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Effects of *Imperata cylindrica* (L.) Beauv. (Cogongrass) Invasion on Fire Regime in Florida Sandhill (USA)

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Natural Areas Journal 20:140–149

ABSTRACT: Fire maintains structure and function in pyrogenic ecosystems. Invasive nonindigenous grasses have introduced fire cycles into nonpyrogenic ecosystems and altered the fire regime in pyrogenic ecosystems, changing structure and function of the invaded ecosystems. Sandhill, a pyrogenic pine savanna ecosystem, occurs on well-drained sands on the southeastern Coastal Plain of the United States. Sandhill sites are managed with relatively frequent low-intensity fires fueled by short caespitose grasses and pine needles ignited in the growing season. *Imperata cylindrica* (L.) Beauv. (cogongrass), a tall rhizomatous grass from Southeast Asia, is invading Florida sandhill. To determine if cogongrass is functionally equivalent to indigenous sandhill grasses, I compared fine-fuel attributes that contribute to fire behavior, a parameter of the fire regime, in uninvaded and invaded sandhill. Sandhill invaded by cogongrass had significantly greater fine-fuel loads, horizontal continuity, and vertical distribution. These fine-fuel changes in invaded sandhill resulted in fires that, compared to those in noninvaded sandhill sites, were more horizontally continuous and had higher maximum temperatures at greater heights. Fire-induced mortality of juvenile *Pinus palustris* Mill. (longleaf pine) was higher for pines growing in invaded sandhill. Rate of fuel accumulation after burning was greater in invaded sandhill. Over time, changes in sandhill fire behavior due to cogongrass invasion could result in higher mortality of native herbaceous and woody plants, shifting sandhill composition from a species-rich pine savanna to a grassland dominated by nonindigenous cogongrass.

Index terms: fire regime, Florida sandhill, *Imperata cylindrica*, invasive species, *Pinus palustris*

INTRODUCTION

Fire in Ecosystems

Recurrent fires are an integral part of the dynamics of many ecosystems (Christensen 1987, Trabaud 1987). Fire maintains ecosystem structure by influencing production, succession, and species composition and diversity (Pickett and White 1985), and fire affects ecosystem function by changing nutrient cycles and water relations (Christensen 1981, Wright and Bailey 1982, Trabaud 1987). Variation in ecosystem response to fire primarily results from differences in parameters of fire regime, that is, fire behavior, type, intensity, frequency, and season (Sousa 1984, Pickett and White 1985, Malanson 1987). When fire regime is significantly altered, the structure or function of pyrogenic ecosystems may consequently change (D'Antonio and Vitousek 1992).

Grass Invasions

Numerous grass species have been carried around the world as forage crops or for control of soil erosion (Hartley and Williams 1956). Many of the traits that agronomists have traditionally used to select promising forages also identify "ideal weeds" (Baker 1965): (1) they regrow rapidly after burning, grazing, and mowing; (2) they can resprout from rhizome fragments after plowing; and (3) they are highly competitive under a variety of environmental conditions (Chapman 1996). As a result, 12% of the world's total agricultural weed species are grasses, and the family Poaceae is a close second to the Asteraceae in number of genera (166) and species (753) that are weeds (Heywood 1989). Indeed, 10 of the 18 most noxious agricultural weeds in the world are grasses (Holm et al. 1977), the majority of these (21 out of 31) in the subfamily Panicoideae, which includes the genus *Imperata* (Chapman 1996). African and Asian grasses, which have evolved perennating organs near or below ground and regrow rapidly after defoliation by intense ungulate grazing (Parsons 1972), were widely distributed because of these aggressive growth traits; these are now some of the most globally widespread plant invaders (Hartley and Williams 1956). Seventeen of the 31 principal weedy grasses worldwide are of African origin (Chapman 1996).

The presence of invasive nonindigenous grasses has initiated fire cycles in ecosystems that were not formerly pyrogenic, resulting in the loss of indigenous species and alteration of important ecosystem processes (D'Antonio and Vitousek 1992, Hobbs and Huenneke 1992, Mack and D'Antonio 1998). In Hawaii, invasion of nonindigenous grasses, such as *Andropogon virginicus* L. (broomsedge), *Melinis minutiflora* Beauv. (molasses grass), *Schizachyrium condensatum* (Kunth) Nees (bush beardgrass), and *Pennisetum setaceum* (Forsk.) Chiov. (fountain grass), led to an increase in the frequency and size of fires in woodlands (Hughes et al. 1991, Smith and Tunison 1992), altering forest structure and nutrient cycles (Asner and Beatty 1996, D'Antonio et al. 1997, Mack and D'Antonio 1997). In Australia, invasive grasses introduced fire into nonpyrogenic tropical forest ecosystems (Humphries et al. 1991). In arid regions of Australia and Mexico, *Cenchrus ciliaris* L. (bur grass) now carries fires along watercourses that previously acted as fire barriers (Gill et al. 1990).

In addition to introducing fire into previously nonpyrogenic ecosystems, invasive nonindigenous grasses have altered the fire regime in pyrogenic ecosystems throughout the world, primarily by increasing fire frequency (Klemmendson and Smith 1964, Whisenant 1990, Humphries et al. 1991, Smith and Tunison 1992). In Brazilian cerrado, invasion of *Imperata brasiliensis* Trin. and other nonindigenous grasses resulted in more frequent fire, which in turn resulted in loss of native cerrado species and consequent dominance by highly flammable and fire-tolerant invasive grasses (Pivello and Coutinho 1996). The invasive *Pennisetum polystachion* (L.) Schultes (giant tussock grass) in forests of wet tropical Australia burns more intensely than the indigenous *Sorghum intrans* Muell. ex Benth. (Macdonald and Frame 1988). *Bromus tectorum* L. (cheatgrass), a highly flammable European grass that displaced less-flammable indigenous grasses across the Intermountain Region of the western United States (Mack 1986), increased the size and frequency of fires, leading to increased flooding, erosion, and displacement of indigenous shrubs and grasses (Klemmendson and Smith 1964, Whisenant 1990). Invasive grasses increased the areal extent of fires in the wet-dry tropics of Australia because of greater continuity of fuels (Gill et al. 1990).

Sandhill Fire Regime

Extensive pyrogenic forests of *Pinus palustris* Mill. (longleaf pine) once dominated the southeastern Coastal Plain of the United States from Virginia to eastern Texas (Christensen 1981, Myers 1990, Robbins and Myers 1990, Streng et al. 1993). By 1993 only about 1 million ha remained of the 22 million ha of longleaf pine forest present prior to European settlement of the Coastal Plain (Frost 1993, Simberloff 1993). Less than 385,000 ha of Florida longleaf pine forest remained by 1995, almost half of which occurred on public land managed for silviculture, hunting, and recreation (Landers et al. 1995).

One type of longleaf pine forest, the high pine ecosystem, is a fire-maintained pine savanna found on soils ranging from loamy sands underlain by clay (clayhill) to well-drained low-nutrient sands (sandhill) (Myers and Ewel 1990). In Florida, sandhill ecosystems extend from the middle of the Florida peninsula to the Panhandle region of the state, where sandhill gradually grades northward into clayhill (Davis 1967). Most Florida sandhill is characterized by an overstory of longleaf pine, a subcanopy of fire-tolerant oaks, and an herbaceous understory (Myers and Ewel 1990).

Prescribed burning in sandhill, modeled after the historic fire regime, consists of low-intensity surface fires ignited during the growing season at 5- to 8-year intervals (Myers 1990, Robbins and Myers 1990). Sandhill fires are primarily fueled by short (≤ 0.5 m tall) caespitose grasses such as *Aristida beyrichiana* Trin. & Rupr. (wiregrass) and *Sporobolus junceus* Michx. Kunth. (pineywoods dropseed) that dominate the ground layer. Sandhill fires are also propagated by needles of longleaf pine. Considered the most fire-tolerant southern pine, longleaf pine exists for its first years in a "grass stage" during which the belowground meristem is protected from fire (Croker and Boyer 1975, Landers 1991). After fire, the juvenile pine "bolts," growing rapidly above the grass layer (Maple 1975). From then on, thickening bark protects the trunk during low-intensity fires (Wade 1986, Boyer 1993). Fuel accumulation due to fire suppression or exclusion increases the possibility of burns that are lethal even to large longleaf pines (Christensen 1981, Wade and Johansen 1986, Myers 1990).

Cogongrass Invasion in Sandhill

Imperata cylindrica (L.) Beauv. (cogongrass) is a tall (to 1.5 m) rhizomatous grass indigenous to Southeast Asia (Gabel 1982). It is known as a noxious weed even where it is native (Holm et al. 1977) because burning after forest clearing maintains cogongrass dominance and prevents succession to forest (Eussen and Wirjahardja 1973). This species has been spread worldwide and is considered one of the most noxious invasive plants, invading agricultural areas as well as deserts, sand dunes, grasslands, forests, river margins, and swamps (Holm et al. 1977).

Many southeastern sandhill ecosystems have been invaded by cogongrass since its intentional and accidental introduction into the southeastern United States in the early 1900s (Tabor 1952a, 1952b). This grass is now naturalized in much of the southeastern Coastal Plain (Bryson and Carter 1993) and is considered a weed in developed areas such as pastures, pine plantations, and roadsides due to its pyrogenic nature (Patterson et al. 1980).

In sandhill ecosystems dominated by pyrogenic grasses and pines, the ecological consequences of cogongrass invasion are unclear. If cogongrass is functionally equivalent to indigenous grasses of the sandhills, then invasion would not significantly change fire regime. However, if cogongrass is not functionally equivalent to sandhill grasses in terms of fire, then fire regime should be altered by its invasion. Since fire is key to maintaining the characteristic structure and function of sandhill, significant changes in fire regime could result in significant alterations to system structure and function.

The purpose of this study was to determine if cogongrass invasion in sandhill significantly changes fire behavior, and fire severity as reflected in juvenile longleaf pine mortality. I compared several fine-fuel (grass and litter < 0.6 cm diameter) (Wade 1989) attributes in invaded and uninvaded sandhill: fuel load, vertical distribution, horizontal continuity, moisture content, and heat of combustion. I related these fine-fuel attributes to rate of fire spread and aspects of fire intensity. To evaluate fire severity in invaded and uninvaded sandhill, I compared maximum burn temperatures and mortality and growth of burned juvenile longleaf pines. I also examined rate of accumulation of fine fuels after burning in invaded and uninvaded sandhill.

METHODS

This study was conducted in sandhill at the 16,600-ha Citrus Tract of the Withlacoochee State Forest in west-central peninsular Florida near Brooksville (Citrus County; 28°65′N, 82°36′W) in 1995 and 1996. The Florida Division of Forestry conducts prescribed burns at the Citrus Tract for forest and game management. Cogongrass was intentionally introduced to the Brooksville area as a forage crop in the early 1900s (Tabor 1952b) and now occurs throughout the Citrus Tract in scattered swards ranging in size from a few square meters to several hectares. Cogongrass is thought to have been inadvertently spread throughout the Citrus Tract as rhizome fragments in road fill (J. Blanchard, Preserve Manager, The Nature Conservancy, Tallahassee, Florida, pers. com.).

This study was performed at four sites encompassing well-established extensive cogongrass swards. Chosen sites consisted of naturally regenerating longleaf pine stands of similar age that had not burned in four years (since 1991), sites occurring on well-drained sandy soils with little or no slope. Frequency of overstory pines and subcanopy oaks was similar across the four sites (Lippincott 1997). Because all four sites had similar forest management history, soil, and vegetation structure and composition, effect of site was not considered in statistical analyses.

Two treatment plots (invaded and uninvaded) were located adjacent to each other in each of the four sites (Figure 1). All eight treatment plots were 35 m wide, but the length of treatment plots within a site was determined by the dimensions of the cogongrass sward at that site, varying from 35 to 145 m in length (Table 1). Consequently, treatment plots were of equal area within each site but varied across the four sites (Figure 1).

Before burning I compared five fine-fuel attributes (load, vertical distribution, moisture content, heat of combustion, horizontal continuity) in two treatments—sandhill dominated by extensive swards of cogongrass (“invaded”) and nearby sandhill not invaded by cogongrass (“uninvaded”). Fine fuels were sampled in 1-m ↔ 1-m quadrats located randomly across the four sites, and different quadrats were sampled for each of the five fine-fuel attributes. For fine-fuel load, I harvested fine fuels (13 samples per treatment), then oven-dried them at 60 °C to constant weight. To determine preburn fine-fuel vertical distribution, I harvested fine fuels (13 samples per treatment) from three height classes (0–0.49 m, 0.50–0.99 m, and 1.00–1.50 m), then oven-dried them at 60°C to constant weight. For fine-fuel moisture content, I harvested live and dead fine fuels (10 samples per treatment), stored them in sealed plastic bags, weighed them the next day (fresh weight), then oven-dried them at 60°C to constant weight. Moisture content was calculated as the difference between fresh weight and dry weight, divided by fresh weight. To measure heat of combustion (kJ/g), I collected green leaves of cogongrass, and of all sandhill grasses combined from each quadrat (nine samples per treatment), oven-dried them at 60°C to constant weight, then ground and sifted them through a 1-mm sieve before a random subsample was oxidized in an oxygen bomb calorimeter (Parr Model 1341, Parr Instrument Company, Moline, Illinois, USA). I estimated fine-fuel horizontal continuity by measuring the total length in centimeters of bare ground under randomly located 100-m line transects (13 samples per treatment).

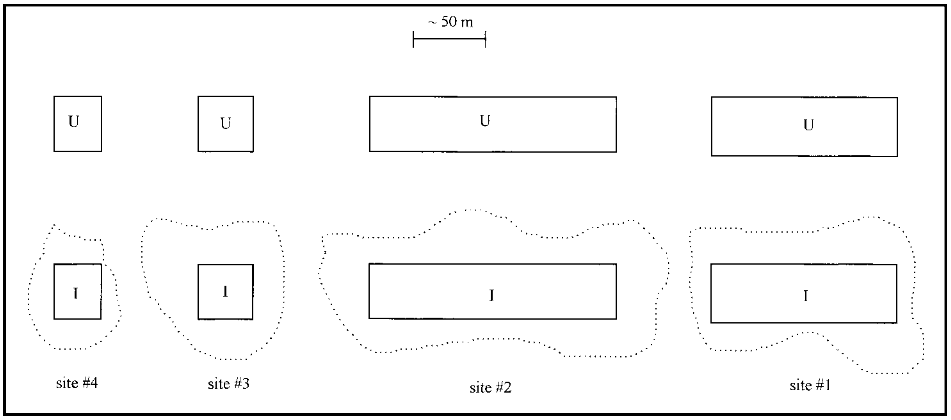

Figure 1. Arrangement of treatment plots within four study sites in Citrus Tract of Withlacoochee State Forest, Florida. Distance between sites varies from 1.6 to 4.8 km. U = univaded sandhill, I = invaded sandhill. Dotted lines are approximate boundaries of cogongrass swards.

Prescribed fires were conducted in the early growing season: sites 1, 2, and 3 in April 1995 and site 4 in March 1996 (Table 1). Each fire was ignited in the mid-morning as a backing fire lit parallel to the width of the treatment plots. Shifts in wind direction after ignition caused the third and fourth fires to become head fires approximately midway through the burn (Table 1); data were collected throughout the burns.

During the fires, I measured maximum temperatures at 0, 0.5, and 1.5 m heights at 13 randomly located points in each of the four treatment plots (52 samples per treatment). Eighteen temperature-indicating

Table 1. Treatment (uninvaded and invaded sandhill) plot size and weather parameters measured during four prescribed burns at Florida study sites.

Site #	Treatment Plot Size (m)	Month & Year Burned	Fire Type	Wind Speed (km/hr)	Relative Humidity (%)	Ambient Temperature (°C)
1	130↔35	April '95	backing	8	32	25
2	145↔35	April '95	backing	13	56–68	29
3	40↔35	April '95	backing/head	16	44–56	24
4	35↔35	March '96	backing/head	8	63	22

paints (Tempilaq , Tempil Division, Air Liquide America Corporation, South Plainfield, New Jersey, USA), each formulated to melt at a specific temperature, were applied in a row to narrow rectangular stainless steel strips (1.9 cm ↔ 30.5 cm) attached horizontally to an iron pole, one strip at each of the three heights. Temperatures tested (°C) were 94, 122, 150, 178, 206, 234, 262, 290, 318, 346, 374, 402, 430, 458, 542, 654, 766, and 878. These were within the range of published values (83°C to over 1,000 °C) for grassland and savanna fire temperatures (Daubenmire 1968, Wright and Bailey 1982, Frost and Robertson 1985). After the fires, the melted paint spot of maximum temperature was recorded for each strip. Mean maximum temperature was then calculated for each treatment (invaded and uninvaded) at each height for all four fires combined.

Rate of spread of the fire front during each of the four burns (four samples per treatment) was timed between two 1.8-m-tall metal poles placed at the opposite edges of each treatment plot, ranging from 35 to 145 m apart. After the burns, I calculated fire intensity (four samples per treatment) for each fire using the following formula (Byram 1973):

$$I = HWR$$

where I = fire intensity in kW/m, H = mean heat of combustion in kJ/g, W = mean fuel load in g/m^2, and R = rate of fire spread for each fire in m/sec.

After the burns, I compared fine-fuel accumulation rates in cogongrass and in sandhill at 3, 6, and 14 months after burning. I randomly selected 1-m ↔ 1-m quadrats (13 samples per treatment) in sites burned in April 1995. I harvested fine fuels in each quadrat and oven-dried them at 60 °C to constant weight.

To compare effects of fire on survival and growth of established longleaf pine juveniles (grass stage to 1.5 m tall), I tagged and measured the height (to top of meristem) and basal stem diameter of randomly located longleaf pine juveniles in burn units 1, 2, and 3 within one month of burning in April 1995. I tagged 150 pines in invaded treatment plots and 150 in uninvaded treatment plots. One year later I relocated all tagged pines, remeasured height and stem diameter of live pines, and compared percent increase.

All statistical tests were analyzed at $\alpha = 0.05$. All pairwise comparisons were considered significantly different at $P < 0.05$. All t-tests were two-tailed. Nonparametric tests were used if transforming did not normalize data. Statistical power values reported for parametric tests are retrospective (Thomas 1997).

RESULTS AND DISCUSSION

The presence of cogongrass in sandhill sites significantly affected several fine-fuel attributes that contribute to fire behavior. Prior to burning, invaded sandhill had a significantly greater fine-fuel load (1163 g

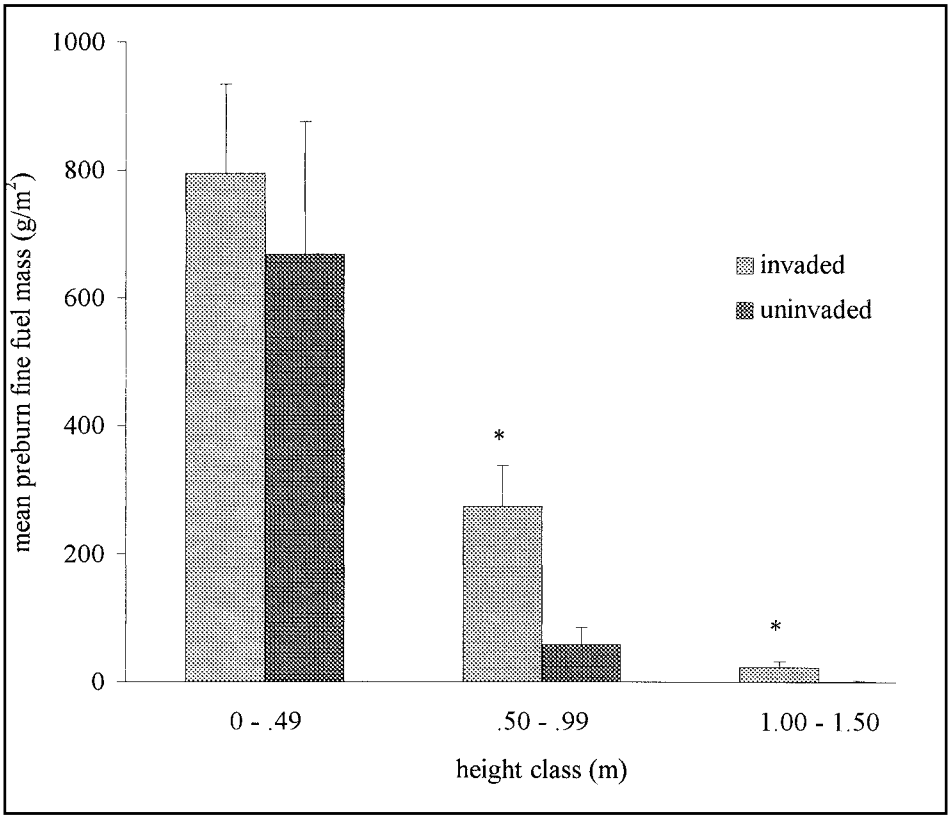

Figure 2. Mean fine fuel mass in three height classes in invaded and uninvaded sandhill. Error bars represent 1 SD. Asterisks denote significant differences between invaded and univaded sandhill at each height.

Table 2. Proportion of stainless steel strips with heat sensitive paint at each height (all fires combined) with temperature < 94 °C (52 samples per treatment). Asterisk indicates significant differences.

Height (m)	Invaded	Uninvaded	Test	Test Statistic	*P*
0	0.00	0.06	Fisher Exact		0.24
0.5	0.02	0.26	Chi-square	$\chi^2 = 10.1$	< 0.01*
1.5	0.12	0.53	Chi-square	$\chi^2 = 16.8$	< 0.01*

m^{-2} ± 285 g m^{-2} SD) than uninvaded sandhill (777 g m^{-2} ± 279 g m^{-2} SD) in sites not burned in four years (t-test: $t = 3.48$, df = 24, $P < 0.01$). Fuel load for uninvaded sandhill in this study was consistent with a study that showed a steady-state fine-fuel load of 750 g m^{-2} in sandhill four to five years after burning (Parrott 1967). Fine-fuel load for cogongrass-invaded sandhill in this study was similar to fine-fuel loads of *Hyparrhenia rufa* Nees. Stapf, an African grass that invades and dominates neotropical savannas (Sarmiento 1984).

Fine fuels in cogongrass-invaded sandhill prior to burning were generally taller than fine fuels in uninvaded sandhill. Fine-fuel loads 0.5–0.99 m tall and 1.00–1.50 m tall were significantly greater in invaded sandhill (Figure 2; Mann-Whitney rank sum test: $T = 260.0$, $P < 0.01$). In contrast, fine-fuel loads 0–0.49 m tall were similar in invaded (795 g m^{-2}) and uninvaded (668 g m^{-2}) sandhill (Figure 2; Mann-Whitney rank sum test: $T = 211.0$, $P = 0.07$).

Prior to burning, mean moisture content in live and dead fine fuels was similar in invaded (46.2% ± 10.7 SD) and uninvaded (42.3% ± 12.3 SD) sandhill (t-test: $t = 0.75$, df = 18, $P = 0.46$, power = 0.05). Mean heat of combustion was slightly higher for sandhill grasses (18.4 kJ g^{-1} ± 0.20 SD) than for cogongrass (18.7 kJ g^{-1} ± 0.22 SD) (t-test: $t = -3.37$, df =16, $P < 0.01$). These values were within the range of published values of heat of combustion for similar grassland fuels (Albini 1993, Glitzenstein et al. 1995).

Fine fuels were significantly more horizontally continuous in invaded than in uninvaded sandhill, accounting for 0.3% and 3.0% total bare ground, respectively (Mann-Whitney rank sum test: $T = 134.5$, $P = 0.04$). In invaded sandhill, only 2 of 13 transects contained bare ground, while 8 of 13 transects in uninvaded sandhill contained bare ground. Consequently, for all fires combined, proportion of strips at 0.5 and 1.5 m that did not reach 94°C (the temperature at which the first paint spot would melt) was higher in uninvaded than in invaded sandhill (Table 2); thus, fires in uninvaded sandhill were more patchy.

Mean maximum temperature in this study was significantly higher in invaded (260.9°C ± 13.7 SD) than in uninvaded sandhill for all three heights combined (218.3°C ± 14.5 SD) (Table 3). Mean maximum temperature at each height, however, was similar for invaded and uninvaded sandhill (Figure 3, Student-Newman-Keuls Method of all pairwise multiple comparisons). Mean maximum temperature tended to decrease significantly as height increased (Table 3). Mean maximum fire temperatures in this study were similar to those measured in a study in central Florida sandhill (Williamson and Black 1981) and were within the range for other grassland fuels (Wright and Bailey 1982). Because of its greater fuel load, invaded sandhill produced higher maximum fire temperatures than uninvaded sandhill (Table 4). Similarly, in Australian ecosystems, greater shoot biomass of non-indigenous grasses also contributed to hotter fires (Macdonald and Frame 1988).

Fuel in invaded sandhill was distributed significantly higher above the ground: 27% of total fuel was above 0.5 m, compared to only 8% in uninvaded sandhill (Figure 2). Cogongrass fuels from 0.50 to 0.99 m

Table 3. Two-way ANOVA (General Linear Model) of mean maximum temperatures at three heights in invaded and uninvaded Florida sandhill. Asterisk denotes significant differences.

Source of Variation	df	*F*	*P*	power
treatment	1	4.57	0.05*	0.42
height	2	4.66	0.02*	0.59
treatment ↔ height	2	0.98	0.40	0.05

Table 4. Highest temperature (°C) recorded for each height for each of the fires (13 samples per treatment) in invaded (INV) and in uninvaded (UNINV) Florida sandhill study sites. During fire #4, no paints reached 94 °C at 1.5 m height in sandhill.

		Height					
		0 m		0.5 m		1.5 m	
Fire #	Fire Type	INV	UNINV	INV	UNINV	INV	UNINV
1	backing	318	290	290	290	262	150
2	backing	290	290	290	262	290	262
3	head	318	290	262	290	458	290
4	head	458	318	458	150	346	< 94

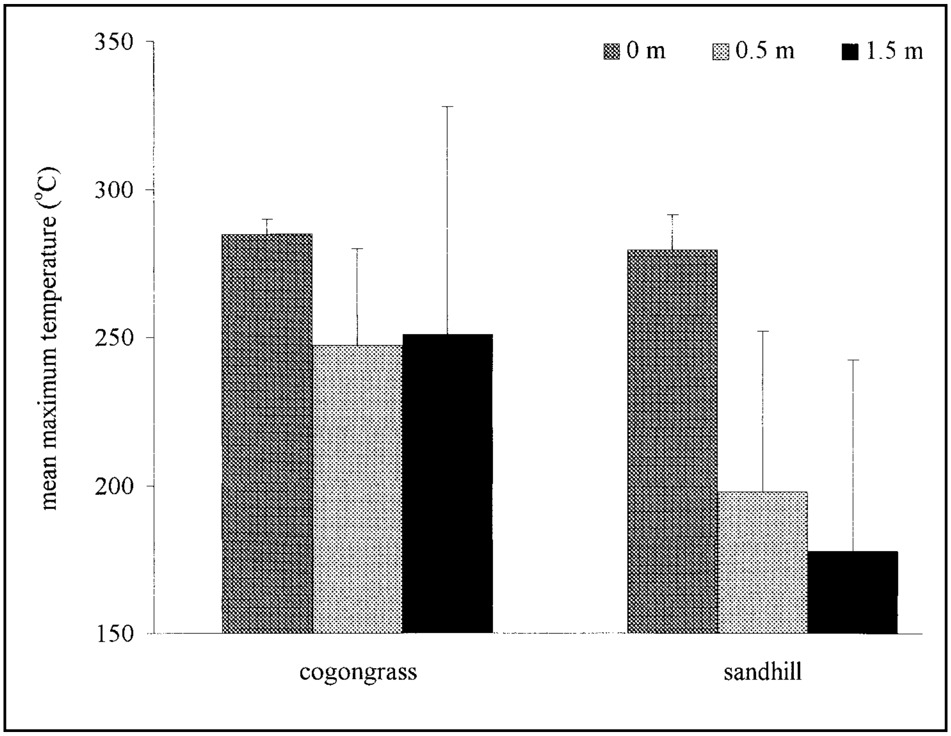

Figure 3. Mean maximum fire temperatures at three heights in invaded and uninvaded Florida sandhill for all four fires combined. Error bars represent 1 SD. None of the differences were significant at alpha = 0.05

height were 4.5 times greater in mass than uninvaded sandhill fuels; consequently, fire temperatures in cogongrass were 50°C hotter at 0.5 m height (Figure 3). Cogongrass fuels from 1.00 to 1.50 m height were six times greater in mass than in uninvaded sandhill, and fire temperatures in cogongrass were 73°C hotter at 1.5 m (Figure 3).

Rate of fire spread measured during the four burns was similar between invaded and uninvaded sandhill (Table 5; Wilcoxon signed rank test: $W = -2.00$, $P = 0.75$). Calculated fire intensity was similar in invaded and uninvaded sandhill (paired t-test: $t = 1.55$, df = 3, $P = 0.22$, power = 0.14). Fire intensity values were consistent with published values for similar grassland ecosystems worldwide (Frost and Robertson 1985).

After burning, fine fuels accumulated more quickly in invaded than in uninvaded sandhill. Invaded sandhill had over 100% more fine fuel than uninvaded sandhill at 3 months after burning (Figure 4; Mann-Whitney rank sum test: $T = 242.0$, $P < 0.01$), 86% more at 6 months (t-test: $t = 4.97$, df = 24, $P < 0.01$), and 50% more at 14 months (t-test: $t = 3.34$, df = 24, $P < 0.01$). Before being burned for this study, invaded sandhill that had not burned in four years had accumulated 50% more fine fuel by weight than uninvaded sandhill. With more rapid accumulation of fuels that are more evenly distributed than in uninvaded sandhill, fire in sandhill invaded by cogongrass has the potential to ignite and spread more frequently in the absence of fire management.

Over the year after burning, percent mortality of longleaf pine juveniles (Figure 5) was significantly greater in invaded than in uninvaded sandhill for pines 0.50 to 0.99 m tall (80% v. 49%) (z-test: $z = 1.98$, $P = 0.05$). Mortality was similar, however, for pines 0 to 0.49 m tall (z-test: $z = 1.50$, $P = 0.13$, power = 0.32) and for pines 1.00 to 1.50 m tall (z-test: $z = -0.48$, $P = 0.68$, power = 0.08). At one year postburn, median increase in height for pines 0 to 0.49 m tall was significantly lower in invaded than in uninvaded sandhill (21% v. 50%) (Mann-Whitney rank sum test: $T = 6162.5$, $P < 0.01$). However, this smaller increase in height for pines to 0.49 m tall is probably due to competition with cogongrass instead of direct fire effects (Lippincott 1997). There was no difference in height increase for pines 0.50 to 1.50 m tall between invaded and uninvaded sandhill (29% vs. 27%) (t-test: $t = 0.18$, df = 19, $P = 0.86$, power = 0.05). Stem diameter growth did not differ between invaded and uninvaded sandhill for pines 0 to 0.49 m tall (Mann-Whitney rank sum test: $T = 666.5$, $P = 0.42$) nor for pines 0.50 to 1.50 m tall (Mann-Whitney rank sum test: $T = 27.5$, $P = 0.15$).

Fire temperature can be an indicator of fire intensity and a predictor of plant tissue death, which occurs at approximately 66°C for unprotected tissues (Albini 1993). Since combustion occurs when fuel temperature reaches 346 °C ± 40°C SD (Albini 1993),

Table 5. Rate of spread (R) and fire intensity (I) for each fire in invaded (INV) and in uninvaded sandhill (UNINV) sites in Florida. Fire intensity was calculated using the formula I = HWR, where H equals mean heat of combustion for invaded (18.4 kJ g^{-1}) and uninvaded (18.7 kJ g^{-1}) sandhill, W equals mean prefire fine-fuel mass for invaded (1163.2 g m^{-2}) and uninvaded (776.9 g m^{-2}) sandhill, and R equals rate of spread for each of the four fires.

		R (m/sec)		I (kW/m)	
Site #	Fire Type	INV	UNINV	INV	UNINV
1	backing	0.0185	0.0235	395.95	341.41
2	backing	0.0208	0.0195	445.18	283.30
3	head	0.1300	0.1300	2782.37	1888.64
4	head	0.1458	0.0280	3120.54	406.78

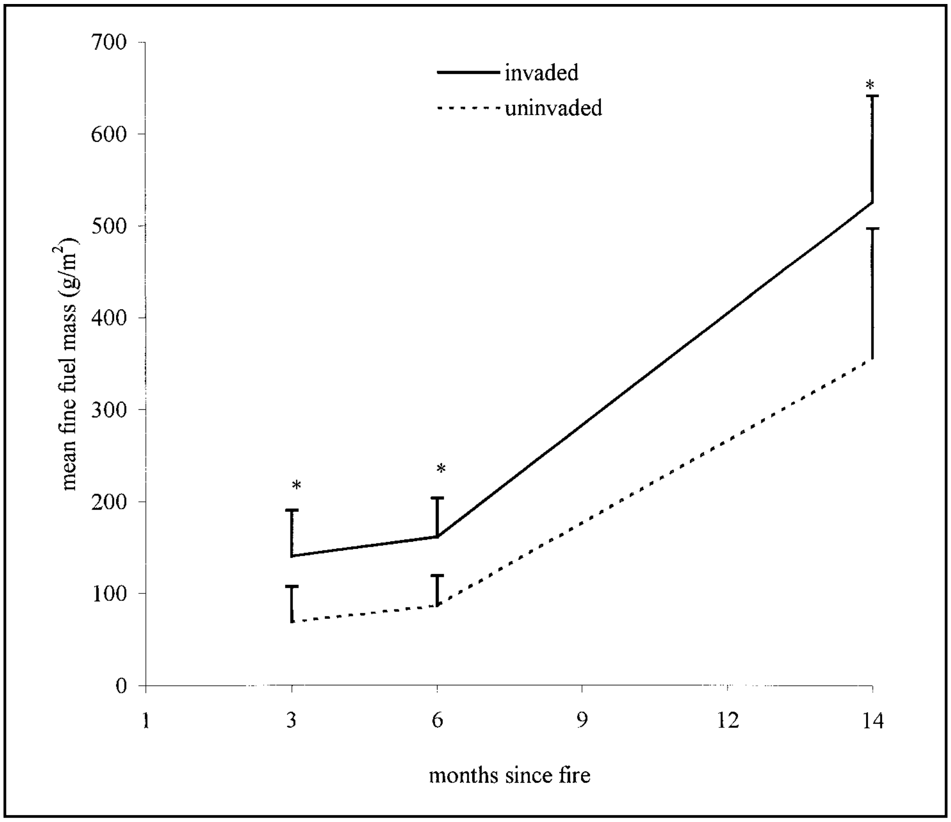

Figure 4. Mean fine fuel mass accumulated at 3, 6, and 14 months after burning in invaded and uninvaded Florida sandhill. Error bars represent 1 SD. Asterisks denote significant differences between invaded and univaded sandhill.

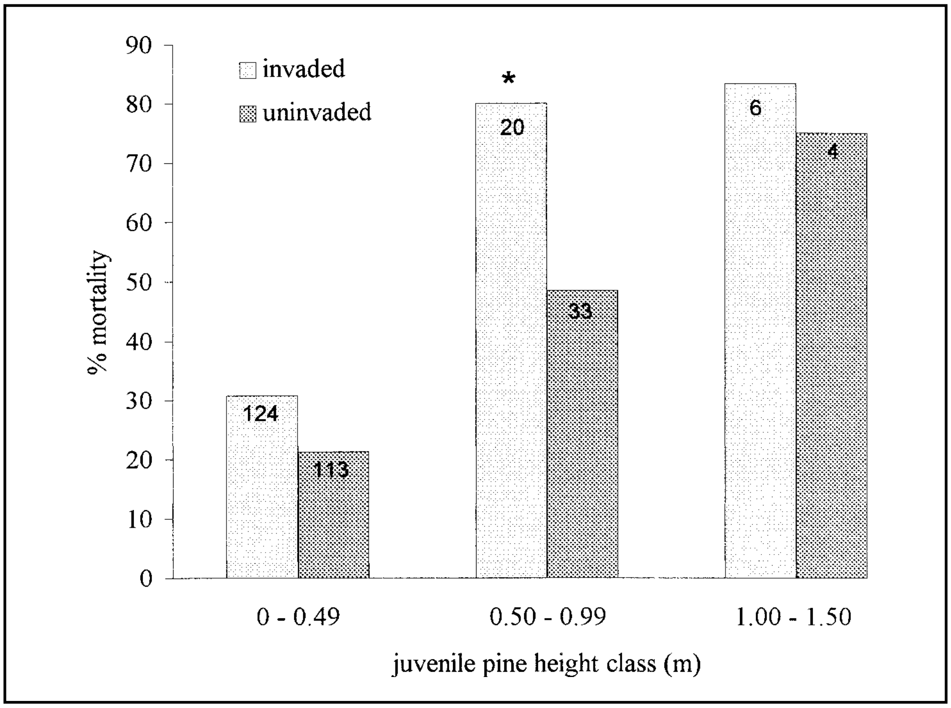

Figure 5. Percent mortality of burned juvenile longleaf pines in three height classes one year after burning in invaded and uninvaded Florida sandhill. Total number of pines sampled in each height class shown at the top of each column. Asterisk denotes significant difference between invaded and uninvaded sandhill.

protected meristematic tissues can be exposed to lethal temperatures when surrounding leaves, pine needles, and bark burn. In this study, fire temperatures in cogongrass reached a maximum of 458 °C on some strips at all heights. These instantaneous temperature measurements at a given point suggest that even fire-tolerant sandhill plant species such as longleaf pine may lose aboveground tissues to cogongrass-fueled fires, although additional data on fire temperature duration (e.g., Jacoby et al. 1992) would help to determine direct mortality effects. Rapid growth out of the grass stage offers longleaf pine juveniles some protection from fire. Longleaf pine juveniles in cogongrass, however, still appear to be vulnerable to fire damage in the 0.50–0.99 m height range because of the greater quantity of fuel and higher fire temperatures. A similar study in northern Thailand (Koskela et al. 1995) examined *Pinus merkusii* Jugh. & de Vriese, which, like longleaf pine, exists for several years in a fire-resistant grass stage. Juvenile pines growing with cogongrass were killed in frequent fires fueled by cogongrass.

CONCLUSIONS

Although cogongrass in sandhill might be viewed as an additional pyrogenic grass in a system already structured by grass-driven fires, this new arrival is distinctly different from sandhill grasses: it is taller, extensively rhizomatous, and faster-growing, in contrast to indigenous grasses of the sandhills, which are primarily short, caespitose, and slow-growing. These traits enable cogongrass to behave in novel ways in sandhill, changing fire regime, as demonstrated in this study, as well as displacing sandhill plants and animals, suppressing seedling recruitment, and limiting resources (Lippincott 1997). In this sense, cogongrass is not just an additional grass species in the functional group that perpetuates fire in the sandhill ecosystem; it also represents a new functional group in sandhill, of extensively rhizomatous pyrogenic grasses. Invasion by this new functional group appears to change the disturbance regime in sandhill (Sousa 1984, Mack and D'Antonio 1998), with consequences for the perpetuation of this indigenous ecosystem.

The purpose of determining the functional equivalence of cogongrass to sandhill grasses was to predict whether cogongrass invasion could shift a pine forest ecosystem to a grassland dominated by cogongrass. This study, coupled with results from related studies (Lippincott 1997), suggests that cogongrass has the ability to dominate and displace most sandhill vegetation, eventually forming treeless fire-prone grassland, as has been the case in previously forested ecosystems in Southeast Asia (Eussen 1980). As mentioned earlier in this paper, the alteration of fundamental ecosystem processes by invasive nonindigenous plant species is increasingly being documented in ecosystems throughout the world (Vitousek 1990, Mack and D'Antonio 1998). These invasions often cause shifts to a new or different community state, with consequences for regional and global biodiversity.

Sandhill Management Implications

Disturbances such as fire are known to facilitate invasion of pyrogenic species (Hobbs and Huenneke 1992). Indeed, the relatively frequent burning essential to sandhill management is a key to cogongrass dominance, which results in hotter, more frequent fires that kill all but the most fire-tolerant species and stimulate vegetative spread (Lippincott 1997). As long as sandhill with cogongrass is burned, cogongrass will spread and dominate.

Management of ecosystems dominated by invasive species requires approaches that integrate control of the invasive species with alteration of processes that facilitate invasion (Hobbs and Humphries 1995). Fire prevention in sandhill, however, will not result in restoration and eventual dominance of characteristic sandhill plant species. Rapid accumulation of dense leaf litter in cogongrass, along with its comparatively large rhizome and root mass (Lippincott 1997), make unassisted recruitment of most sandhill seedling species improbable in cogongrass swards. In Southeast Asia, fire prevention in cogongrass swards allowed eventual succession to nonpyrogenic forest (Eussen and Wirjahardja 1973). This may also be the case in sandhill dominated by cogongrass, where fire prevention would allow eventual succession to nonpyrogenic forest dominated by fire-intolerant tree species rather than pyrogenic sandhill species.

In the southeastern United States, cogongrass is already well established in peninsular Florida and in the Gulf Coast states, and it is apparently moving inland across the Coastal Plain (Watson and Dallwitz 1992). Based on its broad environmental requirements and tolerance of cold temperatures (Patterson et al. 1980), there are no apparent ecological impediments to the invasion of cogongrass across the historic range of longleaf pine forests, threatening dozens of species of rare plants and animals (Engstrom 1993, Folkerts et al. 1993, Walker 1993, Ware et al. 1993).

ACKNOWLEDGMENTS

This study was part of a doctoral dissertation project supported by a National Science Foundation Graduate Research Fellowship to the author. I thank my advisor, Francis Putz, for guidance on this project. I thank the staff of the Florida Division of Forestry at Withlacoochee State Forest for assistance is choosing study sites and for conducting prescribed fires. I appreciate helpful comments on earlier versions of this manuscript provided by Victoria Nuzzo, Ron Myers, Jon Blanchard, George Tanner, Dale Wade, and an anonymous reviewer.

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