

forest ecology

Cogongrass (*Imperata cylindrica*) Affects Above- and Belowground Processes in Commercial Loblolly Pine (*Pinus taeda*) Stands

Adam N. Trautwig, Lori G. Eckhardt, Nancy J. Loewenstein, Jason D. Hoeksema, Emily A. Carter, and Ryan L. Nadel

Cogongrass (*Imperata cylindrica*), an invasive grass species native to Asia, has been shown to reduce tree vigor in loblolly pine (*Pinus taeda*) plantations, which comprise more than 50% of growing stock in commercial forests of the United States. *I. cylindrica* produces exudates with possible allelopathic effects that may influence abundance of *P. taeda* symbionts, such as soil microbes and ectomycorrhizal fungi. Soil microbial communities and root colonization by mycorrhizal fungi were sampled in intensively managed *P. taeda* stands in Greene County, Mississippi, in *I. cylindrica* present and absent plots. *I. cylindrica* present plots had reduced abundance of ectomycorrhizal colonization of pine fine feeder roots in the top 40 cm of soil in comparison to *I. cylindrica* absent plots. Abundance of pine fine feeder roots in the 21–40 cm and 41–60 cm layers of the soil profile was also reduced in *I. cylindrica* present plots. Vegetative diversity was negatively correlated with *I. cylindrica* (% cover), which probably contributed to the reduced microbial diversity in *I. cylindrica* present plots. Because of the variety of roles microorganisms play, changes associated with the invasion of *I. cylindrica* are likely to alter nutrient cycling and reduce site productivity.

Keywords: ectomycorrhizal fungi, allelopathy, vegetation

Economic losses attributable to the nearly 50,000 nonindigenous species in the United States are estimated to be US\$120 billion per year (Pimentel et al. 2005). A large portion of the impacts of invasive species are ecological in nature and often unnoticed, although they can contribute to ecosystem or community transformation over time (Simberloff et al. 2013). In addition to direct impacts on aboveground flora and fauna, effects on belowground symbionts and other organisms that co-occur with native species can magnify the impact of an invasive species. Although a few instances of compounding effects of coinvasion by plants and their symbionts have been well documented (Richardson et al. 2000, Pasternak et al. 2007, Dickie et al. 2010), principles that outline how an invader will affect preexisting communities of mutualists are generally broader in scope (Ehrenfeld 2003, Wolfe and Klironomos 2005, van der Heijden et al. 2008).

The role of diversity in understory vegetation has been thoroughly explored (Nilsson and Wardle 2005, Gilliam 2007, Hector and Bagchi 2007). Monoculture-forming invaders that replace en-

tire communities of native plants have the potential to affect micro-organism communities and canopy vegetation (Callaway and Ride-nour 2004, Stinson et al. 2006). *Imperata cylindrica* invasion of a longleaf pine (*Pinus palustris* Mill.) ecosystem resulted in a loss of the herbaceous plants that make this native ecosystem distinct (Brewer 2008). The loss of these herbaceous species may have significant effects on threatened ecosystems (Brewer 2008). These significant effects have been well established in the literature and include alteration of fire regimes, degradation of habitat, and altered nutrient cycles (Lippincott 2000, Daneshgar and Jose 2009, Hagan et al. 2013b). Cogongrass (*Imperata cylindrica* [L.] Beauv) is classified as a noxious weed in more than 70 countries and represents a tangible threat to biodiversity and resource management (Burrell et al. 2015, Estrada and Flory 2015). In areas where it has successfully invaded, it often forms dense monotypic stands (MacDonald 2004). *I. cylindrica* was introduced accidentally from Japan to the United States in 1912 but later was intentionally introduced for forage crop trials and erosion control (Bryson and Carter 1993, Holzmüller and Jose

Manuscript received January 22, 2016; accepted July 21, 2016; published online December 15, 2016.

Affiliations: Adam N. Trautwig (antrautw@gmail.com), Auburn University, School of Forestry and Wildlife Science, Auburn, AL. Lori G. Eckhardt (eckhlg@auburn.edu), Auburn University. Nancy J. Loewenstein (loewenj@auburn.edu), Auburn University. Jason D. Hoeksema (hoeksema@olemiss.edu), University of Mississippi. Emily A. Carter (ecarter@fs.fed.us), USDA Forest Service. Ryan L. Nadel (ryan.nadel@auburn.edu), Auburn University.

Acknowledgments: We thank Joseph Fan for comments on statistical analysis and the Forest Health Cooperative for funding. We also thank the Westervelt Company for the land base and our contact Robert Greer. Graeme Lockaby, Robin Governo, and Stephen Enloe were instrumental in developing the early study design. In addition, we thank Curtis Hansen for assisting with plant identification and the insightful input of two anonymous reviewers. J. Hoeksema was supported by National Science Foundation DEB Award 1119865.

2011). Because of its high silica content, it was ultimately not selected for use as a forage crop (MacDonald 2004). *I. cylindrica* is a C₄, rhizome-producing, perennial plant that can reach heights of 3 m but typically grows to heights of 1.2 m (Koger and Bryson 2004). It spreads both sexually through seeds and asexually through rhizomes. Seed production can be prolific with most seeds generally dispersed within 15 m of the plant (Daneshgar et al. 2008). *I. cylindrica* can grow on a variety of soils, from nutrient-poor, coarse sands to nutrient-rich, sandy loam soils (Jose et al. 2002). It is particularly difficult to eradicate because it produces a vast network of underground rhizomes from which the plant regenerates. Rhizomes can reach densities of 89 m · m⁻² of soil (MacDonald 2004).

Daneshgar and Jose (2009) found that competition for nitrogen (N) between *I. cylindrica* and loblolly pine (*Pinus taeda* L.) seedlings resulted in a greater reduction in pine seedling growth than competition with native vegetation. *I. cylindrica* also may impact growth of timber species such as *P. taeda* through production of exudates that may have an allelopathic effect (Hussain and Abidi 1991, Koger and Bryson 2004, Holzmueller and Jose 2011, Hagan et al. 2013b). Compounds isolated from exudates of *I. cylindrica* with possible allelopathic effects include seven phenolic acids, two aromatic acids, one trihydroxy anthraquinone, and one *meta*-dihydroxyl phenol (Hagan et al. 2013b). In addition to direct impacts on plant growth, compounds present in *I. cylindrica* exudates may affect growth through influence on mycorrhizae and other soil microbial taxa (Roberts and Anderson 2001, Kourtev et al. 2002, Hagan et al. 2013b). Boufalis et al. (1994) found that the growth of two ectomycorrhizal fungal species, *Cenococcum geophilum* and *Laccaria laccata*, were affected by the applications of several phenolic acids similar to those produced by *I. cylindrica*. For this study, we hypothesized that *I. cylindrica* present *P. taeda* plots would have reduced mycorrhizal and fine *P. taeda* feeder root abundance, a reduction in microbial biomass (N) (mg · liter⁻¹) and *P. taeda* diameter growth rate (mm · year⁻¹), and reduced vegetation diversity compared to *I. cylindrica* absent plots.

Materials and Methods

Site Description

The research site was located East of Leakesville, in Greene County, Mississippi, an area under commercial *P. taeda* production (31.148493, -88.470755). The area receives an average annual rainfall of 1,677 mm.¹ The dominant mid-story vegetation includes yaupon (*Ilex vomitoria* Ait.), scrub oak (*Quercus* spp.), and *P. taeda*. Much of the area has also been invaded by *I. cylindrica*. The soil series was identified as Benndale sandy loam on 8–15% slopes and Benndale sandy loam or McLaurin sandy loam on 2–5% slopes. Benndale soils are classified as a coarse-loamy, siliceous, semiactive, thermic Typic Paleudults, and McLaurin soils are classified as a coarse-loamy, siliceous, subactive, thermic Typic Paleudults. These soils are well drained and generally nutrient poor due to low amounts of organic matter and clay (Soil Survey Report, Greene County, 2012).

A total of eight study plots (16 m × 16 m) were established within two similar stands of *P. taeda*, which have received slightly different management regimens (Table 1).² The plots were situated within the northeast quadrant of larger plots (30 m × 30 m), which were initially established for a study in 2010 (Brunson 2013). *I. cylindrica* was present at this site before the establishment of that study in 2010, but the exact time of invasion is not known. Four plots were located within areas of the stands that were not invaded with *I. cylindrica*; the remaining four were in areas that were invaded

Table 1. Site conditions and treatments listed by plot.

Parameter	<i>I. cylindrica</i> absent	<i>I. cylindrica</i> present (<50% cover)	<i>I. cylindrica</i> abundant (>50% cover)
<i>I. cylindrica</i> cover 2011 (%)	0 (0)	43.00 (43.00)	85.00 (10.54)
Stand age	18.00 (2.00)	21.00 (0)	18.00 (2.00)
Basal area (m ² /ha)	22.43 (1.20)	25.30 (0)	22.43 (1.20)
Trees per acre	245.67 (11.29)	243.00 (0)	245.67 (11.29)
Percent stocking	73.33 (3.33)	80.00 (0)	73.33 (3.33)

Plots were divided into no *I. cylindrica* observed, plots with <50% *I. cylindrica* and plots in which *I. cylindrica* was present at >50%. Average values are displayed with standard errors in parentheses.

with *I. cylindrica*. Over the course of this study, *I. cylindrica* invaded one of the non-*I. cylindrica* plots, and it was determined that *I. cylindrica* density in one of the *I. cylindrica*-invaded plots was lower than in the original larger plot as a whole. Therefore, for analyses, the plots were characterized by whether *I. cylindrica* was present (<50% cover, *n* = 2), abundant (>50% cover, *n* = 3), or absent (*n* = 3). Sites were all in close proximity and represent a high degree of homogeneity with the exception of *I. cylindrica* being present.

Mycorrhizae

Field sampling of roots for mycorrhizae was performed in November 2014 and May 2015. Preliminary studies have shown that May is the most reliable time to survey mycorrhizal communities as this is when mycorrhizal fungi are most active in this region (J. Hoeksema, University of Mississippi, pers. obs., Aug. 4, 2013). Another sampling in November was included to account for seasonal variation (Brundrett et al. 1996). At each plot, nine evenly distributed soil cores (10-cm diameter × 60-cm height) were removed across each of the eight plots using a pneumatic coring device. This method of soil core sampling assured that both the O and A soil horizons were sampled for mycorrhizae. Although the majority of *I. cylindrica* rhizomes were found higher in the soil profile, roots have been found as deep as 120 cm (MacDonald 2004). Therefore, an analysis of multiple layers of soil was necessary. Each soil core was taken approximately 2.5 m from the next core, and each plot contained several trees. Individual cores were sealed and immediately stored at 4°C until processing.

Soil cores were cut into 20-cm increments, and roots were gently washed free of soil with water through a 0.5-mm sieve (Horton and Bruns 1998, Roberts and Anderson 2001). Roots were pooled within each plot by soil core increment (0–20, 21–40, and 41–60 cm). Pine roots were separated and kept in a 2% cetyl trimethyl ammonium bromide (CTAB) lysis buffer (Tedesoo et al. 2006). Because ectomycorrhizal tips were abundant ($7\text{--}72 \times 10^4 \cdot \text{m}^{-2}$) (Taylor 2002), we arbitrarily sampled 100 1-cm root segments for a total of 100 cm of fine roots per 20-cm soil core increment except when there were not enough roots present, in which case we examined all roots (Anderson et al. 2010), to measure the percentage of fine root segments that were colonized. The lengths of fine feeder roots (<2 mm) were measured (cm) for all plots. Mycorrhizal structures on subsampled roots were identified and quantified at ×10–40 magnification using the gridline intercept method (Brundrett et al. 1996).

Vegetation Survey

A vegetation analysis was undertaken in July 2014 to quantify percent cover of vegetation on *I. cylindrica*-invaded and noninvaded plots. Vegetation was assessed using a 10% scale by the line transect

method, where 10 adjacent 1-m² quadrats were sampled on a diagonal transect within each plot (Krebs 1989). Plants that were present but in lower abundance than 10% were given a classification of 5% to ensure they were accounted for in diversity estimates. Vegetation that could not be identified in the field was collected and pressed for later identification by plant taxonomists at Auburn University.

Microbial Biomass N

Four soil samples were collected from each plot to determine organic N levels (mg/liter), which were used to calculate microbial biomass N. Samples were collected 2 m apart in each cardinal direction, in the southwest corner of each plot or the center of the original plot. Before sampling, the top layer of loose organic debris (or duff) was removed. Because target microbial communities are more abundant higher in the soil profile, only the upper layer of soil (≤ 10 cm) was sampled. Samples were placed in plastic bags and transported within 8 hours to the laboratory where they were refrigerated. All tests were performed within 3 days.

Soil samples were sieved using a 2-mm sieve. Each soil sample was separated into two 18.5-g samples and was processed using the chloroform-fumigation extraction technique (Vance et al. 1987). This method measures only the organic N in microbial organisms in the soil by lysing cell walls in one sample (using chloroform) and not disturbing the second sample. Organic N levels were measured utilizing a TNM-1 total N measuring unit (Shimadzo Scientific Instruments, Columbia, MD). The organic N levels from the nondisturbed samples are subtracted from the organic N levels in the fumigated sample. The subtracted value, divided by the efficiency of extraction constant, yielded the microbial biomass N. These values for the four soil samples collected per plot were averaged before plot comparisons.

Tree Radial Growth

Within each of the original 30-m $\times$ 30-m plots, six dominant or codominant trees closest to plot center were selected to evaluate tree growth rate. An increment borer was used to remove a tree core at breast height (1.37 m). Cores were mounted onto blocks and sanded down to show clear annual growth rings. Total radial growth over the last 5 and 10 years was determined by measuring from the early wood of the 5th and 10th annual rings, respectively, to the bark. To account for differences in growth due to relative density of trees on each plot, growth was expressed as a function of percent stocking. Percent stocking standardizes available growing space across plots with trees of various ages and sizes and differing basal area (Gingrich 1967).

Statistical Analysis

Analyses examining mean percent colonization and mean fine root length as response variables were conducted in R version 3.0.2, using the lmerTest package. Graphs were constructed in STATISTICA (2013; StatSoft, Tulsa, OK). Mean values were calculated from multiple cores (nine) in each plot on each sampling date. We performed split-plot, repeated-measures mixed-model analyses of variance (ANOVAs) in which *I. cylindrica* abundance was a whole-plot between-subjects factor, sampling depth was a split-plot between-subjects factor, sampling date was a within-subjects factor, and plot was a random factor. These models included treatment, depth, month, and all two-way interactions between them as fixed factors. The three-way interaction among all three was excluded from final models, as it was always highly nonsignificant.

Models were fit with the lmer function using restricted maximum likelihood. Degrees of freedom and *P* values were estimated using

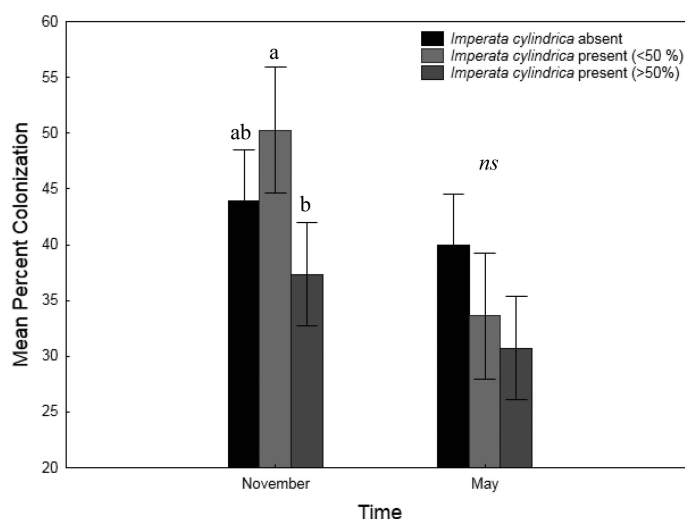


Figure 1. Mean values of percent colonization of mycorrhizal fungi on fine feeder roots of *P. taeda* over the course of two field seasons. Error bars represent standard errors. Letters represent statistically significant different pairwise comparisons between *I. cylindrica* abundances, not between sampling seasons.

the Satterthwaite method. Marginal means and standard errors for significant predictors were obtained using the lsmeans function, and pairwise significant differences between means were estimated using the diffslmeans function. For significant interactions of treatment with depth or month, we only conducted pairwise tests between levels of treatment within each depth or month to minimize the number of pairwise tests conducted. Differences were considered statistically significant at $\alpha = 0.05$.

SAS version 9.3 (2010; SAS Institute, Inc., Cary, NC) and STATISTICA were used for one-way ANOVA on microbial biomass with *I. cylindrica* invasion as the predictor variable. In addition, a factorial ANOVA examining the effect of *I. cylindrica* presence and loblolly stocking percentage was conducted on radial growth measurements. A post hoc Tukey honestly significant difference test ($\alpha = 0.05$) was performed to compare means in pairwise tests. Residuals were tested for normality and response variables were log transformed when found to be nonnormally distributed.

Species richness and diversity for each plot were calculated using both the Shannon-Wiener and Simpson's nonparametric measurements of diversity (Colwell 2013, Magurran 2013). A Student's *t*-test was undertaken to compare mean richness and diversity across invasion category. Percent cover of *I. cylindrica* was regressed against both the Shannon-Wiener and Simpson's diversity indices to determine whether the two were correlated.

Results

Mycorrhizae

Mycorrhizal fungi colonization was affected by a significant interaction between *I. cylindrica* abundance and month [$F_{(2, 29)} = 5.53$, $P = 0.009$] (Figure 1). *I. cylindrica* exercised a different influence on mycorrhizal fungi colonization in November than in May. Overall, there is a trend toward decreased colonization by mycorrhizal fungi in the presence of *I. cylindrica*, but in November mycorrhizal colonization was significantly lower in *I. cylindrica* present plots than in *I. cylindrica* abundant plots. In May, the comparison of mycorrhizal colonization in plots with no *I. cylindrica* versus *I. cylindrica*

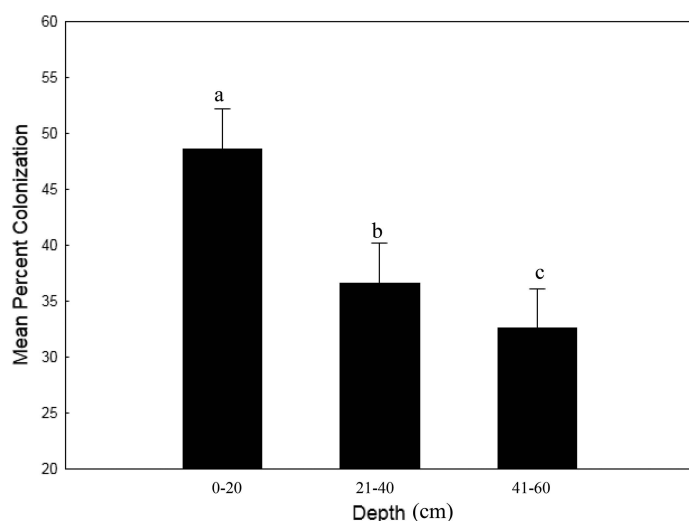


Figure 2. Mean values of percent colonization of mycorrhizal fungi on fine feeder roots of *P. taeda* at each of the three depth classes over the course of two field seasons. Error bars represent standard errors. Letters indicate statistically significant differences.

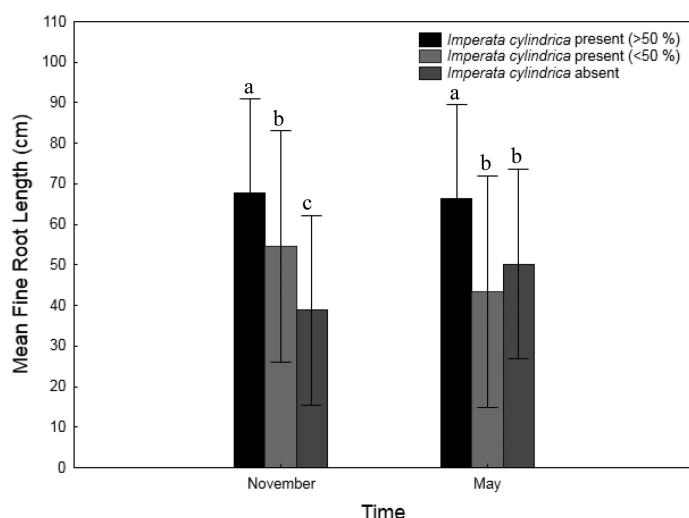


Figure 3. Mean values of recovered fine feeder roots of *P. taeda* over the course of two field seasons. Error bars represent standard errors. Letters represent statistically significant differences between *I. cylindrica* abundances, not between sampling seasons.

present plots was nearly significant ($P < 0.1$), despite very low replication ($n = 3$ plots each). Mycorrhizal fungi colonization was also significantly different across depth classes (Figure 2). Specifically, fine roots at depths of 0–20 cm were more heavily colonized than those at depths of 21–40 cm ($P < 0.0001$) or 41–60 cm ($P < 0.0001$). Similarly, roots in the 21–40 cm depth class were more heavily colonized than those in the 41–60 cm depth class ($P = 0.041$).

Amount of fine roots recovered was significantly affected by an *I. cylindrica* abundance $\times$ month interaction. In both November and May, *I. cylindrica* absent plots yielded significantly more *P. taeda* fine roots than *I. cylindrica* present ($P = 0.038$ and $P < 0.0001$) and *I. cylindrica* abundant plots ($P < 0.0001$ and $P = 0.005$) (Figure 3). Fine root abundance was also affected by a significant interaction between depth class and *I. cylindrica* abundance. In the 21–40 cm depth class *I. cylindrica* absent plots yielded more fine roots than either *I. cylindrica* present or abundant plots ($P < 0.0001$ and $P < 0.0001$,

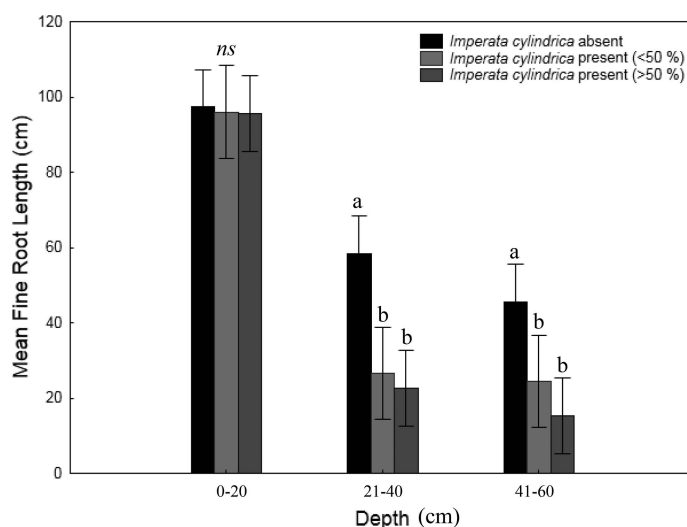


Figure 4. Mean values of recovered fine feeder roots of *P. taeda* over the course of two field seasons. Error bars represent 95% confidence intervals. Letters represent statistically significant differences between depth classes, not between sampling seasons.

Table 2. Percent cover of *Imperata cylindrica* and bare ground on plots, as well as species richness and measures of diversity.

	<i>I. cylindrica</i> absent	<i>I. cylindrica</i> present (<50% cover)	<i>I. cylindrica</i> abundant (>50% cover)
<i>I. cylindrica</i> cover 2015 (%)	0 (0)	17.00 (5.00)	80.67 (13.91)
Bare ground (% cover)	35.33 (12.72)	32.00 (4.00)	9.00 (6.51)
Species richness	13.33 (2.60)	11.50 (0.50)	5.33 (1.67)
Shannon-Wiener index	1.77 (0.32)	1.81 (0.03)	0.49 (0.29)
Simpson index	4.49 (1.54)	4.47 (0.03)	1.39 (0.30)

Average values are displayed with standard errors in parentheses.

respectively). Similarly, in the 41–60 cm depth class *I. cylindrica* absent plots yielded more fine roots than *I. cylindrica* present or abundant plots ($P = 0.008$ and $P < 0.0001$, respectively) (Figure 4).

Vegetation Survey

Plant species richness and diversity differed between the *I. cylindrica* abundant and *I. cylindrica* absent plots for both Shannon-Wiener ($P = 0.049$) and Fisher's α ($P = 0.042$) indices but not Simpson's diversity index ($P = 0.120$) (Table 2).

Individual species and both observed diversity indices were correlated for each species. *I. cylindrica* was the only species significantly negatively correlated with measures of diversity. An inverse correlation was also observed in a linear regression between *I. cylindrica* percent cover and Shannon-Wiener diversity index ($y = 1.8926 - 0.0172x$, $r = -0.9027$, $P = 0.0021$, $r^2 = 0.815$) (Figure 5A) as well as *I. cylindrica* and Simpson's diversity index ($y = 4.6486 - 0.0385x$, $r = -0.7299$, $P = 0.0398$, $r^2 = 0.533$) (Figure 5B).

Microbial Biomass N

A significant interaction was not observed between *I. cylindrica* and month of sampling. Furthermore, no significant differences were observed in either *I. cylindrica* abundance or time on microbial biomass N. There is a consensus in the literature that microbial biomass is related to soil moisture (Wardle 1992, Devi and Yadava 2006). A related study on the same site did not find a relationship

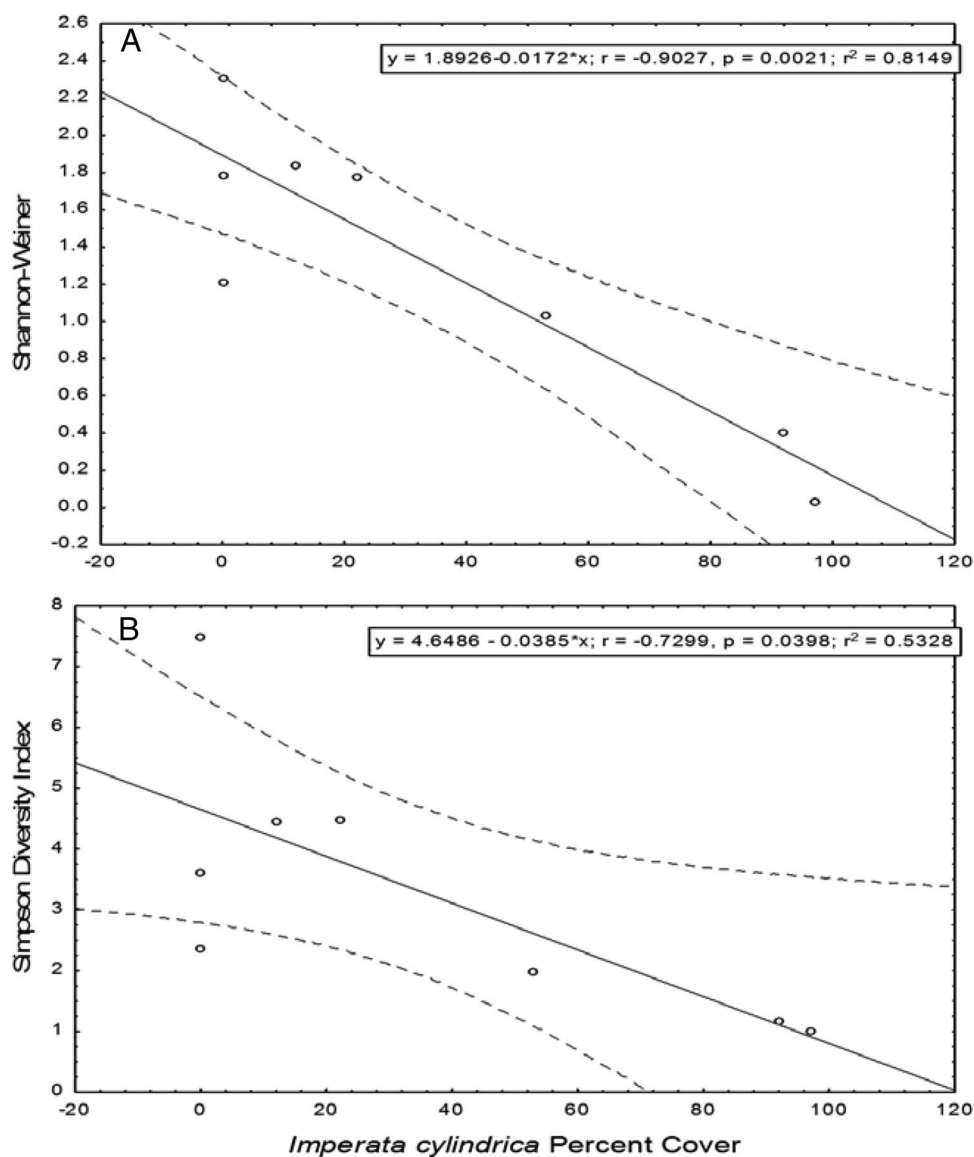


Figure 5. Linear regression of Shannon-Weiner index and *I. cylindrica* percent cover ($n = 8$) (A) and Simpson diversity index and *I. cylindrica* percent cover ($n = 8$) (B).

between microbial biomass N and soil moisture ($y = 4.8233 + 0.1803x$; $r = 0.2919$; $P = 0.1050$; $r^2 = 0.0852$) (Trautwig 2015).

Radial Growth

No significant differences in radial growth were observed between *I. cylindrica* present and absent plots. No *I. cylindrica* present plots were located in stands with lower than 70% stocking (Table 1). Plots in stands with lower stocking densities tended to have higher 5- and 10-year growth rates than higher stocked stands.

Discussion

Mycorrhizae are responsible for many plant functions, in particular nutrient uptake. There is significant consensus within the published literature concerning the role mycorrhizal fungi plays in contributing to nutrient uptake, particularly in the case of immobile nutrients (Bolan 1991, Marschner and Dell 1994, Landeweert et al. 2001). With a significant reduction in colonization by ectomycorrhizal fungi, as observed here in *P. taeda* plots with high abundance of *I. cylindrica* during the November sampling (Figure 1), the

volume of soil the plant is able to exploit is reduced, potentially resulting in reduced uptake of essential nutrients. It is important to note that ectomycorrhizal fungi predominantly colonize a host's fine root tips, more abundant in topsoil (Brundrett et al. 1996). Although the magnitude of the reduction in mycorrhizal colonization density (percent colonization of fine feeder roots) is not dramatic, the reduced abundance of fine feeder roots also observed on the invaded sites, especially deeper in the soil profile and in the November field sampling period (Figures 3 and 4), probably compounds the effect of reduced mycorrhizal colonization in more heavily invaded sites, and hampers the ability of trees to take up nutrients directly. Although significant differences in mycorrhizal colonization were only noted between *I. cylindrica* present and *I. cylindrica* abundant in November, we noted a trend toward increasing cover of *I. cylindrica* leading to decreased mycorrhizal colonization in both field seasons. In particular, the *I. cylindrica* absent and *I. cylindrica* abundant plots showed a nearly significant difference ($P = 0.066$), despite very low replication ($n = 3$). Similar studies have found that *I. cylindrica* reduced belowground root biomass in *P. taeda* seedling and

percent colonization of mycorrhizae in slash pine (*Pinus elliotii* Engelm.) seedlings (Daneshgar et al. 2008, Hagan et al. 2013b). This study supports those trends in an established pine forest environment. We theorize that the differences observed in mycorrhizal abundance and fine root abundance were predominantly attributable to the thick rhizomorphic mats that *I. cylindrica* forms and the potentially allelopathic compounds *I. cylindrica* produces (Hagan et al. 2013b). Several studies have postulated that potentially allelopathic chemicals produced by *I. cylindrica* may play a role in its invasive success (Koger and Bryson 2004, Holzmüller and Jose 2011, Hagan et al. 2013b).

We found that there was no significant difference in plant diversity indices between *I. cylindrica* present, abundant, and absent plots. However, when *I. cylindrica* abundant and *I. cylindrica* absent plots were compared, there was a significant difference. We also found that *I. cylindrica* percent cover was negatively related to vegetation diversity. Decreased plant diversity associated with invading vegetation is not a novel observation (Brewer 2008, Vilà et al. 2011). The effect of such a homogenization of plant diversity on ecology at the landscape scale may be severe (Chapin et al. 2000). It is well documented that diverse plant communities are more microbially active (Kowalchuk et al. 2002, Zak et al. 2003, Eisenhauer et al. 2010). Microorganisms play an imperative role in nutrient cycling, in particular through mineralization and competition for nutrients (van der Heijden et al. 2008). Because dense monocultures of *I. cylindrica* reduce plant diversity, microorganisms associated with extirpated plants, as well as nonassociated beneficial microorganisms, are probably being extirpated simultaneously, disrupting nutrient cycling. Counter to these expectations Hagan et al. (2013a) found that *I. cylindrica* did not have significant direct results on nutrient dynamics although eradication produces significant results with respect to phosphorus (P) and N. Specifically, no differences were observed in pH, NO₂ and NO₃, or NH₄. Significant results observed with regards to N included immobilization in the rhizome tissue in the first 12 months followed by a leveling off and P immobilization occurring immediately. However, it is difficult to determine the exact effects of *I. cylindrica* on the resident microbial population without long-term and physiological research. Regardless of what the specific effects may be, they may have implications on resource management and conservation of biodiversity.

Microbial biomass N was highly variable in all plots and no significant differences were evident between plots; either by treatment or over time. We attributed this observation to the limited number of replications used. A combination of observed effects including reduced plant diversity associated with *I. cylindrica* increased bare space in *I. cylindrica* present plots, and physical differences observed by other researchers (such as reduced light) may have a significant effect on the relationship between the microbial biomass carbon/nitrogen ratio. Microbial processes are linked with nutrient cycling, fertilization, and organic matter transformation (Ěerný et al. 2003), and microbial biomass is often used as an indicator of soil quality. However, high levels of variability in microbial biomass, even among nearby areas, can make generalizations difficult (Xu et al. 2013). This “natural” heterogeneity probably contributed to the variation observed between plots and may have been more influential as a whole than *I. cylindrica*.

Significant differences in *P. taeda* growth were not observed between *I. cylindrica* percent cover by stocking percentages. Although lower growth rates would be expected in the stands with higher stocking levels, growth of trees in the *I. cylindrica* present plots in these stands was not significantly reduced. Although competitive

effects of *I. cylindrica* were expected, an insufficient amount of time may have elapsed since *I. cylindrica* entered the site for the effects of the invasion to be fully expressed. Given the potential long-term effects that may only emerge over time, additional testing covering longer time scales is recommended.

Conclusion

Abundances of mycorrhizal fungi and fine feeder roots were significantly reduced in *I. cylindrica* abundant plots. Vegetative communities were also less diverse in *I. cylindrica* abundant plots. These factors probably contribute to a lower overall microbial diversity and a reduction in the rate of nutrient cycling and affect the soil nutrients present. Although impacts on growth were not observed, it is expected that over time, an impact may be seen. Furthermore, these changes may lead to communities that are more susceptible to disease and secondary invasion. Careful monitoring and *I. cylindrica* control may be necessary to maintain production of *P. taeda* and conservation of biodiversity.

Endnotes

1. For more information, see www.idcide.com.
2. The 16-year-old stand was thinned in 2009 and has not been burned. Diammonium phosphate (DAP) was applied in 2006 at a rate of 280 kg/ha, and urea was applied in 2010 at a rate of 224 kg/ha. The 21/22-year-old stand was thinned before 2006 and had a cool season controlled burn in 2009. It also had DAP applied in 2006 but at a rate of 140 kg/ha and urea was applied in 2007 at a rate of 224 kg/ha.

Literature Cited

- ANDERSON, R.C., M.R. ANDERSON, J.T. BAUER, M. SLATER, J. HEROLD, P. BAUMHARDT, AND V. BOROWICZ. 2010. Effect of removal of garlic mustard (*Alliaria petiolata*, Brassicaceae) on arbuscular mycorrhizal fungi inoculum potential in forest soils. *Open Ecol. J.* 3(1):41–47.
- BOLAN, N.S. 1991. A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant Soil* 134(2):189–207.
- BOUFALIS, A., F. PELLISSIER, AND L. TROSSET. 1994. Responses of mycorrhizal fungi to allelopathy: *Cenococcum geophilum* and *Laccaria laccata* growth with phenolic acids. *Acta Bot. Gallica* 141(4):547–550.
- BREWER, S. 2008. Declines in plant species richness and endemic plant species in longleaf pine savannas invaded by *Imperata cylindrica*. *Biol. Invas.* 10(8):1257–1264.
- BRUNDRETT, M., N. BOUGHER, B. DELL, T. GROVE, AND N. MALAJCZUK. 1996. *Working with mycorrhizas in forestry and agriculture*. Pirie Printers, Canberra, Australia. 374 p.
- BRUNSON B. 2013. *Impact of Imperata cylindrica on populations of root-feeding bark beetle populations and factors associated with loblolly pine decline in a Pinus taeda stand*. MS thesis, Auburn University, Auburn, AL. 83 p.
- BRYSON, C.T., AND R. CARTER. 1993. Cogongrass, *Imperata cylindrica*, in the United States. *Weed Technol.* 7(4):1005–1009.
- BURRELL, A.M., A.E. PEPPER, G. HODNETT, J.A. GOOLSBY, W.A. OVERHOLT, A.E. RACELIS, R. DIAZ, AND P.E. KLEIN. 2015. Exploring origins, invasion history and genetic diversity of *Imperata cylindrica* (L.) P. Beauv. (Cogongrass) in the United States using genotyping by sequencing. *Mol. Ecol.* 24(9):2177–2193.
- CALLAWAY, R.M., AND W.M. RIDENOUR. 2004. Novel weapons: Invasive success and the evolution of increased competitive ability. *Front. Ecol. Environ.* 2(8):436–443.
- CERNÝ, J., J. BALIK, D. PAVLIKOVA, M. ZITKOVA, AND K. SYKORA. 2003. The influence of organic and mineral nitrogen fertilizers on microbial biomass nitrogen and extractable organic nitrogen in long-term experiments with maize. *Plant Soil Environ.* 49(12):560–564.
- CHAPIN, F.S., III, E.S. ZAVALA, V.T. EVINER, R.L. NAYLOR, P.M. VI-TOUSEK, H.L. REYNOLDS, D.U. HOOPER, ET AL. 2000. Consequences of changing biodiversity. *Nature* 405(6783):234–242.
- COLWELL R.K. 2013. *EstimateS: Statistical estimation of species richness and*

- shared species from samples, version 9. Available online at <http://purl.oclc.org/estimates>; last accessed Jan. 21, 2016.
- DANESHGAR, P., AND S. JOSE. 2009. *Imperata cylindrica*, an alien invasive grass, maintains control over nitrogen availability in an establishing pine forest. *Plant Soil* 320(1):209–218.
- DANESHGAR, P., S. JOSE, A. COLLINS, AND C. RAMSEY. 2008. Cogongrass (*Imperata cylindrica*), an alien invasive grass, reduces survival and productivity of an establishing pine forest. *For. Sci.* 54(6):579–587.
- DEVI, N.B., AND P.S. YADAVA. 2006. Seasonal dynamics of soil microbial biomass C, N and P in a mixed oak forest ecosystem of Manipur, North-East India. *Appl. Soil Ecol.* 31(3):220–227.
- DICKIE, I.A., N. BOLSTRIDGE, J.A. COOPER, AND D.A. PELTZER. 2010. Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytol.* 187(2):475–484.
- EHRENFELD, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6(6):503–523.
- EISENHAEUER, N., H. BEßLER, C. ENGELS, G. GLEIXNER, M. HABEKOST, A. MILCU, S. PARTSCH, ET AL. 2010. Plant diversity effects on soil microorganisms support the singular hypothesis. *Ecology* 91(2):485–496.
- ESTRADA, J.A., AND S.L. FLORY. 2015. Cogongrass (*Imperata cylindrica*) invasions in the US: Mechanisms, impacts, and threats to biodiversity. *Global Ecol. Conserv.* 3:1–10.
- GILLIAM, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57(10):845–858.
- GINGRICH, S.F. 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central states. *For. Sci.* 13(1):38–53.
- HAGAN, D.L., S. JOSE, K. BOHN, AND F. ESCOBEDO. 2013a. Cogongrass (*Imperata cylindrica*) invasion and eradication: Implications for soil nutrient dynamics in a longleaf pine sandhill ecosystem. *Invas. Plant Sci. Manage.* 6(3):433–443.
- HAGAN, D.L., S. JOSE, AND C.H. LIN. 2013b. Allelopathic exudates of cogongrass (*Imperata cylindrica*): Implications for the performance of native pine savanna plant species in the southeastern US. *J. Chem. Ecol.* 39(2):312–322.
- HECTOR, A., AND R. BAGCHI. 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448(7150):188–190.
- HOLZMUELLER, E.J., AND S. JOSE. 2011. Invasion success of cogongrass, an alien C₄ perennial grass, in the southeastern United States: Exploration of the ecological basis. *Biol. Invas.* 13(2):435–442.
- HORTON, T.R., AND T.D. BRUNS. 1998. Multiple-host fungi are the most frequent and abundant ectomycorrhizal types in a mixed stand of Douglas fir (*Pseudotsuga menziesii*) and bishop pine (*Pinus muricata*). *New Phytol.* 139(2):331–339.
- HUSSAIN, F., AND N. ABIDI. 1991. Allelopathy exhibited by *Imperata cylindrica* (L.) P. Beauv. *Pak. J. Bot.* 23(1):15–25.
- JOSE, S., J. COX, D.L. MILLER, D.G. SHILLING, AND S. MERRITT. 2002. Alien plant invasions: The story of cogongrass in southeastern forests. *J. For.* 100(1):41–44.
- KOGER, C.H., AND C.T. BRYSON. 2004. Effect of Cogongrass (*Imperata cylindrica*) extracts on germination and seedling growth of selected grass and broadleaf species. *Weed Technol.* 18(2):236–242.
- KOWALCHUK, G.A., D.S. BUMA, W. BOER, P.G.L. KLINKHAMER, AND J.A. VEEN. 2002. Effects of above-ground plant species composition and diversity on the diversity of soil-borne microorganisms. *Antonie Van Leeuwenhoek* 81(1–4):509–520.
- KOURTEV, P.S., J.G. EHRENFELD, AND M. HÄGGBLUM. 2002. Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83(11):3152–3166.
- KREBS, C. 1989. *Ecological methodology*. Harper Collins Publishers, New York. 654 p.
- LIPPINCOTT, C.L. 2000. Effects of *Imperata cylindrica* (L.) Beauv. (Cogongrass) invasion on fire regime in Florida sandhill (USA). *Nat. Area J.* 20(2):140–149.
- LANDEWEERT, R., E. HOFFLAND, R.D. FINLAY, T.W. KUYPER, AND N. VAN BREEMEN. 2001. Linking plants to rocks: Ectomycorrhizal fungi mobilize nutrients from minerals. *Trends Ecol. Evol.* 16(5):248–254.
- MACDONALD, G.E. 2004. Cogongrass (*Imperata cylindrica*)—Biology, ecology, and management. *Crit. Rev. Plant Sci.* 23(5):367–380.
- MAGURRAN, A.E. 2013. *Measuring biological diversity*. Blackwell Publishing, Malden, MA. 264 p.
- MARSCHNER, H., AND B. DELL. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant Soil* 159(1):89–102.
- NATIONAL RESOURCES CONSERVATION SERVICE. 2012. *Soil survey report, Greene County, MS*. US Department of Agriculture, Washington, DC. Available online at <http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx>, last accessed Nov. 15, 2016.
- NILSSON, M.C., AND D.A. WARDLE. 2005. Understory vegetation as a forest ecosystem driver: Evidence from the northern Swedish boreal forest. *Front. Ecol. Environ.* 3(8):421–428.
- PASTERNAK, Z., A. DIAMANT, AND A. ABELSON. 2007. Co-invasion of a Red Sea fish and its ectoparasitic monogenean, *Polylabris* cf. *mamaevi* into the Mediterranean: Observations on oncomiracidium behavior and infection levels in both seas. *Parasitol. Res.* 100(4):721–727.
- PIMENTEL, D., R. ZUNIGA, AND D. MORRISON. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52(3):273–288.
- RICHARDSON, D.M., N. ALLSOPP, C.M. D'ANTONIO, S.J. MILTON, AND M. REJMANEK. 2000. Plant invasions—The role of mutualisms. *Biol. Rev.* 75(1):65–93.
- ROBERTS, K.J., AND R.C. ANDERSON. 2001. Effect of garlic mustard [*Alharia petiolata* (Beib. Cavara and Grande)] extracts on plants and arbuscular mycorrhizal (AM) fungi. *Am. Midl. Nat.* 146(1):146–152.
- SIMBERLOFF, D., J.L. MARTIN, P. GENOVESI, V. MARIS, D.A. WARDLE, J. ARONSON, F. COURCHAMP, ET AL. 2013. Impacts of biological invasions: What's what and the way forward. *Trends Ecol. Evol.* 28(1):58–66.
- STINSON, K.A., S.A. CAMPBELL, JR. POWELL, B.E. WOLFE, R.M. CALLAWAY, G.C. THELEN, S.G. HALLETT, D. PRATI, AND J.N. KLIRONOMOS. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biol.* 4(5):727–731.
- TAYLOR, A.F. 2002. Fungal diversity in ectomycorrhizal communities: Sampling effort and species detection. *Plant Soil* 244(1):19–28.
- TEDERSOO, L., T. SUVI, E. LARSSON, AND U. KÖLJALG. 2006. Diversity and community structure of ectomycorrhizal fungi in a wooded meadow. *Mycol. Res.* 110(6):734–748.
- TRAUTWIG, A.N. 2015. *Microbial communities in cogongrass (Imperata cylindrica (L.) Beauv.) invaded commercial loblolly pine (Pinus taeda L.) stands*. MS thesis, Auburn University, Auburn, AL. 111 p.
- VAN DER HEIJDEN, M.G., R.D. BARDGETT, AND N.M. VAN STRAALEN. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* 11(3):296–310.
- VANCE, E.D., P.C. BROOKES, AND D.S. JENKINSON. 1987. An extraction method for measuring soil microbial biomass C. *Soil Biol. Biochem.* 19(6):703–707.
- VILÀ, M., J.L. ESPINAR, M. HEJDA, P.E. HULME, V. JAROŠÍK, J.L. MARON, J. PERGL, U. SCHAFFNER, Y. SUN, AND P. PYŠEK. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14(7):702–708.
- WARDLE, D.A. 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biol. Rev.* 67(3):321–358.
- WOLFE, B.E., AND J.N. KLIRONOMOS. 2005. Breaking new ground: Soil communities and exotic plant invasion. *BioScience* 55(6):477–487.
- XU, X., P.E. THORNTON, AND W.M. POST. 2013. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Global Ecol. Biogeogr.* 22(6):737–749.
- ZAK, D.R., W.E. HOLMES, DC. WHITE, A.D. PEACOCK, AND D. TILMAN. 2003. Plant diversity, soil microbial communities, and ecosystem function: Are there any links? *Ecology* 84(8):2042–2050.