



Phosphorus addition reduces invasion of a longleaf pine savanna (Southeastern USA) by a non-indigenous grass (*Imperata cylindrica*)

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Abstract

Imperata cylindrica is an invasive C_4 grass, native to Asia and increasing in frequency throughout the tropics, subtropics, and southeastern USA. Such increases are associated with reduced biodiversity, altered fire regimes, and a more intense competitive environment for commercially important species. We measured rates of clonal spread by *I. cylindrica* from a roadside edge into the interior of two longleaf pine savannas. In addition, we measured the effects of fertilization with nitrogen and phosphorus on clonal invasion of one of these sites. Clonal invasion occurred at both sites and at similar rates. Older portions of an *I. cylindrica* sward contained fewer species of native pine-savanna plants. Clonal growth rates and aboveground mass of *I. cylindrica* were reduced by the addition of phosphorus relative to controls by the second growing season at one site. As a group, native species were not affected much by P-addition, although the height of legumes was increased by P addition, and the percent cover of legumes relative to native non-legumes decreased with increasing expected P limitation (i.e., going from P-fertilized to controls to N-fertilized treatments). Clonal invasion was negatively correlated with the relative abundance of legumes in control plots but not in P-fertilized plots. Species richness and percent cover of native plants (both legumes and non-legumes) were dramatically lower in N-fertilized plots than in controls or P-fertilized plots. Species richness of native plants was negatively correlated with final aboveground mass of *I. cylindrica* in control and P-fertilized plots, but not in N-fertilized plots. The results suggest that *I. cylindrica* is a better competitor for phosphorus than are native pine-savanna plants, especially legumes, and that short-lived, high-level pulses of phosphorus addition reduce this competitive advantage without negatively affecting native plant diversity. Ratios of soil P to N or native legume to non-legume plant species may provide indicators of the resistance of pristine pine savannas to clonal invasion by *I. cylindrica*.

Introduction

The invasion and alteration of native communities and ecosystems by non-indigenous species is considered an important type of global environmental change (D'Antonio and Vitousek 1992 Mooney 1998 Mack et al. 2000). Of particular concern to ecologists and land managers are invasions by aggressive species that displace native flora and fauna and lead to fundamental changes in ecosystem function (Vitousek and Walker 1989 D'Antonio and Vitousek 1992 Gordon 1998). Identifying ways to prevent the spread and

establishment of invasive species presents a formidable challenge to conservation (Mack et al. 2000).

How competition for resources influences invasibility of plant communities has been the subject of recent debate (Robinson et al. 1995 Burke and Grime 1996 Tilman 1997). One hypothesis is that increases in resource availability render communities more invulnerable to species with high resource requirements (Burke and Grime 1996). If this hypothesis is correct, then increased anthropogenic nitrogen loading could lead to greater invasibility of plant communities (Huenneke et al. 1990). Another hypothesis is that a non-indigenous species will invade a community if it

and indigenous species are limited by different nutrients (Tilman et al. 1999). Both the overall amount and the type of nutrient added (i.e., nitrogen vs. phosphorus) have been shown to elicit changes in community structure in nutrient-poor grasslands (Tilman 1987 Aerts and Berendse 1988 Huenneke et al. 1990 Bobbink 1991 Willems et al. 1993). Contrasting responses of indigenous and non-indigenous species to changes in resource availability and resource-ratios could provide the basis of an experimental program of competitively-mediated control of aggressive, non-indigenous species (Tilman et al. 1999 Udensi et al. 1999).

Imperata cylindrica (L.) Beauv. (cogongrass, alang-alang) is an invasive C_4 grass, native to subtropical and tropical Asia. It is increasing in frequency in the southeastern USA and throughout tropical and subtropical Asia and Africa (Bryson and Carter 1993 Kuusipalo et al. 1995 Terry et al. 1997 Dozier et al. 1998 Udensi et al. 1999). Such increases concern ecologists and conservationists, because, when abundant, this species displaces native plant and animal species and alters fire regimes (Lippincott (1997, 2000)). In addition, dense swards of *I. cylindrica* create a more intense competitive environment for commercially important species (Bryson and Carter 1993 Kuusipalo et al. 1995 Premalal et al. 1995 Dozier et al. 1998). Shade, repeated herbicide application, and mechanical control have all been used to control *I. cylindrica* (Macdicken et al. 1997 Terry et al. 1997). However, all three methods kill native shade-intolerant vegetation and generally require replanting the manipulated area with other less invasive species. Some authors have suggested the need to explore alternatives to herbicides and mechanical control (Premalal et al. 1995 Dozier et al. 1998 Udensi et al. 1999).

Invasion of longleaf pine savannas by *Imperata cylindrica* represents an ideal system in which to study both limits to community invasibility and the impacts of invasive species on communities. Clones of this species can expand rapidly into undisturbed pine savannas by rhizomes (Lippincott 1997). Thus, the advancing border of a sward of *I. cylindrica* can be readily located, manipulated, and its effects tracked over time. Longleaf pine savannas of the southeastern USA contain extraordinarily species-rich plant communities and are home to numerous threatened endemic plant and animal species (Walker and Peet (1983) and Bridges and Orzell (1989), Brockway and Lewis (1997), references within Hermann (1993)). Thus, the consequences of unchecked inva-

sion of these communities by *Imperata cylindrica* are potentially large, as are the pay-offs from better understanding how to control this species.

In this study, we examined the effects of adding nitrogen or phosphorus on the rate at which *Imperata cylindrica* invaded a pine flatwoods savanna via clonal growth. This species became established along a disturbed edge of our study sites (roadside areas) in the late 1980s and is currently expanding into the interior of these savannas. We monitored invasion over two growing seasons by examining growth in plots established at the advancing border of the sward. We tested the hypothesis that *I. cylindrica* and native pine-savanna vegetation respond differently to the type of nutrient added. Specifically, we hypothesized that *I. cylindrica*'s growth would be limited more by nitrogen, while growth of native plants (in particular, legumes) would be limited more by phosphorus.

Methods

Description of *Imperata cylindrica*.

Imperata cylindrica is an important component of fire-maintained grasslands and savannas in southeast Asia (Wibowo et al. 1997 Peet et al. 1999). It is also considered a nuisance to agroforestry operations in that region, because it suppresses growth of trees and crop plants and increases fire hazard (Kuusipalo et al. 1995 Premalal et al. 1995 Macdicken et al. 1997 Terry et al. 1997 Wibowo et al. 1997). In 1977, it was considered the world's seventh most important weed (Holm et al. 1977). It was introduced to North America in the early 1900s and has since become an invasive component of disturbed sites and native plant communities throughout the southeastern United States (Bryson and Carter 1993 Dozier et al. 1998).

Although seedling establishment of *I. cylindrica* benefits from disturbances such as tilling in pine savannas (King and Grace 2000), clones of this rhizomatous perennial are not restricted to disturbed areas and can invade pristine pine savannas vegetatively from disturbed edges (Lippincott (1997, 2000)). Rates of invasion can vary from site to site, but under optimal conditions, a single ramet can give rise to over 350 descendant shoots in 6 weeks and produce a clone that covers 4 m² in 11 eleven weeks (Eussen 1980).

Study sites

We examined rates of clonal spread into the interior of a longleaf pine flatwoods community at two locations at the University of Mississippi Forest Lands in Stone County in southeastern Mississippi, USA. Flatwoods are mesic, fire-maintained savannas or sparse woodlands with nutrient-poor soils. They are dominated in the overstory by longleaf pine (*Pinus palustris*) and in the ground layer by a diverse mixture of herbs (including grasses, legumes, and composites), low shrubs, and small oaks (*Quercus* spp.; see 'Southern Mesic Longleaf Pine Woodland' of Peet and Alard (1993), for a more complete description).

Both sites were very similar in overstory tree composition and density and in the composition of herbaceous plants in the groundcover. The main difference between the two sites was a modest difference in fire frequency. One site, Henley Park, had been burned every 1 to 2 years in the winter since the early 1980s. The second site, Wolf Branch, had received winter fires every 3 years since the early 1980s. Soils at both sites were nutrient-poor loamy sands with total N and P concentrations of less than 1.5 and 0.25%, respectively (J. S. B., unpublished data).

Sampling design for evaluating site differences in clonal invasion

To evaluate site differences in rates of clonal invasion, we located 20 0.5 × 0.5-m quadrats at the advancing border of *I. cylindrica* swards at Wolf Branch and Henley Park. At Henley Park these unmanipulated quadrats represented the control plots in a nutrient addition experiment (Figure 1). The quadrats were established in May 1998 at Wolf Branch and May 1999 at Henley Park. The advancing border was located by ensuring that all quadrats contained at least three shoots of *Imperata*; none contained adult pine trees. We counted shoots in May 1998 and May 1999 at Wolf Branch and in May, June, and September 1999 and May 2000 at Henley Park. The impact of *I. cylindrica* on native species richness was inferred indirectly by quantifying species richness in border plots and in 20 plots located no closer than 2 m from the advancing border of sward (i.e., interior plots; Figure 1).

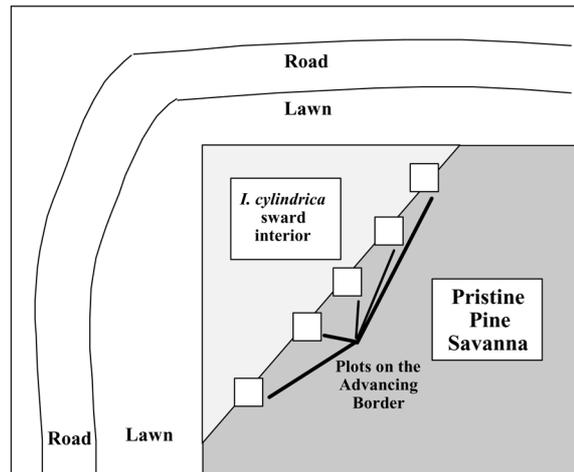


Figure 1. Diagram showing the locations of the *I. cylindrica* sward interior and advancing front, the pristine pine savanna, and the plots in which rates of clonal invasion of the pine savanna by *I. cylindrica* were measured and fertilizer was added.

Design of nutrient addition experiment

Using an approach similar to that of Levine et al. (1998), we examined nutrient limitation of clonal invasion of the pine savanna at Henley Park by measuring responses to nutrient addition along the advancing border of a sward of *Imperata*. In mid-May 1999, we located 60 0.5 × 0.5-m quadrats along this border, 20 of which were the unmanipulated controls mentioned above. As described above, all quadrats contained at least three shoots of *Imperata*. We randomly assigned two fertilizer treatments and a control to the 60 plots. One fertilizer treatment (+ N) received 3 broadcast applications of 60 g of 32% pelletized ammonium nitrate (or 20 g N per application). The other fertilizer treatment (+ P) received 3 applications of 42 g of 46% pelletized superphosphate fertilizer (or 20 g P per application). Fertilizer was applied in May 1999, September 1999, and March 2000. Thus, each treated 0.25-m² plot received 60 g of ammonium nitrate-N or phosphate-P per year.

Plant and light measurements in nutrient addition experiment

We counted shoots and measured the height of the tallest shoot in May, June, and September 1999 and in May 2000. In addition, we measured final dry aboveground mass in July 2000. We harvested all green aboveground shoots of *I. cylindrica* from all plots, and dried and weighed them.

Native plants

In July 2000, we identified all plants to species, to the extent possible, and quantified species richness, percent cover, and height of the tallest erect stem of native plants in each plot. We also examined the responses of legumes to phosphorus addition separately.

Light

We measured photosynthetically-active photon flux density (PPFD) at each plot above and below the *I. cylindrica* canopy. Specifically, we measured PPFD between 1,100 and 1,300 h on a cloudless day in July 2000 at 1 m and 10 cm above the ground at each plot each plot using a Li-Cor optical sensor.

Statistical analysis of clonal invasion

We used one-way analysis of covariance (ANCOVA) to determine the effect of site on changes in shoot density, using distance from the edge as a covariate. We also used ANCOVA to examine the effect of fertilization treatment on changes in shoot density and final dry aboveground mass of shoots of *I. cylindrica* at Henley Park. In the second analysis, covariates included initial shoot density and distance from the edge. The 'edge' occurred along a mowed lawn alongside an unpaved road at both sites (Figure 1). We also examined the relationship between distance from the edge and light intensity above the ground-cover canopy (1 m above the ground). Although changes in shoot density were normally distributed and did not produce significantly different variances among treatments, we performed analyses using both untransformed differences in shoot (i.e., ramet) number (absolute clonal growth rate, ACGR) and log-transformed rates of increase in shoot number (RCGR). The initial and final censuses of shoot density were the May 1999 and May 2000 censuses, respectively.

Statistical analysis of native plant responses

The difference in species richness between border plots and sward-interior plots was analyzed using a two-sample *t*-test, assuming unequal variances. To quantify the direct and indirect effects of nutrient addition on native vegetation, we examined the effects of treatments on species richness, percent cover, and maximum height of native plants, using final aboveground dry mass of *I. cylindrica* as a covariate. We also examined the correlation between native plant

species richness and groundlayer shade (i.e., the log difference in PPFD above and below the *I. cylindrica* canopy). We used two-tailed *t*-tests to evaluate the effect of phosphorus addition on percent cover and height of the tallest legume. The relative percent cover of native non-legumes and legumes in response to fertilizer treatments was examined using log-transformed data. A constant (1) was added to each value before transformation. The relationship between RCGR and the ratio of percent cover of non-legumes to legumes in control and P-addition plots was examined using ANCOVA. Post-ANCOVA comparisons of adjusted least-square means were done using Tukey's tests ($\alpha = 0.05$). All ANCOVAs were analyzed using SuperAnova v. 1.11 (Abacus Concepts, Inc., Berkeley, California).

Results

Clonal invasion of two pine savannas by I. cylindrica

I. cylindrica increased in abundance at two sites by spreading vegetatively into the interior of pine savannas from edges along roadsides. The number of shoots per plot increased by an average of 5.75 shoots over 12 months at Henley Park and by 4.8 shoots at Wolf Branch. Despite modest differences in fire history between the two sites, rates of clonal invasion were not substantially different (two-sample, two-tailed $t_{38} = 1.15$, $p = 0.13$ for ACGR). At Henley Park, older portions of the *I. cylindrica* sward contained fewer species of native pine-savanna plants (1.23 ± 0.28 s.e. vs. 6.15 ± 0.43 s.e. for interior vs. border plots, respectively; two-tailed $t_{32} = 8.99$, $p < 0.0001$).

Response of I. cylindrica to nutrient addition

Growth of *Imperata*, in terms of shoot density, and aboveground mass, was reduced by the addition of phosphorus, relative to controls and N-fertilized plots (Figure 2a). There was a significant effect of fertilizer treatment on all three measurements of growth (Table 1). Much of the effect of fertilizer could be attributed to differences between the N-fertilized and the P-fertilized plots (Figure 2a, Table 1). Phosphorus addition had a significant, negative effect on ACGR and log final mass, compared to both controls and N-fertilized plots (Figure 2a). Relative clonal growth rate

was significantly lower in P-fertilized plots than in the N-fertilized plots (Figure 2a). Shoot densities declined or remained the same in 7 of 20 P-fertilized plots, compared to 4 of 20 control plots and 2 of 20 N-fertilized plots, respectively. Although we found no significant differences in growth between N-fertilized plots and controls, leaves of *I. cylindrica* were noticeably greener in N-fertilized plots. Growth was negatively correlated with distance from the edge of the pine stand (Table 1). Light availability (PPFD) above the *I. cylindrica* canopy did not decline significantly with increasing distance from the edge ($r = -0.198$, $p = 0.13$), however, indicating a relatively sparse overstorey pine canopy. Clonal growth rates were highly density dependent, as evident from the significant, negative correlation between initial shoot density on subsequent increases in shoot density (Table 1). In contrast, log final dry mass was positively correlated with initial shoot density (Table 1).

Responses of native plants to nutrient addition

A total of 41 species of native plants was found within border plots in July 2000 (Table 2). Fertilizer treatments significantly affected native plant species richness and height (Table 3), but not percent cover. Nitrogen significantly reduced final species richness and height of the tallest native plant below that of controls and P-fertilized plots (Figure 2b). Phosphorus addition had no effect on species richness, percent cover, or height of native vegetation as a group (Figure 2b). However, phosphorus addition appeared to have a slight positive effect on the maximum height of legumes ($67.71 \text{ cm} \pm 5.02 \text{ s.e.}$ vs. $50.22 \text{ cm} \pm 4.88 \text{ s.e.}$ in P-fertilized and control plots, respectively; $t_{32} = 2.5$; $p = 0.018$). There was no effect of phosphorus addition on percent cover or richness of legume species. However, there was a trend towards greater relative abundance of non-legume native compared to legumes with greater phosphorus limitation. The log relative cover of non-legumes to legumes increased with increasing expected P-limitation ($0.082 \pm 0.24 \text{ s.e.}$ vs. 0.35 ± 0.16 vs. 0.67 ± 0.16 in the P-fertilized, control, and N-fertilized plots, respectively). A linear contrast of fertilizer treatments on the relative cover of non-legumes and legumes was statistically significant ($F_{1, 57} = 3.43$, $p = 0.035$), although the overall effect of treatment on relative cover was not statistically significant ($p = 0.10$). Relative clonal growth rate of *I. cylindrica* was positively correlated with the ratio of non-legumes to legumes in control plots ($r =$

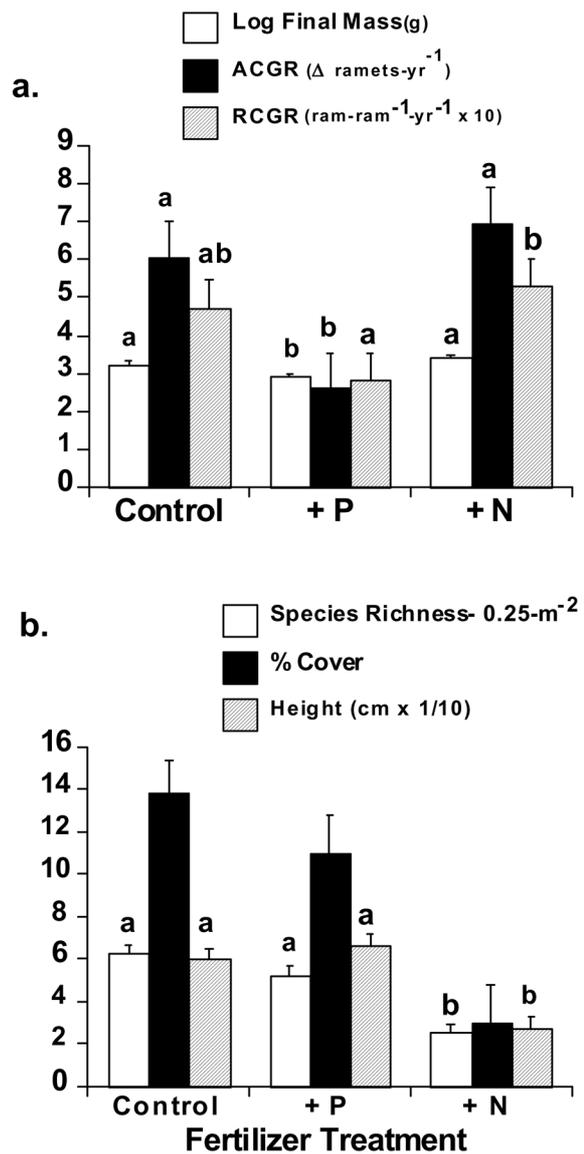


Figure 2. Effects of fertilizer treatments on a) final dry above-ground mass, absolute clonal growth rate (ACGR) and relative clonal growth rate (RCGR) of *Imperata cylindrica* and b) richness, percent cover, and height of the tallest erect stem of native species in July 2000. Values are least-square means adjusted for covariates (initial ramet density and distance from the forest in 2a and log final mass of *I. cylindrica* in 2b). Error bars are +1 standard error. Significant differences among means are denoted by different letters. Post-anova tests were not done for percent cover of natives, since the overall effect of treatment was not significant.

0.55 , $p = 0.012$) but not in P-fertilized plots ($r = 0.13$, $p = 0.58$). Hence, there was a significant phosphorus addition \times non-legume:legume ratio interaction ($F_{1,36} = 5.91$, $p = 0.02$). At least one legume species occurred in 18 of 20 control plots and 17 of 20 P-fer-

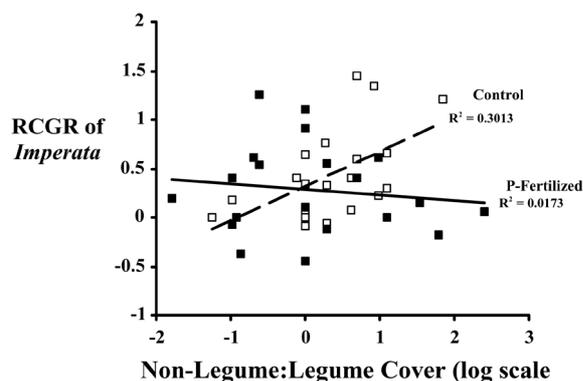


Figure 3. Relative clonal growth rate (RCGR) of *I. cylindrica* in control (open) and P-addition (filled) plots as a function of the ratio of percent cover of native non-legumes to legumes. The dashed regression line best fits the control plots, whereas the solid regression line best fits the P-addition plots. Units on RCGR are ramets per ramet per year.

tilized plots, but only 6 of 20 N-fertilized plots. Although both species richness and percent cover of native plants were negatively correlated with final log mass of *I. cylindrica* in control and P-fertilized plots, this was not true for N-fertilized plots (Table 3). Furthermore, although groundlayer shade was negatively correlated with species richness in control and P-fertilized plots ($r = -0.46$, $p = 0.003$), there was no relationship between groundlayer shade and species richness in N-fertilized plots ($r = -0.097$, $p = 0.68$).

Discussion

Although colonization of new sites by *Imperata cylindrica* often results from the establishment of seedlings and fragments in disturbed areas (Dozier et al. 1998 King and Grace 2000), in this study, *I. cylindrica* increased in abundance at two sites by spreading vegetatively into the interior of pine savannas from edges along roadsides. Rates of clonal invasion were not substantially different between the two sites studied here. Native plant species richness was lower in central portions than at the advancing borders of *I. cylindrica* swards at both sites. Hence, *I. cylindrica* most likely displaced native pine-savanna species at our sites, but the mechanism remains unclear. Lippincott (1997) found that *I. cylindrica* reduced seedling establishment of native longleaf pine-savanna plants in a xeric sandhill community in Florida. A similar mechanism of displacement could have occurred at our mesic flatwoods sites as well. Alternatively, re-

peated fires of higher than normal intensity could have extirpated some native species (Lippincott 2000).

The rate of clonal invasion by *I. cylindrica* decreased farther from the roadside edge at both sites. Thus, the immediate impact of *I. cylindrica* on native species richness apparently diminished as clones extended into the interior of pine savannas. We do not know what was responsible for this pattern. The effects of light quality and nitrogen availability deserve greater attention, however, since we found no significant relationship between the rate of clonal invasion and overhead mid-day shade. In addition to mid-day shade, overhead plant canopy density did not vary significantly with distance from the edge (data not presented), perhaps due to the open canopy of pines at these sites. Regardless of the cause, our results suggest that clones would expand more rapidly along the roadside than into the interior of the savanna at sites similar to ours.

A new and important finding of our study was that adding large amounts of phosphorus slowed rates of clonal invasion of pine savannas by *I. cylindrica* without negatively affecting native plants. Knowing this, we should turn our attention to investigating the mechanisms of inhibition and the relationship between rates of invasion and natural levels of phosphorus availability in the soil. We do not know the cause(s) of the lower rate of invasion of P-fertilized plots, but competitive suppression of *I. cylindrica*, P-toxicity, chemical or microbial changes in the soil, or some interaction among these are possibilities (Willems et al. 1993 Udensi et al. 1999). We suggest that reductions in the rate of clonal invasion by *I. cylindrica* resulted from a mild form of P-toxicity or unknown chemical or microbial changes in the soil. Additional work is needed, however, to elucidate the mechanism of inhibition of *I. cylindrica* by P addition.

Some have recently advocated competitively-mediated control of invasive species, whereby nutrient ratios are altered, if possible, and a nutrient competitor is added (Premalal et al. 1995 Udensi et al. 1999 Tilman et al. 1999). We cannot conclude with certainty, however, that the addition of phosphorus increased the intensity of competition between *I. cylindrica* and native species in this study. The addition of phosphorus increased the height of legumes, and the relative cover of legumes increased with decreasing P-limitation. We did not find a negative relationship between the rate of clonal invasion and the maximum height of legumes in P-fertilized and control plots,

Table 1. Analysis of covariance for the effect of fertilizer on log final mass, absolute clonal growth rate, and relative clonal growth rate. Cell entries include F statistics and partial regression coefficients (β).

	Log final mass (g)	Absolute clonal growth rate	Relative clonal growth rate
Initial ramet	$F_{1,55} = 13.5^{**}$	$F_{1,55} = 32.24^{**}$	$F_{1,55} = 63.33^{**}$
Density (Cov)	$\beta = 0.026$	$\beta = -0.491$	$\beta = -0.051$
Distance from Forest edge (Cov)	$F_{1,55} = 10.49^{**}$	$F_{1,55} = 12.8^{**}$	$F_{1,55} = 13.94^{**}$
Fertilizer	$\beta = -0.017$	$\beta = -0.229$	$\beta = -0.018$
	$F_{2,55} = 11.92^{**}$	$F_{2,55} = 6.15^{**}$	$F_{2,55} = 3.59^*$

** $p < 0.01$, * $p < 0.05$

Table 2. Native Species Encountered and Identified in Plots in July 2000 at Henley Park, with legumes indicated. Nomenclature follows Clewell (1985).

Species	Species (cont.)
<i>Andropogon</i> spp. L.	<i>L. repens</i> (L.) Bart. (legume)
<i>Asclepias</i> sp. L.	<i>Phlox</i> sp. L.
<i>Aster adnatus</i> Nutt.	<i>Pinus elliotti</i> Engelm.
<i>A. concolor</i> L.	<i>Pityopsis graminifolia</i> (Michx.) Nutt.
<i>A. dumosus</i> L.	<i>Prunus serotina</i> Ehrh.
<i>A. tortifolius</i> Michx.	<i>Pycnanthemum albescens</i> T. & G.
<i>Clitoria mariana</i> L. (legume)	<i>Rhus copallina</i> L.
<i>Desmodium lineatum</i> DC. (legume)	<i>Rhynchosia reniformis</i> (Pursh) DC. (legume)
<i>D. marilandicum</i> (L.) DC. (legume)	<i>Rubus trivialis</i> Michx.
<i>D. strictum</i> (Pursh) DC. (legume)	<i>Rudbeckia hirta</i> L.
<i>Diospyros virginiana</i> L.	<i>Schizachyrium scoparium</i> (Michx.) Nash
<i>Elephantopus</i> sp. L.	<i>Smilax glauca</i> Walt.
<i>Eupatorium rotundifolium</i> L.	<i>Solidago odora</i> Ait.
<i>Eupatorium</i> spp. L. (2 species)	<i>Stylosanthes biflora</i> (L.) BSP (legume)
<i>Hypericum suffruticosum</i> Adams & Robson	<i>Tephrosia florida</i> (Dietr.) Wood (legume)
<i>Ilex glabra</i> (L.) Gray	<i>Tragia smallii</i> Shinnery
<i>Ipomoea</i> sp. L.	<i>Vaccinium myrsinites</i> Lam.
<i>Kuhnia eupatorioides</i> L.	<i>Vernonia angustifolia</i> Michx.
<i>Lespedeza angustifolia</i> (Pursh) Ell. (legume)	<i>Viola septemloba</i> LeConte
<i>L. hirta</i> (L.) Hornem. (legume)	Unidentified grass

however, nor was clonal invasion negatively correlated with relative legume cover in P-fertilized plots. The apparent lack of competitive displacement of *I. cylindrica* by legumes following phosphorus addition may reflect slow growth and conservative resource-use by these species (Grime 1979 Huston 1979 Chapin 1980).

In this study, we found that clonal invasion was negatively correlated with the relative abundance of legumes in unfertilized control plots. If *I. cylindrica* is a better competitor for phosphorus than are native pine-savanna species (especially legumes), ratios of soil N to P or non-legume to legume plant species could provide indicators of the vulnerability of pristine pine savannas to clonal invasion by *I. cylindrica*.

Such data could be integrated into programs aimed at reducing the spread of this highly invasive species. Currently, repeated herbicide application and shade are the most common methods of controlling of *I. cylindrica* (Macdicken et al. 1997 Terry et al. 1997). Given that herbicides and shade have profoundly negative effects on the indigenous C₄ grasses and shade-intolerant forbs, minimizing the use of these methods would be desirable in pine savannas.

The results of adding nitrogen to the advancing border of an *I. cylindrica* sward may be cause for some concern, considering the projected increases in nitrogen deposition in terrestrial ecosystems in the eastern United States (Vitousek et al. 1997). Urbanization and intensive forestry practices continue to

Table 3. Analysis of covariance for the effect of fertilizer on richness, percent cover, and height of native species. Cell entries include F statistics and partial regression coefficients (β).

	Species richness	Percent cover	Height
Log Final Mass of <i>I. cylindrica</i> (Cov)	$F_{1,54} = 5.63^{**}$ $\beta = -0.997$	$F_{1,54} = 6.94^{**}$ $\beta = -15.46$	$F_{1,54} = 3.23^*$ $\beta = -34.78$
Fertilizer	$F_{2,54} = 4.21^{**}$	$F_{2,54} = 2.99^*$	$F_{2,54} = 4.2^{**}$
Interaction	$F_{2,54} = 2.42^*$	$F_{2,54} = 2.2$	$F_{2,54} = 2.61^*$
Log final mass (+P, control)	$F_{1,36} = 6.3^{**}$ $\beta = -1.66$	$F_{1,36} = 5.39^{**}$ $\beta = -15.46$	$F_{1,36} = 5.1^{**}$ $\beta = -34.78$
Log final mass (+N)	$F_{1,18} = 0.003$ $\beta = -0.04$	$F_{1,18} = 1.13$ $\beta = -1.69$	$F_{1,18} = 0.91$ $\beta = 7.7$

** $p < 0.05$, * $p < 0.1$

increase in the southeastern United States (Frost 1993). Although nitrogen addition did not increase growth of *I. cylindrica* above that of controls, leaves of *I. cylindrica* were noticeably greener in the N-fertilized plots. In contrast, the species richness and height of natives were dramatically reduced by N addition. The mechanism involved is not known but increased soil acidity (and thus reduced phosphorus availability) or altered mycorrhizal formation rates are possibilities (Hutchinson et al. 1998). Thus, it would appear that native pine-savanna plants and *I. cylindrica* have different requirements for nitrogen and respond differently to N addition. The amounts of nitrogen applied in this experiment, however, far exceeded projected increases in N availability to pine savannas in the southeastern United States. Hence, future experiments will need to include much lower application rates and will need to run longer to assess more precisely the threat posed by current and projected levels of N deposition. If the responses of *I. cylindrica* and native pine savanna plants to N addition in this study are indicative of responses to long-term sustained increases in the biological availability of nitrogen to pine savannas, then *I. cylindrica* will increase within pine savannas, and natives will decline. Further investigation of the causes of the loss of native plant species in response to nitrogen addition is needed.

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