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Cogongrass (*Imperata cylindrica*) Invasion and Eradication: Implications for Soil Nutrient Dynamics in a Longleaf Pine Sandhill Ecosystem

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We assessed pre- and posteradication nitrogen and phosphorus dynamics in longleaf pine sandhill stands severely affected by cogongrass. Across a 7-yr posteradication (glyphosate + imazapyr) "recovery chronosequence," which included untreated cogongrass, uninvaded reference, and treated plots, we analyzed soils for total N, potentially available P (Mehlich-1 [M1]), pH, and organic matter content. We also used resin bags to assess fluxes of plant available N and P in the soil solution. Additionally, we used litterbags to monitor the decomposition and nutrient mineralization patterns of dead rhizome and foliage tissue. Our results indicate similar total N and M1-P contents in both cogongrass-invaded and uninvaded reference plots, with levels of M1-P being lower than in cogongrass plots for 5 yr after eradication. Soil organic matter did not differ between treatments. Resin bag analyses suggest that cogongrass invasion did not affect soil nitrate availability, although a pulse of $NO_2 + NO_3$ occurred in the first 3 yr after eradication. No such trends were observed for ammonium. Resin-adsorbed PO_4 was lowest 3 yr after eradication, and pH was highest 5 yr after eradication. Our litterbag study showed that approximately 55% of foliar biomass and 23% of rhizome tissue biomass remained 18 mo after herbicide treatment. Substantial N immobilization was observed in rhizomes for the first 12 mo, with slow mineralization occurring thereafter. Rapid P mineralization occurred, with 15.4 and 20.5% of initial P remaining after 18 mo in rhizomes and foliage, respectively. Overall, our findings indicate that cogongrass invasion has little to no effect on soil nutrient cycling processes, although some significant—but ephemeral—alterations develop after eradication.

Nomenclature: Glyphosate; imazapyr; cogongrass, *Imperata cylindrica* (L.) Beauv. IMCY; longleaf pine, *Pinus palustris* Mill.

Key words: Decomposition, herbicides, invasive plants, legacy effects, restoration.

Invasive alien (IA) plants typically grow fast, colonize new sites rapidly, compete favorably with native species, and have few natural enemies outside of their home range. While theories abound as to the specific mechanisms alien plants use or traits they possess that enable them to be successful invaders (Bakker and Wilson 2001; Callaway and Ridenour 2004; Davis et al. 2000; Maron and Vilà 2001), a near-universal characteristic is their ability to alter—often dramatically—the species composition of plant communities (D'Antonio and Vitousek 1992; Gordon 1998; Hejda et al. 2009). Differences in resource uptake patterns, as well as the changes in litter quality and quantity that accompany these vegetative shifts, in turn can greatly alter the nutrient cycling dynamics of an ecosystem (Allison and Vitousek 2004; Ehrenfeld 2003; Kourtev et al. 2003). The extent of change depends on how different the invader is from the species that it replaces with respect to traits such as life history, physiology, size, above- and belowground architecture, tissue chemistry, photosynthetic pathways, symbiotic relationships, and other factors (Ehrenfeld 2003). Nitrogen-fixing IA plants have perhaps received the most research attention in this area (Corbin and D'Antonio 2004; Ehrenfeld 2003). In one illustrative study, the invasion of the N_2-fixing actinorhizal IA shrub

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Myrica faya (Aiton) Wilbur to N-poor Hawaiian forests was observed to increase ecosystem N inputs more than 5 times (Vitousek and Walker 1989).

Management Implications

An improved understanding of how invasive alien plant species alter soil properties and of how novel soil properties persist after eradication is essential for practitioners to develop effective restoration strategies for invaded natural communities. Toward these ends, we undertook this study to assess nutrient dynamics in forest stands affected by cogongrass—an invasive alien plant that affects tropical and subtropical ecosystems on six continents. We chose a longleaf pine sandhill ecosystem as the study site because these forests are frequently targeted in restoration efforts and are commonly invaded by cogongrass in the southeastern United States. Because nitrogen (N) and/or phosphorus (P) availability often affect plant establishment after disturbance, we focused on processes that affect N/P availability and uptake. Our results indicate that cogongrass invasion does not substantially alter soil properties. This is intriguing, given that this species is known to be a superior competitor for belowground resources and often forms dense, single-species stands in longleaf pine ecosystems. The decomposition of cogongrass biomass after herbicide treatment resulted in a rapid pulse of P into the soil and the temporary immobilization of soil N. All measured soil properties (N, P, pH, organic matter), however, returned to a preinvasion state within 5 yr. These results suggest that long-term posteradication soil "legacy" effects, which have been observed with other invasive alien plant species (e.g., alterations to the nitrogen cycle and other biogeochemical cycles), might not occur in cogongrass-affected pine ecosystems—at least those that have been invaded for a relatively short period of time. In light of these findings, we see little evidence to indicate that altered soil properties would impede groundcover restoration efforts in sites that have been invaded by cogongrass for 1–2 yr, as long as practitioners give the soil adequate time to recover after eradication.

The body of knowledge on the effects of IA species on soil nutrient cycling processes, while limited, has increased greatly in recent years (Blank 2008; Ehrenfeld 2003; Reinhart and Callaway 2006; Rodgers et al. 2008; Weidenhamer and Callaway 2010; Wolfe and Klironomos 2005). Less attention, however, has been paid to posteradication effects (Maron and Jeffries 2001; Yelenik et al. 2004), although researchers have speculated on the potential for legacy factors (e.g., alterations to nutrient cycles, modifications to mycorrhizal fungal communities) to impede restoration efforts (Corbin and D'Antonio 2004; Mummey and Rillig 2006; Renz and Blank 2004; Yelenik et al. 2004). Maron and Jefferies (2001), for example, reported that elevated soil N levels persist for more than 5 yr after removal of the N_2-fixing IA plant *Lupinus arboreus* Sims in prairie ecosystems in California. This, clearly, is an area that deserves more consideration, in that the restoration of native plant communities after the eradication of IA species (including non-N_2-fixers) is a high priority among land managers (Hartman and McCarthy 2004; Miller et al. 2010; Zavaleta et al. 2001). Much like any other disturbance, if soil processes and properties are altered by an invader, these effects will likely persist for some time after the invader is removed (Corbin and D'Antonio 2004; Jordan et al. 2008). The decomposition of plant biomass after treatment might cause further alterations to soil properties through its effects on soil organic matter (OM), pH, and the mineralization and immobilization of nitrogen (N) and phosphorous (P). These alterations might in turn affect nitrification rates (Chapin et al. 2002) or phosphorus complexation reactions (Brady and Weil 2002). In concert, these changes might impede the re-establishment of desirable native species, increase the potential for reinvasion by either the same or new alien species, or both (Kourtev et al. 2003; Ortega and Pearson 2010).

With invasions reported on six continents, cogongrass [*Imperata cylindrica* (L.) P. Beauv. IMCY]—hereafter referred to as cogongrass—is increasingly recognized as one of the world's most problematic IA plants. In total, some 500 million ha worldwide have some degree of cogongrass infestation (MacDonald 2004), with dense monotypic stands widely reported in tropical and subtropical forests, savannas, grasslands, pastures, and agricultural fields (MacDonald 2004). In the southeastern United States, cogongrass has been observed to alter the species and functional composition of native pine (*Pinus* spp.) ecosystems dramatically by displacing native groundcover species (Collins et al. 2007; Jose et al, 2002), inhibiting the performance of sapling trees (Daneshgar and Jose 2009; Holzmueller and Jose 2011) and altering fire behavior (Lippincott 2000). Little is known, however, about the role of belowground processes in cogongrass-invaded forest communities. Additionally, although standard forestry rates of common herbicides have proven effective at controlling cogongrass (Jose et al. 2002), researchers have yet to assess the changes to soil properties that might occur after these control efforts.

An improved understanding of how cogongrass alters soil properties and how novel soil properties might persist or develop after eradication is essential to develop effective long-term restoration strategies for cogongrass-invaded forest ecosystems. Toward these ends, we undertook this study to assess nutrient dynamics in longleaf pine (*Pinus palustris* Mill.) stands affected by cogongrass. We chose a longleaf pine sandhill ecosystem as the study site because these forests are frequently targeted in restoration efforts (Walker and Silletti 2006) and are commonly invaded by cogongrass (Daneshgar and Jose 2009; Jose et al. 2002). Because the availability of nitrogen, phosphorus, or both often drive ecological succession after a disturbance (Tilman 1985; Vitousek et al. 1993), we focused on processes that affect N/P availability and uptake. The two primary objectives of this study were:

- Analyze how invasion by cogongrass affects soil N and P pools, fluxes, and associated processes in longleaf pine sandhill stands.
- Quantify soil N and P dynamics in the years after cogongrass eradication.

We hypothesized that cogongrass invasion would decrease the availability of soil N and P, likely through reductions in pH, changes to the soil carbon (C) cycle, or both. We also expected these changes in N and P cycling to persist after eradication, perhaps because of the slow decomposition rates of low-quality cogongrass foliage and rhizomes after herbicide treatment.

Materials and Methods

Study Location. The study location was an uneven-aged, naturally regenerated longleaf pine forest in the Croom Tract of Withlacoochee State Forest in Hernando County, Florida (28°36′19.99″N, 82°16′19.73″W). The tract is near one of the original points of cogongrass introduction in the United States and has a history of invasion that spans several decades. Efforts in recent years to eradicate most cogongrass infestations in the tract through chemical means have been successful, and numerous areas are in various stages of recovery throughout, although some untreated cogongrass patches remain. The uninvaded areas are characterized by high levels of understory species richness and diversity, as is typical of an actively managed, frequently burned longleaf pine sandhill community. Predominant understory species in uninvaded areas were wiregrass [*Aristida stricta* Michx. var. *beyrichiana* (Trin. and Rupr.) D.B. Ward], along with various native trees, graminoids, forbs, shrubs, and vines (D. L. Hagan, unpublished data). Soils in the study location were primarily deep, well-drained to excessively drained sands of the Lake and Candler series (hyperthermic coated Typic Quartzipsamments and hyperthermic uncoated Lamellic Quartzipsamments, respectively). Small inclusions of the Arredondo series (Loamy, siliceous, semiactive, hyperthermic Grossarenic Paleudults)—comprising < 20% of the total area—were also present (U.S. Department of Agriculture 1977). Mean overstory basal area for the study location was 10.7 m^2 ha. Longleaf pine constituted approximately 88% of total basal area.

We used cogongrass-invaded and uninvaded reference sites across four longleaf pine sandhill stands in the study location to assess the effect of cogongrass invasion on soil N and P dynamics. Additionally, because some sites within these stands had cogongrass eradicated in previous years, we established a 7-yr "recovery chronosequence" to measure temporal changes in N and P cycling after eradication. Although we recognize the inherent limitations in space-for-time substitution, specifically the assumption that all sites had the same initial condition (Walker et al. 2010), this chronosequence allowed us to speculate on longer term patterns and processes than are typically possible in invasion/eradication studies. Sites selected for the chronosequence treatments were treated in the late summer/early fall—approximately 3, 5, and 7 yr before, respectively—with a tank mix solution (sprayed to the point of runoff) consisting of 2% Roundup Pro™ (Monsanto Co., St. Louis, MO 63167) (41% glyphosate plus surfactant), and 0.4% Arsenal™ (BASF Corporation, Research Triangle Park, NC 27709) (28.7% imazapyr). Glyphosate and imazapyr tank mixes such as this are among the most common and effective methods of chemical control for cogongrass (MacDonald 2004). (A single herbicide treatment does not always completely eradicate a cogongrass patch. However, for young [≤ 2-yr-old] patches in the Croom tract, > 95% control is typical. For the purposes of this study, all such patches were considered "eradicated.") All sites, hereafter referred to as plots, were identified and selected using Geographic Information Systems (GIS) and with the help of state forest personnel. It should be emphasized that plots in the recovery sequence were not assigned randomly to chronosequence treatments. The availability of plots of various "ages" was the result of several years of cogongrass treatment in these stands. Uninvaded reference plots were randomly selected using GIS and were ground-truthed to verify that they were not currently invaded and did not fall on disturbed or degraded sites (e.g., roads, bicycle trails, abandoned rock mines, formerly invaded sites). Plots with live cogongrass were estimated to be 1–2 yr old, which is approximately the same age that those in the recovery chronosequence were when they were treated. Cogongrass was the dominant species in these plots. With the exception of herbicide treatment of the occasional cogongrass resprout, there was no posteradication vegetation management. The dominant species in recovery chronosequences were primarily ruderal graminoids and forbs (e.g., *Setaria* sp., *Eupatorium capillifolium* (Lam.) Small). Desirable species, such as wiregrass and other species that would typically be found before invasion, were generally absent posteradication. Despite the differences in vegetative composition, total percent cover increased after cogongrass eradication and was comparable to reference levels by year 7 (D. L. Hagan, unpublished data).

Study Design. The study was laid out as a complete block design, replicated at two study areas. Each study area consisted of an adjacent pair of 259-ha stands (blocks) with similar management histories (both typically burned every 4 yr, but staggered 2 yr apart). One block in each study area was burned approximately 12 mo before sampling, and the other was burned approximately 36 mo earlier. Each block typically contained two to three plots from each of the five treatments: uninvaded reference, cogongrass-invaded, 3-yr

Table 1. Number of study plots in each in each treatment by block by study area combination in longleaf pine sandhill communities in Hernando County, FL, USA.

	Area 1		Area 2	
Treatment	Block 1	Block 2	Block 1	Block 2
Uninvaded reference	3	3	3	3
Cogongrass-invaded	3	3	1	3
3 yr eradicated	2	3	3	2
5 yr eradicated	3	2	3	3
7 yr eradicated	3	3	3	3

eradicated, 5-yr eradicated, and 7-yr eradicated (Table 1). Within each plot, three subplots were randomly selected, each being at least 2.5 m from the other, at least 8 m from the edge, and distant from any cogongrass resprouts (where applicable; Figure 1). Additionally, four recently treated ($<$ 3 yr) cogongrass patches were selected as locations for a litterbag decomposition study (described below).

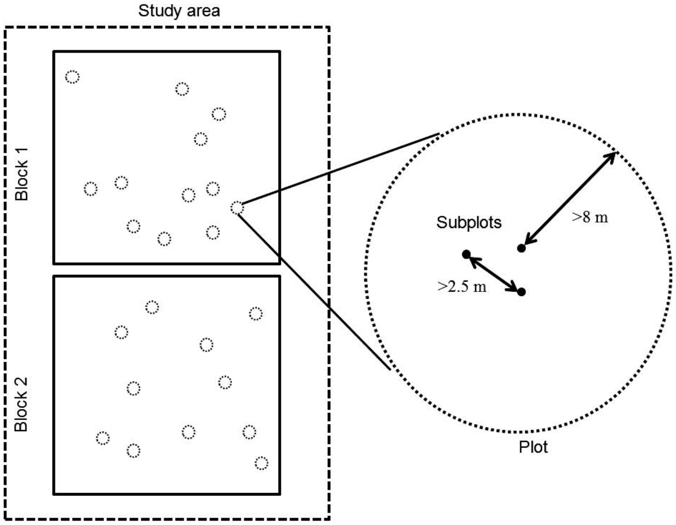

Figure 1. Schematic diagram of one study area (not to scale), with cogongrass-invaded and eradicated plots (3, 5, and 7 yr posteradication) indicated as dashed circles. Uninvaded reference plots, three per block, are randomly scattered among the other plots. Close-up view of a plot indicates the location and arrangement of subplots. Blocks are located in longleaf pine sandhill communities in Hernando County, FL, USA.

Soil Chemistry and Nutrient Pools. Soil samples from the top 15 cm of the profile were collected from subplots in June 2010 using a standard one-piece soil probe. Each sample was a composite of five subsamples—one taken at plot center and the remaining four collected 1 m away in each of the four cardinal directions. Samples were transported to the lab in a cooler and then moved to a freezer, where they remained at −4°C until analysis. Soil OM content was determined by acid digestion, and pH was measured using a 1 : 2 soil : water ratio (Mylavarapu and Moon 2002). Total N (by the Total Kjeldahl N [TKN] method) and potentially available P were quantified using an Alpkem AutoAnalyzer and a Mehlich-1 (M1) extraction, respectively (Mylavarapu and Moon 2002).

Soil Nutrient Availability. The availability of N and P in the different treatments was assessed with mixed cation–anion exchange resin bags, incubated in situ (Harpole and Tilman 2007; Standish et al. 2004) during the 2010 growing season. By integrating microenvironmental factors (e.g., water availability, flow, and plant uptake) during the incubation period (Binkley 1984), this method can shed light on the relative differences in N and P availability between treatments (Binkley et al. 1986; Feller et al. 2003; Gibson 1986). Before incubation, resins were washed in sodium chloride (NaCl) and sodium hydroxide per the procedure outlined in Thiffault et al. (2000). Bags consisted of approximately 10 g (moist weight) of washed resin (Dowex Marathon MR-3) cinched in a square of acid-washed nylon-lycra mesh with a plastic zip tie to make a firm, spherical bag (Thiffault et al. 2000). In early May and September of 2010, a bag was buried at a depth of 5 cm in each subplot. Bags were removed after 33-d incubation periods. Upon return to the lab, they were gently rinsed in de-ionized water to remove adhering soil particles, and then shaken in a 2 M NaCl solution for 2 h. Extracts were analyzed using an autoanalyzer for total adsorbed nitrite + nitrate-N ($NO_2 + NO_3$) and ammonium-N (NH_4) and by inductively coupled plasma mass spectrometry for total adsorbed P (Harpole and Tilman 2007; Thiffault et al. 2000).

Litter Decomposition and Nutrient Mineralization. Initial nutrient cycling after cogongrass eradication may be affected by the decomposition of dead biomass. Therefore, to determine the rates of cogongrass decomposition and nutrient mineralization and immobilization, 40, 1-mm fiberglass mesh litterbags (20 filled with 5 g of air-dried cogongrass rhizomes and 20 filled with 5 g of air-dried cogongrass foliage; Ashton et al. 2005) were incubated in clusters of five in four random locations in recently treated (fall 2009) cogongrass patches scattered across the two blocks and away from plots. Rhizome and foliage tissues used in the litterbags were collected from an adjacent area outside the two blocks that had been treated 2 wk earlier with the glyphosate and imazapyr tank mix. In December 2009, rhizome bags were buried to a depth of 5 cm, and foliage bags were left on the soil surface. After 31, 90, 192, 373, and 544 d (approximately 1, 3, 6, 12, and 18 mo), eight bags were collected (one per tissue type, per location; $n = 40$) and transported to the lab, where their contents were carefully removed, freed from adhering soil, and dried at 65°C. Subsamples were ground to $<$ 1 mm and analyzed for total C, N, and P, per the

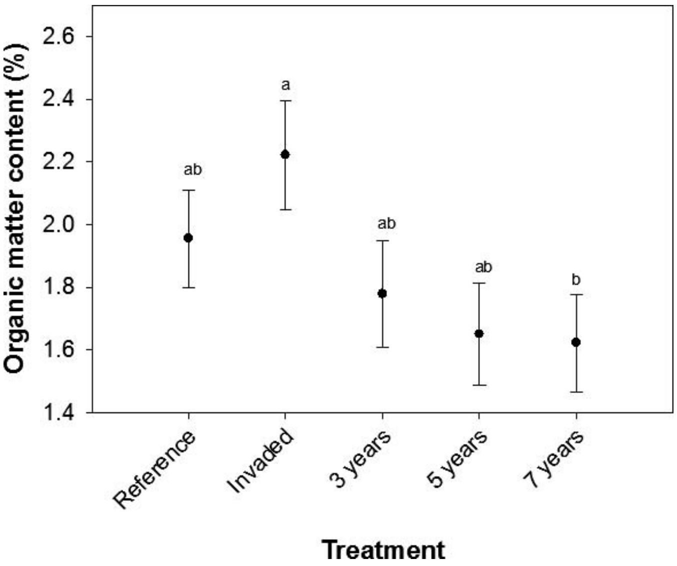

Figure 2. Mean soil organic matter content (%) in uninvaded reference plots, cogongrass-invaded plots, and plots in which cogongrass was eradicated 3, 5, and 7 yr earlier in longleaf pine sandhill communities in Hernando County, FL, USA. Means and standard errors. Means having different lowercase letters are statistically different at $P < 0.05$.

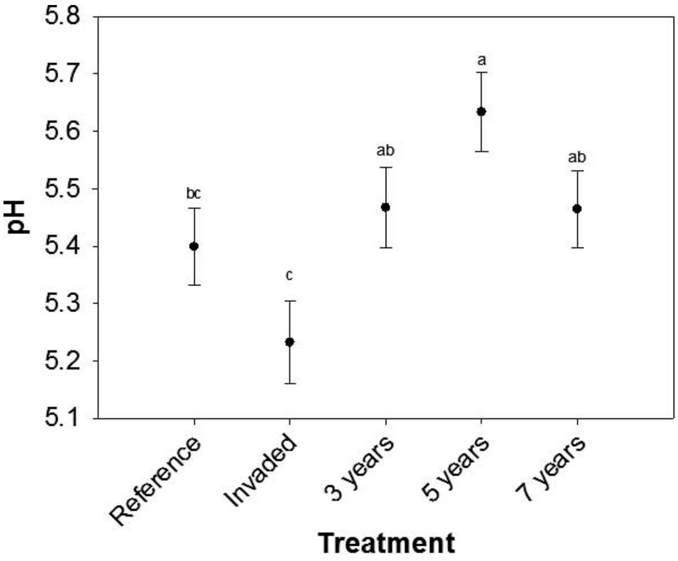

Figure 3. Mean water-extractable soil pH in uninvaded reference plots, cogongrass-invaded plots, and plots in which cogongrass was eradicated 3, 5, and 7 yr earlier in longleaf pine sandhill communities in Hernando County, FL, USA. Means and standard errors. Means having different lowercase letters are statistically different at $P < 0.05$.

procedure outlined in Bray (2005). Mass loss and nutrient mineralization and immobilization, relative to preincubation values, were then determined for each sampling date (Allison and Vitousek 2004).

Statistical Analysis. The three subplot values from the soil sample, resin bag, and litterbag analyses were averaged to obtain plot-level estimates. For the resin bags, plot-level estimates for the May and September deployments were also averaged to generate single growing season estimates of NO_2 + NO_3, NH_4, and P availability. The data were analyzed using the MIXED procedure in SAS 9.2 (SAS 2007). Study area and block(study area) were treated as random effects. Although this study was not designed specifically to tease out the effects of fire, the inclusion of these random effects allowed us to account for variability between treatments associated with location and time since last fire. This, in turn, enabled us to generate more robust estimates for our fixed effects. The Kenward–Roger calculation, a preferred method for unbalanced mixed models (Spilke et al. 2005), was used to estimate denominator degrees of freedom. (This method can result in noninteger values for denominator degrees of freedom.) Differences between means were declared statistically significant at $P < 0.05$, and Tukey's post hoc test was used for pairwise comparisons. Some nonstatistically significant trends were reported in cases of possible ecological importance (e.g., when nonsignificant relationships add evidence to inferences drawn from significant relationships). Decomposition rates (*k*-coefficients) for cogongrass rhizomes and foliage were calculated on the basis of a negative exponential model following Bray (2005).

Results

Organic Matter and pH. Like many of the other measured soil properties, soil OM was highly variable among the five treatments, ranging from 0.83 to 3.17%, with a mean of 1.84%. Differences between treatments were significant ($F_{(4,43.94)} = 2.71$, $P = 0.0417$), with OM content being highest in cogongrass-invaded plots (2.22%) and lowest in plots where cogongrass was eradicated 7 yr earlier (1.62%; Figure 2). Soil pH in the different treatments ranged from 4.87 to 6.00, with a mean of 5.44. Differences in pH between treatments were significant ($F_{(4,43.47)} = 7.34$, $P = 0.0001$), with pH in 5-yr plots (5.63) being significantly higher than that of the uninvaded reference plots (5.40) and cogongrass-invaded plots (5.23; Figure 3).

Nitrogen. Total N content ranged from 666.7 to 1,400.0 mg kg^{-1}, with a mean of 990.1 mg kg^{-1}. Differences between treatments were not significant ($F_{(4,43.52)} = 1.38$, $P = 0.2557$). Resin-adsorbed NH_4 followed a similar pattern, ranging from < 0.01 to 0.08 mg bag^{-1}, with a mean of 0.02 mg bag^{-1} and no significant differences between treatments ($F_{(4,43.38)} = 0.26$, $P = 0.9000$). Resin-adsorbed NO_2 + NO_3 did, however, vary significantly between treatments ($F_{(4,43.15)} = 12.81$, $P < 0.0001$). Contents ranged from < 0.01 to 0.10 mg bag^{-1},

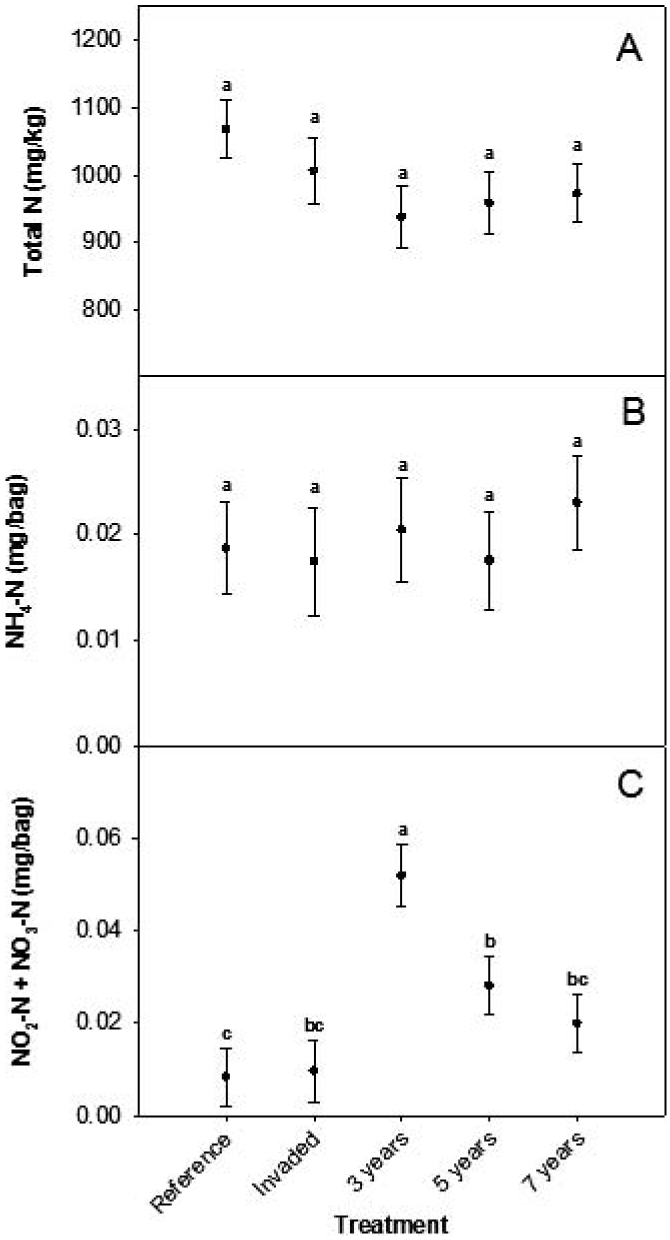

Figure 4. Mean total soil nitrogen (TKN method) (A), resin-adsorbed soil ammonium (B), and nitrite + nitrate (C) in uninvaded reference plots, cogongrass-invaded plots, and plots in which cogongrass was eradicated 3, 5, and 7 yr earlier in longleaf pine sandhill communities in Hernando County, FL, USA. Means and standard errors. Means having different lowercase letters are statistically different at $P < 0.05$.

with a mean of 0.02 mg bag^{-1}. Soil $NO_2 + NO_3$ levels were highest 3 yr after eradication (0.05 mg bag^{-1}) and lowest in the cogongrass-invaded and uninvaded reference treatments (0.01 and 0.01 mg bag^{-1}, respectively. Levels decreased after this initial spike and were not significantly different from the uninvaded reference treatment 7 yr after cogongrass eradication (Figure 4).

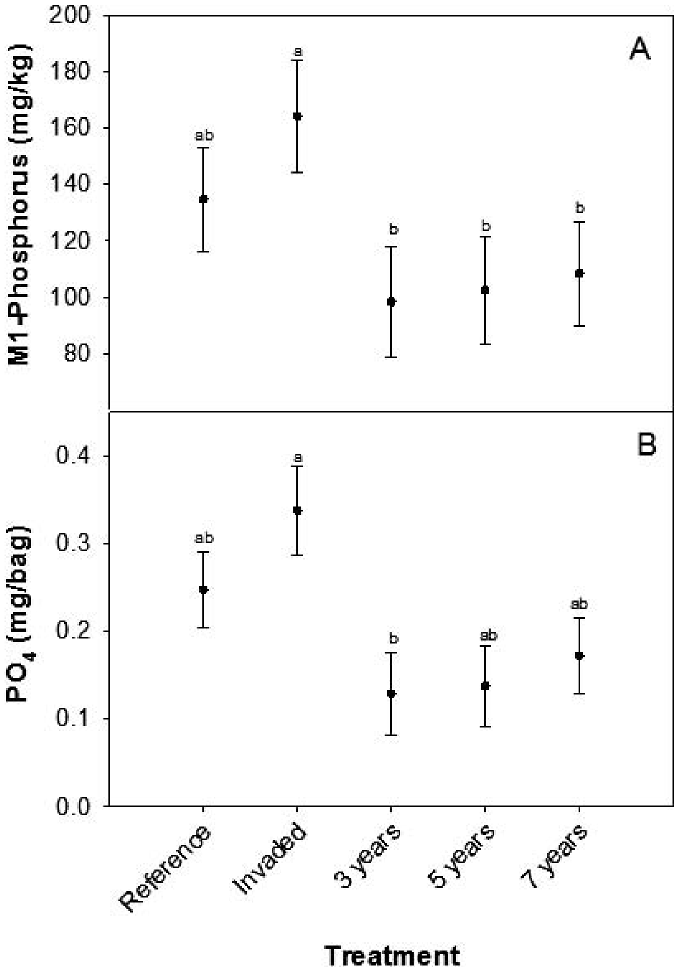

Figure 5. Mean Mehlich-1 (M1)–extractable phosphorus (A) and resin-extracted soil phosphorus (B) in uninvaded reference plots, cogongrass-invaded plots, and plots in which cogongrass was eradicated 3, 5, and 7 yr earlier in longleaf pine sandhill communities in Hernando County, FL, USA. Means and standard errors. Means having different lowercase letters are statistically different at $P < 0.05$.

Phosphorus. Soil M1-extractable P content ranged from 50.8 to 347.3 mg kg^{-1}, with a mean of 120.7 mg kg^{-1}. Differences between treatments were significant ($F_{(4,43.92)} = 3.76$, $P = 0.0102$), with M1-P content being lowest 3 and 5 yr after cogongrass eradication (98.2 and 102.3 mg kg^{-1}, respectively) and highest in cogongrass-invaded plots (164.4 mg kg^{-1}). Resin-adsorbed P ranged from 0.02 to 0.78 mg bag^{-1}, with a mean of 0.20 mg bag^{-1}. It followed a similar pattern as M1-extractable P ($F_{(4,44.04)} = 3.06$, $P = 0.0263$), with the highest values being found in cogongrass-invaded plots (0.33 mg bag^{-1}) and the lowest values found in plots where cogongrass was eradicated 4 and 5 yr earlier (0.13 and 0.14 mg bag^{-1}, respectively; Figure 5).

Tissue Quality, Decomposition, and Mineralization. Cogongrass rhizome and foliage tissue differed with respect

Table 2. Initial mean tissue chemistry (standard deviations in parentheses) of herbicide-treated cogongrass rhizomes and foliage, along with calculated *k*-coefficients for mass loss and N and P mineralization over time.

Tissue	%N	%P	%C	C : N	C : P	k_{biomass}
Foliage	0.94 (0.29)	0.22 (0.05)	43.43 (0.56)	48.70 (12.38)	207.70 (44.72)	0.44 (0.14)
Rhizomes	0.43 (0.14)	0.29 (0.04)	45.06 (0.60)	122.73 (64.25)	147.91 (5.76)	1.01 (0.09)

to chemistry, and they exhibited different patterns of mass loss during the 18-mo field incubation period. Decomposition rates (*k*-coefficients) were 1.01 and 0.44 for rhizomes and foliage, respectively (Table 2). Nutrient mineralization occurred fairly rapidly for cogongrass foliage, with 43.7 and 20.5% of initial N and P remaining, respectively, after 18 mo. A different trend, however, was observed for rhizome tissues. After an initial spike in immobilization, in which tissue N levels were > 2.5 times greater than initial values, tissue N dropped to 70.0% of initial levels after 18 mo. In contrast with N, rapid P mineralization occurred for cogongrass rhizomes, with 15.4% remaining after 18 mo (Figure 6).

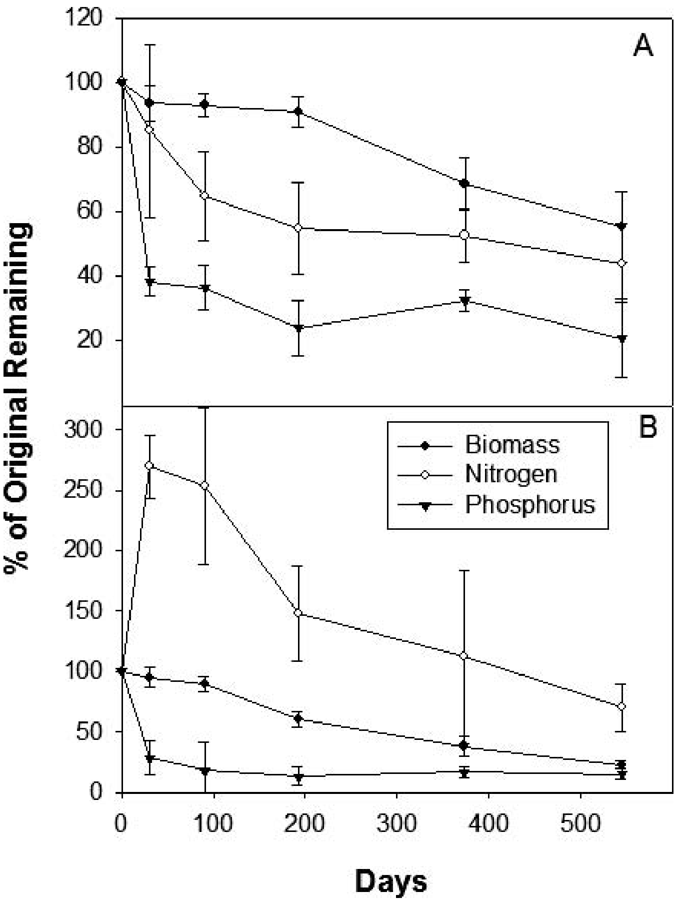

Figure 6. Patterns of mass loss and N and P mobilization/immobilization for foliage (A) and rhizome (B) tissues of cogongrass treated with glyphosate and imazapyr herbicides. Means and standard deviations.

Discussion

Our findings suggest that no substantial changes in soil properties occurred directly as a result of cogongrass invasion in the longleaf pine sandhill ecosystem. This does not support our first hypothesis, and it stands contrary to the findings of other researchers, who have suggested that cogongrass alters soil chemistry in southern pine ecosystems (Collins and Jose 2008; Daneshgar and Jose 2009). Because changes in soil nutrient cycling due to cogongrass invasion were not evident, the persistence of such effects—which we proposed in hypothesis 2—was not possible. Some temporary alterations to N and P dynamics did, however, develop in the years after eradication. These trends, we propose, are most readily explainable by decomposition, mineralization, and nitrification processes, in concert with differences in pH along the chronosequence.

Influence of Cogongrass on Soil Chemistry. Like many IA plants, cogongrass grows faster and produces more biomass than the native understory species that it displaces (Jose et al. 2002). Cogongrass is also suspected to have high nutrient use efficiency (Daneshgar and Jose 2009), which contributes to the production of low-quality tissues that decompose slowly (Bray 2005). Because the carbon cycle is intrinsically linked to other elemental cycles, alterations in biomass production might affect the cycling of soil nutrients—particularly macronutrients such as N and P that are frequently limiting. These differences in biomass production and tissue chemistry would seemingly lead to elevated soil OM levels (Ehrenfeld 2003), although this was not clearly evident in this study. It is difficult to assess why the expected trends were not observed, but it is possible that the invaded plots used for this study had not been affected long enough for substantial alterations to occur.

No characteristic trend of pH alteration appears in invaded systems, in that studies show both decreases (Collins and Jose 2008; Gremmen et al. 1998; Grierson and Adams 2000) and increases (Ehrenfeld et al. 2001; Hector et al. 1999). The apparent lack of effect of cogongrass invasion on soil pH in this study, however, is not consistent with the findings of other cogongrass researchers. Collins and Jose (2008), for example, reported pH values in cogongrass-invaded forest sites to be nearly one quarter unit lower than in uninvaded sites. Although differential NH_4 and NO_3 uptake is commonly cited as an explanation for such effects (Ehrenfeld et al. 2001; Hewins and Hyatt 2010), the fact that we did not observe differences in pH, NO_2 + NO_3 or NH_4 availability between cogongrass-invaded and uninvaded reference plots suggests that this might not be the case for cogongrass. Like many plant species, cogongrass tissues have been shown to contain or exude a variety of different organic acids (Inderjit and Dakshini 1991; Koger and Bryson 2004). Recent research (Hagan et al. 2013), however, indicates that the concentrations of several phenolic acids can be orders of magnitude higher in cogongrass-invaded soils than in similar soils dominated by native species, suggesting that cogongrass would increase soil acidity; however, the reductions in soil pH that we observed were not statistically significant. The reasons we did not observe significant reductions in soil pH in cogongrass-invaded plots, yet Collins and Jose (2008) did, are not entirely clear. Perhaps the soils in our plots had a higher pH buffering capacity, which had the effect of moderating pH fluctuations (Brady and Weil 2002).

Although the superior competitive ability of cogongrass (Daneshgar and Jose 2009; Holzmueller and Jose 2011) would seemingly lead to reductions in soil nutrient levels in invaded areas, total N, M1-P, and resin-adsorbed N and P in this study were not lower in cogongrass-invaded plots than in uninvaded reference plots. In the case of N, it is likely that both systems have highly conservative cycles, in which inputs are limited (because of frequent fire and the preponderance of non–N-fixing vegetation), and that intense competition for this frequently limiting resource leads to internalized N cycling and the maintenance of low levels of soil N (Chapin et al. 2002). Some IA species are more effective at capturing soil P than native species, perhaps because they "mine" it from deeper horizons, have an enhanced scavenging ability, or both (Lambers et al. 2008; Perkins et al. 2011). However, our findings, which showed no significant difference in soil P between cogongrass-invaded and uninvaded reference plots, do not support this assertion.

The Posteradication Legacy of Cogongrass on N and P Cycling. The different patterns of N and P mineralization that we observed in the litterbag study can be attributed to differences in tissue chemistry. The decomposition rates of dead plant tissues are largely controlled by their C : N ratios (i.e., tissue quality; Chapin et al. 2002). For low-quality tissues (e.g., $C:N > 25:1$), N immobilization occurs, for a time, and slow decomposition rates can cause litter to accumulate. For higher quality tissues, N mineralization occurs and decomposition is more rapid (Ehrenfeld 2003). Carbon : phosphorus ratios have less of an effect on decomposition rates, but like N, organic P immobilization and mineralization are governed by a tissue quality threshold (between 200 and 300 : 1; Brady and Weil 2002). Whereas P mineralized quite rapidly for both foliage and rhizome tissues, a substantial amount of N taken up by cogongrass remained immobilized after 18 mo. Daneshgar and Jose (2009) proposed that cogongrass established and maintained dominance in forest ecosystems by monopolizing the soil N pool and storing it in belowground tissues, which constituted the bulk of total biomass. Our findings partially support this claim and further suggest that much of this N remains sequestered for period of time after eradication. The burning of cogongrass "thatch" after treatment, as is often done, releases previously immobilized N into the atmosphere, potentially magnifying an N limitation (Daneshgar and Jose 2009), although available forms of soil N might increase temporarily (Certini 2005).

Because the early stages of succession are often driven by N availability (Vitousek et al. 1993), an increased N limitation due to immobilization in cogongrass biomass (and atmospheric losses from burning) could affect the establishment and growth of desirable nitrophilic species immediately after eradication. The spike in $NO_2 + NO_3$ at 3 yr is probably an example of an "Assart flush" (Li et al. 2003) because the various factors that promote nitrification (e.g., OM mineralization, elevated pH, and temperature), along with decreases in fine root biomass (Attiwill and Adams 1993), likely resulted in a temporary increase in net nitrification. The subsequent decline was likely due to a combination of leaching, plant uptake, and the development of conditions less conducive to nitrification. The rapid decline in M1-P and resin-adsorbed P in the first 3 yr after eradication could be explained by the exploitation of this newly available pool by overstory pines in the absence of most competing understory vegetation (Smethurst and Comerford 1993). It is also possible that the P was not leached or taken up but rather adsorbed onto soil colloids and oxides (Brady and Weil 2002), thereby preventing them from being detected in our M1-P and resin analyses.

Although little is known about posteradication nutrient cycling processes in cogongrass-invaded systems, it can be assumed that they are strongly tied—after the decomposition of dead tissue—to the effects of soil OM (Attiwill and Adams 1993; Tiessen et al. 1994). In terrestrial systems, the OM pool is constantly turning over, with measurable OM content representing the balance between inputs (e.g., litter) and outputs (e.g., carbon mineralization) at a given point in time (Chapin et al. 2002). In the sandy soils typical of longleaf pine systems, soil OM constitutes a major pool of potentially available nutrients (Wilson et al. 1999). Our findings suggest that soil OM levels either were not significantly affected by invasion and eradication, or they equilibrated to near reference levels within 3 yr of eradication.

In highly leached, acidic forest soils of humid regions, slight changes in pH can greatly alter the chemical form, solubility, and mobility of N and P (Attiwill and Adams

1993). Soil pH has been shown to vary predictably with changes in vegetation during forest succession, with the highest pH values typically found in intermediate successional stages (Christensen and Peet 1984). In this study, soil pH increased for 5 yr after cogongrass eradication before declining to near-reference levels by 7 yr. Because nitrification is inhibited at low pH (Chapin et al. 2002), the significant increases in pH observed for 5 yr after eradication could have contributed to the elevated levels of resin-adsorbed $NO_2 + NO_3$ observed across plots. Perhaps this increase in pH is also associated with burning (Raison 1979), in that all 5-yr plots had been burned at least once since cogongrass eradication. Again, however, the limitations of our sampling design did not allow us to isolate the effects of fire effectively.

Synthesis and Implications for Restoration. This study represents one of the first attempts to assess the effects of both invasion and eradication of alien grasses on soil nutrient cycling processes. Overall, our findings suggest that the effects of cogongrass invasion on soil properties in longleaf pine sandhill ecosystems are not substantial, at least in sites where cogongrass was treated within 2 yr of invasion, which is an ideal (and increasingly typical) management scenario. Some novel soil properties developed after cogongrass eradication, perhaps because of the decomposition and mineralization patterns of the dead biomass, but these changes were only temporary, lasting < 5 yr. These findings are encouraging because they suggest that altered soil properties likely do not have any long-term implications for the establishment of desirable native plant species. Because the restoration of formerly invaded sites is a high priority among land managers, a logical next step is to test this hypothesis, either by monitoring successional patterns over a longer period of time or by evaluating the performance of reintroduced native species. Because cogongrass is known to alter fire regimes, which likely has implications for biogeochemical cycling, additional research on the effects of burning would also be useful.

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