WETLANDS, Vol. 27, No. 3, September 2007, pp. 739–748

USE OF HERBICIDES TO CONTROL ALLIGATORWEED AND RESTORE NATIVE PLANTS IN MANAGED MARSHES

Shannon L. Allen[1], Gary R. Hepp[1], and James H. Miller[2]
[1]*School of Forestry and Wildlife Sciences*
Auburn University
Auburn, Alabama, USA 36849
E-mail: smith68@auburn.edu

[2]*USDA Forest Service*
Southern Research Station
Auburn, Alabama, USA 36849

Abstract: Marsh management is used to improve the quality of wetland habitats for a variety of waterfowl and other waterbirds. However, alien plants, such as alligatorweed (*Alternanthera philoxeroides* (Mart.) Griseb.), may impact success of marsh management by competing with and displacing important native plants. In managed marshes, we tested effects of application rate (high, medium, and low) and timing (April and July) of two herbicides (triclopyr amine and imazapyr) on controlling alligatorweed and restoring native plants. In the year of treatment, imazapyr controlled alligatorweed better than triclopyr amine when applied in April, but the herbicides were equally effective when applied in July. High application rate of herbicides in April controlled alligatorweed better than the low application rate, but application rates of herbicides in July did not influence control. In the year of treatment, application of triclopyr amine resulted in greater native plant biomass than imazapyr. High application rate of herbicides in April resulted in greater native plant biomass in the year of treatment than low application rate, but native plant biomass did not differ among rates of herbicides applied in July. One year after treatment, the high application rate of herbicides resulted in less alligatorweed than the low application rate, and July applications of either herbicide generally controlled alligatorweed better than April applications. Application of imazapyr in July resulted in greater biomass of native plants one year after treatment than either imazapyr or triclopyr amine applied in April. This study demonstrates that single herbicide applications can be effective at controlling alligatorweed, and that these applications can have immediate and longer-term benefits for restoring native plants to managed marshes.

Key Words: alien plant species, *Alternanthera philoxeroides*, imazapyr, marsh management, restoration, triclopyr amine

INTRODUCTION

Alien plants are an increasing problem in wetland habitats because they can displace native plants directly by competition (Madsen et al. 1991, Barrat-Segretain 2005, Thomson 2005) and indirectly by altering light levels and water quality (Blindlow 1992, D'Antonio and Vitousek 1992, Barrat-Segretain and Elger 2004). Establishment of alien plants decreases habitat quality for waterfowl, waterbirds, and other organisms (Keast 1984, Madsen 1997, Benedict and Hepp 2000). For example, mono-specific stands of alien plants can negatively affect invertebrate communities by reducing vegetation complexity and oxygen levels (Cheruvelil et al. 2002, Douglas and O'Connor 2003, Strayer et al. 2003).

Marsh management, which has been used to enhance waterfowl habitat since the 1940s (Nyman et al. 1990), is currently used extensively to improve wetland quality for a variety of waterbirds (Rundle and Fredrickson 1981, Laubhan and Fredrickson 1993, Reid 1993, Parsons 2002). Managed marshes are drained in spring or early summer to develop moist-soil conditions to promote establishment of desirable plant species and increase diversity and density of invertebrates that are an important dietary protein source (Haukos and Smith 1993, Ellison and Bedford 1995, Anderson and Smith 2000, Bowyer et al. 2005). Marshes are flooded again in autumn to provide habitat for migrating and wintering waterfowl, and for waterbirds that forage for seeds and invertebrates (Fredrickson and Taylor 1982, Taft et al. 2002). Invasion of alien plants may hinder the success of marsh management. Therefore, control of alien plants and re-establishment of native vegetation often are necessary management goals, and herbicides can be used by marsh managers to achieve these objectives (Netherland and Getsinger 1992, Getsinger et al. 1997).

Alligatorweed (*Alternanthera philoxeroides*) is an alien plant that has invaded many marshes in the southern United States. It is an evergreen, perennial herb native to South America that grows in a variety of conditions (Eggler 1953, Zhang et al. 1993, Julien et al. 1995). Alligatorweed forms dense mats on moist-soil and over open water. It reproduces asexually in the United States, with new plants developing from any piece of root fragment or stem that contains a node (Spencer and Coulson 1976). Alligatorweed alters marsh plant communities by reducing light penetration, lowering oxygen levels in water, and competing with native plants (Quimby and Kay 1977, Vogt et al. 1992, Buckingham 1996, Holm et al. 1997). Unlike many native marsh plants, alligatorweed is not a valuable waterfowl food because it usually does not produce seeds (Holm et al. 1997).

Control of alligatorweed has proven to be difficult because physical control methods such as mowing and disking only redistribute and possibly spread the plant (Holm et al. 1997). Alligatorweed flea beetles (*Agasicles hygrophila*) have been used successfully to control alligatorweed where mean winter temperatures are >11.1°C, but additional control measures are needed in more northerly areas (Coulson 1977, Vogt et al. 1992). Herbicides may be useful for controlling alligatorweed and restoring marsh plant communities, but extensive testing in managed marshes has not been completed (Bowmer et al. 1989, Bowmer et al. 1993, Tucker 1994, Kay 1999). In particular, herbicides recently licensed for use in wetlands have not been evaluated.

The objectives of this study were to 1) evaluate responses of alligatorweed and native plants to variations in timing and rate of application of triclopyr amine and imazapyr herbicides during the year of application and to 2) determine if responses persisted into the year after treatment. Timing of herbicide application is important because it can affect degree of control of alien species and damage to associated native species, and thus impact the suitability of habitat for wintering waterfowl (Harrington and Miller 2005, Judge et al. 2005). For example, we predicted that early season use of herbicides would result in greater biomass and seed production of native plants than late season herbicide use, at least in the year of application.

STUDY AREA

The study was conducted in the Kennedy (182 ha) and Bradley (305 ha) units of Eufaula National Wildlife Refuge (ENWR; 32° N, 85° W) in southeastern Alabama (Barbour and Russell counties) and southwestern Georgia (Stewart and Quitman counties). Eufaula National Wildlife Refuge (4,452 ha) is located on the northern portion of the Walter F. George Reservoir, an impoundment of the Chattahoochee River (Figure 1).

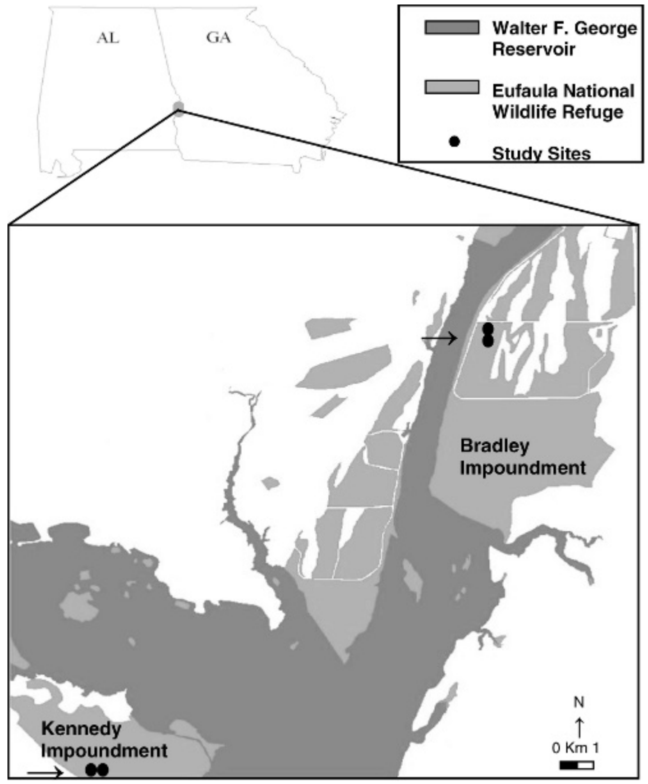

Figure 1. Location of study sites within Eufaula National Wildlife Refuge, Alabama and Georgia.

Marsh management is used at ENWR and drawdown of marshes begins in mid-March to encourage growth of desirable plant species. Reflooding of managed marshes begins in late October. Alligatorweed dominates many of the managed marshes at ENWR, and numerous control methods have been attempted including mowing, disking, burning, herbicide application, and release of alligatorweed flea beetles, with limited success.

METHODS

Experimental Design

We tested the herbicides triclopyr amine (Renovate, SePRO, Carmel, IN 46032) and imazapyr (Habitat, BASF, Florham Park, NJ 07932) in this study because of their recent approval by the Environmental Protection Agency for use in wetlands. Each herbicide was mixed with a nonionic surfactant (Top Surf, Agriliance, LLC, St. Paul, MN 55164). Herbicides were applied with a 2 L CO_2-pressurized backpack spray unit with a five-nozzle boom (2.5 m width). Application rates for triclopyr included: low (4.8 L ha^{-1}), medium (9.6 L ha^{-1}), and high (14.4 L ha^{-1}). These rates were applied using 935 L ha^{-1} of water and 0.25% nonionic surfactant. Application rates for imazapyr included low (1.2 L ha^{-1}), medium (2.4 L ha^{-1}), and high (3.6 L ha^{-1}). These rates were applied using 467 L ha^{-1} of water and 0.25% nonionic surfactant. Application rates were within the range of rates recommended by manufacturers. Non-treated control plots received no herbicide, surfactant, or water.

Herbicide efficacy was assessed in 64 experimental plots arranged in a randomized block design. Four experimental blocks were established in April 2004 within managed marshes of the Kennedy (n = 2) and Bradley (n = 2) units of ENWR (Figure 1). Treatments consisted of herbicide type (triclopyr or imazapyr), application rate (low, medium, high), and application date (28 April or 13 July, 2004). Treatment combinations were randomly assigned the 5 m $\times$ 5 m plots within each block. Four control plots were included in each block.

Alligatorweed Percent Cover, Stem Density, and Height

Percent cover, stem density, and height of alligatorweed for treatment and control plots were estimated one week prior to herbicide application, weekly for one month following treatment, and then monthly in 2004. We randomly placed two subplots (1 m $\times$ 1 m) in each experimental plot and estimated percent cover of all plant species. Height of alligatorweed was measured at the corners of each subplot (n = 4), and stem density was measured by counting individual alligatorweed stems in two 0.25 m $\times$ 0.25 m quadrats within each subplot.

Plant Biomass

In October 2004 and 2005, we estimated plant biomass and species composition in treatment and control plots by clipping all aboveground plant parts in randomly placed quadrats (0.25 m $\times$ 0.25 m; n = 2). Clipped plants were placed into plastic bags, transported to Auburn University where plants were separated and identified to species (Godfrey and Wooten 1978, 1981), and then oven dried (60°C) to constant mass. Alligatorweed and native plants and their seeds were weighed to the nearest 0.01 g. Seed heads and seeds were then separated from native plants and weighed alone to the nearest 0.01 g.

Statistical Analysis

Each year, a four-way analysis of variance (ANOVA)(PROC MIXED; SAS Institute 2003) was used to test effects of block (n = 4), herbicide (n = 2), application rate (n = 3), application timing (n = 2), and all interactions on biomasses of alligatorweed, native plants, and native plant seed. Block was specified as the random variable, while herbicide, application date, and application timing were fixed variables. Biomass of native plants used in the ANOVA included vegetative parts and seeds of native plants. Nonsignificant interactions ($P > 0.10$) were excluded from final models. We tried using pretreatment values of percent cover, stem density, or height of alligatorweed as covariates, but they were not significant ($P > 0.10$) and were not used in the analysis. Tukey-Kramer tests were used to conduct pair-wise comparisons of least squares means to separate significant main effects and interaction effects. Four control plots were included in each block, thus controls were not replicated across all treatments. Therefore, Dunnett's test was used to test for differences in alligatorweed biomass, native plant biomass, and native seed biomass between controls and treatments. Linear regression (PROC REG; SAS Institute 2003) was used to test effects of alligatorweed biomass on native plant biomass and the effect of native plant biomass on native seed biomass. We used $P \leq 0.10$ rather than $P \leq 0.05$ to determine test significance to reduce type II error due to small sample size.

RESULTS

Year of Treatment

Alligatorweed. Alligatorweed biomass was influenced by the interaction of herbicide type and application date ($F_{1,37} = 4.67$, $P = 0.04$). Biomass of alligatorweed was lower ($P = 0.02$) with imazapyr (34.97 $\pm$ 7.85 g/0.25 m^2) than with triclopyr amine (68.79 $\pm$ 7.85 g/0.25 m^2) when applied in April, but alligatorweed biomass did not differ ($P = 1.0$) between herbicides when they were applied in July (imazapyr: 8.69 $\pm$ 7.85 g/0.25 m^2 and triclopyr amine: 8.61 $\pm$ 7.85 g/0.25 m^2).

Biomass of alligatorweed also was affected by the interaction of rate and date of application ($F_{2,37} = 2.72$, $P = 0.08$). In April, the high application rate of herbicides resulted in less ($P = 0.007$) alligatorweed biomass than the low application rate; however, all application rates in July were equally ($P \geq 0.9$) effective at reducing alligatorweed biomass (Figure 2A). Low and high application rates in July provided greater ($P = \leq 0.04$) control of alligator-

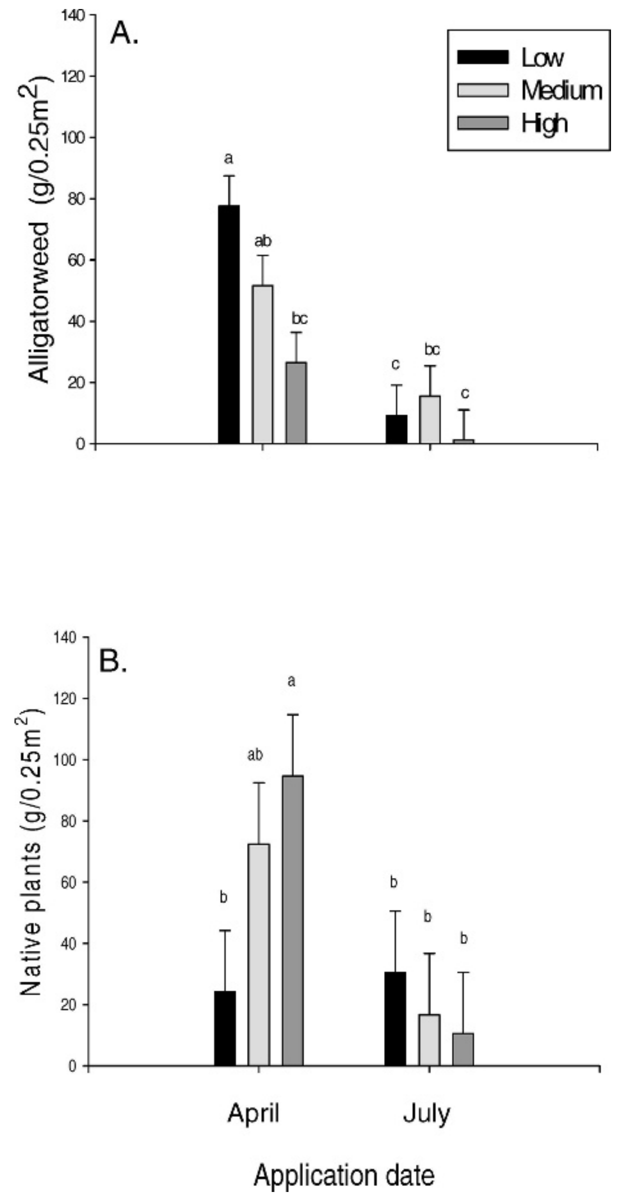

Figure 2. Comparisons of least squares means (±SE) of alligatorweed dry mass (A) and native plant dry mass (B) collected in October 2004 after applying either triclopyr amine or imazapyr at low, medium, and high rates in April and July 2004. Bars with different letters within plant types indicate significance at P ≤ 0.10 level.

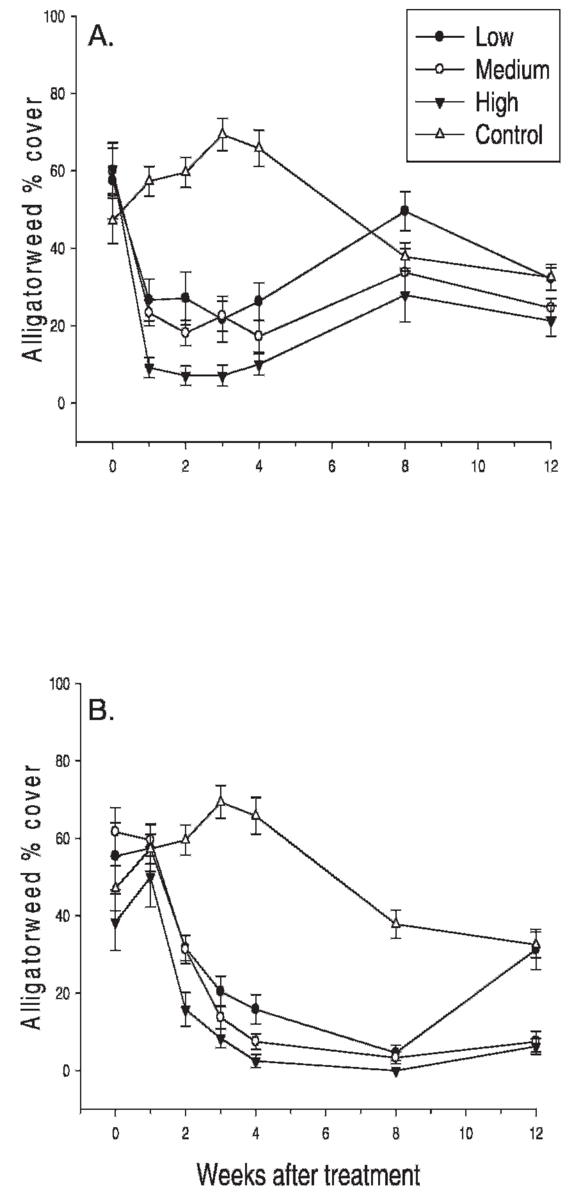

Figure 3. Percent cover ($\bar{x}$ ± SE) of alligatorweed in experimental and control plots following application of triclopyr (A) or imazapyr (B) at low, medium, and high rates in April 2004.

weed than low and medium rates in April, and the medium application rate in July controlled alligatorweed more than ($P = 0.007$) the low rate in April (Figure 2A).

Percent cover of alligatorweed was reduced immediately after applying triclopyr amine at all application rates in April, but cover began increasing three to four weeks later (Figure 3A). Percent cover of alligatorweed actually increased immediately following application of imazapyr in April, but began decreasing about two weeks after application. Percent cover of alligatorweed remained low for medium and high rates of imazapyr, but increased at week 8 for the low application rate (Figure 3B). In July, percent cover of alligatorweed declined immediately after applying either triclopyr amine (Figure 4A) or imazapyr (Figure 4B) and remained below control levels until October.

In April, only imazapyr applied at the high rate reduced ($P = 0.009$) alligatorweed biomass to below that of the control (Table 1). All treatments applied in July reduced ($P \leq 0.04$) biomass of alligatorweed to below that of the control (Table 1).

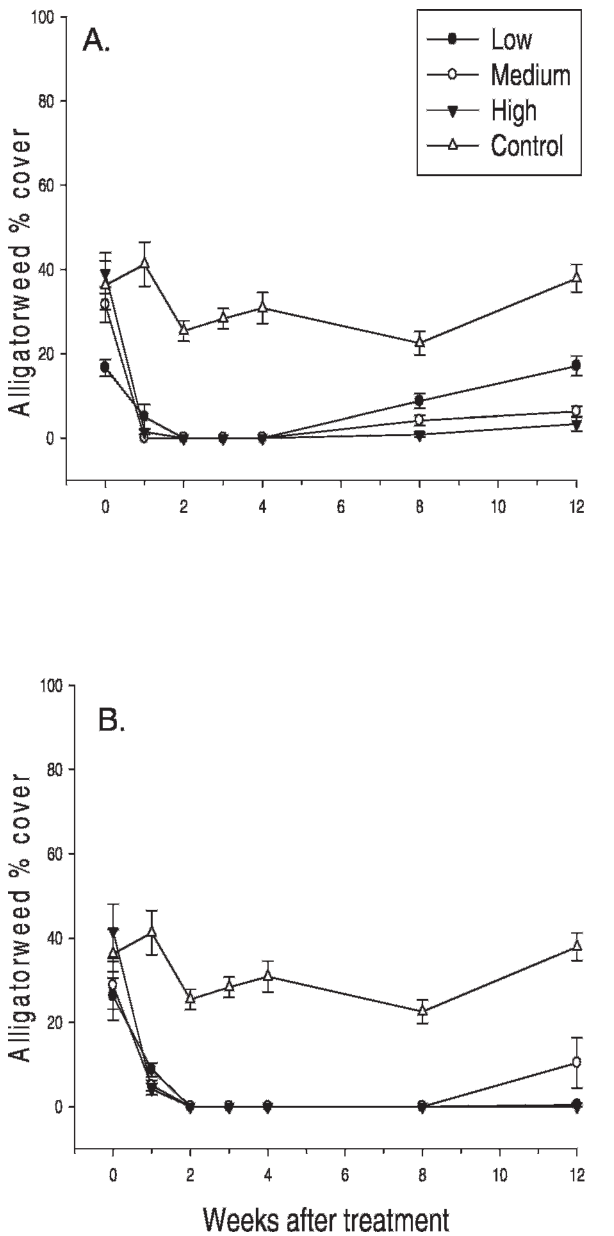

Figure 4. Percent cover ($\bar{x} \pm$ SE) of alligatorweed in experimental and control plots following application of triclopyr (A) or imazapyr (B) at low, medium, and high rates in July 2004.

Native Plants. We collected 13 species of native plants (no alien plants other than alligatorweed were present) in October 2004 (Allen 2006). Biomass of native plants was affected by herbicide type ($F_{1,38}$ = 3.86, P = 0.06). Application with triclopyr amine (55.40 ± 14.14 g/0.25 m^2) resulted in greater (P = 0.06) native plant biomass than application with imazapyr (27.58 ± 14.14 g/0.25 m^2). Biomass of native plants also was affected by the interaction of rate and date of application ($F_{2,38}$ = 3.55, P = 0.04). High application rate of herbicides in April resulted in greater (P ≤ 0.1) biomass of native plants than did low application rate in April and low, medium and high rates in July (Figure 2B). Different application rates in July did not affect (P = 1.0) native plant biomass (Figure 2B). Native plant biomass was highly variable, and treatments applied in either April or July did not increase (P ≥ 0.3) biomass of plants over that of controls (Table 1).

Biomass of native seeds was affected by the interaction of rate and date of application ($F_{2,38}$ = 3.11, P = 0.06). Application of medium rate of herbicides in April (16.99 ± 3.77 g/0.25 m^2) resulted in greater (P ≤ 0.08) biomass of native plant seed than application of low rate in April (2.63 ± 3.77 g/ 0.25 m^2), medium (2.80 ± 3.77 g/0.25 m^2) or high rate (2.81 ± 3.77 g/0.25 m^2) in July. Native seed biomass was highly variable and treatments applied in either April or July did not increase (P ≥ 0.2) biomass of plants over that of controls (Table 1).

There was a slight increase in biomass of native plants as alligatorweed biomass decreased after applying herbicides in April (y = 96.02 − 0.62×; adj r^2 = 0.1, P = 0.07), but there was no relationship (P > 0.1) following the July application. There was a positive relationship between biomasses of native plants and their seeds that did not differ between April (b = 0.16 ± 0.04) and July (b = 0.15 ± 0.03) application of herbicides, so data were combined (y = 1.85 ± 0.17×; adj r^2 = 0.52, P < 0.001).

Year After Treatment

Alligatorweed. We also evaluated effects of treatments applied in 2004 on biomass of alligatorweed in October 2005. Biomass of alligatorweed was affected by application rate ($F_{2,39}$ = 3.54, P = 0.04). High application rate (20.72 ± 9.89 g/0.25 m^2) resulted in less (P = 0.03) alligatorweed than low application rate (40.70 ± 9.89 g/0.25 m^2), but alligatorweed biomass at the medium application rate (31.78 ± 9.89 g/0.25 m^2) did not differ (P ≥ 0.3) from either low or high rates. Biomass of alligatorweed also was affected by the interaction of herbicide and application date ($F_{1,39}$ = 6.37, P = 0.02). Alligatorweed biomass did not differ (P = 0.4) between herbicides after April application, but July application of imazapyr resulted in less (P ≤ 0.007) alligatorweed than either herbicide applied in April (Figure 5A). Further, July application of triclopyr amine resulted in less (P < 0.01) alligatorweed than April application of imazapyr (Figure 5A).

Treatments applied in April 2004 did not reduce (P ≥ 0.7) alligatorweed biomass to below that of the control when compared in October 2005 (Table 1). Only triclopyr amine applied at the high rate and imazapyr applied at medium and high rates in July 2004 reduced ($P \leq 0.01$) alligatorweed biomass to below that of the control in October 2005 (Table 1).

Native Plants. We collected 15 species of native plants (no alien plants other than alligatorweed were present) in October 2005 (Allen 2006). Biomass of native plants was affected by the interaction of herbicide and application date ($F_{1,39} = 7.88$, $P = 0.008$). Within application dates (April or July 2004), native plant biomass measured in 2005 did not differ ($P \geq 0.2$) between herbicides, but application of imazapyr in July resulted in greater ($P \leq 0.1$) native plant biomass than April application of either herbicide (Figure 5B).

Biomass of native plant seed was affected by the interaction of herbicide and application date ($F_{1,39} = 3.53$, $P = 0.07$). Application of imazapyr in April (13.33 ± 5.95 g/0.25 m^2) resulted in less ($P = 0.03$) native plant seed than did application in July (26.27 ± 5.95 g/0.25 m^2). Seed production did not differ ($P = 1.0$) between application dates in plots treated with triclopyr amine. Treatments applied in either April or July did not increase ($P \geq 0.12$) seed biomass of native plants over that of controls (Table 1).

The inverse relationship between biomasses of native plants and alligatorweed did not differ between April ($b = -1.37 \pm 0.27$) and July ($b = -2.09 \pm 0.84$) herbicide applications, so data were combined (Figure 6). There was a positive relationship between biomasses of native plants and native seeds that did not differ between April ($b = 0.16 \pm 0.04$) and July ($b = 0.15 \pm 0.02$) so these data also were combined ($y = 2.42 + 0.14\times$, adj $r^2 = 0.58$, $P < 0.001$). Neither treatments applied in April nor July increased ($P \geq 0.4$) native plant biomass to greater than that of the control plot (Table 1).

DISCUSSION

Three factors may have contributed to the greater biomass of native plants following application of triclopyr amine compared to imazapyr. First, fewer native plant species, especially monocots, may have been killed by triclopyr amine because it is a synthetic auxin selective for broad leaf plants, whereas imazapyr is a broad-spectrum herbicide (Tu et al. 2001). Second, imazapyr is moderately mobile and more persistent in the soil than triclopyr, so plants germinating after imazapyr application may have been affected by residual herbicide activity in the soil (Coffman et al. 1993, Cox 2000). Third, percent cover of alligatorweed was reduced much more quickly in April with triclopyr amine than with imazapyr (Figure 3). Imazapyr inhibits production

Table 1. Comparisons between treatments and control values (least-squares means ±SE) of alligatorweed (Aw), native plant, and native plant seed dry mass (g/ 0.25 m^2). Dry masses of treatments and control were measured in October 2004 and 2005 and treatments were applied in April and July 2004.

		Application date												
		April						July						
		Triclopyr			Imazapyr			Triclopyr			Imazapyr			
		Low	Med	High	Low	Med	High	Low	Med	High	Low	Med	High	Control
2004	Aw	92.45	73.50	40.41	62.74	29.72	12.46***	14.25**	9.22***	2.35***	4.21***	21.86**	$1.3e^{-13}$****	78.11
	SE	16.39	16.39	16.39	16.39	16.39	16.39	16.39	16.39	16.39	16.39	16.39	16.39	8.20
	Native	33.24	88.36	97.59	15.08	56.44	91.67	60.39	31.74	21.09	0.65	1.60	0.04	75.38
	SE	30.96	30.96	30.96	30.96	30.96	30.96	30.96	30.96	30.96	30.96	30.96	30.96	16.03
	Seed	3.10	16.40	16.77	2.17	17.59	13.40	9.83	5.50	5.61	0.0075	0.10	$7.63e^{-20}$	2.89
	SE	5.03	5.03	5.03	5.03	5.03	5.03	5.03	5.03	5.03	5.03	5.03	5.03	3.61
2005	Aw	34.77	42.45	37.99	75.45	50.44	32.95	34.1	28.19	11.78**	18.49	6.03**	0.18***	53.99
	SE	16.77	16.77	16.77	16.77	16.77	16.77	16.77	16.77	16.77	16.77	16.77	16.77	12.96
	Native	135.44	97.04	138.80	31.58	86.89	90.97	114.68	106.32	170.20	160.18	207.78	209.54	128.86
	SE	46.55	46.55	46.55	46.55	46.55	46.55	46.55	46.55	46.55	46.55	46.55	46.55	30.90
	Seed	19.82	14.19	15.75	3.19	21.17	15.63	17.92	17.17	17.73	21.49	24.51	32.81	16.79
	SE	7.39	7.39	7.39	7.39	7.39	7.39	7.39	7.39	7.39	7.39	7.39	7.39	6.46

* $P \leq 0.10$, ** $P \leq 0.05$, *** $P \leq 0.01$, **** $P \leq 0.001$.

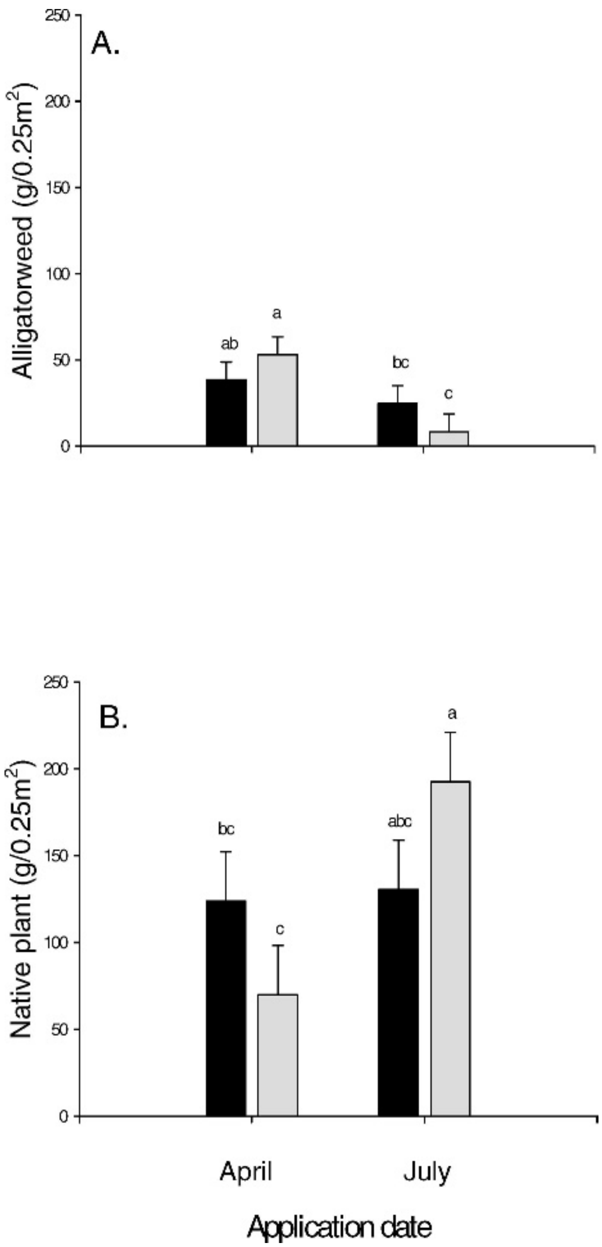

Figure 5. Comparisons of least squares means (±SE) of alligatorweed dry mass (A) and native plant dry mass (B) collected in October 2005 after applying either triclopyr amine (■) or imazapyr (■) in April and July 2004. Bars with different letters within plant types indicate significance at P ≤ 0.10 level.

of amino acids that are stored by plants, so mortality does not occur until those resources diminish (Tu et al. 2001). This difference in timing of herbicide effectiveness in spring could have provided a critical window of opportunity for native plants to become established (Harper 1977). High plant biomass has been shown to negatively affect seedling establishment (Gaudet and Keddy 1988, Weigelt et al. 2002), so decreasing alligatorweed

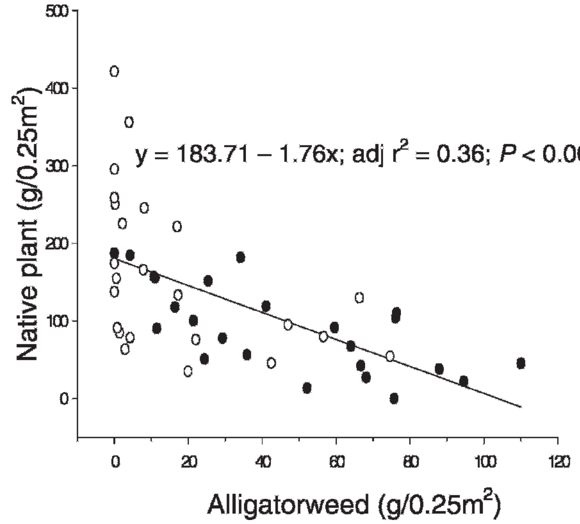

Figure 6. Relationship between dry mass of alligatorweed and native plants in October 2005 following herbicide application in April (solid circle) and July (open circle) 2004.

biomass in the spring, even just for a short time, may have provided suitable growing conditions for native plants. Alligatorweed became re-established from underground nodes following April application of triclopyr amine, but the delay apparently allowed sufficient time for native plants to become established, resulting in increased native plant biomass in October prior to flooding.

Alligatorweed exhibits several traits that may give it a competitive advantage over other plant species. It is evergreen, grows quickly, produces high biomass, and forms dense canopies (Gaudet and Keddy 1988, Tilman 1988, Wisheu and Keddy 1992, Greulich and Bornette 2003) in early spring that effectively block light and space needed by native plants to germinate and grow (Durden et al. 1975, Liu et al. 2004). Other studies have shown increased recruitment and growth of native plant seedlings when more space and light are made available after alien plants are controlled (Walker and Vitousek 1991, Barrat-Segretain 1996, Barrat-Segretain and Elger 2004). Control of Eurasian watermilfoil (*Myriophyllum spicatum* L.) with triclopyr, for example, resulted in increases in native plants that remained dominant for two years after treatment (Getsinger et al. 1997). Similarly, removal of the alien ripgut brome (*Bromus diandrus* (Roth.)) increased seedling recruitment of the endangered dune evening primrose (*Oenothera deltoides* (Torr. and Fremont)) (Thomson 2005). Early alligatorweed control may allow re-established native plants to compete with alligatorweed.

We found that both herbicides applied at any rate in July were effective at reducing alligatorweed

Table 2. Dominant[a] native plant species collected in October 2004 and 2005 after applying either triclopyr amine or imazapyr at low, medium, or high rates in April or July 2004.

Application Date	Herbicide	Rate	Dominant Species 2004	Dominant Species 2005
April	Triclopyr	Low	*Polygonum densiflorum* *Leptochloa panacea*	*Polygonum densiflorum*
		Medium	*Echinochloa crus-galli* *Polygonum densiflorum*	*Polygonum densiflorum* *Polygonum punctatum*
		High	*Echinochloa crus-galli* *Leersia oryzoides*	*Polygonum densiflorum* *Polygonum hydropiperoides*
	Imazapyr	Low	*Echinochloa crus-galli*	*Polygonum hydropiperoides*
		Medium	*Echinochloa crus-galli*	*Polygonum densiflorum*
		High	*Echinochloa crus-galli*	*Echinochloa crus-galli*
July	Triclopyr	Low	*Polygonum punctatum*	*Polygonum hydropiperoides* *Leptochloa panicea*
		Medium	*Polygonum densiflorum*	*Polygonum densiflorum*
		High	*Polygonum densiflorum*	*Polygonum densiflorum* *Leptochloa panicea*
	Imazapyr	Low	*Panicum* sp. *Diodia virginiana*	*Echinochloa crus-galli*
		Medium	*Polygonum densiflorum* *Panicum* sp.	*Echinochloa crus-galli*
		High	*Panicum* sp.	*Echinochloa crus-galli* *Sesbania herbacea*

[a] Plant species that singly or combined comprised ≥50% of total native dry mass (g/0.25 m^2).

biomass. Plants, especially perennials, accumulate carbohydrates and other nutrients in roots and other storage structures in autumn (Chapin III et al. 1990, Wyka 1999); therefore, herbicides are more likely to be transported with them into the roots, resulting in death of the plant. This explains why low application rates of herbicides late in the season worked well to control alligatorweed; however, later use of herbicides did not allow high production of native plants in the year of treatment.

Many of the dominant native plant species (e.g. *Polygonum* sp., *Echinochloa crus-galli*, etc.) in our study are valuable waterfowl foods (Low and Bellrose 1944, Haukos and Smith 1993, Cronk and Fennessy 2001). Species richness of the dominant native plants was greater for plots treated with triclopyr amine in April and imazapyr in July (Table 2). Plots treated with imazapyr in April and triclopyr amine in July were more likely to contain a singe dominant species (Table 2). Additionally, native monocots and annual plants that are the target species of many marsh managers were more common after April application than after July application (Low and Bellrose 1944, Fredrickson and Taylor 1982, Allen 2006). The value of these plants lies in their great production of seeds consumed by waterfowl.

Biomass of native seeds was related positively to native plant biomass, and was affected by interactions both years (rate and date of application in 2004, and herbicide and date of application in 2005). Plots treated with high herbicide rates in April tended to have greater native seed production than plots treated with low rates. For example, plots treated with low rate contained from 87–124 kg/ha of native seeds, while plots treated with high rate contained 536–672 kg/ha. Seed production in plots treated with medium and high rates of herbicide were within the range found in managed marshes elsewhere (Bowyer et al. 2005, Reinecke and Hartke 2005). Plots treated in July had lower seed production (0–393 kg/ha) than plots treated in April because there was less native plant biomass and because plants had less time to produce seed after herbicide application.

Better control of alligatorweed in the initial treatment year resulted in less alligatorweed biomass and greater native plant biomass the year after treatment. We collected 15 species of native plants in the year following treatment (Allen 2006). Plots treated with a high herbicide rate contained less alligatorweed biomass and more native plant biomass than plots treated with a low herbicide rate one year later. These same plots, especially following July application of imazapyr, resulted in the greatest native seed biomass (716–1312 kg/ha). Plots treated with triclopyr amine or imazapyr did not differ in alligatorweed biomass or native plant biomass at April or July application. However, diversity of dominant native plants was greater for plots treated with triclopyr amine than imazapyr at April and July applications. Results indicate that control of alligatorweed in one year allows native plant species to reestablish the next year, probably because of decreased competition with alligatorweed.

MANAGEMENT IMPLICATIONS

One of the primary objectives of marsh management is to improve the quality of wetland habitats for migrating and wintering waterfowl (Reinecke et al. 1989, Kaminski et al. 2003). However, in many cases, alien plant species, such as alligatorweed, can decrease native plant biomass and seed production. Our results suggest that using the herbicides triclopyr amine or imazapyr to control alligatorweed and re-establish native vegetation is a realistic tool for improving managed marshes degraded by alligatorweed. Two potential management strategies were revealed. Marsh managers who want to control alligatorweed and have the greatest improvement in habitat quality in the treatment year should apply triclopyr amine at a high rate in April. Marsh managers who can wait one year after treatment to improve habitat quality should apply a high rate of either herbicide in July. Both methods could be used simultaneously in different areas to improve habitat quality each year. Marsh managers often vary habitat management to enhance diversity of habitats available at any given time for waterfowl and other waterbirds (Laubhan and Fredrickson 1993, Parsons 2002, Taft et al. 2002). Control of alligatorweed and improved quality of managed wetlands over longer terms needs further investigation.

ACKNOWLEDGMENTS

The authors would like to thank Eufaula National Wildlife Refuge staff Frank Dukes and Milton Hubbard for their cooperation and field technicians Erwin Chambliss, Frank Allen, and Frank and Betty Tee Smith for their invaluable help. This project was supported by USFWS, SePro, and BASF.

LITERATURE CITED

Allen, S. L. 2006. Restoration of native plants through chemical control of alligatorweed (*Alternanthera philoxeroides*) at Eufaula National Wildlife Refuge. M.S. Thesis. Auburn University, Auburn, AL, USA.

Anderson, J. T. and L. M. Smith. 2000. Invertebrate response to marsh management of playa wetlands. Ecological Applications 10:550–58.

Barrat-Segretain, M. H. 1996. Strategies of reproduction, dispersion and competition in river plants: a review. Vegetatio 123:13–37.

Barrat-Segretain, M. H. 2005. Competition between invasive and indigenous species: impact of spatial pattern and developmental stage. Plant Ecology 180:153–60.

Barrat-Segretain, M. H. and A. Elger. 2004. Experiments on growth interactions between two invasive macrophyte species. Journal of Vegetation Science 15:109–14.

Benedict, R. J., Jr. and G. R. Hepp. 2000. Wintering waterbird use of two aquatic plant habitats in a southern reservoir. Journal of Wildlife Management 64:269–78.

Blindlow, I. 1992. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshwater Biology 28:15–27.

Bowmer, K. B., P. Eberbach, and G. McCorkelle. 1993. Uptake and translocation of 14 C glyphosate in *Alternanthera philoxeroides* (Mart.) Griseb. (alligator weed) I. Rhizome concentrations required for inhibition. Weed Research 33:53–57.

Bowmer, K. B., G. McCorkelle, P. M. Sale, and P. Eberbach. 1989. Progress in the chemical control of alligatorweed. p. 54–61. *In* R. Dyason and P. Dorham (eds.), 5th Biennial Noxious Plants Conference, Lismore. Australia.

Bowyer, M. W., J. D. Stafford, A. P. Yetter, C. S. Hine, M. H. Horath, and S. P. Havera. 2005. Marsh plant seed production for waterfowl at Chautauqua National Wildlife Refuge, Illinois. American Midland Naturalist 154:331–41.

Buckingham, G. R. 1996. Biological control of alligator weed, *Alternanthera philoxeroides*, the world's first aquatic weed success story. Castanea 61:232–43.

Chapin, S. III, E. Schulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. Annual Review of Ecological Systems 21:423–47.

Cheruvelil, K. S., P. A. Soranno, J. D. Madsen, and M. J. Robertson. 2002. Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte. Journal of the North American Benthological Society 21:261–77.

Coffman, C. B., J. R. Frank, and W. E. Potts. 1993. Crop responses to hexazinone, imazapyr, tebuthiuron, and triclopyr. Weed Technology 7:140–45.

Coulson, J. R. 1977. Biological control of alligator weed, 1959–1972. A review and evaluation. U.S. Department of Agriculture, Agriculture Research Service.

Cox, C. 2000. Herbicide factsheet: triclopyr. Journal of Herbicide Reform 20:12–19.

Cronk, J. K. and M. S. Fennessy. 2001. Wetland Plants: Biology and Ecology. Lewis Publishing, Boca Raton, FL, USA.

D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecological Systems 23:63–87.

Douglas, M. M. and R. A. O'Connor. 2003. Effects of the exotic macrophyte, para grass (*Urochloa mutica*), on benthic and epiphytic macroinvertebrates of a tropical floodplain. Freshwater Biology 48:962–71.

Durden, W. C., R. D. Blackburn, and E. O. Gangstad. 1975. Control program for alligatorweed in the Southeastern states. Hyacinth Control Journal 13:27–30.

Eggler, W. A. 1953. The use of 2,4-D in the control of water hyacinth and alligator weed in the Mississippi delta, with certain ecological implications. Ecology 34:409–14.

Ellison, A. M. and B. L. Bedford. 1995. Response of a wetland vascular plant community to disturbance: a simulation study. Ecological Applications 5:109–23.

Fredrickson, L. H. and T. S. Taylor. 1982. Management of seasonally flooded impoundments for wildlife. U.S. Dept. of the Interior, Fish and Wildlife Service, Washington, DC, USA.

Gaudet, C. L. and P. A. Keddy. 1988. A comparative approach to predicting competitive ability from plant traits. Nature 334:242–43.

Getsinger, K. D., E. G. Turner, J. D. Madsen, and M. D. Netherland. 1997. Restoring native vegetation in a Eurasian watermilfoil-dominated plant community using the herbicide triclopyr. Regulated Rivers: Research and Management 13:357–75.

Godfrey, R. K. and J. W. Wooten. 1978. Monocotyledons. University of Georgia Press, Athens, GA, USA.

Godfrey, R. K. and J. W. Wooten. 1981. Dicotyledons. Aquatic and Wetland Plants of Southeastern United States. University of Georgia Press, Athens, GA, USA.

Greulich, S. and G. Bornette. 2003. Being evergreen in an aquatic habitat with attenuated seasonal contrasts- a major competitive advantage? Plant Ecology 167:9–18.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, London, UK.

Harrington, T. B. and J. H. Miller. 2005. Effects of application rate, timing, and formulation of glyphosate and triclopyr on control of Chinese privet (*Ligustrum sinense*). Weed Technology 19:47–54.

Haukos, D. A. and L. A. Smith. 1993. Marsh management of playa lakes for migrating and wintering ducks. Wildlife Society Bulletin 21:288–98.

Holm, L., J. Doll, E. Holm, J. Pancho, and J. Herberger. 1997. World Weeds: Natural Histories and Distribution. John Wiley and Sons, Inc., New York, NY, USA.

Judge, C. A., J. C. Neal, and J. E. Derr. 2005. Preemergence and postemergence control of Japanese stiltgrass (*Microstegium vimineum*). Weed Technology 19:183–89.

Julien, M. H., B. Skarratt, and G. F. Maywald. 1995. Potential geographical distribution of alligator weed and its biological control by *Agasicles hygrophila*. Journal of Aquatic Plant Management 33:55–60.

Kaminski, R. M., J. B. Davis, H. W. Essig, P. D. Gerard, and K. J. Reinecke. 2003. True metabolizable energy for wood ducks from acorns compared to other waterfowl foods. Journal of Wildlife Management 67:542–50.

Kay, S. H. 1999. Evaluation of SP1001 (pelargonic acid) in combination with glyphosate on cattail and alligatorweed. Journal of Aquatic Plant Management 37:29–31.

Keast, A. 1984. The introduced macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. Canadian Journal of Zoology 62:1289–1303.

Laubhan, M. K. and L. H. Fredrickson. 1993. Integrated wetland management: concepts and opportunities. Transactions of the 58th North American Wildlife and Natural Resources Conferences 58: 323–34.

Liu, C. L., G. Wu, D. Wang, and S. Xia. 2004. Seasonal changes in height, biomass and biomass allocation of two exotic aquatic plants in a shallow eutrophic lake. Journal of Freshwater Ecology 19:41–45.

Low, J. B. and F. C. Bellrose. 1944. The seed and vegetative yield of waterfowl food plants in the Illinois River valley. Journal of Wildlife Management 8:7–22.

Madsen, J. D. 1997. Methods for management of nonindigenous aquatic plants. p. 145–71. *In* J. O. Luken and J. W. Thieret (eds.) Assessment and Management of Plant Invasions. Springer-Verlag, New York, NY, USA.

Madsen, J. D., J. W. Sutherland, J. A. Bloomfield, L. W. Eichler, and C. W. Boylen. 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. Journal of Aquatic Plant Management 29:94–99.

Netherland, M. D. and K. D. Getsinger. 1992. Efficacy of triclopyr on Eurasian watermilfoil: concentration and exposure time effects. Journal of Aquatic Plant Management 30:1–5.

Nyman, J. A., R. H. Chabreck, and R. G. Linscombe. 1990. Effects of weir management on marsh loss, Marsh Island, Louisiana, USA. Environmental Management 14:809–14.

Parsons, K. C. 2002. Integrated management of waterbird habitats at impounded wetlands in Delaware Bay, USA. Waterbirds 25:25–41.

Quimby, P. C. and S. H. Kay. 1977. Hypoxic quiescence in alligator weed. Physiologia Planatarum 40:163–68.

Reid, F. A. 1993. Managing wetlands for waterbirds. Transactions of the 58th North American Wildlife and Natural Resources Conferences 58: 345–50.

Reinecke, K. J. and K. M. Hartke. 2005. Estimating marsh seeds available to waterfowl with double sampling for stratification. Journal of Wildlife Management 69:794–99.

Reinecke, K. J., R. M. Kaminski, K. J. Moorehead, J. D. Hodges, and J. R. Nassar. 1989. Mississippi alluvial valley. p. 203–47. *In* L. M. Smith, R. L. Pederson, and R. M. Kaminski (eds.) Habitat Management For Migrating and Wintering Waterfowl in North America. Texas Tech University Press, Lubbock, TX, USA.

Rundle, W. D. and L. H. Fredrickson. 1981. Managing seasonally flooded impoundments for migrant rails and shorebirds. Wildlife Society Bulletin 9:80–87.

SAS Institute. 2003. SAS User's Guide. SAS Institute, Inc, Cary, NC, USA.

Spencer, N. R. and J. R. Coulson. 1976. The biological control of alligator weed, *Alternanthera philoxeroides*, in the United States of America. Aquatic Botany 2:177–90.

Strayer, D. L., C. Lutz, H. M. Malcom, K. Munger, and W. H. Shaw. 2003. Invertebrate communities associated with a native (*Vallisneria americana*) and an alien (*Trapa natans*) macrophyte in a large river. Freshwater Biology 48:1938–49.

Taft, O. W., M. A. Colwell, C. R. Isola, and R. J. Safran. 2002. Waterbird responses to experimental drawdown: implications for the multispecies management of wetland mosaics. Journal of Applied Ecology 39:987–1001.

Thomson, D. 2005. Measuring the effects of invasive species on the demography of a rare endemic plant. Biological Invasions 7:615–24.

Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ, USA.

Tu, M., C. Hurd, and J. M. Randall. 2001. Weed control methods handbook. The Nature Conservancy, http://tncweeds.ucdavis.edu.

Tucker, T. A., L. Anger, and F. T. Corbin. 1994. Absorption and translocation of ^{14}C-imazapyr and ^{14}C-glyphosate in alligator weed (*Alternanthera philoxeroides*). Weed Technology 8:32–36.

Vogt, G. B., P. C. QuimbyJr, and S. H. Kay. 1992. Effects of weather on the biological control of alligator weed in the lower Mississippi Valley region, 1973–1983. Washington, DC, USA. Department of Agriculture, Agriculture Research Service.

Walker, L. R. and P. M. Vitousek. 1991. An invader alters germination and growth of native dominant tree in Hawaii. Ecology 72:1449–55.

Weigelt, A., T. Steinlein, and W. Beyschlag. 2002. Does plant competition intensity rather depend on biomass or on species identity? Basic and Applied Ecology 3:85–94.

Wisheu, I. C. and P. A. Keddy. 1992. Competition and centrifugal organization of plant communities: theory and tests. Journal of Vegetation Science 3:147–56.

Wyka, T. 1999. Carbohydrate storage and use in an alpine population of the perennial herb, *Oxytropis sericea*. Oecologia 120:198–208.

Zhang, G. C., J. X. Li, and C. H. Cheng. 1993. A study on biology of *Alternanthera philoxeroides* (Mart.) Griseb. Journal of Weed Science 2:10–12.

Manuscript received 17 May 2006; accepted 7 May 2007.