Cogongrass (*Imperata cylindrica*), an Alien Invasive Grass, Reduces Survival and Productivity of an Establishing Pine Forest

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Abstract: A 27-month-long study was conducted to compare the impacts of *Imperata cylindrica* (L.) (Beauv.) and native vegetation competition on the productivity of *Pinus taeda* (L.) seedlings. In March 2003, 1-year-old pine seedlings were planted in the following treatments: vegetation free (VF), native competition (NC), and *I. cylindrica* (IC) competition. At the end of the study, only 26% of the IC seedlings survived, half of what was observed in the NC treatment. The IC seedlings had significantly smaller root collar diameter than the NC seedlings ($P < 0.0001$) after the first growing season and by the end of the third growing season the height and stem volume index were significantly less as well ($P < 0.0001$). After one full growing season, the NC and IC pine seedlings had 21 and 11.5% of the total biomass of the VF seedlings, respectively. After three growing seasons, the IC pine seedling total biomass was 2.4% of that of the VF seedlings and 18% of that of the NC seedlings ($P < 0.0001$). The greatest difference was in the pine needle biomass with the IC pine needle biomass being only 11% of that of the NC. During the first growing season, the IC pine seedlings maintained the lowest levels of light-saturated net photosynthesis and stomatal conductance. These results may be explained by reduced amounts of foliar nitrogen and water stress that result from *I. cylindrica* competition. The pines in the IC treatment had the lowest total foliar surface area and the lowest specific leaf area, which may explain the reduced productivity. Evidence from this study suggests that *I. cylindrica* competition significantly reduces the productivity and growth of *P. taeda* seedlings compared with that from native vegetation. FOR. SCI. 54(6):579–587.

Keywords: cogongrass, *Pinus taeda*, photosynthesis, stomatal conductance, soil water potential, foliar nitrogen

INVASION BY nonindigenous species can have major impacts on native ecosystems with both ecological and economic consequences (Mack et al. 2000). The structure and function of an ecosystem can be altered by the presence of an exotic invasive species (Vitousek et al. 1997) owing to changes in system-level rates of resource supply, trophic structure, and disturbance regime (D'Antonio and Vitousek 1992). Such changes are clear in forests, where invasive plants affect the establishment, growth, and productivity of new seedlings, which represent the future canopy species.

Several studies have been conducted to test the impacts of invasive plants on forest regeneration and growth and their mechanisms of action. In Hawaii, it was observed that the dominant native tree *Metrosideros polymorpha* (Gaud.) was not able to establish a single seedling beneath the canopy of the invasive nitrogen-fixing *Myrica faya* (Ait.) because of the physical characteristics of the leaf litter (Walker and Vitousek 1991). Increasing biomass of *Tradescantia fluminensis* (Vell.) led to an exponential decrease in the species richness and abundance of native forest seedlings in New Zealand by rapidly reducing the light availability (Standish et al. 2001). Competition for light was also implied to be the mechanism by which *Lonicera maackii* (Rupr.) was reducing survival and biomass of *Acer saccharum* (Marsh.) in Ohio, USA (Gorchov and Trisel 2003). The shrub *Rhamnus frangula* (L.) reduced the growth and survival of *Acer rubrum* (L.), *A. saccharam*, *Fraxinus Americana* (L.), and *Pinus strobus* (L.) in New Hampshire, USA, which the authors suggested might be due to belowground competition from *Rhamnus* with its extensive shallow root system (Fagan and Peart 2004).

A species that is making a significant impact on forests in the southeastern United States is *Imperata cylindrica* (L.) (Beauv.), cogongrass, a perennial rhizomatous grass thriving in both undisturbed and disturbed areas with soil types ranging from nutrient-poor coarse sands to nutrient-rich sandy loams (Jose et al. 2002). *I. cylindrica* spreads by both sexual and asexual mechanisms. *I. cylindrica* is a prolific producer of seeds, with as many as 3,000 1-mm-long grains per plant, which generally are dispersed within 15 m of the plant (Holm et al. 1977) but may be carried by wind up to 24 km over open country (Hubbard et al. 1944). Established plants spread vegetatively through rhizomes, which are long, tough, white underground stems with short internodes. They comprise >60% of the plant's biomass, resulting in a high root/shoot ratio that allows it to survive and thrive after fire or cuttings (Sajise 1976). Regeneration of new plants can occur from rhizome fragments weighing as little as 0.1 g (Ayeni and Duke 1985). The extensive growth of *I. cylindrica* results in dense mats of rhizomes in the soils, forming dense monocultural patches with fresh weights ranging up to 40 Mg ha^{-1} (Terry et al. 1997), producing approximately 4.5 million shoots (Soerjani 1970).

I. cylindrica can negatively affect forests in a variety of ways. The density of the belowground rhizome network makes *I. cylindrica* a mechanical hindrance to growth of roots of native species. The rhizome tips are sharp; they may even penetrate the roots of native species, leading to damage or mortality by infection (Eussen and Soerjani 1975). *I. cylindrica* occupies significant space belowground, which may prevent root growth of germinating seeds. Lippincott (1997) showed that *I. cylindrica* replaced most understory species in a Florida sandhill savanna and greatly reduced the diversity. The leaf blades of *I. cylindrica* have been observed to reach heights of 1.5 m under good moisture and fertility conditions (Holm et al. 1977), which suggests that *I. cylindrica* may compete for light on the forest floor, especially with understory species and young tree seedlings. The dense carpet of leaf blades may prevent sunlight from reaching the upper soil layer, eliminating the opportunity for seedling germination.

Allelopathy has been suggested to be another mechanism by which *I. cylindrica* gains dominance over native species. Several studies have demonstrated the impacts of *I. cylindrica* extracts on the germination, growth, and survival of crop plants (Hubbard et al. 1944; Soerjani 1970; Eussen et al. 1976). It was shown that *I. cylindrica* suppressed tomatoes (*Solanum lycopersicum* [L.]) and cucumbers (*Cucumis sativus* [L.]), especially at low pH (Eussen and Wirjahardja 1973). Koger and Bryson (2004) demonstrated that extracts of *I. cylindrica* roots and foliage with concentrations as low as 0.5% inhibited germination of *Cynodon dactylon* (L.) and *Lolium multiflorum* (Lam.) by up to 62%.

I. cylindrica has been shown to alter disturbance regimes of forests. Lippincott (2000) observed that fires from swards of *I. cylindrica* could reach higher temperatures (e.g., 450°C) and greater heights than those for native vegetation. If fires this hot persist longer than a few seconds in any given area, not only will the understory species die but juvenile trees will also die. Mortality was even observed for juvenile *Pinus palustris* (Mill.), which normally are fire tolerant (Lippincott 2000). Because *I. cylindrica* allocates significant carbon belowground, it is able to recover quickly after fire, which is why Lippincott (2000) suggested that frequent intense fires could convert a pine savanna into an *I. cylindrica*-dominated grassland. *I. cylindrica* is also favored by disturbances other than fire. King and Grace (2000) showed that *I. cylindrica* can germinate, survive, and grow in wet pine savanna communities after several types of disturbance including mowing, tilling, and light gaps created by cutting or natural stand mortality.

All of the evidence thus far has demonstrated that *I. cylindrica* does pose a threat to forests by altering the trophic structure and disturbance regime and by belowground interactions. Most of the studies, however, have focused on the impacts of this invasive plant on crop or understory species and less on how it affects the species that will represent the canopy. *I. cylindrica* is having an impact on pine forests throughout the southeastern United States, and little work has been done to quantify the impact of the invasive species on the pines themselves. In this study, we examined how *I. cylindrica* affects the survival, growth, and productivity of young *Pinus taeda* (L.) seedlings. We compared how the seedlings performed in the absence of competition, with competition from native species, and with competition from *I. cylindrica*. With pine seedlings growing in the absence of competition as a reference for their growth potential for our site, we hypothesized that *I. cylindrica* competition would have a much greater impact on seedling growth and productivity than competition from native species by reducing their photosynthetic and growth rates.

Methods
Site Description

This field study was conducted on an industrial plantation site in Santa Rosa County, Northwest Florida, USA (30°50′N, 87°10′W). The site was a 60-ha cutover area (site index = 24.4 m), which quickly became infested with *I. cylindrica* after harvesting of the 17-year-old *P. taeda* in early 2002. The climate in this area is temperate with moderate winters and hot, humid summers. Total annual precipitation in 2003 was 1,928 mm with the wettest month being June (418 mm), and the mean annual temperature was 19.4°C and with August being the hottest (27.3°C) (National Oceanic and Atmospheric Administration). The soils on the site were mapped as a Lakeland series (Typic Quartzipsamment: 89% sand, 7.8% silt, and 3.4% clay). Native species on the site included *Smilax rotundifolia* (L.), *Smilax aspera* (L.), *Rubus occidentalis* (L.), *Ilex glabra* (L.) (A. Gray), *Andropogon virginicus* (L.), *Asclepias veriagata* (L.), *Carphephorus paniculatus* (J.F. Gmel), *Ilex vomitoria* (Aiton), and *Erechtites hieraciifolia* (L.) (Raf.).

Cultural Treatments

The experimental design consisted of 15 plots (7.9 × 10.4 m), with each of the following three treatments assigned to five plots:

VF—vegetation free: maintained by weekly hand weeding
NC—native competition: natural establishment and growth of native vegetation was allowed. The major native species on site included *S. rotundifolia*, *S. aspera*, *R. occidentalis*, *I. glabra*, *A. virginicus*, *A. veriagata*, *C. paniculatus*, *I. vomitoria*, and *E. hieraciifolia*.
IC—*I. cylindrica* competition: a dense *I. cylindrica* cover established from local seed or rhizome sources

In fall 2002, a uniform patch of *I. cylindrica* of about 1 ha in size was selected for the five IC plots. Five VF and five NC treatment plots were randomly established in an area 20 m away from the advancing front of the *I. cylindrica* patch. The 20-m buffer zone was considered appropriate since *I. cylindrica* spread had been estimated to be about 2 m year^{-1} at this site (Collins et al. 2007).

Although five plots were randomly established within each of the treatment areas, the treatment areas themselves represented locations within a single cutover site. Thus, the five plots were not randomly distributed in space. This raises the problem of pseudoreplication (Hurlbert 1984; van Mantgem et al. 2001), in which differences among treatments could be due to uncontrolled sources of variation inherent to each area. However, the study area was uniform

with similar soil and similar vegetation before cogongrass started invading from an access road nearby, after harvesting in early 2002 (Ramsey et al. 2003). The area further represents typical upland sandhills, which are quite common throughout the southeastern coastal plain where *I. cylindrica* is invading. We wanted to capture the naturally invaded site with adjacent native vegetation to eliminate issues involved in conducting such an experiment in an artificial setting (e.g., field mesocosm or greenhouse). Further, we used this invaded site to make intensive physiological measurements to understand the mechanisms of competition. The growth rates and net photosynthesis reported in our study are comparable to data reported from similar sites in Louisiana (Tang et al. 2003), North Carolina (Murthy et al. 1997), and Florida (McGarvey et al. 2004). The *I. cylindrica* at our study site exhibited growth characteristics similar to those observed in other invaded sites as well (Willard et al. 1996).

All of the plots, except for the IC treatment, were site prepared in October 2002 with a tank mix of imazapyr and triclopyr at a rate of 936.2 ml ha^{-1} to ensure that there was no *I. cylindrica* infestation. All treatment plots had a 3-m buffer around them. Because of the close proximity of the plots (all were within an area of approximately 2 ha), the soil conditions were assumed to be uniform before installment of the treatments.

On March 6, 2003, 1-year-old bareroot *P. taeda* seedlings, purchased from a local nursery, were planted in four rows of eight seedlings in each plot (32 seedlings per plot) with spacing of 1.1 m $\times$ 2.0 m. Nitrogen fertilization of short-rotation woody biomass species at establishment has become common practice (Jokela et al. 1991, Lee and Jose 2005), particularly for *P. taeda* (Martin and Jokela 2004, Jokela et al. 2004), so the pine seedlings were fertilized with ammonium sulfate fertilizer at the rate of 55 kg of N ha^{-1} in March 2003. Four randomly selected seedlings were fertilized with ^{15}N-labeled ammonium sulfate (5% enrichment) instead of the nonenriched ammonium sulfate fertilizer at the same rate for a companion project.

Competitor Abundance

To assess the degree of competition on the pine seedlings, percent cover and above- and belowground biomass of the competing vegetation were determined. Percent cover of each plot was estimated monthly, for the duration of the study, by placing a square meter quadrat randomly in four locations within each plot and estimating the mean percentage of vegetative cover. Above- and belowground biomass of the competing vegetation was collected monthly from each plot. Aboveground *I. cylindrica* and native vegetation were clipped at ground level from two quadrats (0.5 m^2). Live and dead foliage was separated and all samples were dried at 65°C for 72 hours and weighed. Belowground biomass was collected using soil augers from the same plots used for aboveground biomass harvesting. Three soil cores (5-cm diameter) were taken within each quadrat up to a depth of 18 cm. Roots and rhizomes were washed, dried at 65°C for 72 hours and weighed.

Growth and Gas Exchange Measurements

The root collar diameter (RCD) and height were measured for every pine seedling at planting and remeasured at the end of the growing season in 2003, 2004, and 2005. These values were used to calculate stem volume index (SVI) (RCD^2 $\times$ height). Seedling survival was quantified during each measurement period. In December 2003 and June 2005, four seedlings from each plot were harvested. The needles of all of the seedlings harvested in December 2003 were scanned with a LI-3100 leaf area meter (LiCor, Inc., Lincoln, NE) to estimate total leaf area. The roots, leaves, and stems of all the harvested seedlings were separated, dried at 65°C for 72 hours, and weighed. The dried foliage of the December 2003 harvest was ground using a Wiley mill to pass through a 1-mm screen. The foliar nitrogen concentration was determined using an isotope ratio mass spectrometer (UC Davis Stable Isotope Laboratory) as we also quantified foliar ^{15}N of the same samples for the companion study.

Light saturated net photosynthesis (A_{max}), stomatal conductance (g_s), and internal leaf CO$_2$ concentration (C_i) of four pine seedlings per plot were measured using a portable open leaf gas exchange system (LI-6400, LiCor, Inc.) with a photosynthesis photon flux density of 1,600 μmol m^{-2} s^{-1} and a flow rate of 500 μm/s of CO$_2$ with a reference concentration of 370 ppm. Measurements were taken between 1,000 and 1,400 hours monthly from July 2003 through October 2003. The uppermost fully developed needles were measured. Approximately three fascicles (nine needles) were used for each measurement. The gas exchange measurements were recalculated using the total surface area of the needles, which was calculated on the basis of the assumption that each fascicle was a cylinder (Madgwick 1964).

Statistical Analysis

Seedling growth parameters (height, RCD, and SVI) and physiological variables (light-saturated net photosynthesis, stomatal conductance, and leaf internal CO$_2$) for the three treatments were compared using a repeated-measures analysis of variance (ANOVA). Competitor cover and biomass were also analyzed using a repeated-measures ANOVA. An adjusted Tukey's post hoc test was used for mean separation.

Data collected only once at harvesting (biomass, specific leaf area [SLA], and % foliar nitrogen) were analyzed using one-way ANOVA. Differences were declared significant at $\alpha < 0.05$. Levene's test for homogeneity among variances was used to determine which pairwise post hoc comparison method should be used. For homogenous variances, Duncan's post hoc test was used; for heterogeneous variances, Dunnett's T3 test (Dunnett 1980) was used. We also used a regression approach to analyze total seedling biomass as a function of competing vegetation biomass. This approach avoids the problem of pseudoreplication, but the inferential power of ANOVA is lacking. All analyses were performed using the SAS statistical software package (1999; SAS Institute, Cary, NC).

Results

Competitor Abundance

There was significantly greater ground cover in the IC treatment compared with the NC treatment. The mean percent cover of *I. cylindrica* in all of the plots for the duration of the study was 95.4%, whereas native species covered 81.9% ($F_{1,8}$ = 19.44, P = 0.002). There was no difference in the aboveground biomass of the competing vegetation. The aboveground biomasses of *I. cylindrica* and the native species were 239.7 and 234.8 g m^{-2}, respectively ($F_{1,8}$ = 0.02, P = 0.879). However, *I. cylindrica* had significantly greater belowground biomass (1,117.3 g m^{-2}) than native species (143.7 g m^{-2}) ($F_{1,8}$ = 93.50, P < 0.0001).
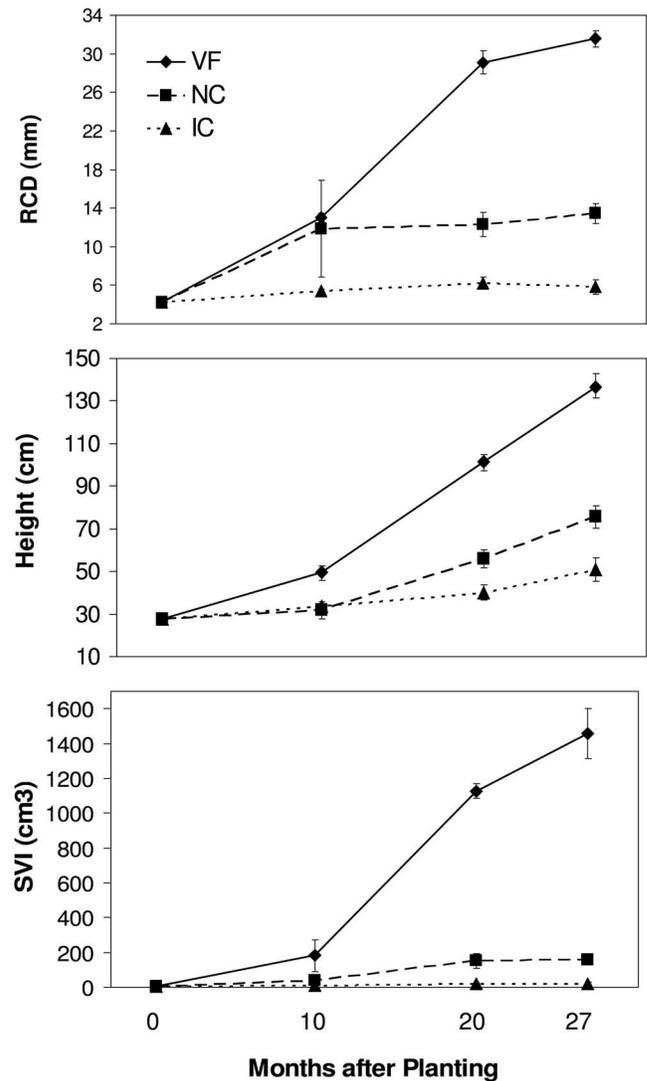
Survival and Growth of P. taeda

At the end of the study, approximately 27 months after planting, only 26% of the seedlings growing in the IC treatment survived compared with 51 and 61% survival observed in the NC and VF treatments, respectively (Table 1). At planting, the seedling mean RCD was 4.23 mm and grew to 31.5, 13.4, and 5.9 mm for the VF, NC, and IC treatments, respectively (Figure 1A) by the end of the study. Repeated measures analysis revealed that RCDs were significantly different among treatments ($F_{2,12}$ = 58.75, P < 0.0001). There was an interaction between treatment and time for RCD. Mean seedling height at the start of the study was 27.7 cm and grew to 136.6, 75.7, and 50.8 cm by the end of the study for the VF, NC, and IC treatments, respectively ($F_{2,12}$ = 140.06, P < 0.0001) (Figure 1B). The seedling heights for the IC and NC treatments did not differ after the first growing season but did so by the end of the second growing season. There was an interaction between treatment and time for seedling height ($F_{4,24}$ = 17.16, P < 0.0001). Mean SVI for the seedlings in all treatments was 4.95 cm^3 at planting and rose to 1,455.8, 158.6, and 21.8 cm^3 for the VF, NC, and IC treatments, respectively, with significant treatment effects ($F_{2,12}$ = 297.98, P < 0.0001) (Figure 1C). The SVI did not differ between the IC and NC treatments until the second growing season.

Above- and Belowground Biomass

After one full growing season, pine seedlings growing in the VF treatment had a mean foliar ($F_{2,12}$ = 71.14, P < 0.0001), stem ($F_{2,12}$ = 49.22, P < 0.001), and root biomass ($F_{2,12}$ = 101.29, P < 0.0001) that differed from those with the other two treatments (Figure 2). Foliar and stem biomass did not differ between the NC and IC treatments, whereas root biomass did differ between the two. By the end of the

Figure 1. *Pinus taeda* seedling root collar diameter (RCD), height, and stem volume index (SVI) means (SE) for vegetation free (VF), native competition (NC), and *I. cylindrica* competition (IC) treatments from planting through the end of the third growing season.

third growing season, all treatments showed significant differences in foliar ($F_{2,12}$ = 40.31, P < 0.0001), stem ($F_{2,12}$ = 37.00, P < 0.0001), and root biomass ($F_{2,12}$ = 49.41, P < 0.0001) (Figure 2). Seedlings in the VF treatment had the highest biomass (612 ± 79.9 g) followed by those in the NC (83.3 ± 12.8 g) and IC (14.0 ± 3.8 g) treatments, with significant differences ($F_{2,12}$ = 59.4, P < 0.0001) detected among them. A strong negative relationship (R^2 = 0.85) was observed between seedling biomass and belowground competing vegetation biomass (Figure 3).

Gas Exchange and Leaf Characteristics

There was a significant difference in the summer means of A_{max} between the treatments (Figure 4). The A_{max} summer means were 3.97, 5.07, and 5.85 μmol m^{-2} s^{-1} for the IC, NC, and VF treatments, respectively ($F_{2,12}$ = 17.32, P = 0.0006). The seedlings growing in the IC treatment maintained the lowest levels of A_{max} each month and always differed significantly from the seedlings growing in the

Table 1. Percent survival of *P. taeda* seedlings in vegetation free (VF), native competition (NC), and *I. cylindrica* competition (IC) after each growing season

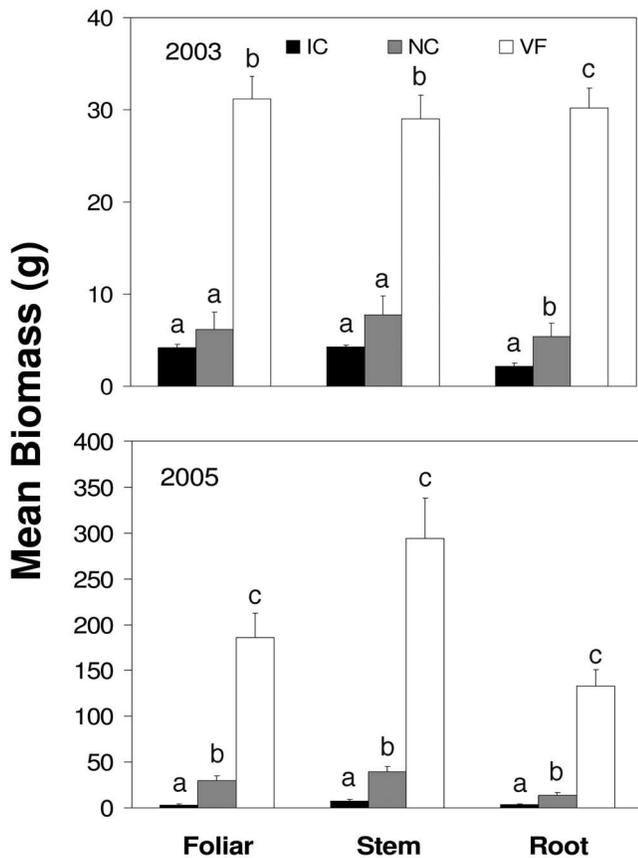| Treatment	Growing Seasons		
	1	2	3
VF	63	62	61
NC	62	57	51
IC	57	51	26

Figure 2. Mean (SE) biomass of *Pinus taeda* foliage, stems, and roots for vegetation free (VF), native competition (NC), and *I. cylindrica* competition (IC) treatments after one growing season (2003) and three growing seasons (2005). Different letters represent significant differences in means ($\alpha = 0.05$) between treatments.
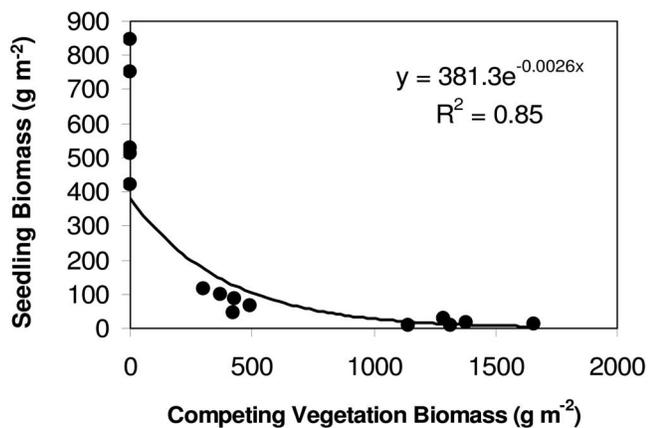

Figure 3. Relationship between belowground competing vegetation biomass and seedling biomass (stem + foliage + roots) after three growing seasons.

Figure 4. Mean light-saturated photosynthesis (A_{max}), stomatal conductance (g_s), and internal leaf CO_2 concentration (C_i) for pine seedlings for all 4 months measured in vegetation free (VF), native competition (NC), and *I. cylindrica* competition (IC) treatments. Different letters represent significant differences in means ($\alpha = 0.05$).
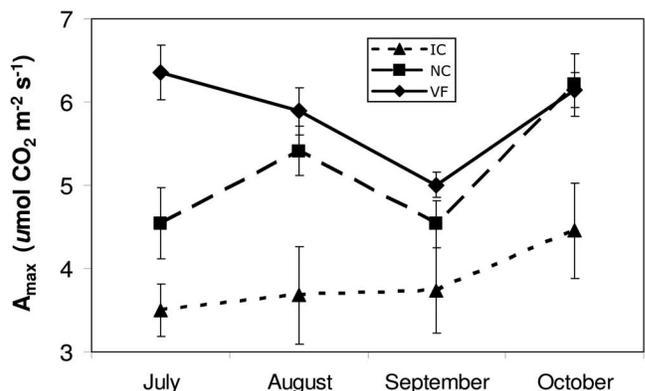
Figure 5. Monthly light-saturated photosynthesis (A_{max}) of *P. taeda* seedlings in vegetation free (VF), native competition (NC), and *I. cylindrica* competition (IC) treatments.

absence of competition (Figure 5). Repeated-measures analysis indicated significant differences for A_{max} among months ($F_{2,12} = 17.32$, $P = 0.0013$), but there was no interaction between treatments and time.

Stomatal conductance of the pine seedlings in the VF treatment was higher than that in the other treatments but was only significantly higher than that in the IC treatment ($F_{2,12} = 5.98$, $P = 0.0157$) (Figure 4). There were no
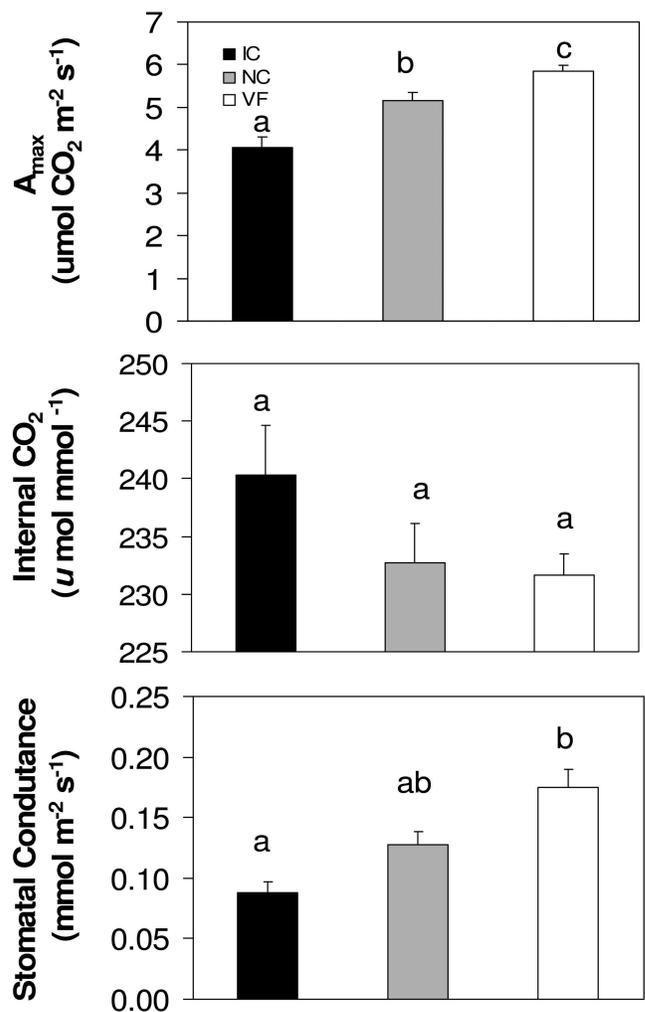
significant differences in the summer means of the three treatments for internal CO_2.

After one growing season, the seedlings in the VF treatment had significantly greater total leaf area ($F_{2,12} = 70.45$,

Table 2. Mean (SE) leaf area, specific leaf area (SLA) and % foliar nitrogen of 9-month-old *P. taeda* seedlings for different treatments

Treatment	Total leaf area (mm²)	SLA (mm²/g)	% N
VF	3450.8(279.6) a	50.63(2.4) a	1.71(0.03) a
NC	631.1(223.8) b	14.58(4.6) b	1.57(0.09) a
IC	265.8(33.1) b	7.06(0.8) b	1.10(0.1) b
P	<0.0001	<0.0001	0.0004

Different letters represent significant differences in means (α = 0.05) between treatments.

$P < 0.0001$) and SLA than those in the other two treatments ($F_{2,12} = 57.62$, $P < 0.0001$) (Table 2). There were no differences in leaf area and SLA between the NC and IC treatment seedlings. The pine seedlings in the IC treatment had the lowest nitrogen concentration ($F_{2,12} = 16.24$, $P = 0.0004$) compared with those for the other two treatments, which were not significantly different.

Discussion

Competition from native species and *I. cylindrica* prevented the pine seedlings from reaching the full growth potential that was observed in the VF treatment. It was evident, as early as 9 months after planting, that competition limited the growth of *P. taeda* seedlings. The seedlings growing in the presence of competition had reduced height, diameter, and mean SVI compared with the seedlings in the VF treatment. Interspecific competition impacts on *P. taeda* seedlings has been well documented in experiments using weed control to create competition-free treatments (Britt et al. 1990, Cain 1991, Miller et al. 1991, Morris et al. 1993, Martin and Jokela 2004), and these results support previous findings that the growth of seedlings is heavily affected by competing vegetation.

Because all seedlings experience a reduction in growth because of competition, the impacts of *I. cylindrica* on the pine seedlings are better seen when compared with the impacts of native vegetation. Nine months after planting, the IC treatment seedlings had a smaller mean RCD (44% of NC) and smaller mean SVI (27% of NC) than the NC treatment seedlings. The total biomass of the seedlings grown in the IC treatment was 54% of seedling biomass in the NC treatment. All of the growth parameter measurements became significantly different between the two treatments by the end of the second growing season, and the differences increased with time. By the end of the third growing season, the seedlings in the IC treatment had smaller diameters (44% of NC), had lower SVI (15% of NC), were shorter in height (71% of NC), and had a much lower total biomass (18% of NC) than the seedlings in the NC treatment. For the component biomass, the foliage biomass of the seedlings in the IC treatment was most reduced compared with that for seedlings in the NC treatment (12% of NC).

Competition, as demonstrated by both the NC and IC treatments, affected the rates of photosynthesis of the young pines within the first year after planting. For the first 3 months of measurement, the seedlings growing free of com- petition maintained the highest rates of $A_{\max}$. This finding conflicts with the findings of Green et al. (1991), who observed that competition control had no effect on 4-year-old *P. taeda* photosynthesis and Munger et al. (2003) who reported a decrease in *P. taeda* light-saturated photosynthesis with competition control.

In October, pine seedlings in the NC treatment exhibited their highest rate of $A_{\max}$, a rate that was higher than that with the VF treatment. The IC treatment pine seedlings also showed an increased level of photosynthesis compared with how they had been performing all season. This significant increase in $A_{\max}$ in the two treatments may be explained by the decrease in temperature (from 26.7°C in the summer to 20.1°C in October) or by dieback of competing vegetation. Because several of the competing species in the NC treatment were annuals, it is possible that their mortality at the end of the season would result in an increase in light, nutrients, and moisture, which would favor an increase in photosynthesis of the remaining species. As temperature declines, *I. cylindrica*, like most grasses, shifts its allocation of nutrients and biomass belowground (Ramsey et al. 2003), resulting in browning and death of the aboveground biomass. This action may favor pine seedlings that are still capable of photosynthesizing.

The results of the gas exchange measurements demonstrated that *I. cylindrica* competition affects the physiological function of the pine seedlings more than NC competition does. Every month, the seedlings in the IC treatment had lower rates of light-saturated photosynthesis than those in the other two treatments. The lower rates of photosynthesis were matched by lower stomatal conductance (g_s), and the lower stomatal conductance is most likely due to limited water availability brought about by *I. cylindrica* invasion. In a companion study, with the same three treatments, it was observed that *I. cylindrica* reduced water availability, leading to the lowest soil water potential of the three treatments at 30- and 60-cm soil depths throughout the summer (P. Daneshgar and S. Jose, University of Florida, Gainesville, FL, unpublished data, Aug. 2005). The water stress was more severe at shallower depths, where most of the belowground biomass of *I. cylindrica* occurs (Holm et al. 1977).

Water limitation most likely played a role in the decreased photosynthetic capacity of pine seedlings; however, a stronger case might be made for nutrient deficiencies that result from *I. cylindrica* invasion. *I. cylindrica* was shown to decrease soil nitrate and potassium levels in invaded compared with noninvaded pine flatwoods (Collins and Jose 2008). The invasive species was shown to be more competitive for phosphorus than native pine savanna species in the southern United States (Brewer and Cralle 2003), implying that phosphorus levels in the soil may drop with the presence of this invasive species. Brewer and Cralle (2003) also demonstrated that the extent of *I. cylindrica* invasion was negatively correlated to the number of legumes present, which would lead to the assumption that species that are capable of obtaining nitrogen from other sources (fixation) are better able to compete with the invasive grass. *I. cylindrica* may be efficient at gathering nitrogen and thus may be hindering competing species from taking up nitrogen. In our

study, seedlings growing in the IC treatment had significantly lower levels of foliar nitrogen than seedlings growing in either the VF or NC treatments. Because a large proportion of nitrogen in the leaves occurs in photosynthetic enzymes, reduced nitrogen concentrations in the IC pine seedlings may account for the reduced levels of photosynthesis. Several authors have demonstrated that the capacity for photosynthesis correlates with leaf nitrogen concentration for several tree species around the world (Field and Mooney 1986, Reich et al. 1999, Henderson and Jose 2005), which was also observed in this study across the three treatments (Figure 6). The reduced levels of foliar nitrogen may also have contributed to the reduced total leaf area and SLA that were observed for the IC treatment seedlings. Reduced SLA and leaf area imply reduced light-capturing ability and productivity, which explains why the biomass of the seedlings was reduced.

The decrease in photosynthesis in pines in the IC treatment, whether it was due to decreased nutrients or water stress or both, does indicate belowground stress caused by the invasive species, which had a larger proportion of its biomass belowground. Dillenburg et al. (1995) demonstrated that *Liquidambar styraciflua* (L.) reduced leaf photosynthetic capacity not only from aboveground competition with vines *Lonicera japonica* (Thunb.) and *Parthenocissus quinquefolia* (L.) (Planch) but also from belowground competition. After a full growing season, the roots of the seedlings grown in the IC treatment were the most affected part of the seedling compared with seedlings in the NC treatment. This result suggests that in the presence of *I. cylindrica* emerging juvenile trees experience the greatest competitive stress belowground. *I. cylindrica* retains more of its biomass belowground (>60% according to Sajise 1976, approximately 80% on this site), which has been reported to be 5 to 10 times that of native understory belowground biomass in southeastern forests (Ramsey et al. 2003). We observed nearly eight times more belowground *I. cylindrica* biomass in the IC treatment compared with that for the native species in the NC treatment. This finding clearly indicates that the intensity of resource competition belowground

between *I. cylindrica* and pine seedlings could be far greater than that between pine seedlings and native vegetation.

Species that maintain high levels of biomass either above- or belowground decrease the growth of competing trees. After one season, *P. taeda* growing with *Andropogon virginicus* showed decreases in SVI with increasing *A. virginicus* density; 4 individuals m^{-2} reduced pine SVI by 60% compared with a competition control and 16 individuals m^{-2} reduced pine SVI by an additional 22% (Perry et al. 1993). *I. cylindrica* maintained >90% cover of the ground in all plots during the course of their study, suggesting that its high density, both above- and belowground, could be a factor in the reduced growth of pine seedlings.

The nitrogen fertilization used in our study has the potential to enhance growth of both native understory and *I. cylindrica*, which may undermine the positive effect on pine growth. Nitrogen fertilization at planting of pines has become a common practice in the Southeast (Allen 1987, Jokela et al. 1991, 2004, Martin and Jokela 2004, Lee and Jose 2005). However, in the absence of an effective understory vegetation management strategy, the desirable effect on the overstory may be short-lived. The VF treatment in our study showed the maximum potential growth of *P. taeda* in the best possible scenario of fertilization combined with weed control. The IC and NC treatments in our study had the potential to reduce the growth of pine seedlings more aggressively than in an unfertilized stand. However, our competitor biomass data fall within the range reported for similar age stands that are unfertilized. For example, Nelson et al. (1981) reported mean aboveground weed biomass of $150-1,100$ g m^{-2} in young loblolly pine plantations across the Southeast. A cogongrass study by Willard et al. (1996) reported a mean foliar biomass of 220 g m^{-2} and rhizome biomass of 2,420 g m^{-2}. Data collected from a companion study near our study area showed that *I. cylindrica* foliar biomass averaged 525 g m^{-2} and belowground biomass averaged 1,832 g m^{-2} in a 1-year-old unfertilized *P. taeda* plantation (C. Ramsey, USDA Animal and Plant Health Inspection Service, Fort Collins, CO, and S. Jose, University of Florida, Gainesville, FL, unpublished data, Aug. 2003). Visual observations also did not reveal any differences in percent cover or vigor of the understory native species or that of *I. cylindrica* between the fertilized area and nearby unfertilized area.

Conclusions

Only recently has attention been focused on the potential impact of *I. cylindrica* invasion on establishing forests. Although forest managers have acknowledged the negative effect of this species on new plantations (Jose et al. 2002), this is the first work to demonstrate the impacts of *I. cylindrica* on establishing pines. Compared with native vegetation, competition from this alien grass reduced survival of pine seedlings by half after 3 years. Pine seedlings competing with *I. cylindrica* were significantly smaller in RCD, height, and biomass than those competing with native species. We believe that *I. cylindrica* reduces the productivity of young pines by altering conditions (water and nutrient availability) belowground where its root/rhizome
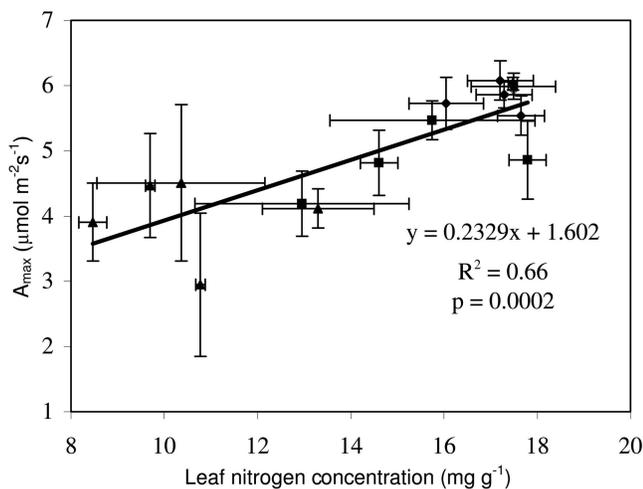
Figure 6.   Relationship between leaf nitrogen concentration and light-saturated net photosynthesis (A_{max}). Each point represents a plot mean (◆, vegetation free; ■, native competition; ▲, *I. cylindrica* competition).

biomass is much higher than that of native vegetation. We showed evidence of *I. cylindrica* lowering soil water availability and foliar nitrogen, which resulted in a reduction in the photosynthetic capacity of pine seedlings. Detailed examination of *I. cylindrica* impacts on belowground resources is essential to fully understand the mechanisms responsible for the observed reduction in seedling growth.

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