

TECHNICAL REPORT

Characterization and quantitative assessment of interspecific and intraspecific penetration of below-ground vegetation by cogongrass (*Imperata cylindrica* (L.) Beauv.) rhizomes

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Cogongrass (*Imperata cylindrica* (L.) Beauv.), an invasive C4 perennial grass, negatively influences native plant communities by forming dense monotypic stands that alter ecosystem properties and lower local species diversity. A hypothesized mechanism by which cogongrass achieves competitive dominance is a novel use of below-ground vegetative disturbance of neighboring vegetation (i.e. puncturing). However, very little empirical evidence is found in the peer-reviewed literature to quantify this phenomenon, much less establish it as a true form of competitive interaction. The present field study was conducted to quantify the occurrence of rhizome-mediated, below-ground vegetative penetration, both interspecifically and intraspecifically, document how this phenomenon is influenced by spatial location relative to the cogongrass stand, and determine the role that above-ground and below-ground biomass might have in the process. Analyses of 100 sod samples indicated that rhizome-mediated, below-ground vegetative penetration is a much larger intraspecific phenomenon than an interspecific one. The data also strongly suggested spatial location as a significant factor, with most penetrations occurring in the interior of a cogongrass stand as opposed to the advancing border. Significant correlations between rhizome-mediated, below-ground vegetative penetration and above-ground cogongrass biomass were found in the overall plot analysis and most strongly in the advancing border of the cogongrass stands.

Keywords: below-ground interactions, competition, invasive plant species, penetration, rhizome growth.

INTRODUCTION

Cogongrass (*Imperata cylindrica* (L.) Beauv.) is an invasive perennial grass that threatens agriculture, forestry, and native plant assemblages in many regions of the world. Cogongrass exerts its negative effects upon the landscape by forming dense monotypic stands that can lower local species diversity and alter fire regimes (Lippincott 2000). The general explanation given for the formation of monotypic cogongrass stands is that it is a superior competitor against native vegetation. Some authors have hypothesized that allelopathic interactions (Koger *et al.*

2004), versatile dispersal ability (Shilling *et al.* 1997), and efficiency at nutrient acquisition (Brewer & Cralle 2003) all can lead to an increased competitive advantage for cogongrass.

Cogongrass also has been hypothesized to utilize a unique form of below-ground competitive interaction to compete against native forms of vegetation. In this hypothesized competitive interaction, cogongrass uses its extensive rhizome system to physically rupture the below-ground vegetative tissue (roots, rhizomes, tubers, bulbs) of neighboring plants. Many critical reviews have referenced this phenomenon, suggesting that the rhizomes interfere with the growth and nutrient uptake of neighboring plants, as well as facilitate the invasion of pathogens into the tissues of damaged plants (Bryson & Carter 1993; Dozier *et al.* 1998; MacDonald 2004). However, little if any empirical evidence has been

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provided to substantiate these claims. Most references to this unique form of inhibitory plant interaction are supported only by scientists having observed the phenomenon in the field. The first step in determining whether cogongrass actually exhibits a mechanistic below-ground vegetative interference strategy is to quantify the actual occurrence of the process. Later studies, involving analyses of growth and other fitness correlates, would be necessary to establish below-ground vegetative penetration by cogongrass rhizomes as an effective form of competitive interaction.

The purpose of this study was to address the lack of empirical evidence supporting the occurrence of rhizome-mediated puncturing of below-ground vegetation by cogongrass. The four main objectives of our study were to: (i) quantify the interspecific occurrence of rhizome-mediated penetration of below-ground vegetation; (ii) quantify the intraspecific occurrence of rhizome-mediated penetration of below-ground vegetation; (iii) determine if the spatial location (interior vs edge of cogongrass stand) influences the penetration frequency; and (iv) determine if rhizome-mediated penetration of below-ground vegetation is influenced by the above or below-ground biomass of cogongrass or neighboring vegetation.

STUDY SITES AND DESIGN

The study was conducted on three cogongrass populations located in Oktibbeha County, Mississippi, USA: North Farm (33.47393°N, -088.77078°W), Ramsey Bottom (33.46641°N, -088.75828°W), and Highway 182 (33.47771°N, -088.67453°W). The first two sites, North Farm and Ramsey Bottom, were located on experimental farm land owned by Mississippi State University and the Highway 182 site was located on a highway shoulder. Each site contained a mature stand of undisturbed cogongrass as evidenced by the tall swards in the interior of the population. Visual inspection, weeks prior to the actual experiment, also confirmed the populations had not been recently disturbed (i.e. mowed) in the area of sampling.

The design to quantify the occurrence of rhizome-mediated penetration of below-ground vegetation, both interspecifically and intraspecifically, consisted of examining 100 0.25 m × 0.25 m plots that were exhumed from the field and returned to the laboratory for analysis. The sods were excavated to a constant depth of 35 cm and were examined for penetration frequency within 2 days of sampling. All sampling was conducted during July 2005 in order to excavate the below-ground vege-

tation at a time of year when the plants were actively growing and allocating resources to underground growth. This allowed us to capture the below-ground interactions during a time when the plants were growing, competing for resources, and potentially, when direct physical below-ground interactions were taking place.

The sampling design called for an equal number of samples to be collected from within a cogongrass stand and from along the edge of the monotypic stand in order to provide evidence for the spatial relationship of penetration frequency, as outlined in the third objective of the study. In accordance with this design, 30 interior and edge plots were obtained from the North Farm site and 10 interior and edge plots were obtained from both the Ramsey Bottom and the Highway 182 locations, leading to a total of 100 0.25 × 0.25 m plots (50 interior and 50 edge plots). The sampling design did not call for equal numbers of samples to be obtained from each study site, as the differences between the sites were unimportant for testing our hypotheses. Thus, three cogongrass populations were used to allow for more spatial heterogeneity in the overall sampling and greater generality to the conclusions.

The interior sampling was restricted to areas ≥ 1 m within the edge of the monotypic stand and which contained ≥ 99% cogongrass coverage. The sampling was randomized by using a random number generator to provide for possible sample points within the available space at each site. The edge of a stand was defined as that area where the percentage cover of cogongrass was between 25–75% and did not exceed farther than 0.5 m into what had been defined as the interior of the stand. Randomization was achieved, as in the interior stand, by preliminary surveying of the site to define the sample space and the use of a random number generator to provide possible sample points.

After the samples had been removed from the field, they were immediately brought back to the laboratory, sorted, and processed. The processing of samples consisted of sieving away all soil and inspecting the resulting underground biomass for possible vegetative penetration. Only penetrations that involved a live cogongrass rhizome penetrating another live root or rhizome at the time of sampling were considered in the analysis. Roots and rhizomes were the only below-ground vegetative structures encountered in the study and, thus, the only below-ground anatomical components mentioned throughout the remainder of the paper. Live roots and rhizomes were considered to be those that were white and turgid at the time of sampling. Also, nearly all of the

rhizomes counted as living were attached to green above-ground tissues.

The above and below-ground biomass were recorded to determine if penetration was correlated with cogongrass biomass. The above and below-ground composition of cogongrass was recorded for both the interior and edge plots; additionally, the above and below-ground biomass of non-cogongrass vegetation was analyzed in the edge plots. As the percentage cover of cogongrass approached 100% in the interior plots, only the edge plots received the additional non-cogongrass vegetation analysis. These measurements were taken in the laboratory after penetration numbers had been counted. The above and below-ground tissue was dried at a temperature of 100°C for at least 48 h after being sorted. After drying, the tissue was then weighed and recorded to the nearest 0.01 g.

Data analysis was carried out using SYSTAT (version 11; Systat Software, Richmond, CA, USA). In order to determine if rhizome-mediated penetration occurred more frequently in the interior of a cogongrass stand or along the edge of the stand adjacent to native vegetation, an ANOVA was performed among the two population means. The penetration data were not completely normally distributed, but despite the large sample size ($n = 100$), which should have justified the use of parametric analyses, the non-parametric Mann–Whitney test also was applied. Regression analyses were conducted in order to find correlations between the measured biomass variables and the penetration frequency. As a result of the abnormal distribution of our penetration data, a Robust-Rank-type regression analysis, which uses the ranks of residuals rather than the observations themselves in order to find a predictive relationship between a response variable and a predictor variable, also was used.

RESULTS AND DISCUSSION

Interspecific penetration was recorded in 10 of the 100 plots. Although this is not an excessive occurrence, it is 10% of the total sample space and, thus, relatively common. As a result of the low number of recorded occurrences of this interspecific event, further analyses beyond mere percentages were not possible. The most common type of vegetation punctured by the cogongrass rhizomes was bahiagrass (*Paspalum notatum* Fluegge), accounting for six of the 10 interspecific penetrations and all occurring through the rhizomes of this species. The other penetrations were through the rhizomes of bermudagrass (*Cynodon dactylon* (L.) Pers.), the roots of goldenrod (*Solidago* sp.), and the roots of two unidentifiable grass (Poaceae) species.

The occurrence of intraspecific rhizome-mediated penetration was recorded in 42 of the 100 plots in our survey and greatly exceeded that of the interspecific phenomenon. There were 67 total accounts of cogongrass rhizomes puncturing the living rhizomes of adjacent cogongrass (Table 1). The mean number of penetrations per plot was 0.77 (median = 0). In the interior plots, there was a mean of 1.04 (median = 1) intraspecific penetrations per plot, whereas the edge plots contained a mean of 0.30 (median of 0) intraspecific penetrations (ANOVA $P = 0.001$, Mann–Whitney $P = 0.002$). The large amount of intraspecific penetration found in the edge plots is very important given the fact that the edge plots contained nearly equal amounts of cogongrass and neighboring vegetation (Table 1). Thus, there should have been an almost equal chance for the penetration phenomenon to be one of an interspecific or intraspecific nature.

Regression analysis indicated that the above-ground cogongrass biomass was significantly correlated with the overall number of penetrations ($P = 0.03$, $r^2 = 0.05$) and intraspecific penetrations ($P = 0.004$, $r^2 = 0.08$) in the combined plot data analysis. When the data were divided into interior and edge plot components, only the above-ground biomass of cogongrass in the edge plots was found to be a significant factor. The edge plot above-ground cogongrass correlated with the overall number of penetrations ($P = 0.001$, $r^2 = 0.19$). The non-parametric rank regression for the total plot intraspecific penetrations yielded a coefficient value for the above-ground cogongrass variable of 0.021 that corresponds

Table 1. Overview of plot vegetation and penetration data

Variable	Interior plots	Edge plots
Intraspecific penetration	52.00	15.00
Interspecific penetration	3.00	7.00
Mean above-ground biomass (g plot ⁻¹)		
Cogongrass	21.36	9.43
Native vegetation	NA	7.25
Mean below-ground biomass (g plot ⁻¹)		
Cogongrass	38.80	22.98
Native vegetation	NA	23.54

Penetration, the penetration of a cogongrass rhizome through the root or rhizome of another plant; NA, there were no biomass calculations performed on these plots for non-cogongrass vegetation.

with the parametric coefficient of 0.022. The rank regression for the edge plot overall penetrations yielded a coefficient value for the above-ground cogongrass variable of 0.048 that also corresponds with its parametric counterpart of 0.046. As a result of the low number of interspecific penetrations found among all plots, further analyses such as the ones performed for intraspecific penetrations were not statistically justifiable.

The results clearly indicate that the predominance of rhizome-mediated penetration of below-ground vegetation by cogongrass is a largely intraspecific phenomenon. In this survey, intraspecific penetration far exceeded interspecific penetration (Table 1). It is important to point out that in the edge plot survey, nearly equal amounts of below-ground cogongrass and below-ground neighboring vegetation tissue were observed, yet there was still a higher degree of intraspecific penetration. These data lend credit to the sampling design used and indicate that the observed intraspecific predominance is not merely a sampling artifact. However, it is important to stress that one cannot interpret these results as indicative of proof that this phenomenon is a method of competition, either intraspecific or interspecific. The present study, as outlined in the introduction, merely sought to quantify this phenomenon and not to establish it as a mechanistic competitive function.

Beyond establishing rhizome-mediated penetration of below-ground vegetation by cogongrass as a mainly intraspecific phenomenon, the data also point out several more significant relationships. For instance, below-ground vegetation penetration by cogongrass occurred most often in the interior of an established cogongrass stand rather than along the advancing front. The data also indicated that the above-ground biomass of cogongrass is a weak predictor of the total and intraspecific numbers of rhizome-mediated penetrations found beneath the soil (low correlation coefficients) and that the below-ground biomass was uncorrelated with the number of penetrations. Although below-ground penetration was more frequent in the interior of these stands, the above-ground cogongrass biomass was more strongly correlated with the total number of penetrations along the advancing border than in the interior. This apparent discrepancy might be attributable to a biomass-dependent threshold beyond which the chances of observing an increase in the penetration phenomenon decrease significantly. Thus, it could be the case that in the interior plots, a “saturated” population existed, whereas along the advancing border, the cogongrass was still showing detectable responses to biomass allocation.

The study also supported the widely observed claim that cogongrass allocates most of its biomass to below-ground tissues, with roughly two-thirds of the cogongrass mass represented by below-ground tissues (Table 1). The fact that cogongrass allocates so much of its biomass to below-ground tissues would support competitive hypotheses that emphasize nutrient uptake, resource utilization, and competitive displacement. These competitive mechanisms might be responsible for the complete dominance of cogongrass in our interior plots and the lack of interspecific competitors and, consequently, penetration. Finally, the data would appear to contradict any purported hypotheses regarding pathogen introduction via rhizome-mediated penetration of below-ground tissue. Though we did not directly test pathogen introduction in our experimental design, pathogen infection would presumably be much higher in cogongrass than in neighboring plants because of the high frequency of intraspecific rhizome penetration.

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