50	0.30	0.583	0.47	0.495
Cyperus iria	60.79	29.51	104.23	72.68	35.09	30.29	270.13	229.16	3.24	0.074 *	1.36	0.245
Cyperus spp.	0.00	0.00	0.14	0.14	0.00	0.00	0.00	0.00	1.25	0.265	1.04	0.309
Dichromena colorata	0.11	0.08	0.04	0.04	1.67	1.66	0.04	0.03	0.56	0.456	4.18	0.043 *
Distichlis spicata	29.35	19.84	0.62	0.62	10.34	10.24	0.00	0.00	1.97	0.162	3.09	0.081 *
Echinochloa crus-galli	16.25	11.87	68.01	40.06	24.09	21.69	30.91	16.24	3.31	0.071 *	0.37	0.543
Eleocharis quadrangulata	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.61	0.435	0.97	0.326
Fimbristylis annua	22.37	16.66	18.76	8.88	2.73	2.52	48.18	30.94	4.86	0.029 *	3.01	0.085 *
Fuirena squarosa	5.99	4.65	6.44	4.18	0.00	0.00	0.62	0.62	1.02	0.314	0.71	0.401
Juncus canadensis	0.66	0.63	0.00	0.00	0.27	0.27	1.36	0.94	0.05	0.831	1.92	0.168
Juncus coriaceous	13.66	9.51	0.57	0.57	0.98	0.71	0.00	0.00	1.59	0.209	0.05	0.829
Juncus marginatus	0.18	0.18	0.36	0.26	0.00	0.00	0.00	0.00	0.30	0.584	0.31	0.581
Juncus megacephalus	0.56	0.41	0.60	0.60	5.79	3.43	4.83	2.78	0.00	0.992	0.12	0.731
Juncus tenuis	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.26	2.10	0.149	0.92	0.339
Panicum dichotomoflorum	7.78	4.65	31.08	19.60	5.50	3.80	26.60	15.89	4.71	0.032 *	0.42	0.520
Panicum spp.	1.10	0.59	0.68	0.51	0.00	0.00	0.00	0.00	0.03	0.869	0.33	0.566
Panicum virgatum	58.82	42.76	0.00	0.00	3.24	3.24	2.64	2.64	0.60	0.441	1.90	0.170
Polygonum pensylvanicum	9.15	5.14	1.02	1.02	8.52	7.56	2.41	1.73	0.15	0.699	1.47	0.228
Rhynchospora spp.	0.59	0.39	0.77	0.70	3.56	3.56	4.03	3.59	0.68	0.412	0.01	0.921
Sacciolepsis spp.	0.00	0.00	0.02	0.02	0.06	0.06	0.00	0.00	0.26	0.610	1.70	0.195
Scirpus americanus	2.34	0.68	5.40	2.90	3.93	0.93	4.76	1.84	0.81	0.370	0.00	0.967
Scirpus olneyi	0.00	0.00	6.07	5.30	3.80	2.67	0.42	0.42	0.04	0.851	3.61	0.059 *

Table 3.3 Cont'd.

	1996				**1997**					**Year x**
	Control		**Disced**		**Control**		**Disced**		**Treatment**		**Treatment**	
Species	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	***F***	***P***	***F***	***P***
Scleria verticillata	0.31	0.31	0.08	0.06	0.00	0.00	0.00	0.00	0.17	0.681	0.41	0.522
Setaria spp.	1.81	1.69	0.76	0.59	0.44	0.30	1.07	0.54	0.13	0.717	1.80	0.182
Spartina patens	9.95	3.03	3.87	1.50	11.87	4.67	16.06	8.51	0.07	0.793	0.45	0.504
Xyris spp.	0.00	0.00	0.00	0.00	0.32	0.32	0.40	0.40	0.03	0.858	0.00	0.970

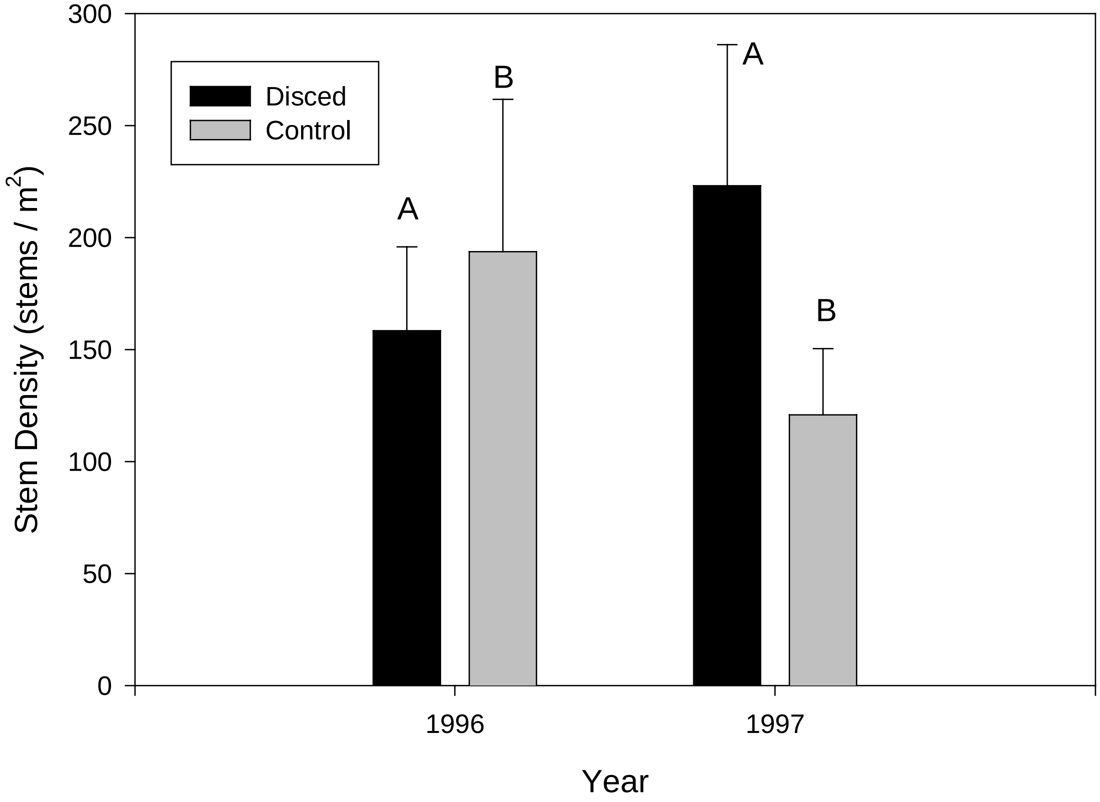

Figure 3.4. Mean (+ SE) stem density of moist-soil plants in disced and control plots (*n* = 8 per treatment) at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Treatment means with similar capital letters do not differ (*P* > 0.10) within years.

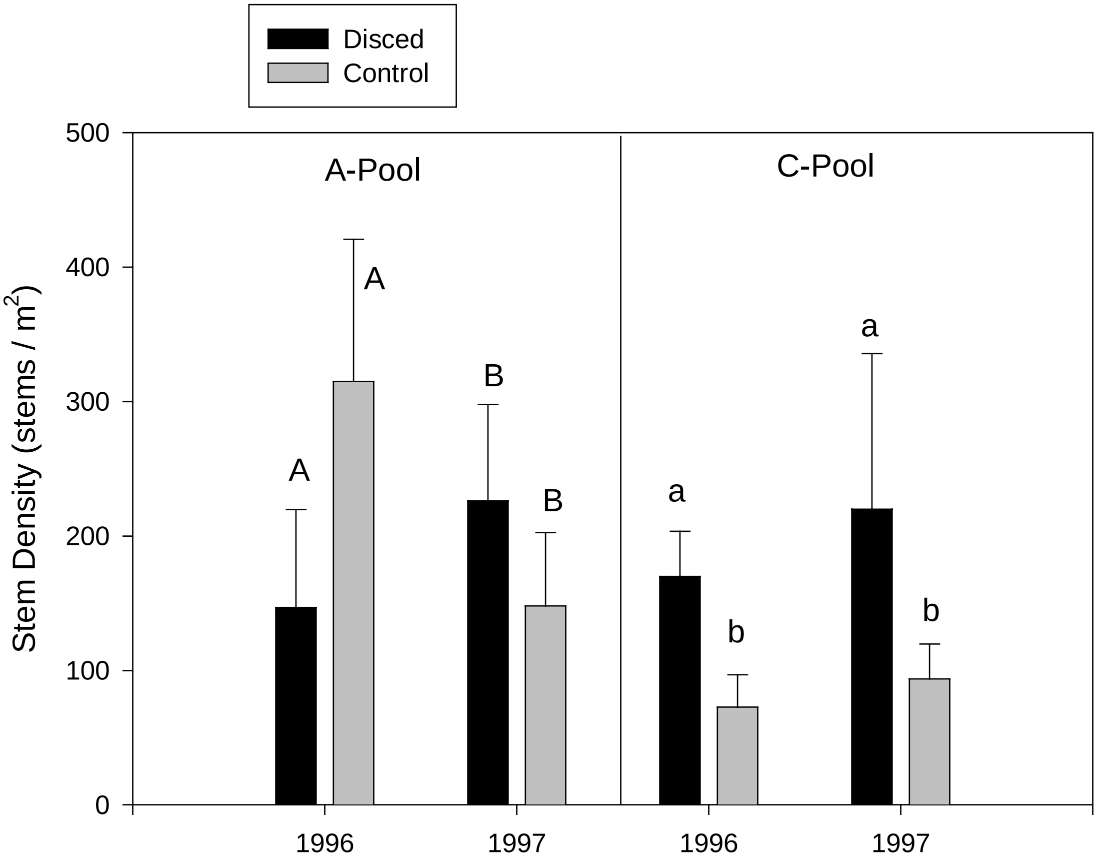

Figure 3.5. Mean (+ SE) moist-soil plant stem density in 2 treatments (disced and control) and 2 pools (*n* = 4 per treatment x pool) at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Means with similar capital letters do not differ (*P* > 0.10) within pools and between years. Means with similar lowercase letters do not differ (*P* > 0.10) within pools and between treatments.

Table 3.4. Results of the repeated measures mixed model ANOVA for total moist-soil plant stem density at Back Bay National Wildlife Refuge, 1996-97. Analysis was conducted on log-transformed variables using PROC MIXED (Littell et al. 1996).

Source	***df***	***F***	***P***
Between Plots			
Pool	1,12	0.30	0.593
Treatment	1,12	1.80	0.205
Pool x Treatment	1,12	1.67	0.220
Within Plots			
Year	1,75	0.95	0.332
Year x Pool	1,75	0.01	0.944
Year x Treatment	1,75	3.77	0.056
Year x Pool x Treatment	1,75	7.43	0.008
Covariate			
Plant Height	1,75	20.86	0.0001

to 1997 in control plots ($F = 8.19$, $P = 0.0054$), but did not differ ($F < 0.74$, $P > 0.391$) between years for either treatment in C-Pool (Fig. 3.5). Among individual species, discing effects on stem density were significant only for *Cyperus erythrorhizos*, *Echinochloa crus-galli*, *Fimbristylis annua*, and *Panicum dichotomiflorum* (Table 3.5). Year x Treatment interactions were significant for *Dichromena colorata*, *Fimbristylis annua,* and *Scirpus olneyi* (Table 3.5). Total stem density and total seed production were highly correlated ($r = 0.701$, $P < 0.0001$) among plot-years (Fig. 3.6).

Plant Distribution

Mixed models for percent cover of individual plant species revealed significant treatment effects or interactions with treatment for *Cyperus iria*, *Fimbristylis annua*, *Fuirena squarrosa*, *Juncus marginatus*, *J. roemerianus*, *Panicum dichotomiflorum*, *P. virgatum*, *Rhynchospora* spp., and *Spartina patens* (see Appendix E for F-statistics and P-values). Percent cover of *Fimbristylis annua*, *Fuirena squarrosa*, and *Panicum dichotomiflorum* was higher in disced than in control plots, whereas percent cover of *Juncus roemerianus*, *Panicum virgatum*, and *Spartina patens* was higher in control plots (Table 3.6). There was annual variation in percent cover of nine species (Year effect; $3.24 \leq F \leq 12.84$, $0.0038 \leq P \leq 0.097$; see Appendix E). *Bidens cernua*, *Juncus marginatus*, *Panicum virgatum*, and *Spartina patens* were more abundant in 1997, whereas *Cyperus esculentus*, *Distichlis spicata, Echinochloa crus-galli*, *Eleocharis obtusa*, and *Fuirena squarrosa* were more abundant in 1996. Variation in abundance among impoundments was evident (significant Pool effect or interaction with Pool) for 21 of 26 species (Table 3.7).

Vegetation Height

Mean vegetation height did not differ ($F = 2.98$, $P = 0.110$) between disced and control plots, but increased ($F = 29.70$, $P < 0.001$) from 1996 to 1997 (Fig. 3.7). Vegetation height did not differ between pools ($F = 0.40$, $P = 0.541$). All interaction terms were nonsignificant (Table 3.8).

DISCUSSION

Seed Production

Although high seed production is recognized as an important impoundment management goal, few published estimates of moist-soil seed production are available. Reinecke et al. (1989:236) concluded that 450 kg/ha is a “reasonable estimate of average food production” for

Table 3.5. Mean stem density (stems / m^2) for 30 species of moist-soil plants in disced (n = 8) and control (n = 8) study plots at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. *F*- and *P*-values are from mixed model analysis of variance for each species. Mixed models included Year, Treatment and Pool as main effects, as well as all 2- and 3- way interactions. *P*-values with asterisks were considered statistically significant ($P < 0.10$). Complete ANOVA tables for each species are provided in Appendix E.

	1996				**1997**						**Year x**	
	Control		**Disced**		**Control**		**Disced**		**Treatment**		**Treatment**	
Species	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	***F***	***P***	***F***	***P***
Bidens cernua	17.80	13.12	7.40	2.82	17.20	9.20	13.00	9.26	0.17	0.684	0.00	0.954
Carex albulotescens	0.60	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.568	0.94	0.335
Carex tribuloides	0.00	0.00	0.20	0.20	0.00	0.00	0.00	0.00	1.57	0.212	1.05	0.306
Cyperus erythrorhizos	3.20	1.63	15.80	9.65	0.00	0.00	0.20	0.20	6.17	0.014 *	1.71	0.194
Cyperus esculentus	2.00	1.16	9.20	7.85	0.40	0.26	0.20	0.20	0.90	0.344	0.55	0.461
Cyperus iria	11.20	5.17	23.40	16.76	6.40	5.72	51.40	40.37	2.40	0.123	2.25	0.135
Cyperus sp.	0.00	0.00	0.40	0.40	0.00	0.00	0.00	0.00	1.25	0.265	1.04	0.309
Dichromena colorata	0.80	0.43	0.40	0.40	6.20	5.97	0.40	0.26	0.66	0.419	3.48	0.064 *
Distichlis spicata	61.60	41.27	1.40	1.40	33.00	30.14	0.00	0.00	2.30	0.131	2.11	0.149
Echinochloa crus-galli	1.20	0.99	3.80	2.03	2.20	1.98	4.00	1.96	3.55	0.062 *	0.18	0.676
Eleocharis quadrangulata	0.00	0.00	0.60	0.60	0.00	0.00	0.00	0.00	0.61	0.435	0.97	0.326
Fimbristylis annua	24.60	15.51	32.60	17.83	3.40	2.97	87.00	56.64	3.96	0.048 *	4.91	0.028 *
Fuirena squarosa	9.40	5.13	16.00	11.24	0.00	0.00	1.60	1.60	0.51	0.477	0.46	0.498
Juncus canadensis	0.40	0.26	0.00	0.00	0.80	0.80	2.00	1.34	0.05	0.817	1.54	0.216
Juncus coriaceous	7.40	5.23	1.40	1.40	1.40	1.02	0.00	0.00	1.22	0.271	0.08	0.782
Juncus marginatus	0.40	0.40	0.60	0.42	0.00	0.00	0.00	0.00	0.13	0.719	0.15	0.700
Juncus megacephalus	0.60	0.42	0.60	0.60	1.60	0.80	2.80	1.38	0.33	0.568	0.11	0.740
Juncus tenuis	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.40	2.10	0.149	0.92	0.339
Panicum dichotomiflorum	3.20	2.16	10.00	5.93	4.80	3.27	18.40	11.90	2.94	0.088 *	0.68	0.410
Panicum sp.	1.80	0.93	0.80	0.60	0.00	0.00	0.00	0.00	0.12	0.725	0.64	0.425
Panicum virgatum	13.40	10.29	0.00	0.00	1.00	1.00	0.60	0.60	0.82	0.367	1.72	0.192
Polygonum pensylvanicum	3.20	1.68	0.40	0.40	2.60	2.18	0.60	0.42	0.52	0.472	0.49	0.487
Rhynchospora sp.	1.60	1.39	2.20	1.57	1.60	1.60	1.80	1.40	0.62	0.431	0.05	0.832
Sacciolepsis sp.	0.00	0.00	0.20	0.20	0.40	0.40	0.00	0.00	0.11	0.745	1.86	0.174
Scirpus americanus	11.60	3.50	21.20	8.80	19.60	7.17	18.20	6.16	0.53	0.468	0.28	0.595
Scirpus olneyi	0.00	0.00	0.80	0.60	0.80	0.60	0.20	0.20	0.10	0.756	3.18	0.077 *

Table 3.5. Cont'd.

	1996				1997						Year x	
	Control		**Disced**		**Control**		**Disced**		**Treatment**		**Treatment**	
Species	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	***F***	***P***	***F***	***P***
Scleria verticillata	3.00	3.00	1.40	0.93	0.00	0.00	0.00	0.00	0.04	0.835	0.12	0.730
Setaria sp.	1.60	1.21	1.20	0.99	0.40	0.26	2.20	1.28	0.41	0.525	2.16	0.144
Spartina patens	13.20	4.24	6.40	2.36	16.60	6.71	17.40	8.65	0.10	0.757	0.21	0.647
Xyris sp.	0.00	0.00	0.00	0.00	0.40	0.40	0.80	0.80	0.17	0.680	0.09	0.764

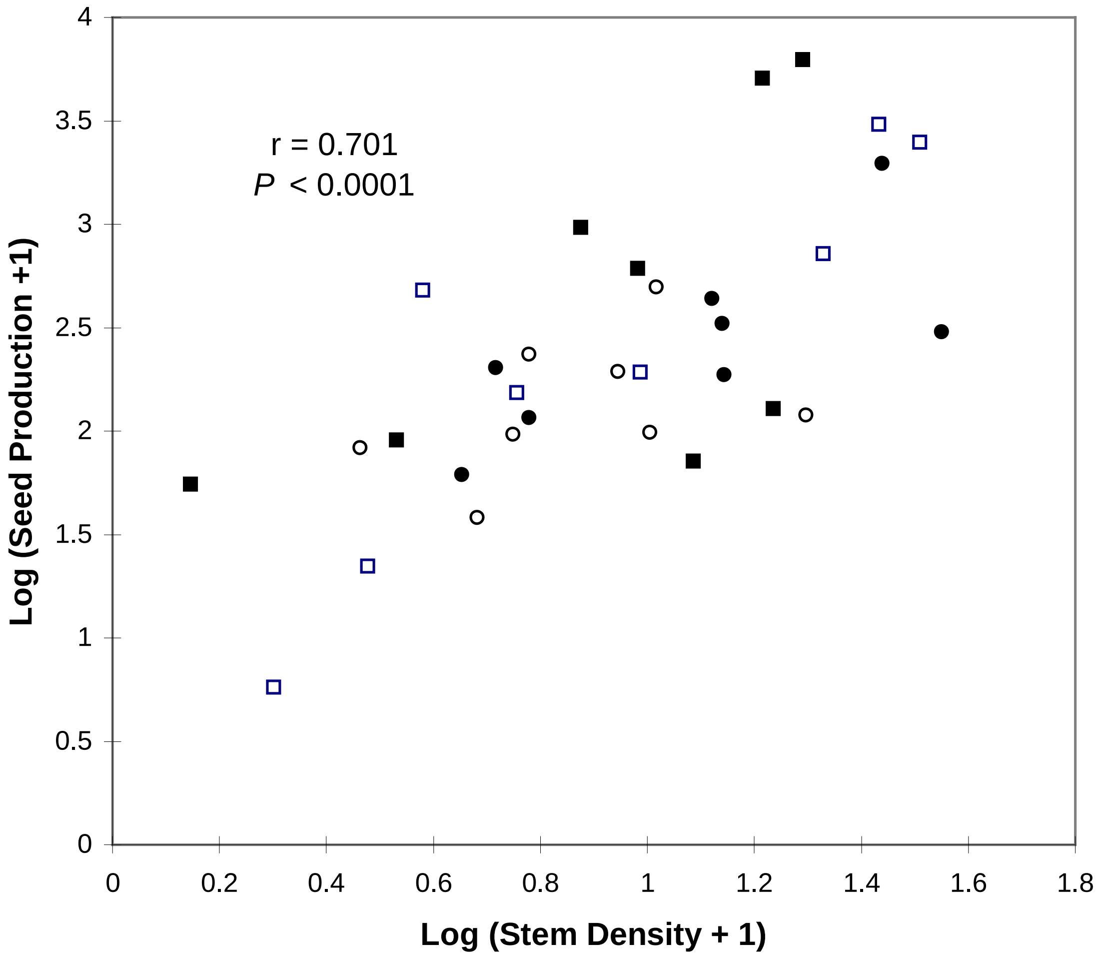

Figure 3.6. Correlation between seed production and stem density of moist-soil plants in impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Data were collected during 1996 (squares) and 1997 (circles) in disced (solid symbols) and control (open symbols) plots. Each observation represents the mean of both variables for 1 study plot.

Table 3.6. Percent cover of moist-soil plants in disced and control study plots, Back Bay National Wildlife Refuge, Virginia Beach, Virginia, September 1996 and 1997. Data were combined by year and pool to generate treatment means. Complete ANOVA tables for each species are provided in Appendix E.

	Control		**Disced**	
Species	**Mean**	**SE**	**Mean**	**SE**
Bidens cernua	4.2	1.9	2.7	1.2
Cyperus erythrorhizos	1.1	0.4	1.3	0.7
Cyperus esculentus	1.3	0.6	1.9	1.4
Cyperus iria[b,d]	0.5	0.3	0.9	0.5
Dichromena colorata	1.5	1.2	0.3	0.1
Distichlis spicata	5.4	2.9	2.4	1.3
Echinchloa crus-galli	1.1	0.5	1.4	0.6
Eleocharis obtusa	13.5	5.6	16.8	6.1
Fimbrystilis annua[a]	2.5	0.7	12.7	5.2
Fuerina squarrosa[a,b,c,d]	0.5	0.2	2.5	1.0
Juncus canadensis	0.5	0.2	0.8	0.3
Juncus marginatus[c,d]	0.3	0.1	0.1	0.1
Juncus megacephalus	0.9	0.4	0.8	0.3
Juncus roemerianus[a]	1.8	0.7	0.1	0.1
Leerzia oryzoides	3.5	1.9	0.9	0.7
Miscellaneous species	12.4	2.2	14.8	3.5
Panicum dichotomoflorum[a]	1.2	0.5	4.1	1.8
Panicum virgatum[a,b]	3.8	1.5	0.6	0.4
Phragmites australis	3.8	1.5	2.5	1.8
Pluchea purpurescens	2.0	0.7	3.8	1.4
Polygonum pensylvanicum	2.1	1.2	1.1	0.6
Rhynchospora spp.[d]	0.6	0.3	0.9	0.5
Scirpus americanus	5.8	1.3	7.5	2.0
Scirpus olneyi	1.0	0.8	0.5	0.2
Setaria spp.	0.5	0.4	0.7	0.4
Spartina patens[a]	21.5	5.1	15.3	5.4
Thelypteris thelypteroides	6.7	2.7	2.4	1.1

[a] Treatment effect significant ($P < 0.10$).

[b] Pool x Treatment effect significant ($P < 0.10$).

[c] Year x Treatment effect significant ($P < 0.10$).

[d] Year x Pool x Treatment effect significant ($P < 0.10$).

Table 3.7. Percent cover of moist soil plants for 2 moist-soil impoundments, Back Bay National Wildlife Refuge, September 1996 and 1997. Data were combined by treatment and year to generate pool means. Complete ANOVA tables for each species are provided in Appendix E.

	Pool A		**Pool C**	
Species	**Mean**	**SE**	**Mean**	**SE**
Bidens cernua[c]	4.8	2.0	2.1	1.0
Cyperus erythrorhizos[c]	2.0	0.7	0.4	0.2
Cyperus esculentus	2.7	1.4	0.5	0.2
Cyperus iria[b,d]	1.1	0.5	0.2	0.1
Dichromena colorata[a]	0.0	0.0	1.9	1.2
Distichlis spicata[a,c]	7.9	2.9	0.0	0.0
Echinchloa crus-galli	1.5	0.6	1.1	0.5
Eleocharis obtusa[c]	19.5	7.2	10.8	3.7
Fimbrystilis annua[c]	3.1	1.1	12.1	5.2
Fuerina squarrosa[a,b,d]	0.4	0.3	2.6	1.0
Juncus canadensis[a]	0.1	0.1	1.1	0.4
Juncus marginatus[a,c,d]	0.0	0.0	0.4	0.1
Juncus megacephalus[a,c]	0.1	0.1	1.7	0.5
Juncus roemerianus	0.5	0.2	1.3	0.7
Leerzia oryzoides[c]	1.6	1.4	2.8	1.5
Miscellaneous species	10.8	2.4	16.4	3.2
Panicum dichotomoflorum[c]	3.9	1.8	1.4	0.5
Panicum virgatum[a,b]	0.6	0.4	3.8	1.5
Phragmites australis	1.7	0.9	4.6	2.1
Pluchea purpurescens[a]	5.5	1.3	0.3	0.1
Polygonum pensylvanicum	1.4	0.9	1.8	1.0
Rhynchospora spp.[d]	0.2	0.1	1.3	0.5
Scirpus americanus[a]	2.3	0.5	10.9	1.8
Scirpus olneyi[a]	1.5	0.8	0.0	0.0
Setaria spp.[c]	0.8	0.4	0.4	0.3
Spartina patens[a,c]	25.2	6.7	11.5	2.3
Thelypteris thelypteroides[a]	0.6	0.5	8.5	2.6

[a] Pool effect significant (P < 0.10).

[b] Pool x Treatment effect significant (P < 0.10).

[c] Pool x Year effect significant (P < 0.10).

[d] Year x Pool x Treatment effect significant (P < 0.10).

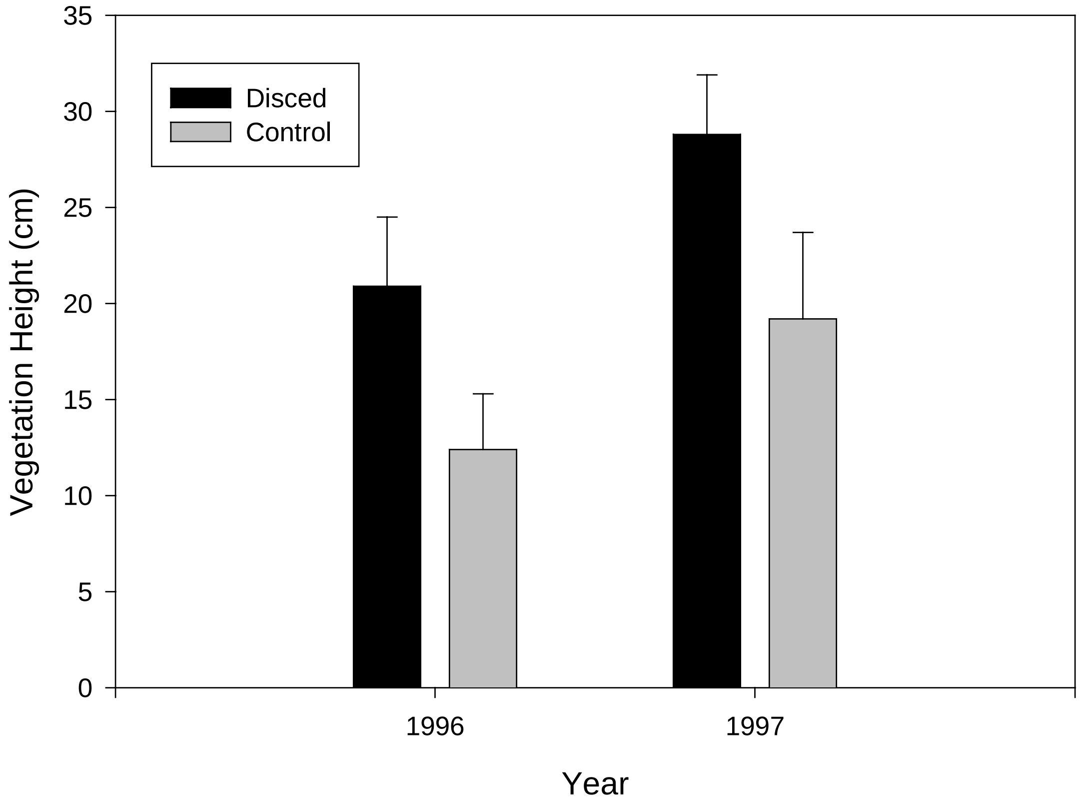

Figure 3.7. Mean (+ SE) moist-soil vegetation height in disced and control plots (*n* = 8 per treatment) at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Table 3.8. Results of the repeated measures mixed model for total moist-soil plant stem density at Back Bay National Wildlife Refuge, 1996-97. Analysis was conducted on log-transformed variables using PROC MIXED (Littell et al. 1996).

Source	***df***	***F***	***P***
Between Plots			
Pool	1,12	0.40	0.541
Treatment	1,12	2.98	0.110
Pool x Treatment	1,12	0.00	0.962
Within Plots			
Year	1,76	29.70	0.0001
Year x Pool	1,76	0.06	0.805
Year x Treatment	1,76	0.03	0.853
Year x Pool x Treatment	1,76	0.35	0.554

Mississippi Alluvial Valley moist-soil impoundments. Total seed production estimates in this study (disced mean = 1052 kg/ha, control mean = 529 kg/ha) were moderately higher than those of Gray (1995) for Mississippi impoundments (range 172 - 612 kg/ha), and an order of magnitude higher than the estimates of Mushet et al. (1992) for California impoundments (range 21 - 38 kg/ha). However, the magnitude of treatment effect observed in this study (2.0x greater seed production in disced areas) was similar to that of Gray (1995) (2.3x greater seed production in disced areas). Similarly, Buckner and Landers (1979) report 2.0 - 3.5x higher seed production by herbaceous plants in a longleaf pine (*Pinus palustris*) forest during the second year after discing.

Reinecke et al. (1989) present assumptions that may be used to estimate duck use-days from field estimates of moist-soil seed production. These assumptions include 1) a uniform metabolizable energy of 2.5 kcal/g for all plant species; 2) an unused fraction of seed production equal to 50 kg/ha; and, 3) an average daily energy expenditure of 292 kcal/day per duck for adult mallards. Using the overall means of seed production from this study, estimated duck use-days per hectare would be 8578 ± 3578 and 4101 ± 1506 for disced and control areas, respectively. Because the relative importance of assumption 2) decreases with increasing seed production, the magnitude of difference in estimated duck use-days (2.1x) is slightly greater than the magnitude of the observed treatment effect (2.0x). A reasonable estimate of true moist-soil habitat (i.e., the substrate is exposed during drawdowns) in the two impoundments is 200 ha. Applying the observed treatment responses uniformly across this area, total estimated duck use-days would be approximately 1.7 million and 0.8 million for disced and control treatments, respectively. Assuming a residence period of 120 days for migrant and wintering birds, disced and control treatments would provide adequate food for about 14,100 and about 6700 birds, respectively. Beyond the assumptions of Reinecke et al. (1989), this exercise assumes 1) no difference in habitat selection for disced or control treatments; 2) equal energetic costs for foraging and thermoregulation between treatments; and, 3) similar levels of seed production response to treatment in unstudied portions of the 2 impoundments. Because these assumptions can not be verified, these estimates should be viewed as indicators of the relative value of the 2 treatments to wintering birds, rather than absolute estimates of potential bird use at the study site. However, it is clear that the magnitude of seed production effect observed is adequate to be considered of biological significance.

Although there was no overall treatment effect on stem density (Fig. 3.3), seed production and stem density were highly correlated among plot-years (Fig. 3.6). The squared correlation coefficient (0.49) between these variables indicates that approximately half of the variation in seed production can be explained simply by variation in the number of seed producing plants per unit area. The remaining variation presumably reflects variation between treatments in seed production per plant (and would also include sampling error). As the method of seed production estimation relied on single specimens of each species within quadrats, variance in seed production within species can not be estimated. The observed correlation pattern suggests that management practices that maximize stem density would maximize seed production. However, extremely high stem density may negatively influence seed production. For example, maximum ear weight of corn (*Zea mays*) occurs at intermediate values of shoot dry weight, but is relatively low in both the upper and lower extremes of shoot dry weight (Raven et al. 1981:581).

Spatial and Temporal Variation

Despite the lack of significant pool effects on total seed production or stem density, 21 of 26 species exhibited variation in percent cover between pools (i.e., significant Pool main effect or interaction with Pool; Table 3.7). Variation between pools in hydrology, salinity, or substrate grain size and organic matter content may have created habitat conditions that favored germination of different species assemblages. Localized variation in seed bank composition also may have contributed to the observed differences among pools. Van der Valk and Davis (1978) observed that only 24% of plant species recruits were common to submerged and exposed marsh substrate, suggesting that hydrology can have a pronounced effect on seed bank recruitment. Plant communities that become established during marsh drawdowns are nonuniform, even in the absence of disturbance (van der Valk and Davis 1978, Galinato and van der Valk 1986). Seed bank composition often does not reflect floristics, particularly in undisturbed sites that are dominated by perennial species that produce few seeds (Leck 1989).

Vegetation height was the only among-species variable that varied among years (Table 3.8). Vegetation height increased from 1996 to 1997 (Fig. 3.7), yet this increase could not be attributed to discing (Treatment x Year interaction $F = 0.47$, $P = 0.504$). Annual plants generally dominate the early stages of marsh succession, with increasing dominance by perennial plants over time (van der Valk 1981). This progression occurs in response to natural hydrological cycles, and has been attributed to variation in seed dormancy among species (van der Valk and Davis 1978). Removal of a late-successional plant community provides habitat conditions under which seed bank annuals may germinate (van der Valk 1981). The observed increases in vegetation height with time are consistent with advancing succession, leading to an increasing prevalence of taller plants.

The timing of stem density responses to discing differed among pools (Year x Treatment x Pool interaction; Table 3.4). Within Pool x Year combinations, discing effects on stem density were only evident in C-Pool, whereas annual variation in stem density within Pool x Treatment combinations was only evident for A-Pool (Fig. 3.5). Variation in stem density response between pools may have resulted from differences in hydrology and substrate composition. The substrate in A-Pool consisted of fine organic matter and sand, whereas C-Pool substrate was primarily coarse sand with sparse organic matter. During drawdowns, C-Pool substrate became exposed prior to A-Pool substrate, and by late summer was completely dry in many locations. Although A-Pool substrate also was eventually exposed during drawdowns, residual moisture content near the surface remained higher. Drawdown timing and reflood depth are important factors in determining plant species composition in subsequent years (Merendino et al. 1990, Merendino and Smith 1991).

Seed production and stem density did not exhibit the same pattern of response to discing. The stem density response showed a temporal pattern consistent with a one-year delay in response to discing. Stem density did not differ between disced and control areas the first year after discing (1996), but was 86% higher in disced areas the second year after discing (1997; Fig. 3.4). However, this pattern was not observed for seed production (i.e., nonsignificant Year x Treatment interaction, Table 3.2). Although discing may initially expose dormant seed, a complete drawdown-reflood cycle may be required to stimulate germination. Alternatively, the plant community in disced areas during the second year may represent a transitional stage between dominance by annuals and perennials. Any perennial plants recruited during the first year after discing would persist to the second year, while recruitment of seed-bank annuals would continue after the second drawdown cycle.

Habitat Structure

Where providing waterfowl nesting cover within impoundments is a management objective, discing may initially compromise the availability of suitable nesting sites, particularly for species that favor dense cover (Kruse and Bowen 1996). Although maintaining dense stands of moist-soil vegetation is not a management objective at Back Bay NWR, such stands may be valuable in more northerly refuges as nesting cover for waterfowl. Increases in stem density in disced areas during the second year of this study suggest that the technique may provide long-term benefits to nesting birds. However, the value of impoundments to nesting birds will be dictated by water level management. Complete dewatering in dense stands of annual vegetation may provide habitat for upland-nesting waterfowl, whereas flooded perennial vegetation (e.g., cattail [*Typha* sp.]) may provide nesting habitat for diving ducks, grebes, and other overwater nesters. The former condition may simultaneously enhance production of seed-bearing plants, whereas the latter is inconsistent with the goal of maximizing seed production (Fredrickson and Taylor 1982). Thus, selection of an appropriate hydrological regime will depend on the relative importance of nesting cover and seed production at a given refuge.

Several studies have documented waterfowl responses to manipulated cover:water ratios in prairie marshes (Kaminski and Prince 1981, Murkin et al. 1982, Solberg and Higgins 1993, Linz et al. 1996, Murkin et al. 1997). Studies on the wintering grounds also have shown disproportionate use of managed vs. unmanaged habitats (Haukos and Smith 1993, Gordon et al. 1998) and increased production of waterfowl food plants in response to manipulation (Harrison and Chabreck 1988, Mushet et al. 1992, Gray 1995, de Szalay and Resh 1997). Although integrated studies that demonstrate direct responses of wintering birds to habitat management are lacking, the value of interspersed open water and cover for wintering birds is recognized

(Hindman and Stotts 1989). In the absence of discing, other factors [e.g., water level manipulation, feral hog (*Sus scrofa*) grubbing, goose grazing] may create openings favored by foraging birds. Further, openings created by discing will be ephemeral in nature, as shown by the marked increase in stem density in disced plots during the second year of this study. The benefit of increased seed production appears to be realized more rapidly and to last through at least two growing seasons after discing, and therefore may be of more substantial benefit to waterfowl than structural habitat changes alone.

Bias and Variance in Seed Production Estimates

Stem density was likely measured with minimal error, whereas there are several sources of measurement error inherent in the methodology for seed production estimation. Nondetection of present plant species and taxonomic inaccuracy are the most likely source of error in stem density measurement. As seed production estimates were based directly on stem density counts, these errors would apply equally to both response variables, and thus can not explain the differences in temporal responses to discing between variables. The regression equations used to predict seed production generally were of high precision ($r^2 > 0.90$). However, the estimation method relied on a single specimen of each species within quadrats, and thus does not account for variation in seed production among plants. Recognizing that seed production within species might vary with treatment, an attempt was made to select a “representative specimen” (Laubhan and Fredrickson 1992) of each species within quadrats. Where seed production among individuals was highly variable, this selection method may nonetheless have introduced researcher bias toward specimens with higher seed production.

Several factors may have introduced bias in estimating bur-marigold seed production. Substantial variation in flowering phenology occurred within and among plants in sampling frames. Seed production was estimated by counting both mature and immature inflorescences, and assuming unit biomass production from measured biomass of mature seed heads ($\bar{x} \pm SE =$ 0.04389 ± 0.00610 g / head, $n = 16$). Although this method assumes no variation in seed production among impoundments or experimental treatments, no such differences were detected among the remaining 29 plant species. Evidence of browsing on bur-marigold plants, presumably by feral horses (*Equus caballus*) or white-tailed deer (*Odocoileus virginianus*), was noted on several occasions. To the extent that browsers favored 1 experimental treatment, herbivory may have biased seed production estimates.

Dabbling ducks generally acquire plant material at or below the water surface, suggesting that their consumption of seeds prior to dehiscence would be minimal. Extensive Canada goose (*Branta canadensis*) grazing on spikerushes (*Eleocharis* spp.) was noted, confounding estimation of seed production for these species. Geese also may have selectively removed newly emerging stems of other species, although other direct evidence of grazing was not observed. The observed activity pattern of resident geese on the refuge suggests that grazing effects would be localized. Given the spatial distribution and number of sampling locations, goose herbivory impacts on the outcome of statistical analyses should be minimal.

Distribution of Plant Species

Many study plots contained salt-tolerant vegetation, suggesting the historical occurrence of tidal inundation. Because the seeds of these species are consumed by relatively few waterfowl species (but see Mendall 1949, Afton et al. 1991), impoundment management is frequently aimed at encouraging production of freshwater plants. In this study, there was little statistical evidence for a negative influence of discing on distribution of salt-tolerant species. *Distichlis spicata* was essentially absent from control areas during both years of the study, although treatment effects on stem density could not be detected due to high variance in disced plots (Table 3.5). *Spartina patens* was twice as abundant in control areas during 1996 and occurred at similar density in disced and control areas during 1997, although the Year x Treatment interaction was nonsignificant (Table 3.5). Seed-bearing stems of *Juncus roemerianus* were rarely encountered during sampling, and no production of viable seed was observed in sampling quadrats. Despite its relative rarity, this species occurred almost exclusively in control plots (Table 3.6). Ocular estimates of plant cover were significantly higher in control areas for *Spartina patens*, but did not differ between disced and control areas for *Distichlis spicata* (Table 3.6). Similarly, there was no demonstrable effect of discing on distribution of invasive species (e.g., *Phragmites australis*, *Pluchea purpurescens*; Table 3.6). De Szalay and Resh (1997) found that *Distichlis spicata* stem density was higher in mowed than in unmowed areas. Gray (1995) suggested that mowing is an appropriate management tool where annual plants dominate due to its effect on stimulating shoot and seed production, whereas discing is more appropriate where reducing abundance of perennial plants is desirable. Discing may not be an appropriate management tool where removal of salt-tolerant and invasive species is desirable, although some such secondary benefits may accrue.

Among the plant species traditionally considered high-quality waterfowl foods (Reid et al. 1989, Reinecke et al. 1989), *Echinochloa crus-galli* and *Panicum dichotomiflorum* had higher seed production and stem density in disced areas (Tables 3.3, 3.5). Higher seed production in disced areas was detected for *Cyperus iria* (Table 3.3), and higher stem density in disced areas was detected for *Cyperus erythrorhizos* (Table 3.5). *Scirpus olneyi* was encountered only in disced areas during 1996, and almost exclusively in control areas during 1997 (Table 3.5). The magnitude of discing effects on *Fimbristylis annua* was greater than any other species (Tables 3.3, 3.5), although use of this species by foraging waterfowl has not been documented in the literature. Reduced abundance in disced areas did not occur for any waterfowl food plants. To the extent that production of the above species is desirable, fall discing appears to be an effective management tool.

Potential Causative Factors

Natural freshwater marshes are dynamic habitats, exhibiting spatial and temporal variation in distribution and abundance of plants. Van der Valk (1981) presented a conceptual model for marsh succession, which stated that floristic changes can result from 1) physical manipulation of vegetation; 2) change in habitat conditions (e.g., water levels); 3) interactions among plants (e.g., competition or allelopathy); or, 4) establishment of new species. Responses among species to the above factors are highly variable, and are primarily a result of life history characteristics (e.g., seed germination, growth rate). Succession and variable life history traits cause increased vigor of some species in response to disturbance, while inhibiting growth of others (van der Valk and Davis 1980). The foregoing analysis assumes that discing is the primary source of the observed differences between disced and control areas. The other factors in van der Valk's (1981) model were either controlled by interspersion of treatments (e.g., water levels) or could not be assessed within the scope of this study (e.g., species interactions).

Among potential causative factors, variation in hydrology is recognized as an important determinant of seed bank recruitment (van der Valk and Davis 1978). There is extensive variation among species in both the influence of inundation on seed viability (Leck 1989) and in the germination response to timing, duration and extent of reflood-drawdown cycles (Merendino et al. 1990, Merendino and Smith 1991). Diversity in life history allows many species to coexist in marsh communities with annual variation in hydrology and disturbance rate (van der Valk and Davis 1980). There was substantial variation in water depth within and between the impoundments in this study. The plots were interspersed along one axis of the depth gradient, and sampling was stratified along the other axis. This feature of the sampling approach should have minimized spurious treatment effects due to hydrological variation.

Depth of seed burial in the substrate affects seed bank recruitment rate, particularly for small-seeded species (Galanato and van der Valk 1986). Consequently, exposure of dormant seed is probably an important function of soil manipulation. The extensive drawdowns required for discing may also enhance oxidation of the deeper soil layers that remain reduced under typical water-level management. Discing reduces soil compaction, likely enhancing germination rate of seed that remains shallowly buried by promoting oxygen uptake (Leck 1989) and further contributing to oxidation of deeper soil layers. Subsurface oxidation favors biogeochemical processes such as nitrogen fixation and sulfide oxidation that enhance nutrient availability to plants (Mitsch and Gosselink 1986). These indirect effects on nutrient cycling may be an important proximate factor in determining growth rate of seed-bank recruits.

Physical manipulation of marsh vegetation may directly affect patterns of nutrient distribution. Emergent plants provide significant storage of nutrients, particularly during the growing season (Mitsch and Gosselink 1986). Discing would be expected to release nutrients held in emergent plants, potentially increasing their availability during the subsequent growing season. Soils with high organic matter content have a greater potential capacity for uptake of released nutrients (Mitsch and Gosselink 1986), suggesting that an interaction between soil composition and nutrient release may be a factor in spatial variability of seed bank recruitment.

MANAGEMENT RECOMMENDATIONS

Discing has been identified as an appropriate method for stimulating growth of annual plants from the seed bank (Reid et al. 1989, Kelley 1990, Gray 1995). Although density and seed production of several annuals increased in response to discing in this study, there was little evidence for reduced production of perennial plants. The coarse-bladed disc used in this study may have been insufficient to deter rhizomatous growth of perennials. Further, litter accumulation can depress recruitment from the seed bank (van der Valk 1986). Mowing generates abundant plant litter but does not expose unvegetated soil, and consequently may have relatively little impact on recruitment of annuals from the seed bank (Gray 1995, de Szalay and Resh 1997). Substantial accumulation of surface litter was noted in areas dominated by *Juncus roemerianus*, and coarse woody debris was abundant in several plots in C-Pool. These observations suggest that methods designed to stimulate seed bank recruitment while minimizing coarse litter accumulation may maximize increases in annual plant production. Multiple passes with a coarse disc (Gray 1995), use of fine-bladed implements, or pre-disc burning (de Szalay and Resh 1997) should be investigated as potentially desirable modifications to single-pass coarse discing.

Despite the known influence of drawdown date and reflood depth on seed bank recruitment (Merendino et al. 1990, Merendino and Smith 1991), control of these factors was beyond the scope of this study. Because complete dewatering of treatment areas is required to support heavy machinery, discing may require a compromise between desired water-level management and the anticipated resource benefits from discing. The drawdown period for Atlantic Coastal impoundments generally includes late summer and early fall, although a more extensive drawdown is generally required to facilitate discing (J. Gallegos, Back Bay NWR, personal communication). Where availability of water for post-discing flooding is questionable, such drawdowns may inhibit the ability to provide appropriate water depths for fall migrant waterfowl. An approach to discing that is analogous to rotational grazing systems might therefore be considered, assuming that water-level control among impoundments is independent. Several impoundments could be selected for rotational discing, with one completely dewatered and disced each year. This approach would allow less extensive drawdowns in impoundments being “rested”, affording some assurance that shallowly flooded habitat will be available for waterfowl even under limited water availability.

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