

THE EFFECTS OF GAP SIZE AND DISTURBANCE TYPE ON INVASION OF WET PINE SAVANNA BY COGONGRASS, *IMPERATA CYLINDRICA* (POACEAE)¹

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Cogongrass is a nonindigenous species perceived to threaten native communities of the southeastern United States through modification of species composition and alteration of community processes. To examine how gap size and disturbance type influence the invasion of wet pine savannas by cogongrass, we performed three field experiments to evaluate the response of cogongrass seeds and transplanted seedlings to four different gap sizes, four types of site disturbance, and recent burning of savanna vegetation. Cogongrass germinated, survived, and grew in all gap sizes, from 0 to 100 cm in diameter. Similarly, disturbance type had no effect on germination or seedling and transplant survival. Tilling, however, significantly enhanced transplanted seedling growth, resulting in a tenfold increase in biomass over the other disturbance types. Seedling survival to 1 and 2 mo was greater in burned savanna than unburned savanna, although transplant survival and growth were not affected by burning. Results of this study suggest that cogongrass can germinate, survive, and grow in wet pine savanna communities regardless of gap size or type of disturbance, including burning. Burning of savanna vegetation may enhance establishment by improving early seedling survival, and soil disturbance can facilitate invasion of cogongrass by enhancing plant growth.

Key words: disturbance; exotic species; gap size; germination; invasion; prescribed burning; seedling survival.

The invasion of natural communities by exotic species is a topic of increasing worldwide concern and research (Kareiva, 1996; Williamson, 1996; Luken and Thieret, 1997; Bright, 1998). Although numerous authors have attempted to determine species' characteristics or community characteristics that contribute to invasion by nonnative species (Fox and Fox, 1986; Swincer, 1986; Rejmánek and Richardson, 1996), there is general consensus that successful invasion is a context-specific process (Bazzaz, 1986; Crawley, 1987; Noble, 1989; D'Antonio, 1993; Hobbs and Humphries, 1995), depending on both the invaders' life-history attributes and favorable site conditions. Thus, site-specific and species-specific studies to determine factors that contribute to ecosystem invasion are warranted for predicting the invasion potential of communities at risk from exotic species (Pierson and Mack, 1990; Hobbs and Humphries, 1995). This study investigates the potential for cogongrass [*Imperata cylindrica* (L.) Beauv.], an exotic perennial, to invade wet pine savanna communities of the southeastern United States by evaluating how gap size and disturbance type influence cogongrass establishment by seed.

Imperata cylindrica var. *major* was first introduced into the United States in 1911 at Mobile, Alabama, when the plant arrived accidentally as shipping material in a crate of satsuma oranges from Japan. A second, intentional introduction of cogongrass from the Philippines occurred sometime before 1920 at the McNeil Mississippi Agricultural Experiment Station, where it was introduced as a potential forage crop (Tabor,

1949). Since its introduction, cogongrass has become established in Florida, Alabama, Mississippi, and Louisiana (MacDonald and Chandler, 1994; Shilling, Gaffney, and Waldrop, 1995) and was recently estimated to cover several thousand hectares in the southeastern United States (Bryson and Carter, 1993). Shilling (1996) reports that cogongrass in the United States can displace other vegetation in forests, rangelands, pastures, roadsides, reclaimed mining areas, and natural areas. In a study of cogongrass invasion of Florida sandhill communities, Lippincott (1997) determined that cogongrass is not functionally equivalent to native sandhill species and is capable of altering community function by changing vegetation structure, soil processes, resource availability, fire regime, and native seedling recruitment. Other ecologically sensitive communities in the Southeast are also at risk from cogongrass invasion, including coastal wet pine savanna.

Wet pine savanna communities are some of the most diverse in North America (Peet and Allard, 1993). They are characterized by an open canopy of pines (*Pinus palustris* P. Mill. and/or *P. elliotii* Engelm.) and a diverse understory of grasses and forbs maintained by frequent fires. Frequent fires and wet soils of low pH and relatively low nutrients provide conditions favorable to many unique endemic species including carnivorous pitcher plants (*Sarracenia* L. spp.) and sundews (*Drosera* L. spp.), and the endangered Mississippi sandhill crane (*Grus canadensis pulla*). Maintenance of open, wet pine savanna requires active management, particularly by prescribed burning (Brockway and Lewis, 1997). Concern exists that the site conditions and management practices conducive to maintaining these communities may also favor the establishment and growth of cogongrass.

Most studies of cogongrass invasion in the United States have examined communities already infested with cogongrass, and no studies have attempted to assess what site characteristics contribute to cogongrass invasion in native communities.

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Although it is generally known that cogongrass invades sites with disturbed soils, such as reclaimed mining lands and roadways, it is unknown whether cogongrass can invade vegetatively intact native communities by seed without some form of disturbance. The effects of small-scale disturbances on germination and establishment of many native and exotic species have been examined in numerous studies (Fenner, 1978; Pickett and White, 1985; Goldberg, 1987; Peart, 1989; Hobbs, 1991; D'Antonio, 1993), and in many cases, germination and seedling growth were found to be dependent on gap size or disturbance intensity (Goldberg and Werner, 1983; McConnaughay and Bazzaz, 1987; Rice, 1987; Klinkhamer and DeJong, 1988; Burke and Grime, 1996). Hobbs and Huenneke (1992, p. 325) point out the conundrum of disturbance and nonnative species invasions: "the continued existence of particular species or communities often requires disturbance of some type . . . but disturbance may simultaneously lead to the degradation of natural communities by promoting invasions." This issue is of primary importance in wet pine savannas, which require periodic burning to maintain the unique and diverse species assemblages associated with this community type, but which may be at risk of invasion by cogongrass. The objectives of this study were to examine the potential for establishment of cogongrass in wet pine savannas by evaluating the response of cogongrass seeds and transplanted seedlings to (1) four sizes of vegetation gaps, from 0 to 100 cm in diameter; (2) four types of small-scale disturbance including no disturbance, mowing, vegetation removal with no soil disturbance, and tilling; and (3) burning of savanna vegetation.

MATERIALS AND METHODS

To assess the response of cogongrass seeds and transplants to gap size and type of disturbance, including burning of savanna vegetation, we conducted three field experiments in a wiregrass savanna on Grand Bay National Wildlife Refuge in Jackson County, Mississippi (30°30' N, 88°30' W). Botanical nomenclature used for this study followed that of the PLANTS database (United States Department of Agriculture, 1997). The herbaceous vegetation of the study site is typical of wet pine savannas in the region, dominated by wiregrass (*Aristida* L. sp.) with a diverse mix of other herbaceous species throughout (see description of southern longleaf savannas in Peet and Allard, 1993). The savanna contains no cogongrass, although established stands exist ~0.5 km away on the refuge property. *Sphagnum* moss (L.) on the soil surface is indicative of moderately wet soils of low pH, as soil analyses confirmed. The sandy loam soil has a pH of 4.3 and a low nutrient content, typical of wet pine savannas. The savanna had not been burned in over 5 yr and contains no mature pines, however pine saplings and woody shrubs including inkberry [*Ilex glabra* (L.) Gray] and yaupon [*Ilex vomitoria* Ait.] are common throughout. Relative elevation across the entire study site varies by 0.31 m.

Environmental characterization—To characterize the effects of treatments on light availability to seeds and seedlings, relative percentage of photosynthetically active radiation (PAR, 400–700 nm) reaching the soil surface at each plot was determined using LI-COR quantum sensors and a data logger (LI-COR inc., Lincoln, Nebraska, USA). Simultaneous readings were taken with a sensor placed in the plot at surface level and a sensor mounted on a pole that reached above the canopy; percentage PAR reaching the surface was determined from these two readings at each plot. We used ANOVA and Tukey's multiple comparison tests to determine whether light availability differed among treatments in the gap size experiment and the disturbance type experiment. Differences in PAR between treatments in the burning experiment were tested with a *t* test using Satterthwaite's approximation, because the data were distributed unequally between treatments (SAS, 1989).

Elevation of each plot was determined using a Spectra-Physics laser level (Spectra-Physics Laserplane, Inc., Dayton, Ohio, USA) prior to planting seeds

or transplants. Since surface irregularities common to this habitat type result in localized ponding, actual elevation may not give true estimates of plot flooding. Therefore, flooding depth at each plot was measured with a ruler on a single day when the site was inundated following heavy rain. Elevation and microsite flooding were analyzed with seed germination data as described below for each experiment. Statistical analyses in all experiments were performed in SAS (SAS, 1989) using an alpha level of 0.05.

Containment barriers—All field experiments used seed plots to examine germination and seedling survival and transplant plots to examine establishment and growth. To reduce the risk of cogongrass escaping into the savanna, all seeds and transplants were planted inside of containment barriers similar to the root-exclusion tubes used by Cook and Ratcliff (1984) and Reichenberger and Pyke (1990), which they used to reduce root competition between seedlings and surrounding plants. Barriers were 46-cm long cylinders of PVC (polyvinyl chloride) sewer pipe, each with two 0.79-cm drainage holes drilled opposite from the other, 1 cm from the top edge. Seed plot barriers were 10-cm in diameter and were covered with fine white nylon mesh (<0.5 mm) secured by heavy rubber bands to prevent seeds from washing out during extreme rainfall events. Transplant plot barriers were 15-cm in diameter and were left uncovered. For each seed or transplant plot in the experiments, a single barrier was pounded into the ground until drainage holes were approximately flush with the soil surface. All barriers were placed in the savanna before treatments (gap sizes, types, or burning) were administered. We conducted a pilot study in 1997 using these barriers and determined that neither the PVC tubes nor the mesh covering seed plots impeded rainfall or significantly altered surface flooding.

Cogongrass inflorescences were collected haphazardly by hand in the first week of April 1997, from cogongrass flowering within 8 km of the study site, along the shoulder and median of Interstate Highway 10 East in Jackson County, Mississippi, USA. Cogongrass inflorescences were stored intact in paper bags at 5°C. Because production of unfilled florets is common in this species (Shilling et al., 1997), caryopses were removed by hand from florets, counted into groups of 20, and placed in storage vials prior to planting. Each seed plot was planted by emptying the 20 cogongrass seeds onto the soil surface at the center of the containment barrier. Mesh covers were secured immediately after planting. All seed plots were planted the second week of April 1998.

Transplant plots were established at the same time as seed plots by planting two, 3-wk-old seedlings (2–3 cm tall) at the center of each containment barrier. Seedlings were started in trays of commercial potting mix (Lambert Peat Moss Inc., Quebec, Canada) in the greenhouse from the same seed collected for seed plots. After 1 wk in the field, one seedling was removed from each plot or a new seedling was transplanted if none survived, so that every transplant plot contained a single cogongrass plant.

Experiment 1—Gap size—Circular gaps of 10, 30, and 100 cm in diameter were created in the vegetation with the herbicide glyphosate, N-(phosphonomethyl)-glycine, trade name Roundup (Monsanto Co., St. Louis, Missouri, USA), with subsequent clipping to the soil surface and hand removal of clipped material. A 2% concentration of Roundup was applied once to vegetation in 30-cm and 100-cm diameter plots using a backpack sprayer and by hand application several weeks prior to planting seeds and transplants. Plots of 10-cm diameter were too small to allow the use of herbicide and were cleared by hand. All standing-dead vegetation and live vegetation not killed by the herbicide was removed from plots by clipping with hand pruners to ground level. A single seed or transplant plot was placed at the center of a each gap-size treatment. Although barriers for the transplant plots were 15-cm in diameter, the parted wiregrass canopy was repositioned after planting using hand-held cultivators (small rakes) so openings were no larger than the treatment opening sizes. An additional 0-cm gap treatment was evaluated with barriers placed in undisturbed vegetation, again with the canopy returned to its original position after parting for barrier insertion and planting. Openings were maintained canopy-free for the duration of the experiment by hand removal of regrowth as needed. The four treatments were assigned in a ran-

domized block design with eight blocks, each containing one replicate of both seed and transplant plots.

Seed plots—The number of seedlings was recorded weekly for 2 mo. Percentage germination was determined for all plots by taking the maximum number of seedlings counted in each plot at any time during the experiment and dividing by 20 (the number of seeds planted). Data were screened for deviations from the parametric assumptions of normality and homoscedasticity (Zar, 1996). Data fit all assumptions, and treatment means were tested by ANCOVA with microsite flooding and measured elevation as covariates. Seedling survival to 1 and 2 mo was calculated by dividing the number of living seedlings by the maximum number of germinants up to that time for each plot. To ensure that survival of seedlings was not adversely affected by seedling density, we used linear regression to test the relationship between percentage germination and survival of seedlings to 2 mo in each plot. Survival to 2 mo was square-root transformed to meet normality assumptions prior to regression analysis. Results of the regression showed that these two variables were significantly, positively related ($P < 0.005$, $r^2 = 0.73$, slope = 1.24), suggesting that plot conditions favorable for seed germination were also conducive to seedling survival. Since the density of seedlings did not negatively affect seedling survival, seedling density was not used as a covariate in tests of treatment effects on survival. The survival data required no transformation to meet parametric assumptions before testing treatment effects by a repeated-measures ANOVA.

Transplant plots—Survival, number of shoots, and maximum height of each shoot were recorded once every 14 d for all transplants for 5 mo. Surviving transplants were harvested intact, rinsed with water to remove soil from roots and crowns, dried at 105°C to constant mass, and weighed to the nearest 0.001 g. Final number of surviving transplants by treatment was analyzed by chi-square analysis using Fisher's Exact Test to determine association between survival and treatment. Shoot number, shoot length, and total biomass of surviving transplants were assessed for univariate normality and homoscedasticity, and a correlation analysis was used to verify correlations between variables. All three measures of growth were linear-rank transformed and analyzed together in a MANOVA using Wilks' Lambda to detect overall differences in growth among treatments. The general linear models (GLM) procedure in SAS was used to account for the unbalanced design resulting from the unequal numbers of surviving transplants in each treatment (SAS, 1989; Scheiner and Gurevitch, 1993). The 100-cm treatment was excluded from the analysis because only one transplant survived to the end of the experiment resulting in no within-treatment variance.

Experiment 2—Type of disturbance—This experiment examined types of site disturbance that occur naturally and with active management of this community: no disturbance, mowing, vegetation removal without soil disturbance (bare), and tilling. All treatments were applied as circles of 100 cm in diameter with either a seed or transplant plot placed at the center. For the no-disturbance treatment, seed and transplant plots were inserted without removing or altering vegetation or ground litter. These plots were the same as the 0-cm gap plots described previously. The mowing treatment was created using a gas-powered weed eater to reduce standing vegetation to a height of ~10 cm. Cut vegetation was left on the plot where it fell. The bare treatment was the same as the 100-cm diameter treatment in the gap-size experiment. Tilling was accomplished by weed-eating and removing standing vegetation, then turning the soil over with shovels to a depth of 30 cm. Treatments were assigned in a randomized block design with eight blocks, each containing one replicate for both seed and transplant plots. Data from seed and transplant plots were collected and analyzed as in the gap-size experiment. Again, linear regression of percentage germination and seedling survival to 2 mo showed a significant, positive relationship ($P < 0.005$, $r^2 = 0.78$, slope = 1.18) suggesting no density-dependent constraints on seedling survival. Data from seed and transplant plots met parametric assumptions for all tests, except for MANOVA of growth responses for surviving transplants. These data were inverse transformed prior to analysis with the GLM procedure. A priori contrasts identified which treatments differed. Analysis of surviving transplant growth did not

include the bare treatment because only one plant survived to the end of the experiment.

Experiment 3—Burning—Six 10 × 10 m areas of savanna were burned in a prescribed burn on 6 April 1998, and six comparable areas of the same size were left unburned. Ten transplant plots were planted in each of the treatment areas 2 d after the burn, and ten seed plots were planted in each treatment area 3 d after the burn. The basic statistical design was a randomized block design with two blocks, each containing three treatment replicates per block with ten subsamples (seed and transplant plots) per replicate.

Seed plots—The number of seedlings was recorded weekly for 2 mo. Seed germination data fit parametric assumptions and required no transformation before analysis. To determine whether germination success differed between burned and unburned savanna, percentage germination was analyzed in a nested ANCOVA with burning treatment as the main effect and water depth and measured elevation as covariates. Survival of germinants to 1 and 2 mo was calculated by dividing the number of surviving seedlings by the maximum number of germinants up to that time for each plot. As in the other two experiments, to determine whether seedling density adversely affected seedling survival, we tested the relationship between percentage germination and survival of seedlings to 2 mo (square-root transformed) with linear regression. Survival was not constrained by the number of germinants in a plot ($P < 0.005$, $r^2 = 0.57$, slope = 1.09), and data on survival to 1 and 2 mo were arcsine square-root transformed and analyzed in a repeated-measures nested ANOVA (Zar, 1996).

Transplant plots—As in the previous experiments, transplant survival, number of shoots, and maximum height of each shoot were recorded at 14-d intervals for 5 mo. Aboveground and belowground biomass were harvested, rinsed with water to remove soil from roots and crowns, dried at 105°C, and weighed to the nearest 0.001 g. Categorical data analysis of a 2 × 2 × 2 contingency table (block × treatment × survival) with a chi-square test was used to detect differences in the total number of surviving transplants by block and treatment. Transplant growth data were screened for outliers and adherence to normality assumptions. A single outlier was detected in the burned treatment and was removed prior to analysis. This excessively robust plant was over twice as tall and had over three times greater total biomass than the next largest plant in the experiment. The data were linear rank transformed to meet parametric assumptions, and a correlation analysis on number of shoots, shoot height, and biomass confirmed that these growth variables were correlated. All three responses were analyzed with the GLM procedure using a nested MANOVA and Wilks' Lambda to detect differences in growth between treatments.

RESULTS

Experiment 1—Gap size—Light availability differed among all gap sizes ($P < 0.001$). Average light penetration in the 0-cm gaps was 20% of full sun. The 10-cm gaps provided 66% of full sunlight, compared with 76 and 89% in the 30- and 100-cm gaps, respectively. Measured elevation within the blocks for this experiment varied by 31 cm, although for seed plots alone there was a difference of only 11 cm between highest and lowest plots. Microsite flooding varied by 7 cm across the site and ranged from 0 to 5.6 cm in seed plots.

Seed plots—Percentage germination was ~40% across all treatments (Fig. 1) and did not differ by gap size, microsite flooding depth, or measured elevation ($P > 0.05$). Survival of germinants to 1 and 2 mo differed by time, but not by gap size. A near-significant interaction effect of Time × Gap Size ($P = 0.059$) suggested that survival between months may differ among treatments (Table 1). The greatest drop in survival between months was observed in the 100-cm gaps (Fig. 1).

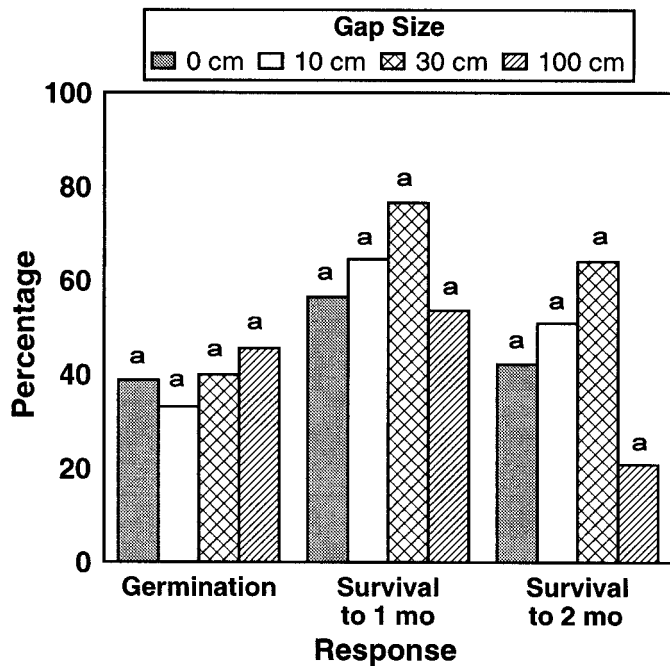


Fig. 1. Mean percentage germination and germinant survival to 1 and 2 mo for cogongrass seeds planted in gaps of different sizes in wet pine savanna. Comparisons of treatment means revealed no significant differences ($P < 0.05$) as indicated by the letter "a" above all bars (see Table 1).

Transplant plots—The number of surviving transplants was not significantly associated with gap size ($P = 0.23$). Number of survivors ($N = 8$) was 1, 4, 5, and 4 in the 100-, 30-, 10-, and 0-cm gaps, respectively. Growth of surviving transplants in 0-, 10-, and 30-cm gaps also did not differ significantly among treatments ($P = 0.79$; Fig. 2).

Experiment 2—Disturbance type—Percentage PAR differed among treatments ($P < 0.001$), with ~89% of above-canopy light reaching the surface in tilled and bare plots and 56 and 20% light penetration in mowed and undisturbed plots, respectively. Overall, elevation varied by 13 cm, and microsite flooding differed by 7.1 cm between the most flooded and least flooded plots. In seed plots alone, elevation varied by 11 cm, and flooding varied by 5.6 cm.

Seed plots—Germination did not differ significantly by disturbance type, microsite flooding depth, or measured elevation ($P > 0.05$) and averaged 44% across all treatments (Fig. 3). Survival of germinants to 1 and 2 mo differed by time ($P < 0.001$) but not by disturbance type ($P = 0.45$; Fig. 3).

Transplant plots—Survival of transplants was ~38% across all treatments, ranging from one (bare treatment) to four survivors (no-disturbance and mowed treatments). The tilled treatment had three surviving transplants at the end of the experiment. Differences in survival among treatments were not statistically significant ($P = 0.40$). However, growth of transplants differed among no-disturbance, mowed, and tilled treatments (Table 2). Total shoot length and final biomass were five and ten times greater, respectively, in the tilled treatment than the other disturbance types (Fig. 4).

Experiment 3—Burning—As expected, significantly more

TABLE 1. Repeated-measures ANOVA source table for cogongrass seedling persistence to 1 and 2 mo in gaps of 0-, 10-, 30-, and 100-cm diameter in wet pine savanna (see Fig. 1).

Source of variation	df	Type III SS	F	P
Between-subjects				
Block	7	0.543	0.49	0.834
Gap size	3	0.926	1.93	0.157
Error	20	3.194	—	—
Source of variation				
df	Wilks' λ	F	P	
Within-subjects				
Time	1	0.339	38.97	0.0001*
Time \times Gap Size	3	0.695	2.92	0.059

* Asterisks indicate statistical significance at the $P < 0.05$ level.

light reached the soil surface in burned plots than unburned plots ($P < 0.001$). Percentage PAR in burned and unburned treatments was 78 and 30%, respectively. Elevation varied by 23 cm and microsite flooding ranged from 0 to 15.9 cm. In seed plots alone, elevation differed by 12 cm, and flooding ranged from 0 to 8.5 cm.

Seed plots—Percentage germination did not differ between burned (23%) and unburned (28%) savanna and was not affected by microsite flooding or elevation ($P > 0.05$); however, survival of germinants to both months was greater in burned than unburned savanna (Fig. 5, Table 3).

Transplant plots—The number of surviving transplants did not differ between burned and unburned savanna, which had 29 and 27 survivors, respectively ($N = 60$, chi-square = 0.13, $P = 0.72$). Growth of transplants was greater in unburned than

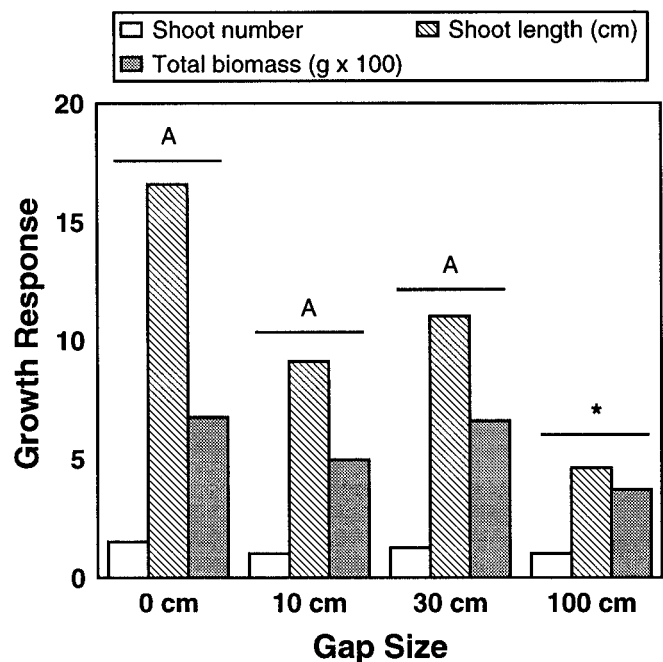


Fig. 2. Growth of cogongrass transplants after 140 d growing in different-sized gaps in wet pine savanna. Comparison of treatments using MANOVA ($P < 0.05$) based on the three growth responses shown revealed no significant differences as indicated by the letter "A" above all groups. * indicates that the 100-cm gap treatment was not included in analysis because measurements were on one surviving plant.

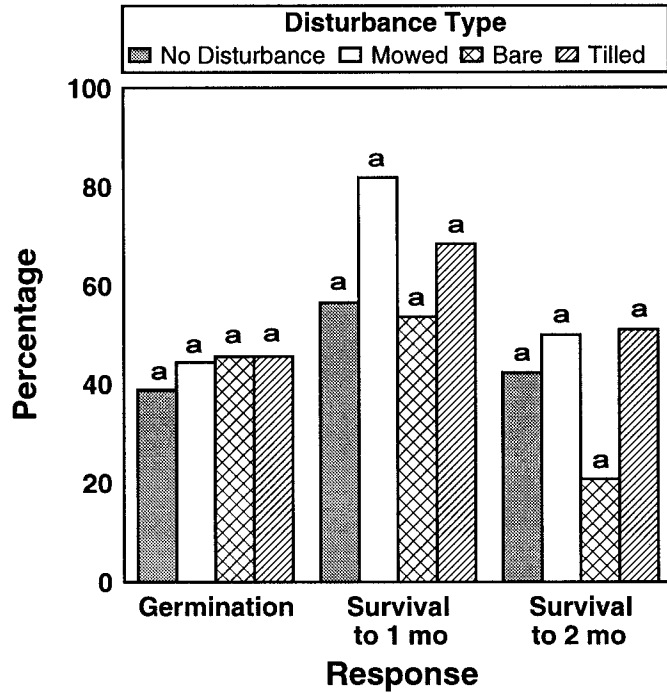


Fig. 3. Mean percentage germination and germinant survival to 1 and 2 mo for cogongrass seeds planted in 1-m openings of different disturbance types in wet pine savanna. Comparisons of treatment means revealed no significant differences ($P < 0.05$) as indicated by the letter “a” above all bars.

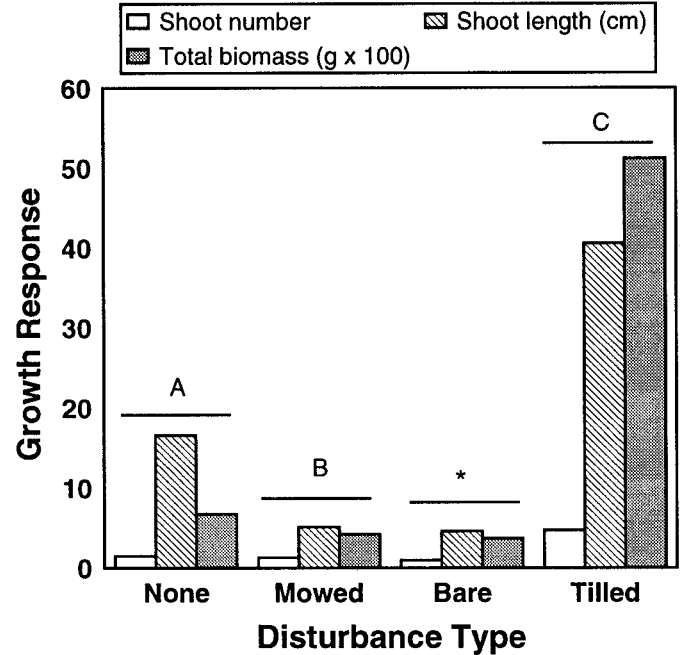


Fig. 4. Growth of cogongrass transplants after 140 d growing in 1-m openings of different disturbance types in wet pine savanna. Different letters represent differences among treatments as determined by MANOVA based on the three growth responses shown with a priori contrasts at the $P < 0.05$ level (see Table 2). * indicates bare treatment was not included in analysis because measurements were on one surviving plant.

burned savanna ($P = 0.007$) due to greater mean shoot length of cogongrass in the unburned treatment (Fig. 6).

DISCUSSION

This study examined how site conditions affect invasion of pine savanna by cogongrass. Gap size, type of disturbance, and burning could potentially affect invasion at several stages during the development of a cogongrass population, as depicted in the conceptual model shown in Fig. 7. The site conditions we examined had only moderate effects on cogongrass performance. Results of this study clearly demonstrate that cogongrass can germinate and survive in wet pine savanna irrespective of gap size, disturbance type, or burning of savanna vegetation. Overall, cogongrass germination was high, averaging over 38% across all three experiments. Over 90% of the

TABLE 2. (A) MANOVA source table and (B) a priori contrasts for cogongrass transplant growth after 140 d growing in 1-m openings of different disturbance types in wet pine savanna. Disturbance types were none, mowed, and tilled. Response variables included in model were transplant shoot number, total shoot length, and total biomass (see Fig. 4).

A) Source of variation				
	df	Wilks' λ	F	P
Block	15	0.000	51.5	0.003*
Disturbance type	6	0.000	632	0.002*
B) Contrasts				
	Num. df	Wilks' λ	F	P
Till vs. none	3	0.000	1926.3	0.017*
Till vs. mow	3	0.000	417.936	0.001*
None vs. mow	3	0.000	363.121	0.001*

* Asterisks indicate statistical significance at the $P < 0.05$ level.

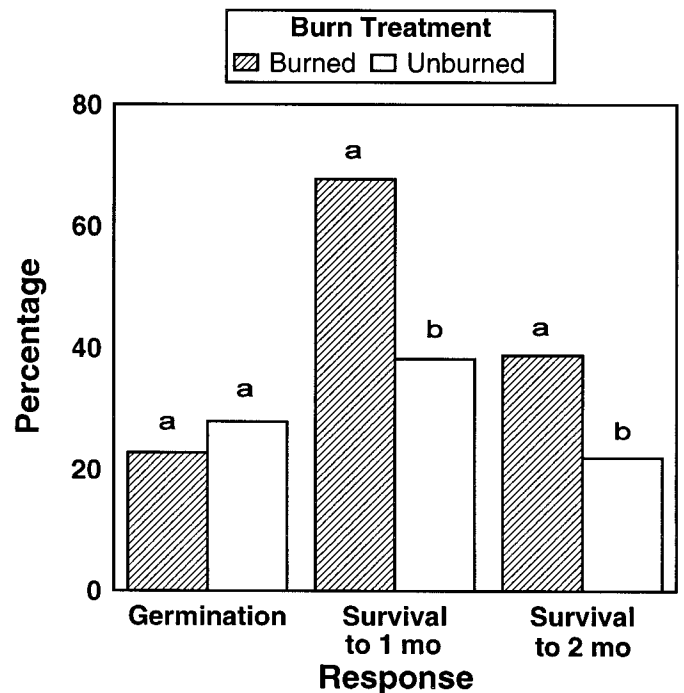


Fig. 5. Mean percentage germination and germinant survival to 1 and 2 mo for cogongrass seeds planted in burned and unburned wet pine savanna. Different letters represent differences between treatment means at the $P < 0.05$ level (see Table 3).

TABLE 3. Repeated-measures ANOVA source table for cogongrass seedling persistence to 1 and 2 mo in burned and unburned wet pine savanna (see Fig. 5). Tests of between-subjects treatment effect and within-subjects interaction use subplot (plot within treatment) Type III sums of squares as the error term.

Source of variation	df	Type III SS	F	P
Between-subjects				
Burning	1	2.380	25.44	0.0001*
Source of variation	df	Wilks' λ	F	P
Within-subjects				
Time	1	0.565	53.04	0.0001*
Time \times Burning	1	0.715	7.16	0.015*

* Asterisks indicate statistical significance at the $P < 0.05$ level.

168 seed plots planted for the three experiments produced at least one cogongrass seedling. In conjunction with successful germination, the overall survival of germinants to at least 2 mo was over 20% in all treatments from all experiments. Transplant survival was also high, averaging >43% across all experiments.

Numerous studies report poor seedling germination and establishment in undisturbed vegetation, particularly for small-seeded species (Winn, 1985; Goldberg, 1987; D'Antonio, 1993). Sajise (1972) reported that cogongrass germination requires light and is favored by light quality characterized by a red to far-red ratio of 1.0 or greater, qualities that are characteristic of open or partly shaded environments. Although cogongrass has tiny seeds (1–1.3 mm long) and requires light to germinate, in this study seeds germinated just as well in undisturbed savanna as in created gaps of all sizes and types, despite receiving only 20–30% of available PAR. Because we scattered bare caryopses under the vegetation canopy, observed germination rates may be higher in this study than would be expected from natural seed dispersal events where spikelets or caryopses would have to fall through the vegetation to reach the soil surface. Pierson and Mack (1990) reported that recruitment of seedlings of the invasive grass *Bromus tectorum* in forest habitats may be determined largely by whether a caryopsis falls through the forest litter layer and germinates in mineral soil. Thus, although disturbance of savanna had no direct facilitating effect on cogongrass seed germination, disturbance of the canopy would likely promote invasion simply by improving the chances for seed to reach the soil surface unimpeded.

Survival of cogongrass germinants was not significantly affected by gap size or any disturbance type other than burning. Significantly more seedlings survived in the burned treatments to months 1 and 2. Although burning can result in an overall loss of nutrients due to oxidation, volatilization, and increased leaching, fire is reported to cause a short-term increase in mobility and availability of various nutrients. Christensen (1993) reported that burned wiregrass savanna soils were enriched in PO_4 -P, K, Ca, and Mg 2 mo following fire, particularly in the top 10 cm of the soil profile where new seedlings would be rooted. This agrees with the immediate post-fire soil fertility increases and greater plant growth in burned vs. unburned soils reported in an earlier study by the same author (Christensen, 1977). Other studies report the positive effects of burning on soil microbial activity and microclimate (Old, 1969; Peet, Anderson, and Adams, 1975), which may be important for seed preparation. Christensen (1993) suggested that microclimatic conditions for successful establishment of native savan-

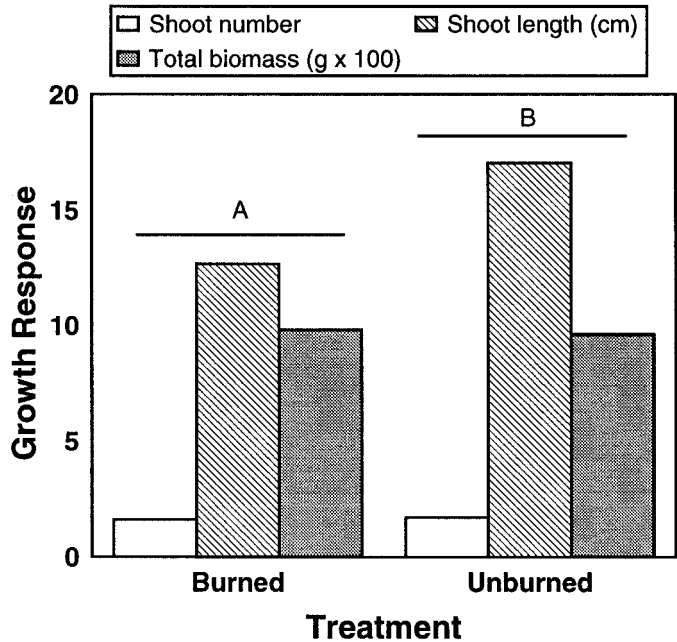


Fig. 6. Growth of cogongrass transplants after 140 d growing in burned and unburned wet pine savanna. Different letters represent differences between treatments as determined by MANOVA ($P < 0.05$) based on the three growth responses shown.

na species are most favorable in the second post-fire year when native herb seed production is highest due to increased flowering in the first post-fire growing season. The results of this study suggest that cogongrass seedlings could already be established by the second post-fire year since cogongrass seed ripens quickly, requires no dormancy for germination, and germination and early seedling survival were high in burned savanna. Thus, spring burning of pine savannas in proximity to flowering stands of cogongrass could promote invasion by giving cogongrass seedlings an early advantage over other species. Long-term studies are needed to further evaluate cogongrass seedling survival and seedling interactions with native savanna vegetation.

We used cogongrass transplants in this study to examine how older seedlings, which had successfully grown past the two-leaf stage (as per Shilling et al., 1997), would respond to site conditions. Overall, cogongrass transplant survival was high (~40%), and no differences among treatments were detected in any experiment, despite only one transplant surviving in the bare, 100-cm gaps. Most seedling deaths began to occur at the end of July, 9 wk after transplants were put in the field.

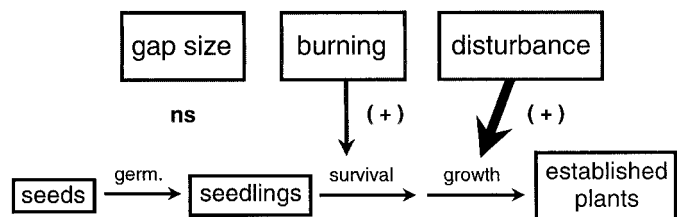


Fig. 7. Conceptual model of the effects of disturbance on early stages of cogongrass invasion in wet pine savanna. "ns" denotes no significant effects detected. Size of arrows depicts magnitude of effect and "+" or "-" denotes enhancing or limiting effects, respectively.

Thus, we believe that seedling deaths were not related to transplant shock, rather they were associated with stress from the hot summer weather conditions. Had our seedlings been older at the time of transplanting, they may have had even higher rates of survival. Interestingly, transplants in the largest gaps, as well as in the tilled and burned plots, appeared stressed during most of the experimental period, having red leaves and high leaf turnover (King, personal observation). Although not included in the growth analyses, the single surviving plant from the 100-cm gap was smaller (in shoot length and biomass) than the survivors from the other gap sizes and disturbance types (Figs. 2, 4). The poor performance of cogongrass in the more open treatments may have been caused by exposure to more stressful microsite temperature, light, and/or moisture conditions. Franco and Nobel (1989) reported improved performance for plants in microsites moderated by neighboring vegetation, and Suding and Goldberg (1999) found that direct effects of either vegetation or litter on seedling establishment were consistently facilitative. Fowler (1986) reported that safe-site requirements for germination, survival, and growth of two native grass species were microhabitat characteristics that prevented desiccation: mainly the presence of litter and/or rocks. Interestingly, although transplants in the tilled plots also appeared stressed for much of the experiment, this did not result in decreased performance. In fact, growth as measured by shoot number, shoot length, and total biomass was greatest with tilling. Results also suggest that cogongrass growth was significantly greater in unburned savanna than in burned savanna, however, this was likely just a morphological effect of shoot elongation from shading, because total biomass showed no corresponding increase in the unburned treatment (Fig. 6). A similar trend of shoot elongation was discernible in the undisturbed treatments of the other experiments. Thus, the only significant effect on cogongrass growth and subsequent spread may be from tilling, which undoubtedly enhances invasion.

The positive effects of soil disturbance on cogongrass growth and spread may be due in part to loosening of the upper soil layer, which in this ecosystem is very dense and may physically impede root and rhizome penetration. Tilling also may improve drainage and may reduce root competition of seedlings with neighboring vegetation, which was effectively eliminated from the plot in the process of turning over the soil. Reichenberger and Pyke (1990) demonstrated that root competition can impact seedling survival and subsequent reproductive performance for semiarid species in the Great Basin sagebrush ecosystem. Their study used PVC tubes, similar to the containment barriers used in this study, to segregate roots of seedlings and neighboring vegetation. Root competition in our study also may have been reduced by the PVC tubes used to prevent the escape of cogongrass into the savanna, although native vegetation that grew inside of the containment barriers with seedlings was allowed to grow unaltered. The greatest impact of the barriers would have been the exclusion of wiregrass roots competing with seedlings since most plots were located between wiregrass tussocks. However, in this ecosystem soil moisture is readily available in spring and early summer, thus we would likely not see the same effects of root competition observed by Reichenberger and Pyke (1990) in their study of arid rangeland in Utah. The effects of the barriers on modifying the interactions of cogongrass with the native community might have been problematic if we had wanted to measure the development of our seedlings and trans-

plants longer, through all life stages. Although the barriers may have lessened the consequences of underground competition, they effectively prevented the escape of cogongrass into this yet-uninfested savanna, providing valuable insight on invasion of this species into a community before it has occurred, information that is sorely lacking for most exotic species and community types.

Although more replicates in our transplant experiments might have allowed us to include all treatments in our analyses, providing stronger statistical support for our findings, we believe that our results address the issue of *Imperata cylindrica*'s potential to establish in wet pine savanna. This study did not evaluate cogongrass survival and performance beyond the first growing season; however, the number of survivors and the vigorous appearance of the surviving seedlings and transplants when harvested suggests that a large number of these plants would have successfully established if left in place. Clearly, the fact that cogongrass was able to germinate and grow in all treatments, including the undisturbed treatments, suggests that coastal wet pine savanna is indeed at risk of invasion by this species. Further study on the long-term persistence of cogongrass seedlings under closed-canopy conditions and the competitive ability of cogongrass seedlings with native seedlings is warranted for predicting how invasion will proceed in these communities. Results from this study suggest that efforts to prevent cogongrass invasion should focus on preventing cogongrass disseminules (seeds and rhizomes) from reaching sensitive communities.

LITERATURE CITED

- BAZZAZ, F. A. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. In H. A. Mooney and J. A. Drake [eds.], *Ecology of biological invasions of North America and Hawaii*, Ecological studies, vol. 58, 96–110. Springer-Verlag, New York, New York, USA.
- BRIGHT, C. 1998. *Life out of bounds*. W.W. Norton, New York, New York, USA.
- BROCKWAY, D. G., AND C. E. LEWIS. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96: 167–183.
- BRYSON, C. T., AND R. CARTER. 1993. Cogongrass, *Imperata cylindrica*, in the United States. *Weed Technology* 7: 1005–1009.
- BURKE, M. J. W., AND J. P. GRIME. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776–790.
- CHRISTENSEN, N. L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the Coastal Plain of North Carolina. *Oecologia* 27: 27–44.
- . 1993. The effects of fire on nutrient cycles in longleaf pine ecosystems. In S. M. Hermann [ed.], *Proceedings of the 18th Tall Timbers Fire Ecology Conference, The longleaf pine ecosystem: ecology, restoration, and management*, 205–214. Tall Timbers Research, Inc., Tallahassee, Florida, USA.
- COOK, S. J., AND D. RATCLIFF. 1984. A study of the effects of root and shoot competition on the growth of green panic (*Panicum maximum* var. *trichoglume*) seedlings in an existing grassland using root exclusion tubes. *Journal of Applied Ecology* 21: 971–982.
- CRAWLEY, M. J. 1987. What makes a community invisable? In A. J. Gray, M. J. Crawley, and P. J. Edwards [eds.], *Colonization, succession, and stability*, 429–453. Blackwell Scientific Publications, Boston, Massachusetts, USA.
- D'ANTONIO, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* 74: 83–95.
- FENNER, M. 1978. A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. *Journal of Ecology* 66: 953–963.

- FOWLER, N. L. 1986. Microsite requirements for germination and establishment of three grass species. *American Midland Naturalist* 115: 131–145.
- FOX, M. D., AND B. J. FOX. 1986. The susceptibility of natural communities to invasion. In R. H. Groves, and J. J. Burdon [eds.], *Ecology of biological invasions*, 57–66. Cambridge University Press, London, UK.
- FRANCO, A. C., AND P. S. NOBEL. 1989. Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* 77: 870–886.
- GOLDBERG, D. E. 1987. Seedling colonization of experimental gaps in two old-field communities. *Bulletin of the Torrey Botanical Club* 114: 139–148.
- , AND P. A. WERNER. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia* 60: 149–155.
- HOBBS, R. J. 1991. Disturbance a precursor to weed invasion in native vegetation. *Plant Protection Quarterly* 6: 99–104.
- , AND L. F. HUENNEKE. 1992. Disturbance, diversity and invasion: implications for conservation. *Conservation Biology* 6: 324–337.
- , AND S. E. HUMPHRIES. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* 9: 761–770.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- KAREIVA, P. [ED.]. 1996. Special feature: developing a predictive ecology for non-indigenous species and ecological invasions. *Ecology* 77: 1651–1652.
- KLINKHAMER, P. G. L., AND T. J. DE JONG. 1988. The importance of small-scale disturbance for seedling establishment in *Cirsium vulgare* and *Cynoglossum officinale*. *Journal of Ecology* 76: 383–392.
- LIPPINCOTT, C. L. 1997. Ecological consequences of *Imperata cylindrica* (cogongrass) invasion in Florida sandhill. Ph.D. dissertation, University of Florida, Gainesville, Florida, USA.
- LUKEN, J. O., AND J. W. THIERET [EDS.]. 1997. Assessment and management of plant invasions. Springer-Verlag, New York, New York, USA.
- MACDONALD, S. K., AND I. E. CHANDLER. 1994. Element stewardship abstract for *Imperata cylindrica* cf. var. major. Nature Conservancy, Arlington, Virginia, USA.
- MCCONNAUGHAY, K. D. M., AND F. A. BAZZAZ. 1987. The relationship between gap size and performance of several colonizing annuals. *Ecology* 68: 411–416.
- NOBLE, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. In J. A. Drake, and H. A. Mooney [eds.], *Biological invasions, a global perspective*, 301–310. John Wiley and Sons, New York, New York, USA.
- OLD, S. 1969. Microclimate, fire and plant production in an Illinois prairie. *Ecological Monographs* 39: 335–384.
- PEART, D. R. 1989. Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds and grazing on colonization. *Journal of Ecology* 77: 267–289.
- PEET, R. K., AND D. J. ALLARD. 1993. Longleaf pine vegetation of the Southern Atlantic and Eastern Gulf Coast regions: a preliminary classification. In S. M. Hermann [ed.], *Proceedings of the 18th Tall Timbers Fire Ecology Conference, The longleaf pine ecosystem: ecology, restoration, and management*, 45–81. Tall Timbers Research, Inc., Tallahassee, Florida, USA.
- , M. R. ANDERSON, AND M. S. ADAMS. 1975. Effect of fire on big bluestem production. *American Midland Naturalist* 94: 15–26.
- PICKETT, S. T. A., AND P. S. WHITE. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, California, USA.
- PIERSON, E. A., AND R. N. MACK. 1990. The population biology of *Bromus tectorum* in forests: effect of disturbance, grazing, and litter on seedling establishment and reproduction. *Oecologia* 84: 526–533.
- REICHENBERGER, G., AND D. A. PYKE. 1990. Impact of early root competition on fitness components of four semiarid species. *Oecologia* 85: 159–166.
- REJMÁNEK, M., AND D. M. RICHARDSON. 1996. What attributes make some plant species more invasive? *Ecology* 77: 1655–1661.
- RICE, K. J. 1987. Interaction of disturbance patch size and herbivory in *Erodium* colonization. *Ecology* 68: 1113–1115.
- SAJISE, P. E. 1972. Evaluation of cogon [*Imperata cylindrica* (L.) Beauv.] as a seral stage in Philippine vegetational succession. I. The cogonal seral stage and plant succession. II. Autecological studies on cogon. Ph.D. dissertation, Cornell University, Ithaca, New York, USA.
- SAS. 1989. SAS/STAT user's guide, version 6, 4th ed., SAS Institute, Cary, North Carolina, USA.
- SCHEINER, S. M., AND J. GUREVITCH [EDS.]. 1993. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- SHILLING, D. G. 1996. Integrated management of cogongrass. Integrated Pest Management Florida, Winter 1996, 2(4): 1–2. University of Florida Cooperative Extension Service, Gainesville, Florida, USA.
- , T. A. BEWICK, J. F. GAFFNEY, S. K. McDONALD, C. A. CHASE, AND E. R. R. L. JOHNSON. 1997. Ecology, physiology, and management of cogongrass (*Imperata cylindrica*). Final report prepared for the Florida Institute of Phosphate Research, Bartow, Florida, USA.
- , J. F. GAFFNEY, AND P. WALDROP. 1995. Cogongrass: problem and solutions. Alabama's treasured forests, Fall 1995: 8–9.
- SUDING, K. N., AND D. E. GOLDBERG. 1999. Variation in the effects of vegetation and litter on recruitment across productivity gradients. *Journal of Ecology* 87: 436–449.
- SWINCER, D. E. 1986. Physical characteristics of sites in relation to invasions. In R. H. Groves and J. J. Burdon [eds.], *Ecology of biological invasions*, 67–76. Cambridge University Press, London, UK.
- TABOR, P. 1949. Cogon grass, *Imperata cylindrica* (L.) Beauv. in the southeastern United States. *Agronomy Journal* 41: 270.
- UNITED STATES DEPARTMENT OF AGRICULTURE. 1997. PLANTS database. <http://plants.usda.gov>. National Plant Data Center, Baton Rouge, Louisiana, USA (7 April 1998).
- WILLIAMSON, M. 1996. Biological invasions. Chapman and Hall, New York, New York, USA.
- WINN, A. A. 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. *Journal of Ecology* 73: 831–840.
- ZAR, J. H. 1996. Biostatistical analysis, 3rd ed. Prentice Hall, Inc., Upper Saddle River, New Jersey, USA.