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The Effects Of Phragmites Australis Litter On Seed Emergence In The Erie-Huron Corridor, Michigan

Travis White
Wayne State University,

THE EFFECTS OF *PHRAGMITES AUSTRALIS* LITTER ON SEED EMERGENCE IN THE ERIE-HURON CORRIDOR, MICHIGAN

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TRAVIS J WHITE

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Introduction

Coastal marshes of the Great Lakes are highly productive ecosystems. They provide habitat for a wide variety of aquatic and terrestrial species and a suite of other ecosystem functions, such as serving as spawning habitats and refuges for juvenile fish species (Jude 1992), and providing nesting habitats for waterfowl (Steen et al. 2006). These ecosystems experienced widespread habitat loss during the 19th and 20th centuries. Most areas in the region have lost at least 50% of their coastal wetlands (Hecnar 2004) with Michigan losing at least 50% and up to 70% (Noss et al. 1995), primarily due to land use changes related to agriculture and urbanization (Noss et al. 1995). More recently, additional habitat loss and loss of biodiversity has resulted from invasions by non-native plant and animal species (Wilcox 2012).

A non-native invasive subspecies of *Phragmites australis* (*P. australis*), likely introduced to the east coast of the United States in the early 19th century has spread to nearly every state in the United States impacting wetlands across the country (Saltonstall 2001). The native subspecies, *Phragmites australis* subsp. *americanus*, typically occurs as scattered plants among broader plant communities in Great Lakes marshes and coastal fens in addition to other wetland habitats (Kulmatiski et al. 2010). The spread of invasive *P. australis* was likely hastened by the construction of railways and roads across the US (Saltonstall 2001). Furthermore, Sellinger (2008) suggested that the spread of *P. australis* could be attributed to multiple abiotic factors such as global climate change, declining water levels, changes in winter ice cover and land use changes. The impacts of both *P. australis* and a hybridized genotype (Saltonstall 2001) has led to extensive habitat degradation in the Great Lakes region (Wilcox 2003). *P. australis* forms dense

monocultures capable of dominating wetlands within a few years of an initial occurrence (Ailstock et al. 2001).

Invasion of *P. australis* into native wetlands results in losses of biodiversity due to its ability to outcompete native plants (Torbick et al. 2010). Furthermore, *P. australis* is a highly productive and can produce up to 50% more biomass than its most productive competitor, another non-native species, narrow-leaved catail (*Typha angustifolia;* Findlay et al. 2002), and has been documented to be an order of magnitude more productive than most other wetland plants. Where the main competitor of *P. australis* is a plant other than *T. angustifolia*, *P. australis* has been documented to exceed the biomass accumulation rate of other species by as much as ten to one (Windham 2001). The annual accumulation of litter associated with *P. australis* invasion can have multiple effects on the ecosystem including reduced nutrient availability (Windham and Ehrenfeld 2003), exclusion of native species via shading and the obstruction of seed deposition and germination (Minchinton 2006), decreased decomposition rates, altered hydrological regimes, increased evapotranspiration, and increased thermal regimes (Pose et al. 2003).

Site dominance by *P. australis* occurs through several different mechanisms. Although *P. australis* stands tend to produce few viable seeds, it aggressively reproduces vegetatively via rhizome and stolon growth (Ailstock et al. 2001). Vegetative reproduction allows dense *Phragmites* stands to develop and can lead to the creation of a thick litter layer (Holdredge and Bertness 2010). This litter layer may decompose slowly because of the high amount of cellulose in *P. australis* culms (Agoston-Szabo and Dinka, 2008), and tends to make eradication difficult, costly and largely ineffective by requiring multiple treatments of herbicide and clearance of dead vegetation via prescribed burns or mechanical means. The dense litter layer generated by *P.*

australis gives it a competitive advantage over native vegetation by suppressing the underlying seed bank (Holdredge and Bertness 2011) and limiting access to sunlight (Ailstock et al. 2001).

Factors controlling the decomposition rate of many wetland systems are unable to compensate for this higher production and a thick litter mat can therefore develop (Holdredge and Bertness 2010). Accelerated litter accumulation in wetland systems may reduce the possibility of native plant reestablishment and decrease diversity while also sequestering nutrients in forms unavailable to plants (Findlay et al. 2002). The ability of *P. australis* to produce greater amounts of biomass than its competitors and to produce litter with slow decomposition rates more slowly can have large impacts on native vegetation establishment by suppression of the underlying seedbank (Holdredge and Bertness 2010).

Previous studies have shown that intact native seed banks may persist for at least 40 years following high levels of disturbance (Brown 1998). Siegly et al. (1988) showed that up to 90 species and >1700 germinable seeds can be found in 1.5-2.0 liters of wetland soil. Although seed bank composition has been shown to be an unreliable predictor of ecological succession in wetlands (Brown 1998), it is a viable source of potential propagules following invasive species removal. Remnant seed banks almost certainly contain viable seed stocks of historically present plant species, and can provide an easily accessible source of potential propagules with which to reestablish biologically diverse stands of native vegetation (Leck 1989). In contrast, *P. australis* seeds have low viability and generally occur at lower densities than other wetland species (Baldwin et al. 2010) and are not likely to germinate in large numbers following its removal. *P. australis* control is a high priority of wetland scientists, conservation biologists, and resource managers because of its tendency toward rapid proliferation and exclusion of native species (Ailstock et al. 2001).

The overall objective of this study was to investigate the effects of *P. australis* litter on seed emergence in wetlands; specifically, comparing seed bank emergence under various litter depths of the less aggressive non-native *T. angustifolia* to that of *P. australis.* In addition, I evaluated the effects of *P. australis* litter on seed emergence at five locations in the Great Lakes along the Erie-to-Huron waterway to identify whether location influenced the effects of litter on seedling emergence among coastal marshes.

Phragmites australis is a highly invasive species that greatly reduces the biodiversity and ecological integrity of coastal marshes in the Great Lakes region. Removal of *P. australis* is therefore a high priority for resource managers and conservation biologists. This study seeks to observe the effects of *Phragmites* litter upon soils from coastal marshes. Understanding how the litter layer affects regeneration of wetland vegetation once *P. australis* establishes a litter layer is important for management considerations regarding treatment of live biomass and the potential legacy effects it creates.

Methods

To examine the impacts of the litter layer in stands of *P. australis* on emergence of plants from the seed bank, I designed two complementary experiments. The first experiment investigated the effects of the litter layer on seed bank emergence from a single location, with respect to the two dominant species there: *P. australis* and *T. angustifolia*. The second experiment examined potential regional factors of *P. australis* invasion by looking at *P. australis* litter and its effects on seedling emergence in soils from five coastal wetlands throughout the Huron to Erie waterway.

Study Locations:

Five coastal marshes along the Erie -Huron waterway in southeastern Michigan dominated by *P. australis* were selected to investigate the effects of *P. australis* litter on seed emergence (Figure 1). The physical nature patches within a location were similar in density and is in close proximity (<100m) of each other, to minimize environmental variables among the patches moving north to south, locations included:

Lake St. Clair Metropark (SCMP) in Harrison Township, Michigan is the northernmost location and is located on the shores of Lake St. Clair near the mouth of the Detroit River (Figure 1). This location is one of the largest remaining coastal marshes remaining in Southeast Michigan (Albert 2003). The marsh has a long history of disturbance and degradation including filling, construction of drainage ditches, and alterations to its hydrological connection with the lake the largest of which was the channelization of the Clinton River, which prevents runoff and direct flow from reaching it. The park has been the subject of aggressive removal of *P. australis* within the last five years; however, it is still present, especially in the northernmost reaches of the park where this location is located.

Belle Isle city park (BICP) in Detroit, Michigan located in the Detroit River. The park has a history of *P. australis* control although documentation of control efforts including herbicide application and controlled burns could only be obtained anecdotally.

Lake Erie Metropark (LEMP) is located in Monroe, Michigan (Figure 1). This location is near the southern boundary of the Detroit River and northwest Lake Erie. The park has a history of *P. australis* control including controlled burns and herbicidal treatment (Muelle 2013).

Private property (PPGI) on Grosse Ille island in Grosse Ille Township, Michigan near the

outflow of the Detroit River into Lake Erie (Figure 1). This location is located on the eastern edge of the island next to a marina and has likely had no control measures enacted.

Sterling State Park (STSP) in Luna Pier, MI (Figure 1). It is located in the northwest corner of Lake Erie south of Lake Erie Metro Park (LEMP). Within the last five years, this location has been subjected to aggressive *P. australis* treatment of controlled burn and herbicidal treatment.

Experiment 1: **Litter depth comparison of *Phragmites* vs. *Thypha*:**

Soil cores from SCMP were harvested on January 2012, from two locations inside LSCMP based on the presence of two large monocultures of 1) *P. australis*; [N 42° 35.435', W 82° 48.091] and 2) *T. angustifolia* [N 42° 35.245', W 82° 48.048'] approximately 300m apart for a laboratory study examining seedling emergence with respect to varying depths and types of litter coverage. To capture as much seed bank heterogeneity as possible at each monoculture, 10 sites were identified within 20 meters of each other to collect soil samples. At each of the ten patches, I collected 5 soil core samples, totaling 50 samples at each monoculture.

Twenty-five measurements of litter depth were taken at each location to determine average litter depth for the litter depth comparison experiment (6.0±0.27 cm at the *P. australis* site and 2.8±0.12 cm at the *T. angustifolia* site). Litter depth was measured as the distance from the surface of the litter layer to the top of the mineral soil to determine how much litter should be used in each of the litter cover treatments (0%, 25%, 50% and 100% litter depth) in the seed bank and litter layer seedling emergence experiment. Immediately prior to collecting the soil all litter was scraped from the ground in an area of approximately $0.25m^2$ and then the five cores were harvested using a 7 cm x 12 cm cylindrical bulb-planter. This method extracted soil cores

to about 7 cm. When 50 cores from each site were harvested, they were brought back to the laboratory while kept cool and dark in coolers. Soil cores were processed in the laboratory using procedures developed by Liu et al. (2005) in preparation for the greenhouse-based seed bank and litter layer seedling emergence experiment. Woody material, litter, rhizomes and stolons were removed from each core, then pooled and homogenized by site in preparation for the experiment. Standing litter of both *P. australis* and *T. angustifolia* was harvested from each site and processed in the lab by separating leaves and cutting culms to no more than 20 cm for use in the experiment.

Seed Bank and Litter Layer Seedling Emergence Experiment:

I followed the seedling emergence method developed by Roberts (1981) for the germination experiment. Pooled soils were spread equally among three 20cm x 25cm x 5cm trays with 1.5 cm sand mixed with pearlite in the bottom to assist with draining. Soils from each location were mixed with 250 ml of water to create a soil slurry and then poured over 1.5cm of sand and pearlite to create a layer of soil approximately 5mm thick. To use the same volume of soil for each soil type, this required 183 g of soil from the *P. australis* site and 83 g of soil from the *T. angustifolia* site. Different soil masses were used to keep the volume of soil from each site type consistent. Soil from each location was separated into 40 trays for a total of 80 trays. For each location soil samples (n=5) of each soil type were subjected to one of 8 experimental treatments which include 0%, 25%, 50% and 100% of average litter depth of either *P. australis* litter or *T. angustifolia* litter and monitored daily for seedling emergence under varying levels of litter cover. Therefore, there were eight potential treatments in all for each location representing a 2 x 2 x 4 factorial design (n=5; 80 trays).

Once soils were distributed to all trays, litter batches were assembled according to the average litter depth of each site (6 cm at the *P. australis* site and 3 cm at the *T. angustifolia* site). This was done by taking the average mass of each litter species at 100% depth using litter harvested from each monoculture sampled. Litter from each species was sorted by stems and leaves and cut to the appropriate maximum size (<20cm) for the trays used in the experiment. Equal proportions of stems and leaves were used when assembling the litter batches. Portions were determined by filling trays used in the experiment to the maximum litter depth (*T. angustifolia*: 3.0 cm; *P. australis*: 6.0 cm) for each species with either stems or leaves. Each treatment received half the average mass of stems and leaves for its respective depth. For *P. australis*, the average stem mass was 80.3 g and the average leaf mass was 19.9 g. The 100% litter cover (6.0 cm) treatment using *P. australis* litter received 40 g stems and 10 g leaves. The 50% litter cover (3.0 cm) treatment using *P. australis* litter was given 20 g stems and 5 g leaves. The 100% litter cover (1.5 cm) treatment using *P. australis* litter received 10 g stems and 2.5 g leaves. For *T. angustifolia*, the average stem mass was 52 g and the average leaf mass was 23 g. The 100% litter cover (3.0 cm) treatment using *T. angustifolia* litter was given 26 g stems and 11.5 g leaves. The 50% litter cover (1.5 cm) treatment using *T. angustifolia* litter received 13 g stems and 5.75 g leaves. The 100% litter cover (0.75 cm) treatment using *T. angustifolia* litter was given 6.5 g stems and 2.88 g leaves.

When appropriate litter treatment was placed over the soil in each tray, trays were then randomly placed in pairs in a 20cm x 40cm x 5cm water containment tray to prevent water spillage to the ground and allow the tray to absorb the water. Position in the greenhouse was determined using a random number generator for each table (1-8 for table number; 1-7 for table position). All pairings were watered daily (500ml) to ensure that proper conditions for seedling

emergence were continuously present in all trays. Greenhouse vents were opened and closed manually to keep the temperature as consistent as possible. The maximum and minimum temperature in the greenhouse was monitored daily. Emergence was documented as any seedling that was visible within the tray without disturbing the litter. Seedling emergence was documented daily for six weeks.

Data Analysis:

Differences among tested factors were compared using a log-linear model containing three independent variables: soil type (*Phragmites* soil or *Typha* soil), litter type (*Phragmites* or *Typha*) and percent litter cover (0, 25, 50, 100). The number of observed emergences was the dependent variable. Independent and interaction effects were determined. All statistical analyses were conducted using IBM SPSS Premium Version 21 (SPSS Inc., 2011) with $\alpha = 0.05$.

Regional Seed Bank and Litter Layer Seedling Emergence Experiment:

To understand if location differences among coastal marshes in this region affect seedling emergence with respect to the litter layer, I evaluated seedling emergence from soils collected from 5 coastal marshes along the Huron-Erie corridor (Figure 1). Soils were harvested from SCMP, BICP, LEMP, SMP and PPGI during February 2013.

Using the same methods as described in experiment one, soils were harvested from patches dominated by either *P. australis* or *T. angustifolia*; however, only *P. australis* litter was used in this study, based on results from experiment one which indicated that the species of litter was not a factor in observed emergence counts. Soil processing, litter preparation and distribution were conducted using the same procedures as the previous experiment except where noted. Each tray received 100g of soil and one of three different amounts of litter (0 g, 20 g, 40 g) for each treatment. This mass selected for the 100% litter cover treatment was between the

100% litter cover treatments used for *T. angustifolia* and *P. australis* litter in the first experiment. For this experiment, a 25% litter cover treatment was not included to keep the number of samples at 120. There were three potential treatments for each soil type harvested from each location representing a 5 x 2 x 3 factorial design (n = 4; N = 120 trays). All replicates were watered once daily with 500 ml of water. Seedling emergence was recorded weekly over the course of six weeks.

Data Analysis:

Differences among tested factors were compared using a log-linear model containing three independent variables: location (SCMP, BICP, LEMP, SMP or PPGI) soil type (*P. australis* soil or *T. angustifolia* soil), and percent litter cover (0, 50, 100). All instances of recorded seedling emergence were included in the data analysis. All statistical analyses were conducted using IBM SPSS Premium Version 21 (SPSS Inc., 2012) with $\alpha = 0.05$.

Table 1: Summary of log-linear model analysis for soil + litter type + litter cover emergence experiment at Lake St. Clair Metropark. The difference between the value generated by the model and the degrees of freedom determines the significance. If the value in the significance column is greater than 0.95 (P<.05) then the factor (litter type, percent cover, soil type and interaction) is considered significant with respect to seedling emergence in the soils tested.

Experiment 1: Seed Bank and Litter Layer Germination			
Factor	Pearson Chi-Square	Degrees of Freedom	P-Value
Litter Species	10.89	11	0.453
Percent Cover	113.307	13	< 0.001
Soil Type	89.213	11	< 0.001
Interaction	10.803	10	0.373

Results

Litter-Seed Bank Seedling Emergence Experiment:

Litter species did not significantly impact the number of seeds emerging (p=0.453; Table 1,). Regardless of litter cover depth, the mean number of emergences beneath *T. angustifolia* and *P. australis* litter were nearly identical over the six-week experiment (Figure 2). There was no effect on observed emergence counts under any of the examined litter depths (Figure 3). The number of observed emergences continued to decrease with increasing depth with nearly the same number of observed emergences regardless of the species of litter used in the treatment (Figure 4).

Litter cover was a significant factor with respect to the number of observed emergences ($p < 0.001$; Table 1). Increasing litter cover significantly reduced the number of emergences at the 50% and 100% treatments, without regardless of the species of litter (Figure 5). In general, an increase in depth for either *T. angustifolia* or *P. australis* litter resulted in declines in the number of emergences from the soils (Figure 6). Seeds in the soil collected from the site dominated by *T. angustifolia* with a 50-100% depth in litter cover had significantly fewer observed emergences than the treatments with no cover or only 25% depth (Figure 6). Likewise, seeds in the soil collected from the site dominated by *P. australis* also had significantly less observed emergences with each increment in litter depth (Figure 6).

The location from which the soil originated had a significant impact ($p< 0.001$) on the number of observed emergences (Table 1). The soil from the *T. angustifolia* dominated sites averaged over two times (mean = 10.2) the number of observed emergences per tray compared to the soil from the *P. australis* dominated site (mean = 4.2) when all treatments were averaged

based on soil type (Figure 7). Soils collected from the *T. angustifolia* stand had significantly higher average emergences across all litter cover treatments; even though each treatment used less soil mass than the *P. australis* samples (Figure 8). Overall, both *T. angustifolia* and *P. australis* soil types exhibited declines in emergences with the exception of the 25% litter cover treatments on *P. australis* soils (Figure 9). Independently, soil type and litter cover were significant factors with respect to the number of emergences in the experiment. Litter species was not significant.

Table 2: Summary of log-linear model analysis for the regional soil + litter seedling emergence experiment. The difference between the Pearson chi-square value generated by the model and the Degrees of Freedom determines the significance. If the value in the significance column is greater than 0.95 (P<.05) then the factor (location, litter amount, soil type and interaction) is considered significant with respect to seedling emergence in the soils tested.

Experiment 2: Regional Seed Bank and Litter Layer Comparison			
Factor	Pearson Chi-Square	Degrees of Freedom	P-Value
Site Location	7482.484	26	< 0.001
Soil Type	1304.976	23	< 0.001
Percent Cover	5143.006	24	< 0.001
Interaction	1253.848	22	< 0.001

Regional Seed Bank Emergence Experiment:

The locations where the soil came from had a significant effect on the number of emergences (P < 0.001; Table 2; Figure 10). The number of emergences varied widely among locations. Soils collected from Sterling State Park had highest number of observed emergences (mean = 148.0) and was over an order of magnitude higher compared to GIPP which was the location with the lowest average emergences (mean = 10.3; Figure 10). The two northern locations, SCMP and BISP, each had average emergence counts similar yet still significantly different from each other (p< .001). The number of observed emergences from the two central locations, GIPP and LEMP, were also similar but still significantly different from each other (p=

.004). Sterling State Park had the highest average of emergences for each soil type (Figure 11). The average emergences from *P. australis* soils from STSP (mean = 215.0) are over two orders of magnitude larger than those from GIPP (mean =1.0). Generally, in the sites sampled, *T. angustifolia* soils had higher observed emergences than *P. australis* soils, but the average among all soils was higher for *P. australis*. These results are somewhat misleading because the Sterling State Park (STSP) *P. australis* patch yielded hundreds of observed emergences in each tray with 0% and 50% litter cover. When the data are analyzed without STSP observed emergences, *T. angustifolia* patches shows greater average observed emergence numbers.

Litter cover had a significant impact on emergences considering all litter treatments together ($p < 0.001$; Table 2). There were also significant differences in average emergence at both the 50% and 100% litter cover depths ($p < 0.001$; Figure 12). All litter cover treatments within each location was significantly different from each other with $P<0.002$ for all sites and treatment combinations. Each location except GIPP experienced a 59%-64% decrease in observed emergence from 0% litter cover to 50% litter cover. All locations saw at least an 84% drop in observed emergence in the 100% litter cover treatment with the location average being a 93% reduction.

Different soil types yielded significantly different number of emergences ($P < 0.001$; Table 2). In all locations except Sterling State Park, *T. angustifolia* soils had more emergences than *P. australis* patch-dominated soils. All soils from all locations had significant differences in the number of emergences between soil type ($p < .007$; Figure 11). Emergences for both soil types tended to follow a similar decreasing pattern of decreasing emergence with respect to increasing litter cover (Figure 13).

When comparing averaged emergences with respect to soil types across all sites, trends were observed with increasing litter cover (Figures 15-17). The average emergences for the 0% litter cover treatments were all significantly different except for the Belle Isle State Park – Lake Erie Metropark and Grosse Ille Private Property – Lake St. Clair Metropark comparisons (Figure 15). Clearly, sites are reacting similarly to increased litter cover regardless of their initial number of observed emergences.

Interaction effects of the factors tested (site location, soil type, litter cover amount) were significant with respect to the number of observed emergences observed ($p < 0.001$; Table 2). The only non-significant result obtained from the experiment was that of litter species. However, since the results do indicate that amount of litter present alone can affect the number of emergences a seed bank can produce, species such as *P. australis* that accumulate deep litter layers should be considered especially problematic and targeted for intense management practices.

Discussion:

Understanding the changes that invasive species can have on ecosystems is of the utmost urgency for land managers, environmental scientists and restoration ecologists. The litter layer produced by *P. australis* can remain for several years even after efforts to remove live biomass, such as pesticide treatment, and thus understanding its potential legacy effects upon ecosystems is important. Results from this study indicate that there was no difference in effect between *P. australis* and *T. angustifolia* on seed emergence from the litter layer when comparing the maximum depths for each species as measured in the field. To my knowledge, there have been no documented studies of a species-specific effect of either *P. australis* or *T. angustifolia* litter

being detrimental to seed emergence aside from litter amount present on the landscape. Previous studies have found that *P. australis* litter and *T. angustifolia* litter did suppress the seed bank, but because of the sheer amount present, not because of any species-specific biochemical effect (Holdredge and Bertness 2011, Farrer and Goldberg, 2009). The dense litter layer generated by *P. australis* provides a competitive advantage over native vegetation by suppressing the underlying seed bank and limiting access to sunlight under the dense canopy it creates (Ailstock et al. 2001).

The results from this study suggest that the depth of the litter layer present in a wetland environment in this region can impact seed emergence, with an increase in litter depth causing a decrease in emergence from the litter layer. These results are consistent with Weltzin et al (2005) who found increasing plant cover with removal of litter in a fen. Both *P. australis* and *T. angustifolia* produce large amounts of litter (Agoston-Szabo and Dinka, 2008). It is possible that the biomass production that leads to monocultural dominance of these species is reinforced by the litter layer that prevents seed emergence. This in turn could promote vegetative reproduction which *P. australis* and *T. angustifolia* excel at (Holdrege and Bertness 2011 Vaccaro, Bedford and Johnston 2009). The ability of *P. australis* to produce recalcitrant litter that decomposes slowly (Agoston-Szabo and Dinka, 2008) could further promote its ability to dominate a landscape by rapid growth, expansion and litter cover.

Ailstock et al (2001) noted that accumulated litter in patches of *P. australis* could cause a lag in regeneration time with living biomass is killed via herbicide. This is likely the result of accumulating litter preventing seeds from germinating by not allowing desirable conditions to become present; chiefly the removal of adequate light (Farrer and Goldberg 2009). Viable seeds are then buried under accumulating litter which inhibits their ability to germinate. Patches of *P.*

australis had nearly twice the litter depth (6.0 cm) than those of *T. angustifolia* (3.0 cm). *Phragmites australis* litter accumulates rapidly and decomposes more slowly than native species competing in the same niche (Agoston-Szabo and Dinka, 2008). If *P. australis* is able to invade a landscape, halt native seedling emergence by becoming the dominant species, and establish a dense litter layer, then native seeds would not be produced and would become buried further under annual accumulations of litter. This could explain why fewer instances of emergence were observed in the *P. australis* dominated soils versus *T. angustifolia* soils.

Asaeda et al. (2002) found the litter layer of a wetland invaded by *P. australis* can be up to 1600 $g*m^{-2}$ in a stand that is around two years old. Here we observe significant decreases in observed emergence counts with as little as 25 g (400 $g*m^{-2}$) of dry litter (50% litter cover in seed emergence experiment and 50% litter cover in regional seed bank experiment). My results suggest that *P. australis* can negatively impact the seed bank through litter accumulation levels much less than what has been recorded in the field.

It is possible that the cumulative effects of litter accumulation over several growing seasons could lead to seeds being buried deeper under the litter layer which eventually decomposes into soil. Since *P. australis* tends to accumulate litter rapidly (Windham 2001), this could cause the low seed density in soils immediately below non-decomposed litter that were observed in this study. Since the average litter depth of the *P. australis* location was deeper than that of *T. angustifolia*, this could suggest that the bulk of the seed bank is found at a greater soil depth than was sampled for this experiment. Depending on the age of the *P. australis* stand sampled, the native seed bank could be buried much deeper due to a persistent accumulation of litter. This would be consistent with previous studies undertaken by Holdredge and Bertness (2010) that showed that the litter legacy because of a *P. australis* invasion could inhibit the

ability of the seed bank to reestablish a native plant community. Additional sampling would be needed to test this hypothesis.

It is likely that the annual accumulation of litter in the *P. australis* soil contributes to the establishment of a monoculture and the submergence of the native seed bank underneath the litter layer. By contrast, *T. angustifolia* litter decays at a faster rate and thus accumulates more slowly (Agoston-Szabo and Dinka, 2008) allowing native seeds the opportunity to germinate, grow and propagate their species more effectively.This may explain the observed differences in seed emergence from the different soils. In all treatments *T. angustifolia* soils yielded higher average number of emergencesand the likely explaination for this is the decreased litter accumulation of *T. angustifolia* relative to *P. australis* (Agoston-Szabo and Dinka, 2008). Less litter accumulation decomposing faster could lead to a higher concentration of seeds closer to the soil surface.

As previously stated, *P. australis* soils yielded on average fewer emergences that *T. angustifolia.* These results support Gervais (19913) research which found that *P. australis* produces a high number of low-viability seeds, and can also present variability in seed viability between populations (Kettenring and Whigham 2009). If the stand sampled for this experiment has been dominated by *P. australis* with weak seed viability for multiple growing seasons, then the low number of emergence observed in the soils sampled from that patch should be expected due to exclusion of native species and the creation of a dense litter mat containing primarily non-viable *P. australis* seeds.

The study, which covered a nearly 60 mile expanse of the Huron to Erie waterway, showed large differences in the number of seed emergences among locations. Altough, all the

sites had similar stands of *P. asutralis* and *T. angustifolia*, one sampling location, Sterling State Park, had a very large number of emergences (greater than 148) while another, Grosse Ille Private Property, had nearly zero. Locations did tend to have similar emergence that were close together which would tend to suggest that regional variations in capability of the seeds to be emergent from litter or seed viability do exist as reported previously by Kettenring and Whigham (2009). One factor is that there could also be variations in the density of seeds within the seed bank. Seed density differences could be caused by patch genetics with respect to seed fitness (Kettenring and Whigham 2009), latitudinal gradients affecting fitness or patches of different ages having litter layers of varying thickness. Because of the rapid expansion of *P. australis* over the last several decades (Saltonstall 2001), it is possible that sites may represent different stages of invasion or different stages of recovery and/or treatment. Of the five locations sampled, *T. angustifolia* soils had more average observed emergences than *P. australis* soils in four which suggests that in the Huron to Erie water waterway, *T. angustifolia* soils have a greater number of viable seeds in the seed bank closer to the soil surface than soils dominated by *P. australis*.

From a regional perspective, each location exhibited similar reactions to the litter treatments, even if their average number of emergences was not the same. Little is known about how seed banks react to litter depths, which is one of the primary questions this study sought to answer. Litter cover can suppress the germination of seeds within the seed bank (Gorbani et al 2006, Holdredge and Bertness 2011) and the regional seed bank data suggests that there lacks a specific threshold of litter cover that affects the ability of a set number of seeds in the seed bank to germinate. Rather, the litter cover proportionally affects the number of emergences that may occur. Soils with high numbers of emergence saw similar proportional decreases emergences

with increasing litter when compared to soils with low numbers of emergences. This could also be a result of a combination *P. australis* not producing viable seeds on its own (Gervais 1993) and *T. angustifolia* litter decomposing faster than *P. australis* (Agoston-Szabo and Dinka 2006) thus allowing more seed into the seed bank that can eventually germinate.

Soils from *P. australis* patches in the regional experiment showed significantly fewer observed emergences across all locations. This is likely due to the increased litter layer deposited by *P. australis* invasions that can persist for extended periods of time (Agoston-Szabo and Dinka 2006) due to its rate of litter accumulation and the presence of material that is not easily decomposed (Minchinton et al 2006). *Typha angustifolia* displays the same pattern of invasion (Farrer and Goldberg 2009) as *P. australis;* however, the decreased litter layer which is a result of faster decomposition times and lower primary production (Agoston-Szabo and Dinka 2006) leads to a shallower seed bank. These results (STSP withstanding) are consistent with what was observed in the seed bank and litter layer seedling emergence experiment and with what would be expected due to *P. australis'* high litter production and prolonged litter legacy (Asaeda, T., et al. 2002; Holdredge and Bertness, 2011).

Conclusions

Phragmites australis is of particular concern to environmental scientists and conservationists because it is an aggressive, invasive competitor that can quickly dominate a landscape, and form a thick litter layer (Kulmatiski et al 2010). This research demonstrates that a dense litter layer can inhibits the ability of seeds contained in the seed bank to germinate. Even when *P. australis* is no longer present as living biomass, its effect upon a landscape can be pronounced through the inhibition of seedling emergence from the seed bank. The wide regional variations in the seed

bank suggests that not all landscapes are affected equally by *P. australis* invasion. The small latitudinal gradient may have an effect on the development of the seed bank. Also, the invasion history of each location used in the study is different as is the response of the land managers. Some sites have been heavily managed with documented treatment regimes (SCMP, STSP, LEMP) while others show evidence of treatment (BISP) and others none at all (GIPP). The duration of time in which a particular site is infested will impact the seed bank when *P. australis* is present as longer periods of time may impact the possibility seeds will be able to emerge from the seed bank through the litter layer. The results of this study indciate how an invasive plant species may alter not only the current biodiversity and function of a coastal marsh but also have long-term future impacts on a marsh through inhibition of seedling emergence from the seed bank.

FIGURES

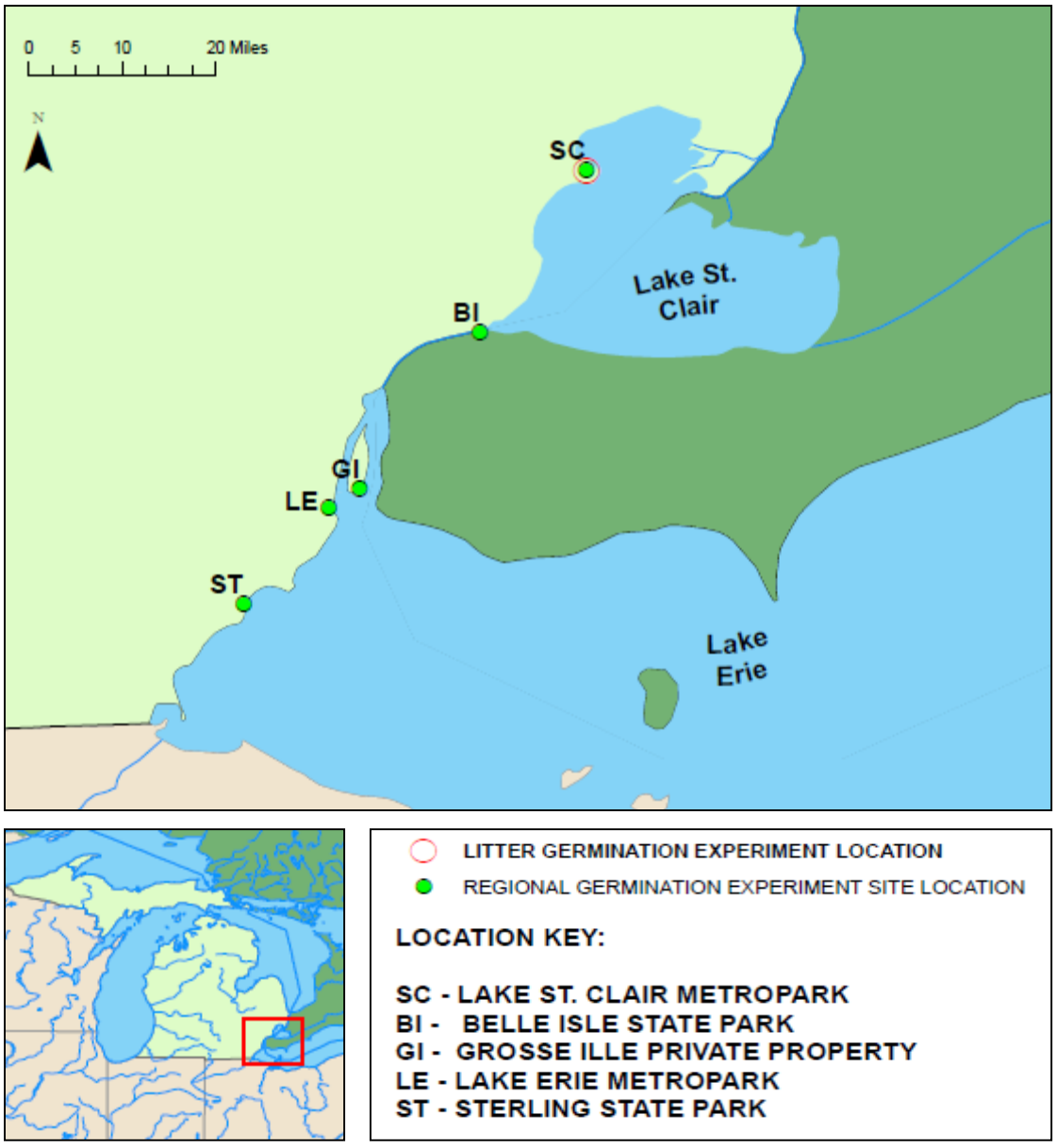

Figure 1: Sampling locations along the Erie -Huron corridor in Southeastern Michigan.

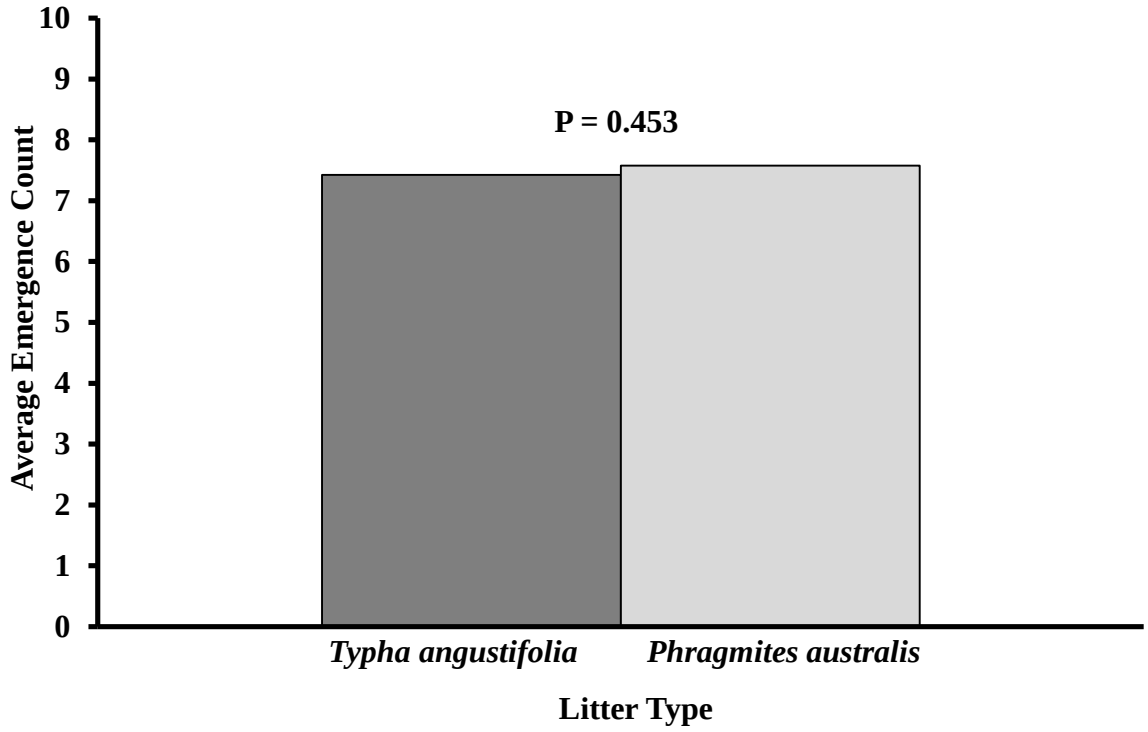

Figure 2: Average number of observed emergences from soils collected from locations dominated by either *Typha angustifolia* or *Phragmites australis* after 6 weeks ($p = 0.453$; $N = 40$). Significance ($p < 0.05$) determined by a Pearson chi-square test.

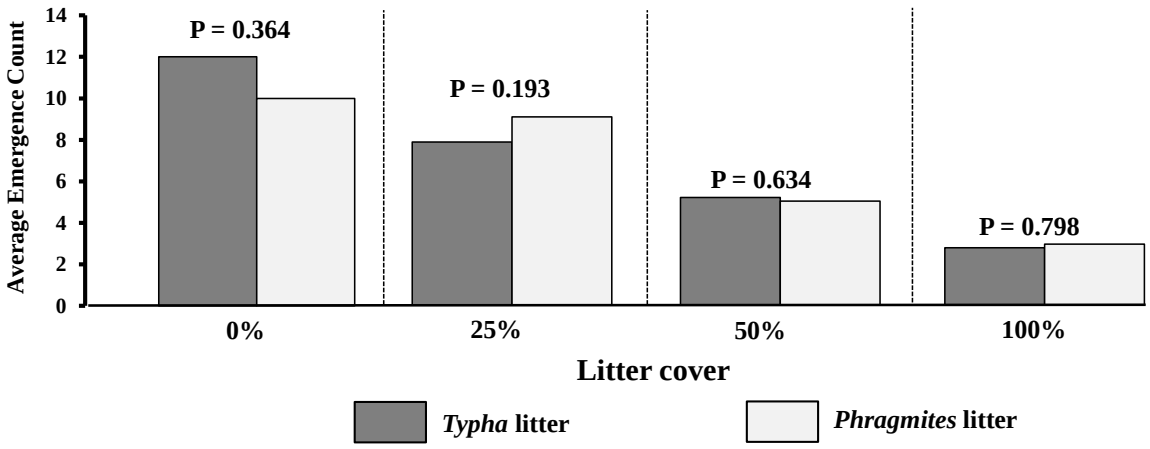

Figure 3: Average numbers of observed emergences over a 6-week period under various litter cover depths. Significance ($p < 0.05$) determined by a Pearson chi-square test between species of litter within each depth.

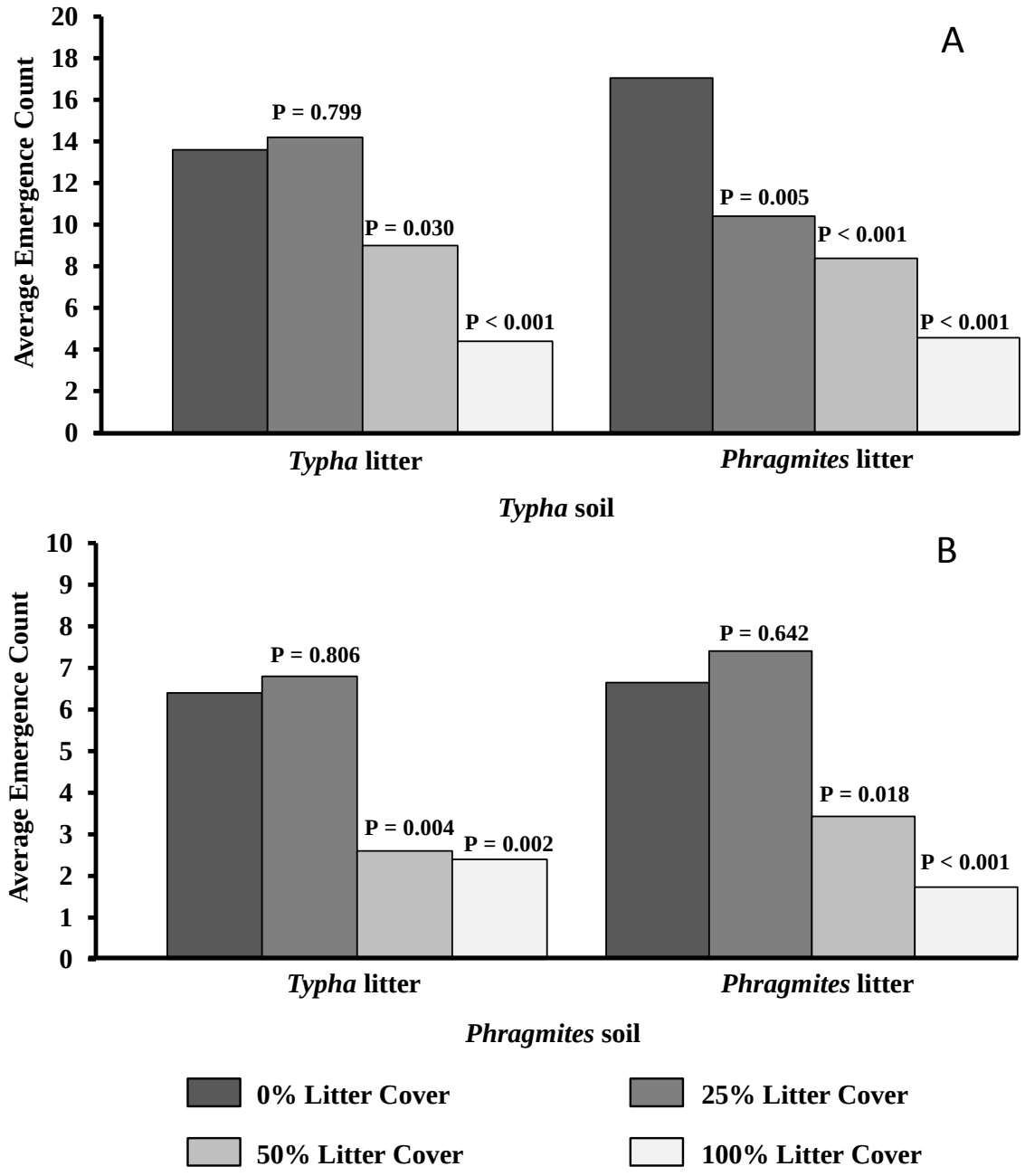

Figure 4: Average number of observed emergences under various litter depths from soils collected from locations dominated by either *Typha angustifolia* (A) or *Phragmites australis* (B). Comparisons made within each soil type and litter species made against 0% litter cover treatment. Significance ($p < 0.05$) determined by a Pearson chi-square test.

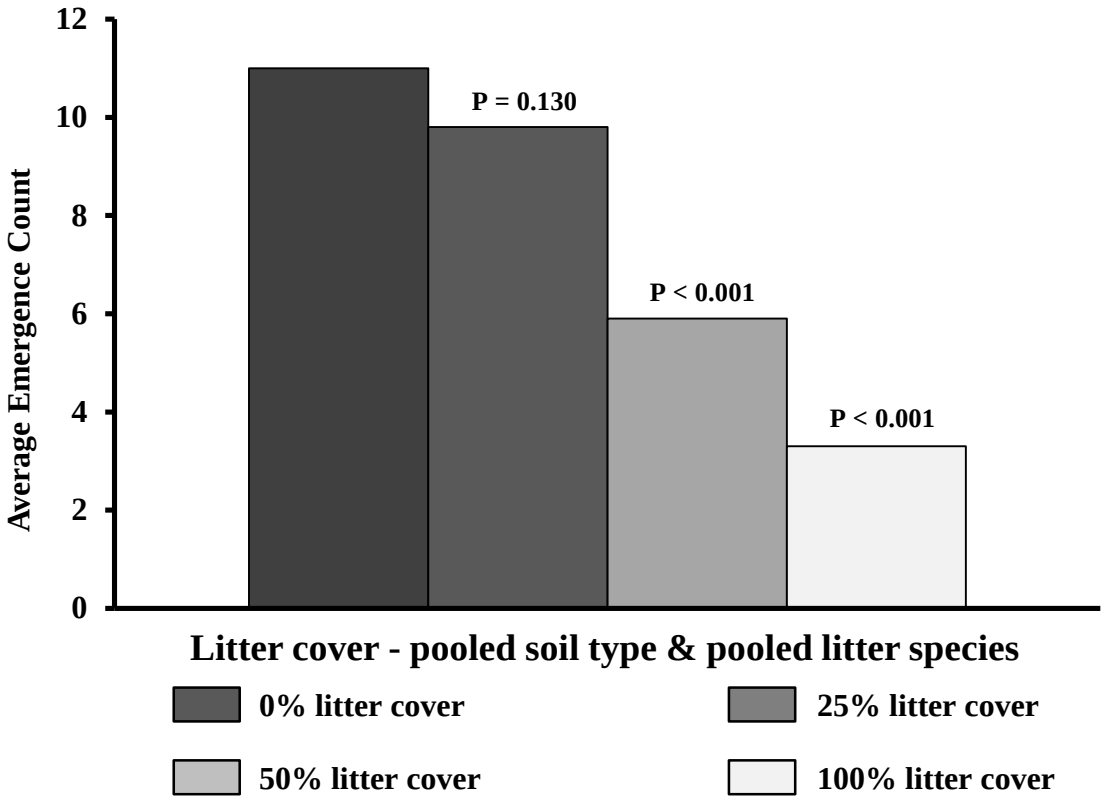

Figure 5: Average number of observed emergences under various percentages of litter cover. Differences between litter cover treatments analyzed using a Pearson chi-square test ($p < 0.05$). Comparisons made against 0% litter cover treatment. Soils collected from locations dominated by either *Typha angustifolia* or *Phragmites australis* were pooled for the statistical analysis (N = 20).

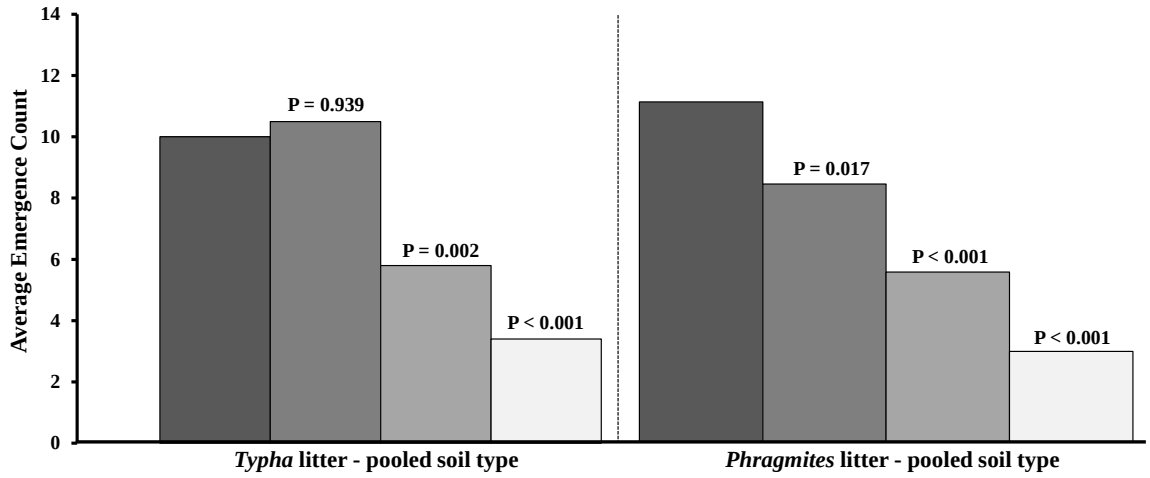

Figure 6: A comparison of the average number of observed emergences under either *Typha angustifolia* or *Phragmites australis* litter by percent litter cover depth. Difference between litter cover depths were compared using a Pearson chi-square test ($p < 0.05$), soils collected from locations dominated by either *Typha angustifolia* or *Phragmites australis* were statistically pooled for the analysis ($N = 20$). Comparisons made within each soil type and litter species made against 0% litter cover treatment.

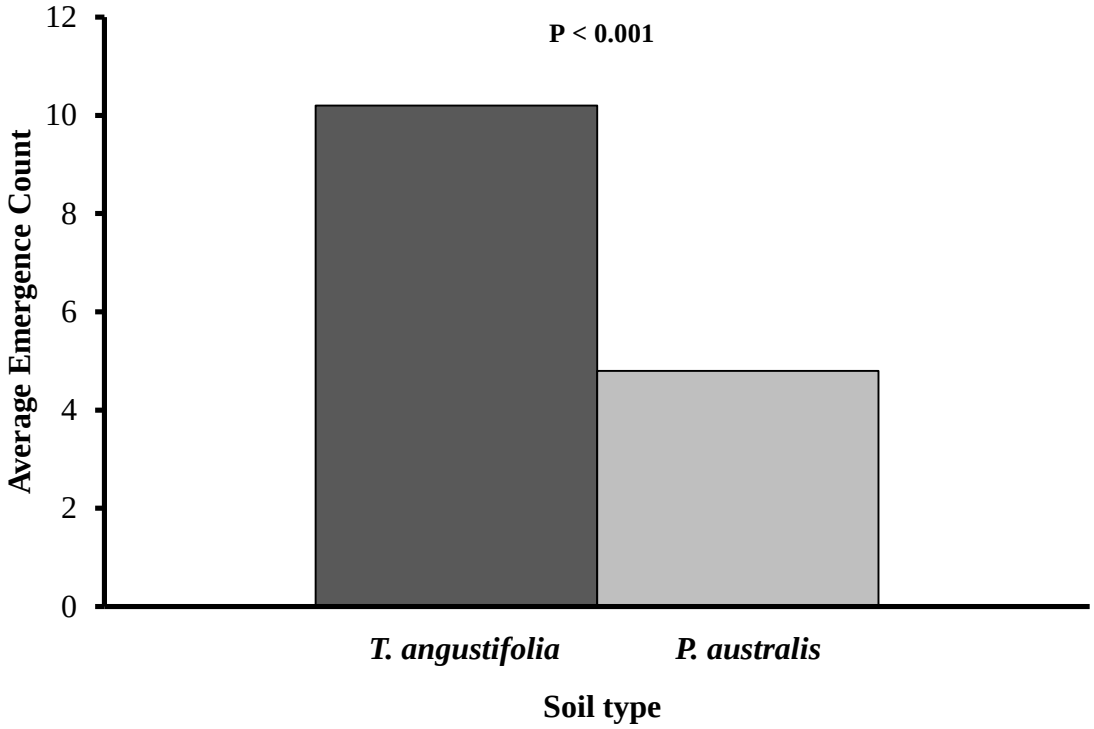

Figure 7: A comparison of the average number of observed emergences from soil collected from a site either dominated *Typha angustifolia* or *Phragmities australils* over six weeks (N = 40). Significance ($p < 0.05$) determined by a Pearson chi-square test.

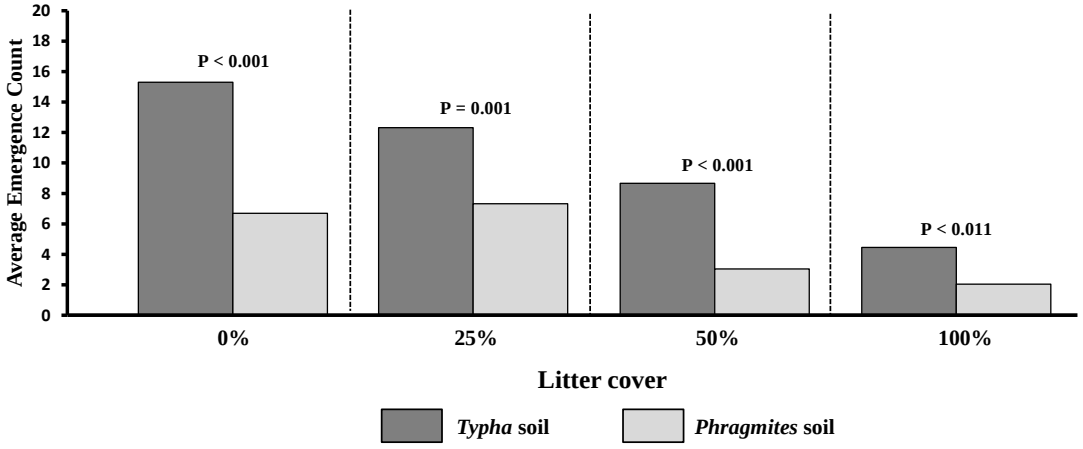

Figure 8: Average number of observed emergences from soil collected from a site either dominated *Typha angustifolia* or *Phragmites australils* over six weeks and various depths of litter cover (N = 10). Significance ($p < 0.05$) determined by a Pearson chi-square test.

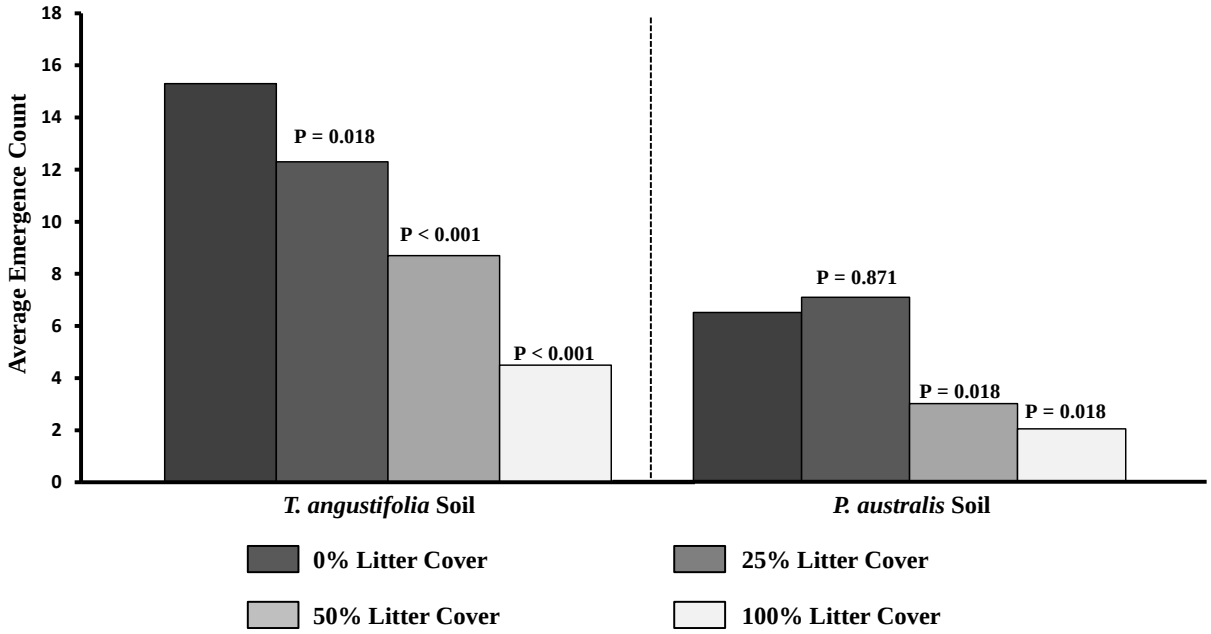

Figure 9: Average number of observed emergences across all litter treatments for 6 weeks in *Typha angustifolia* and *Phragmities australis* soil (N = 10). Significance ($p < 0.05$) determined by a Pearson chi-square test. Comparisons made within each soil type made against 0% litter cover treatment.

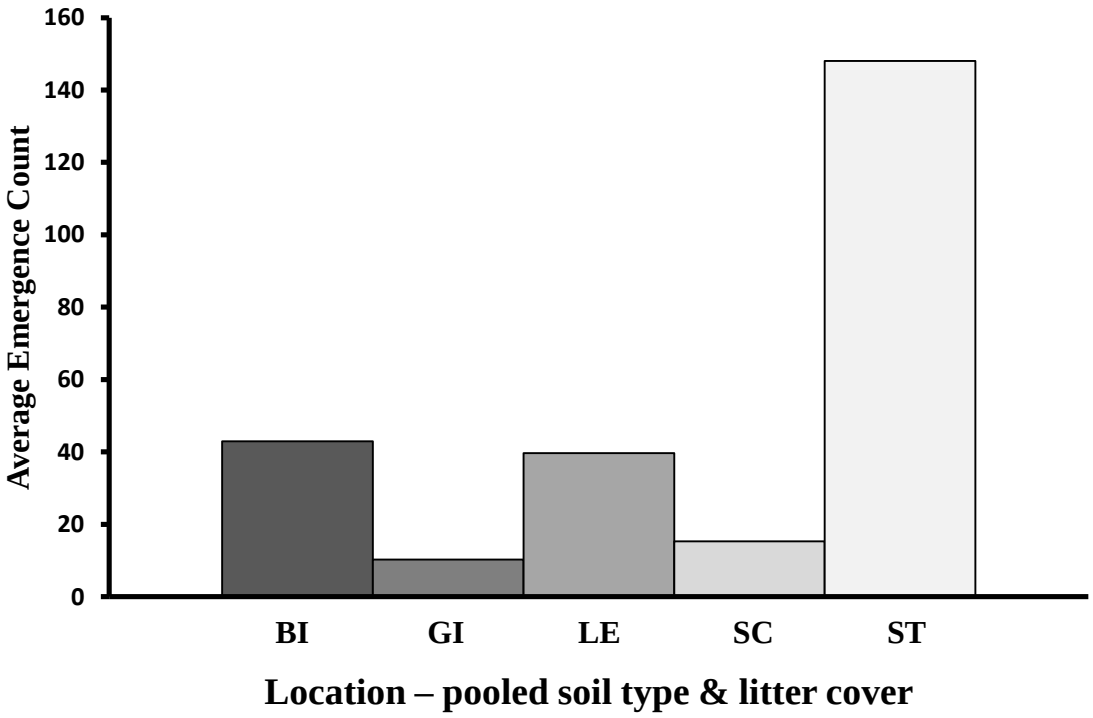

Figure 10: Average number of observed emergences for each location during regional seed bank and litter emergence experiment (6 weeks). Both soil types (*Phragmities australis* and *Typha angustifolia*) and all litter treatments (0%, 50%, 100%) are pooled (N = 24; BI: Belle Isle City Park; GI: Grosse Ille Private Property; LE: Lake Erie Metropark; SC: Lake St. Clair Metropark; ST: Sterling State Park). Significance ($p < 0.05$) determined by a Pearson chi-square test.

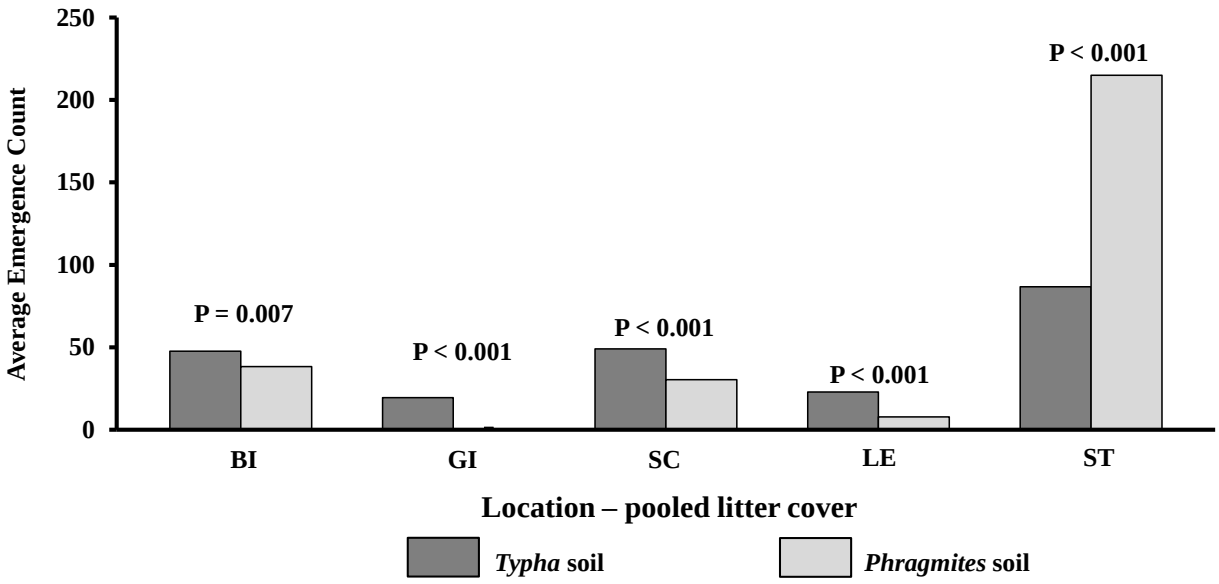

Figure 11: Average number of observed emergences within both soil types (*Typha angustifolia* and *Phragmities australis*) at each site (BI: Belle Isle City Park; GI: Grosse Ille private property; SC: Lake St. Clair Metropark; LE: Lake Erie Metropark; ST: Sterling State Park) over 6 weeks (N = 12). Significance ($p < 0.05$) determined by a Pearson chi-square test.

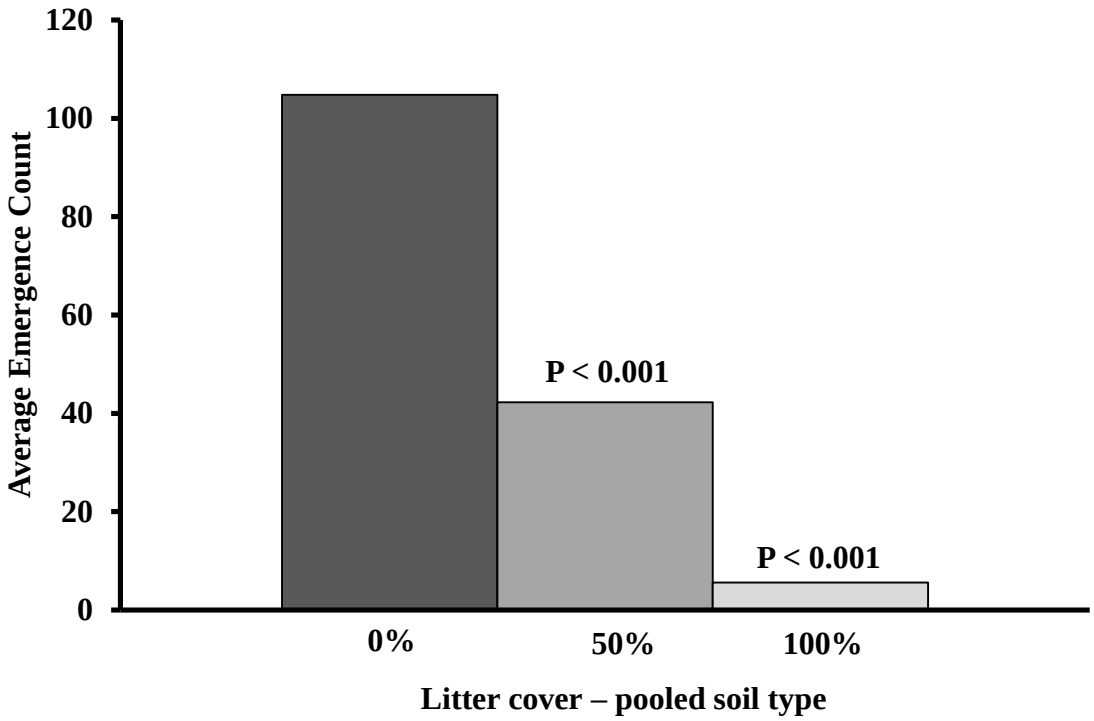

Figure 12: Average number of observed emergences for each litter cover treatment, regardless of soil type or location, over the duration (6 weeks) of the experiment (N = 40). Comparisons made against 0% litter cover treatment. Significance ($p < 0.05$) determined by a Pearson chi-square test.

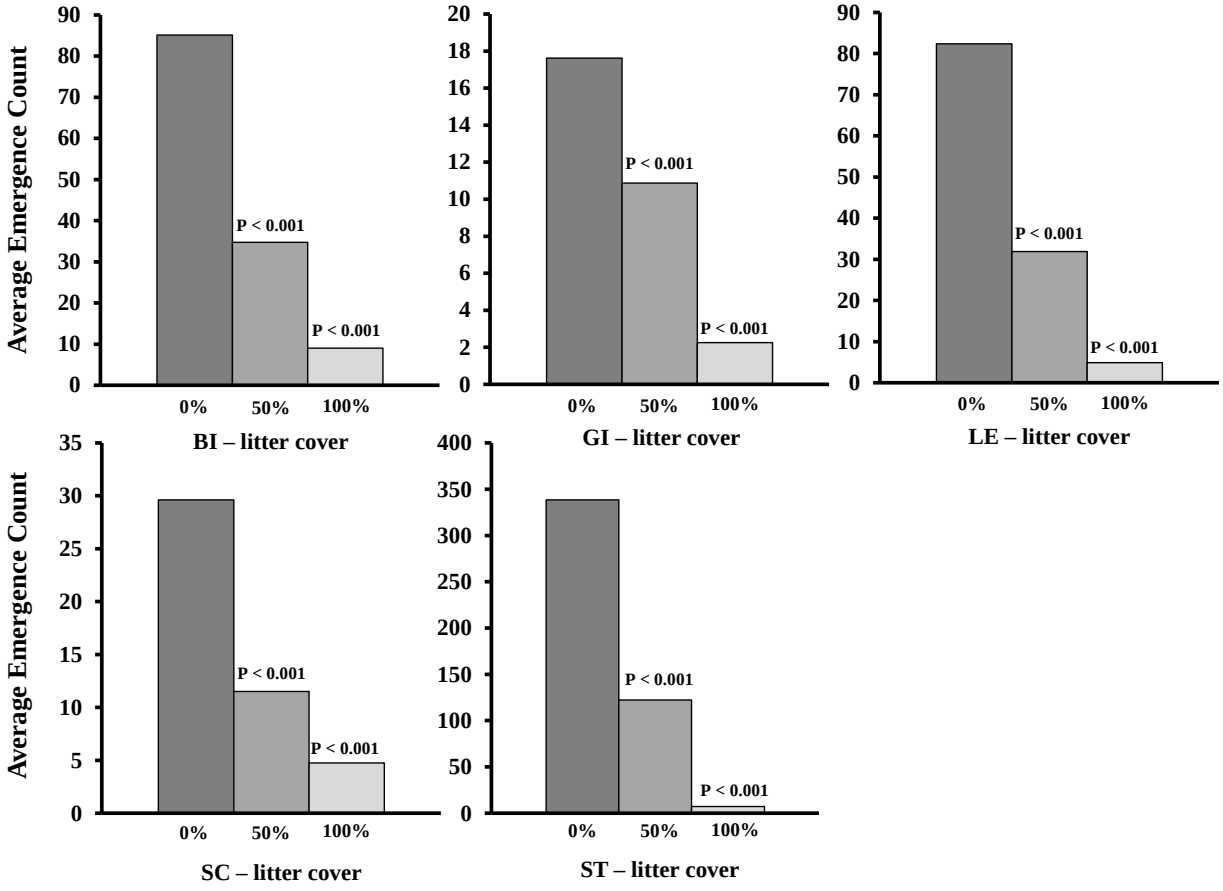

Figure 13: Pooled observed emergences for each site based on litter cover treatment (BI: Belle Isle City Park; GI: Grosse Ille Private Property; SC: Lake St. Clair Metropark; LE: Lake Erie Metropark; ST: Sterling State Park). Comparisons within each site made against 0% litter cover treatment. Significance ($p < 0.05$) determined by a Pearson chi-square test.

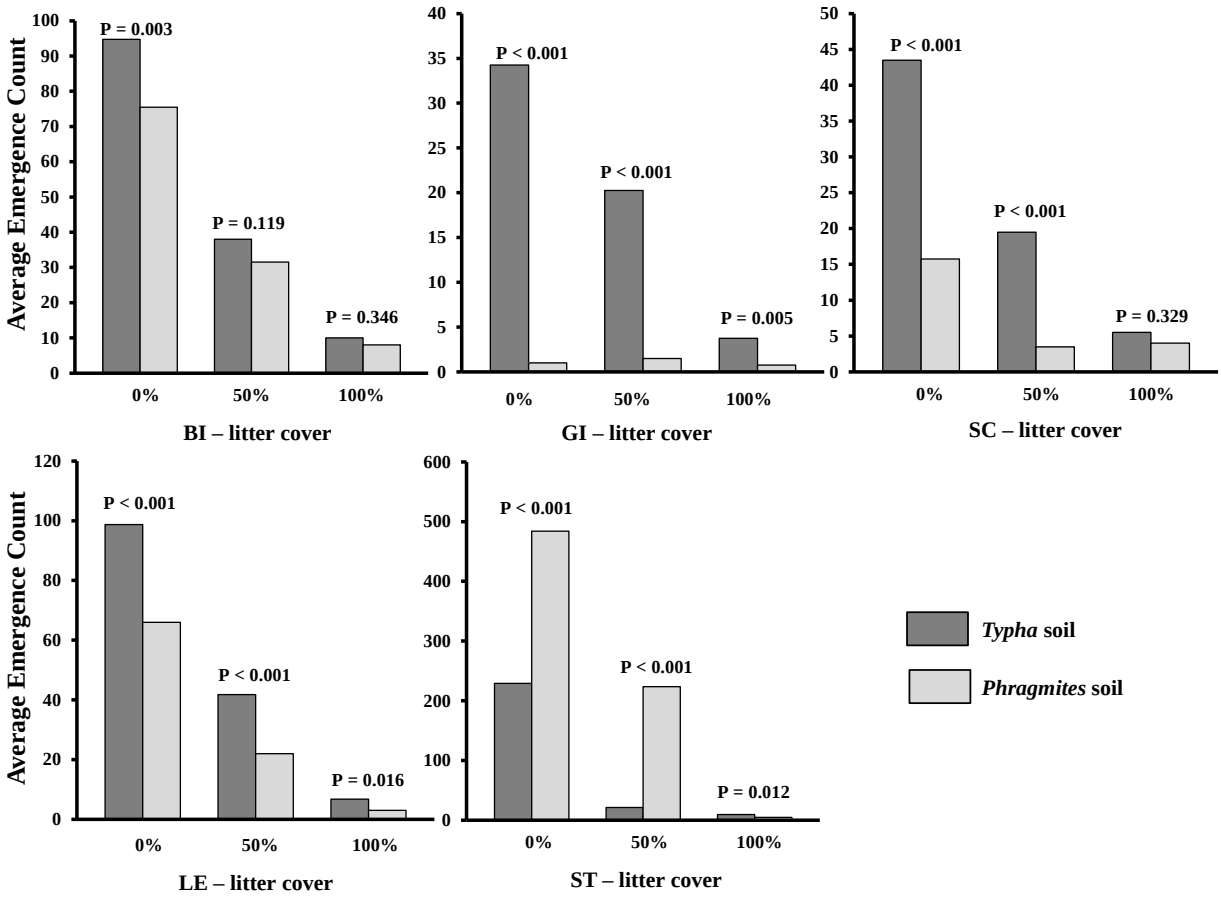

Figure 14: Average number of observed emergences within both soil types at each site (BI: Belle Isle City Park; GI: Grosse Ille Private Property; SC: Lake St. Clair Metropark; LE: Lake Erie Metropark; ST: Sterling State Park) and for each litter treatment over the duration of the experiment (6 weeks; N = 4). Significance ($p < 0.05$) determined by a Pearson chi-square test.

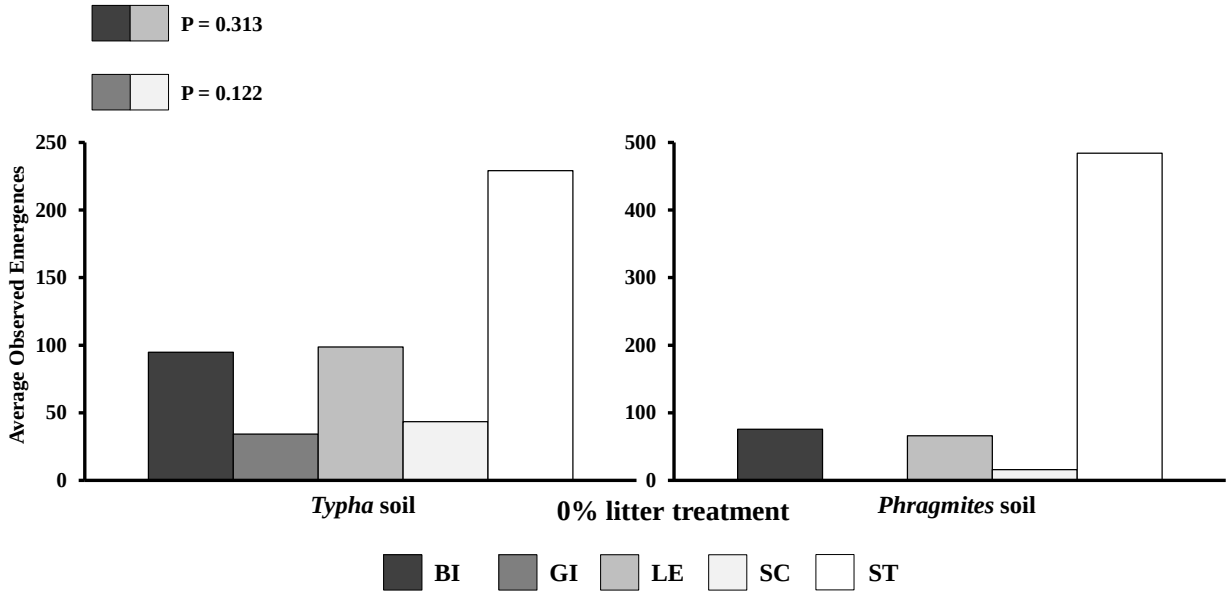

Figure 15: Comparison of average observed emergences across sites, for each soil type, at 0% litter cover. Sites are significantly difference unless noted in the boxes above the graph (N = 4). Significance ($p < 0.05$) determined by a Pearson chi-square test.

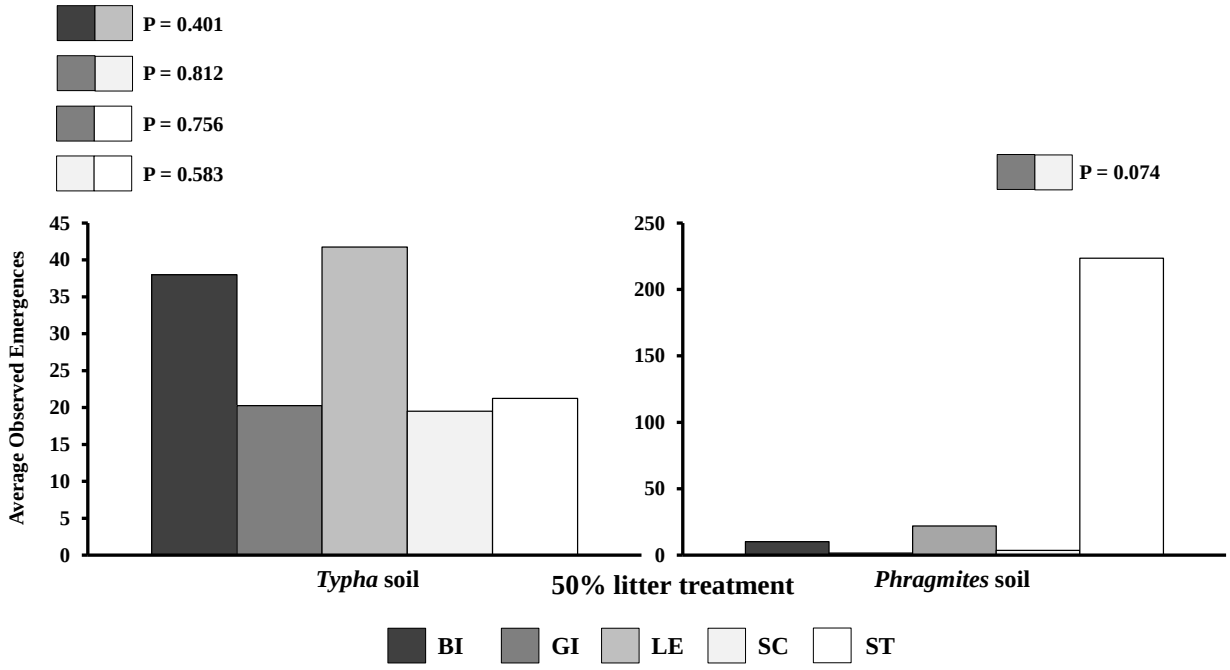

Figure 16: Comparison of average observed emergences across sites, for each soil type, at 50% litter cover. Sites are significantly difference unless noted in the boxes above the graph (N = 4). Significance ($p < 0.05$) determined by a Pearson chi-square test.

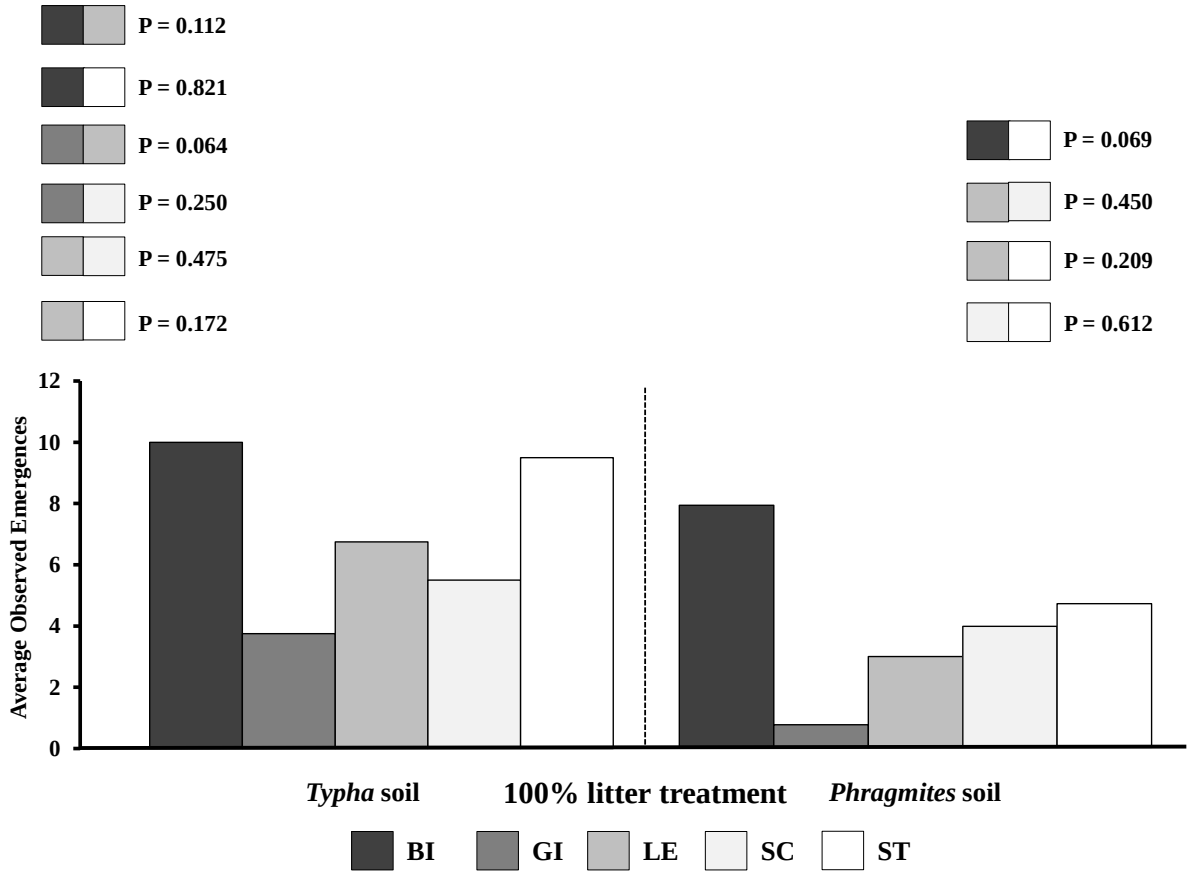

Figure 17: Comparison of average observed emergences across sites for each soil type, at 100% litter cover. Sites are significantly difference unless noted in the boxes above the graph (N = 4). Significance ($p < 0.05$) determined by a Pearson chi-square test.

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ABSTRACT

THE EFFECTS OF *PHRAGMITES AUSTRALIS* LITTER ON SEED EMERGENCE IN THE ERIE-HURON CORRIDOR, MICHIGAN

by

TRAVIS J WHITE

May 2014

Advisor: Dr. Donna Kashian

Major: Biological Sciences

Degree: Master of Science

The invasive reed, *Phragmites australis,* is widespread within the Great Lakes region, and is often blamed for habitat degradation. Once established, it creates dense litter mats that may persist following remediation efforts of living stock removal. We investigated the effects of *P. australis* and *Typha angustifolia,* narrow-leaf cattail, litter on seedling emergence from the native seed bank by harvesting soils from five Great Lakes coastal marshes densely populated by either *Phragmites* or *Typha* and exposing them to *Phramities* or *Typha* litter in treatments of varying litter depths. Seedling emergences were quantified for six weeks. Soils from *Phragmites* dominated sites had significantly less instances of emergence regardless of litter depth compared to soils from *Typha* dominated sites, and in general the deeper the litter fewer seeds emerged regardless of litter species. These results indicate that *Phragmites* can have a negative impact on the viability of the seedbank in a Great lakes coastal marsh.

AUTOBIOGRAPHICAL STATEMENT

Robert Frost – *The Road Not Taken*

TWO roads diverged in a yellow wood,
And sorry I could not travel both
And be one traveler, long I stood
And looked down one as far as I could
To where it bent in the undergrowth;

Then took the other, as just as fair,
And having perhaps the better claim,
Because it was grassy and wanted wear;
Though as for that the passing there
Had worn them really about the same,

And both that morning equally lay
In leaves no step had trodden black.
Oh, I kept the first for another day!
Yet knowing how way leads on to way,
I doubted if I should ever come back.

I shall be telling this with a sigh
Somewhere ages and ages hence:
Two roads diverged in a wood, and I—
I took the one less traveled by,
And that has made all the difference.

I am an unconventional student of biology. Upon graduating from high school in 1999, I attended Michigan State University until exiting before completion of my Bachelor's degree in 2005. I meandered from East Lansing to Virginia and worked as an innkeeper before returning to my hometown of Toledo, Ohio in late 2006. I was employed as a warehouse teamster when I decided to return to school at the University of Toledo. An online course on climate change got me in contact with Dr. Michael Weintraub who hired me to work as a field technician at an Arctic research station in Northern Alaska during the summer of 2010. Prior to leaving for Alaska, I finished my undergraduate degree, earning Student of the Year honors in my college and was accepted to Wayne State University where I joined Dr. Donna Kashian's lab. The road has been long, winding and certainly rough in patches – but it has been a wonderful journey. I have finally arrived. And that has made all the difference