FACILITATING NURSE PLANT SURVIVAL WITH MYCORRHIZAL INOCULUM FOLLOWING ERADICATION OF A NON-NATIVE GRASS

By

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Abstract: Tallgrass prairies of North America are under threat from numerous anthropogenic disturbances including, but certainly not limited to, the introduction and expansion of non-native species. One potential mechanism for successful invasion by non-native plants is alterations of native soil microbial communities, including symbiotic arbuscular mycorrhizal (AM) fungi. In my study, I compared prairie sites invaded by a non-native grass to nearby undisturbed prairie, assessing underlying biological mechanisms of successful non-native plant invasion. I also evaluated the influence of native AM fungal communities on establishment and survival of native plant species following eradication of the invasive grass. Specific objectives of my study were: 1) compare biotic and abiotic characteristics following invasion by a non-native grass species (*Bothriochloa bladhii*) with undisturbed adjacent prairie, and 2) assess the effectiveness of AM fungal inoculum on survival of native grasses and forbs. I established replicate plots in invaded and adjacent undisturbed sites at Konza Prairie Biological Station (KPBS), Manhattan, KS. Plant species richness was reduced from 12-14 species/m^2 in native prairie, to a monoculture of *B. bladhii* in invaded areas. Aboveground biomass production was greater, but root biomass lower, for *B. bladhii*, compared to native prairie. Invasion by *B. bladhii* reduced total microbial biomass, all microbial functional groups, including the relative abundance of AM fungi. To re-establish native plant species following eradication of *B. bladhii*, I inoculated native nurse plants, established under greenhouse conditions prior to outplanting, with AM fungal communities as follows: 1) a suite of AM fungal taxa isolated directly from KPBS soil; 2) fungal spores specifically selected as beneficial for native warm-season grasses and propagated under greenhouse conditions; 3) whole soil freshly collected from KPBS, including all soil microbial communities, and 4) a non-inoculated treatment. I found significant increases in survival of legume and non-leguminous forb species inoculated with either whole prairie soil or selected AM fungal spores, compared to non-inoculated plants. This suggests successful restoration may be achieved through propagation of AM taxa specifically selected for target native species, with fewer disturbances to native grasslands, potentially improving management decisions following removal of non-native species.

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CHAPTER I

FACILITATING NURSE PLANT SURVIVAL WITH MYCORRHIZAL INOCULUM FOLLOWING ERADICATION OF A NON-NATIVE GRASS

INTRODUCTION

The tallgrass prairie of the North American Great Plains historically occupied vast tracts of land from Texas to southern Canada; however, this ecosystem now occupies as little as 1% of its native range (Samson and Knopf 1994). Tallgrass prairie remnants, as well as most grasslands across the globe, are under continued threats from numerous anthropogenic disturbances including, but not limited to, introduction and expansion of non-native species (Monroe *et al.* 2017). Non-native species alter habitat quality, landscapes, and ecosystem functions, often resulting in less productive and less diverse grasslands (D'Antonio and Vitousek 1992; Kulmatiski *et al.* 2008; DiTomaso *et al.* 2017). This is particularly true for grasslands in North America, where non-native plants can dominate and become persistent problems. Underlying biological mechanisms facilitating non-native species are still largely unknown; however recent evidence suggests that most invasive species have negative impacts on soil physical and biological properties (Montserrat *et al.* 2011, Grove *et al.* 2017, Broadbent *et al.* 2018). Therefore, expanding our fundamental and applied understanding of soil degradation is critical for improved grassland restoration success following invasion by non-native species.

One possible mechanism for successful invasion by non-native plants is alterations of native soil microbial communities on which native plant species depend, including symbiotic arbuscular mycorrhizal (AM) fungi (Hartnett and Wilson 1999; Hartnett and Wilson 2002; Wilson *et al.* 2012). While much attention has been placed on the potential roles of disturbance, competition, and aboveground herbivory (Seabloom *et al.* 2015), there is growing acknowledgement that interactions with belowground microorganism, such as AM fungi, can play fundamental roles in the success of invasive species. Arbuscular mycorrhizal fungi form symbiotic associations with plant roots, increasing plant uptake of limiting resources such as phosphorus, nitrogen, and water, in exchange, plants deliver carbon to the fungi (Smith and Smith 2008). Mycorrhizal symbioses are imperative to most native tallgrass prairie plant species (Wilson and Hartnett 1998), and disruptions to these beneficial relationships may create opportunities for non-native plant species (Vogelsang and Bever 2009). Uncoupling of the symbiosis between the native plants and AM fungi due to disturbance by non-native plant species may reduce AM diversity and fungal propagules available to native species, with resultant loss of native plant species that are dependent on locally adapted AM fungal taxa (Wagg *et al.* 2015). In addition, loss of AM fungal hyphae also reduces soil carbon storage and aggregate stability (Wilson *et al.* 2009). Therefore, restoration of native AM fungi may be essential to restoring native plant richness and soil quality following invasion by non-native plants.

Bothriochloa bladhii (Caucasian bluestem), a Eurasian warm-season perennial grass from a group of grasses collectively known as Old World Bluestems, were widely planted in the southern and central Great Plains of the United States for soil stabilization, road side cover, and as a livestock forage, subsequently spreading throughout many southern stats including Texas, Oklahoma, Kansas, and Missouri (USDA; NRCS 2004). *Bothriochloa* spp. are highly competitive

and invasive through several biological mechanisms such as potential production of allelopathic chemicals that reduce native seed germination (Greer *et al.* 2014), and increased seed production and cold tolerance (Coyne *et al.* 1982). In addition, high nitrogen use efficiency of *Bothriochloa spp.* often results in substantially greater annual aboveground biomass production, compared with native C_4 grasses, and this, combined with annual burning, results in reduced soil N-availability due to volatilization, allowing further advantage over native grasses (Reed *et al.* 2005).

Clemente et al. (2004) suggested that to successfully reintroduce native plant species diversity in a tallgrass prairie resoration, AM fungal inoculum must be utilized, as it re-initiates important relationships between plants and the soil microbial community. Furthermore, Middleton and Bever (2012) found that when native AM fungal inoculum was used in a grassland restoration, surrounding non-inoculated native plants benefited from this AM fungal inocula as well, presumably via the spread of the AM fungi into surrounding soil and to non-target plants.

The specific objectives of my study were: 1) to compare soil biotic and abiotic characteristics of a grassland invaded by a non-native grass species with native undisturbed adjacent sites, and 2) assess the effectiveness of AM fungal inoculum on nurse plant survival post eradication of the non-native invasive grass species. The implications of my findings will aid in management decisions following removal of non-native plant species in grasslands. I selected several native grassland grass and forb species as nurse plants representing several functional groups present in the tallgrass prairie. Koziol and Bever (2016) reported that reintroducing native AM fungi can increase nurse plant survival and seed recruitment of grasses. I expanded on this methodology to include three AM inocula from native prairie soil. The native inoculum treatments I selected were: 1) a suite of fungal taxa isolated directly from Konza Prairie soil; 2) fungal spores and root fragments specifically selected as beneficial for native warm-season grass species biomass production, propagated under greenhouse conditions; and 3) whole soil freshly

collected from Konza Prairie, which included local soil microbial communities, including local taxa of AM fungi; and 4) a non-inoculated treatment as a control.

Previous research suggests *Bothriochloa spp.* inhibit native host-plant partnerships with AM fungi and other soil microbes (Wilson *et al.* 2012). Therefore, I hypothesized invasion by *B. bladhii*, prior to restoration (baseline assessments) would reduce total soil microbial biomass, particularly AM fungal biomass. Previous research has indicated loss of AM fungal biomass, decreased soil organic matter, or reductions in plant diversity, can reduce soil aggregate stability (Wilson *et al.* 2009, Siddiky *et al.* 2012, Pérès *et al.* 2013, Daynes *et al.* 2013). Therefore, I hypothesized invasion by the non-native grass will decrease soil aggregate stability, as compared to adjacent native prairie. I also hypothesized *B. bladhii* would produce greater aboveground biomass, compared to native prairie, based on previous research indicating *Bothriochloa spp*. mature more quickly and produce relatively greater biomass, compared to native grasses (Schmidt *et al.* 2008). For objective two (restoration), I hypothesized that native AM fungal inoculum would be more effective on nurse plant survival following eradication of the non-native invasive grass species, compared to non-inoculated nurse plants. In cross-site studies, Johnson *et al.* (2010) reported local adaption in AM fungal symbioses maximizes benefits to host plants.

My research will improve our understanding of local and ecosystem-level consequences of invasion by a non-native invasive grass species. Understanding how mycorrhizal associations are affected by plant invasions may be a critical aspect of the conservation and restoration of native ecosystems and aid restoration management practices. Knowledge gained from my study may allow selection of effective inoculant, possibly with fewer disturbances to native grasslands through propagation of selected AM taxa.

MATERIALS AND METHODS

Site description: Konza Prairie Biological Station, a National Science Foundation Long-Term Ecological Research site located in Manhattan, Kansas, USA, is a 3,487 ha tallgrass prairie preserve in the Flint Hills of northeastern Kansas (39 05' N, 96 35' W). This area is owned by The Nature Conservancy and managed by Kansas State University, Division of Biology. My study was conducted at the "Belowground Plot Experiment," initiated in 1986 to determine the long-term above- and belowground consequences of several grassland management practices (Figure 1). Treatments consist of burning (annually burned or non-burned), mowing (annually mowed or non-mowed), ammonium nitrate fertilization (10 g N m^{-2} annually or non-fertilized), and superphosphate fertilization (1 g P m^{-2} annually or non-fertilized) arranged in a split-split plot with burning as the whole plot treatment, mowing as the subplot treatment, and N and P amendments as factorial sub-subplot treatments. Whole plots are arranged in a randomized complete block design. Burning is performed in April of each year and fertilizer amendments were applied from 1986-2008, and mowed biomass was removed from plots. In the "Belowground Plot Experiment", there are 64 (12 m^2 x 12 m^2) total plots, with four replicates for each of 16 treatment combinations. My study utilized a sub-set of the belowground plots (historically mowed plots), as mowing facilitated invasion by a warm-season non-native invasive grass, *Bothriohloa bladhii*. Prior to the initiation of my restoration study, I determined baseline abiotic and biotic factors of *B. bladhii* invaded sites and adjacent native prairie.

Baseline:

Abiotic and biotic assessments prior to eradication of the non-native grass (baseline) included: AM extraradical hyphae biomass, total microbial biomass, fungal storage mechanisms, percent AM fungal root colonization, water-stable soil macroaggregates, soil nutrient analysis,

soil bulk density, soil temperate and moisture, above- and belowground plant biomass production, and plant species composition.

Sampling for biotic and abiotic assessments: At the end of the 2015-growing season, 8 replicate (non-permanent) 0.25 m^2 sub-plots were established in *B. bladhii* dominated areas of each mowed plot and randomly selected adjacent native prairie. In each replicate 0.25 m^2 sub-plot, plant species composition (percent cover by species) was assessed. Aboveground biomass was determined by placing a ½ m x ½ m sampling frame and clipping biomass 1 cm above the soil surface; all samples were collected at the end of the 2015-growing season. Biomass was dried at 60°C for 48 hours and dry weights determined. Following aboveground biomass collection, soil was collected using a 15 cm diameter soil core to a 10 cm depth to determine belowground biomass (roots and rhizomes). Plant roots were extracted from soil cores approximately 10 cm deep, washed free of soil, and oven-dried for 48 hours at 60°C. Three soil cores per replicate plot (5 cm diameter x 10 cm depth) were collected and homogenized to assess chemical, physical, and microbial soil parameters. Soil chemical and physical parameters processed at Oklahoma State University included: pH, plant-available N and P, soil organic matter (SOM), bulk density, and soil aggregate size distribution. Soil biotic parameters included: relative abundance of soil microbial functional groups, including gram negative and gram positive bacteria, saprophytic fungi, and AM intra- and extra- radical fungal abundance.

Quantification of soil chemistry: Baseline soil samples were analyzed at the Soil, Water, and Forage Analytical Laboratory (SWFAL) at Oklahoma State University. Soil pH was measured using a pH electrode in a 1:1 soil to water suspension. Soil NO_3-N and NH_4-N were extracted by 1M KCl solution and analyzed using the Lachat Quickchem 8000 Flow Injection Autoanalyzer (Kachurina et al. 2000)). Two grams of soil were extracted with 20 ml Mehlich 3 solution (Mehlich 1984) for plant-available P and the concentration of P in the extract were measured by an inductively coupled plasma emission spectroscopy (ICP) (Pittman *et al.* 2005).

Soil organic matter (SOM) was determined by dry combustion using the LECO Truspec CN analyzer (Nelson *et al.* 1996).

Quantification of soil bulk density: Bulk density soil samples were collected using a 10.8 cm diameter core to a depth of 10 cm. Samples were oven-dried for 24 hours and bulk density calculated in accordance to the original volume of the cylinder (McKenzie *et al.* 2002).

Quantification of soil aggregates: Soils (10.8 cm diameter x 10.2 depth) were wet-sieved with a modified Yoder wet-sieving apparatus that utilizes stacked sieves of four sizes: 4 mm and 2 mm to capture macroaggregates; 0.5 mm, and 0.25 mm to capture microaggregates. Each sample weighed 50 g and was placed into the uppermost sieve. The Yoder apparatus is modified to use stacked sieves of the four sizes listed above. The stacked sieves were connected to the Yoder apparatus and slaked in water for 10 minutes (Elliot 1986), and wet sieved for 10 minutes (30 rotations per minute) with a stroke length of 4 cm (Mikha and Rice 2004). Once removed from the Yoder device, soil was removed from each individual sieve and dried at 90° C for 24 hours prior to weighing. Since organic matter left behind in the last three sieves was considered part of the aggregate structure it was not removed from the samples. To calculate sand-free water stable aggregate subsamples (2.0 g each) of each *B. bladhii* and native prairie samples were dried at 105°C for 24 hours, allowing a correction for the dry-weight. The subsample of each intact aggregate (2.0 g) was added to 10 mL of 5 g L^{-1} sodium hexametaphosphate and set for 16 hours. This sample was then shaken at 350 rpm in an orbital shaker for 4 hours. The dispersed organic matter was collected on a 53- μm mesh sieve, rinsed with distilled water and dried at 105°C for 24 hours. The remaining aggregate samples were weighed to estimate sand-free correction.

Quantification of soil microbial communities: March 2016, six soil samples were collected directly from the roots of warm-season non-native grasses to a depth of 10 cm. Samples were homogenized for each invaded plot and for each native plot. . For each invaded plot and

each corresponding native prairie site, relative abundances of soil microbial functional groups (gram negative, gram positive, saprophytic fungi, and AM fungi), and total microbial biomass were assessed using phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA). PLFA's are within cell membranes that are used to estimate active biomass of bacteria and fungi, because biovolume and cell surface are correlated (Frostegård *et al.* 2011). NLFA's are storage mechanisms of many fungi and are the primary energy source in AM fungi (Larsen and Bødker, 2001; Sharma and Buyer, 2015).

Phospholipid fatty acid and neutral lipid fatty acid were analyzed through soil extraction using a modification of the Bligh and Dyer (1959) methodology (White and Ringelberg 1998). Total lipid extracts were separated into PLFA's and NLFA's using silicic acid chromatography; the fatty acids were cleaved from the glycerol backbone using KOH saponification; and the harvested fatty acids methylated to form fatty acid methyl esters (FAME) (White and Ringelberg 1998; Allison and Miller 2005). The FAME's will then be analyzed by gas chromatography and mass selection detection using a GCMS unit Agilent MS 5975C/GC 7890A. Biomarkers used to select for the functional group of gram positive bacteria consisted of i-15:0, a-15:0, i-17:0, and i-16:0. For gram negative bacteria, selected biomarkers consisted of 6:1ω7, cy19:0, cy17:0ω9, 2-OH 14:0, 2-OH 16:0, 3-OH 14:0, and 18:1ω9 trans. For extra-radical AM fungal biomass, biomarkers consisted of 16:1ω5c, 20:1ω9. Biomarkers for saprophytic fungi were 18:2ω9, 12 and 18:1ω9c. Abundances associated with these biomarkers were used to calculate total nmol g^{-1} soil for each functional group and total microbial biomass when all functional groups were combined with non-specific markers (14:0, 15:0, 16:0, 17:0, 18:0, and 20:0).

Quantification of AM fungal root colonization: Arbuscular mycorrhizal fungal root colonization was determined from approximately 0.5 g live roots of uniform size and appearance (approximately 0.25 – 0.50 mm in diameter) isolated from homogenized soil samples and washed free of soil. Six 4 cm samples of live roots were examined from each soil sample collected from

B. bladhii or native prairie plot. Samples were soaked in 10% KOH solution at room temperature for 24 hours. A 1% HCl solution was then added for acidification of the staining solution, roots were stained with trypan blue (0.05%) in lacto-glycerol for 10 minutes at 110°C, and stored in 30% lactic acid. Root colonization was assessed using a modified grid-line intersect method at 200x magnification (McGonigle *et al.* 1990) using a Hirox KH 7700 digital microscope to measure the percentage of root length colonized by vesicles, hyphae, and arbuscules. These measurements are combined to determine the total colonization of each grass root sample (Reinhardt and Miller 1990).

Restoration Study:

At the onset of the restoration experiment plant species composition was assessed in each invaded plot and in eight adjacent native prairie plots. I assessed cover of plant functional groups (C_4 annual, C_4 perennial, C_3 annual, C_3 perennial grasses, annual non-leguminous forbs, perennial non-leguminous forbs, annual legumes, and perennial legumes) and total *B. bladhii* cover. Each invaded plot contained at least 75% *B. bladhii*. Each experimental invaded plot was 12 m^2 x 12 m^2, for a total of 12 'invaded' plots, each delineated into nine 2m x 2m sub-plots with a 2 m buffer between plots. Following baseline assessments, plots were covered with a clear UV resistant polyethylene solarization tarp (16'x 32'; poolsupplies.com) to eradicate *B. bladhii* through soil heating. Solarization of soil will also presumably eradicate native plant species, reduce soil microbial communities, and reduce native and invasive species seed bank. In each of the 12 experimental invaded plots, the solarization tarp was removed from one sub-plot to allow survival of *B. bladhii* as a control.

The solarization of the invaded plots effectively decreased total microbial biomass, including extramatrical AM fungal biomass, as compared to native prairie plots that were not solarized (Table 1). Soil moisture was not affected by solarization, at either 5 cm or 10 cm depth.

However, temperature (°C) was significantly increased by solarization, as compared to plots that were not solarized (Table 1). Tarps were removed after one full growing season.

Arbuscular Mycorrhizal Inocula: Inoculating every plant in acres of restoration is not feasible. My approach was to inoculate nurse plants initiated under greenhouse conditions for 12 weeks prior to transplant into replicate field plots, following *B. bladhii* eradication, allowing the native AM fungi to benefit adjacent non-inoculated plats. I assessed benefits of inoculation with local fungi by comparing inoculation with AM fungi isolated from the native prairie soil; fresh soil collected from nearby native prairie; AM fungi selected as beneficial to warm-season prairie grasses and propagated in the greenhouse on *Sorghum bicolor* (L.); and a non-inoculated sterile control.

AM fungi isolated directly from KPBS soil incorporated a community of AM fungal spores isolated from freshly collected KPBS soil. This natural AM fungal community contains multiple Glomus species as well as representatives of other genera including Acaulospora, Entrophospora, Gigaspora, and Scutellospora (for complete species list see Eom et al. 1999). Spores were isolated by wet-sieving, decanting, and centrifugation in a 20:40:60% sucrose density gradient (Daniels & Skipper 1982) and suspended into distilled water. For each of the three inocula, approximately 100 spores were added to each nurse plant seedling (described below).

Nurse plant propagation: Nurse plants were propagated at Oklahoma State University greenhouses. I selected the following species: *Ratibida columnifera* (Nutt) Wooton and Stample. (forb), *Andropogon gerardii* Vitman (C_4 grass), *Lespedeza capitata* Michx. (legume) *Pascopyron smithii* (Rydb.) Á. Löve (C_3 grass), *Asclepias syriaca* L. (forb). Each of these plant species have been reported to be hosts for AM fungi (Wilson and Hartnett 1998). After a 30-day cold-moist stratification, seeds were germinated in vermiculite. At the two-leaf stage, seedlings were

transplanted into plastic pots (6 cm diameter x 25 cm deep: DeePots; stuewe.com, Tangent, Oregon) containing approximately 100 g of steam-pasteurized (80°C for 2 hours and allowed to cool for 72 hours) soil (a Chase silty clay loam, fine mont-morillonitic, mesic Aquic Argiudoll) freshly collected from Konza Prairie Biological Station, Manhattan KS. Seedlings were inoculated with one of the three AM inoculums by adding inoculum in direct contact with seedling roots at transplant. One fourth of the nurse plants were left non-inoculated as controls.

Nurse plant out-planting: Following eradication of *B. bladhii*, nurse plant seedlings were transplanted into experimental plots in May following spring burning in 2017. Each of the 8 sub-plots within the 12 treatment plots received two nurse plant seedlings of each of the five plant species (10 seedlings per sub-plot). The four AM inoculum treatments were randomly assigned to two of the eight sub-plots contained within each of 12 experimental plots. Nurse plants were planted in the center of each sub-plot, following a shotgun pattern.

Nurse plant survival data collection: Following transplant (2017), survival of nurse plants were determined each month (June-November) throughout the growing season.

Statistical analysis: Data were analyzed using R 3.3.2 (R Core Team 2017). Nurse plant survival, was analyzed using a one-way Analysis of Variance (ANOVA) with a Tukey's honest significant difference (HSD) performed post-hoc with significance assessed at $p \leq 0.05$. Sole factor in the analysis plot type is the inoculum treatments. The baseline measurements included microbial functional groups, soil nutrient analyses, soil temperature and moisture, and above- and belowground plant biomass. These characteristics were analyzed using analysis of variance for each site (invaded, non-invaded) x fertilization. Because interactions involving fertilization treatment (+N; +P; +N and P; control) were not significant, the data were reanalyzed as a one-way analysis of variance with a HSD performed post-hoc with significance assessed at $p \leq 0.05$. to compare invaded vs non-invaded.

Results

Soil baseline: No significant differences were present due to long-term nutrient additions, therefore all plots with >75% invasion were combined and considered "invaded". Plant-available nitrogen was not significantly different between invaded and native sites (Table 2). Bulk density (Native: 1.366 + 0.042; Invaded: 1.333 + 0.065) or pH (Native: 6.775 + 0.175; Invaded: 6.5 + 0.116) were not significantly different. However, soil organic matter (SOM) was significantly greater in the native prairie, compared to invaded sites (Table 2).

Microbial biomass analysis: AM fungal biomass, total microbial biomass, and saprophytic fungal biomass were significantly greater in native prairie as compared to *B. bladhii* invaded sites (Table 2).

Plant biomass assessments: While aboveground biomass production of native and invaded sites did not significantly differ, root biomass was significantly greater in native prairie sites, compared to invaded sites (Table 2).

Nurse plant survival: At year two, there were significant increases in nurse plant survival of nurse plants inoculated with AM fungi compared to nurse plants not inoculated with AM fungi (Figure 2). Generally, grass species had very high and similar survival rates regardless of soil amendment, whereas forb and legume species had significantly increased survival rates with propagated and whole soil inocula amendments (Figure 2).

Discussion

My research has substantial implications for grassland restoration as this research indicates preservation of locally adapted complexes of soils, plants, and soil organism is crucial, and restoration of native fungi may be a fundamental consideration for successful re-establishment of native prairie plant species. I found a significant increase in survival of forb and legume nurse plants inoculated with selected AM fungal spores, compared to non-inoculated nurse plants. Importantly, plants associated with propagated spores performed similarly to plants amended with live (whole) native prairie soil. The whole native soil included a suite of native prairie bacterial and fungal communities, while the cultivated inoculum contained AM spores selected as highly beneficial to native warm-season grasses, and propagated from small amounts of live soil. This suggests nurse plant success is possible with minimal disturbance of the remaining areas of intact tallgrass prairie. A previous study reported AM fungal amendments derived from native tallgrass prairie soils significantly increased nurse plant survival during restoration efforts (Koziol and Bever 2017), with a focus on re-establishment of grasses. My research provides evidence that locally adapted AM fungi provide critical benefits to native legumes and non-leguminous forbs, and can be utilized to enhance successful establishment and persistence in prairie restorations. These sub-dominant forbs are notoriously difficult to re-establish following disturbance, limiting the plant community diversity of restored sites as compared to native tallgrass plant communities (McCain *et al.* 2010).

I found clear evidence that invasion by the non-native grass *B. bladhii* reduced soil organic matter and soil microbial biomass, particularly both extramatrical and storage biomass (e.g. spores) of AM fungi. Soil organic matter (SOM) is important as it assists in the decomposition of other organic residues, soil stabilizations, the increases the ability of soil to hold moisture and carbon dioxide released through microbial respiration (Nelson and Sommers 1982). Reductions in SOM may have been at least partially driven by reduced root biomass of the non-

native grass, as root biomass, reflected by rhizosphere exudates (or rhizosphere priming), have been shown to be a key control on mineralization of N from SOM in grassland soils (Bird *et al.* 2011), and may accelerate SOM decomposition by as much as 380% (Zhu and Cheng 2011). I also found a significant decrease in total microbial biomass, particularly saprophytic and AM fungi, and gram negative bacteria. My findings support my hypothesis that non-native grasses reduce soil organic matter and AM fungal biomass, and highlight the need to address belowground factors for successful establishment of native plants in tallgrass prairie restorations.

My research lays a baseline that indicates successful reintroduction of forb and legume species can be improved by determining the specific AM fungal taxa that will benefit specific forb species. Benefits a given plant receives can depend on the identity of its AM fungal associates (e.g. Johnson *et al.* 2010; Hoeksema *et al.* 2010), and non-native invasive plant species have been shown to alter the density and/or composition of the AM fungal communities, which may feedback on the subsequent spread of the introduced plant species (Bever 2002, 2003; Reinhart and Calloway 2006). It is possible that invasive plants alter AM fungal communities to promote their own success, as plants can allocate preferentially to the most beneficial fungal partner (Bever *et al.* 2009; Kiers *et al.* 2011). For example, Moora et al. (2011) found a non-native invasive plant associated with non-host specific AM fungi, while the native plant-host species associated with a more diverse community of AM fungi, a change which may increase the success of the non-native species. As soil alterations following *B. bladhii* invasion are expected to continue negatively affecting establishment of native plant species (Wilson et al. 2012), a targeted AM fungal inoculum may mitigate this invasion legacy. Increasing restoration success by enhancing native plant community diversity is critical for reversing the extensive loss of grasslands worldwide. The technique of propagating beneficial AM fungal taxa from small amounts of native soil is an effective strategy, reducing the disturbance of prairie remnants required with restoration practices that utilize large amendments of native soil. Therefore, the

methodology of selecting and propagating highly beneficial and local AM taxa, examined in my research, has substantial restoration and conservation implications.

Hilderbrand *et al.* (2005) discussed common restoration fallacies, including "the myth of the field of dreams". These authors challenge the myth that ecosystems self-assemble without direct intervention. My research indicates alterations in soil microbial communities may not restore themselves and successful restorations following eradication of non-native invasive plant species have significantly altered local microbial communities.

New and important research questions have emerged based on my results. For example, genetic assessments of AM fungal communities in future studies will elucidate potential shifts in AM fungal taxa following non-native plant invasion. Understanding these alterations in AM taxa will allow selection of highly beneficial AM taxa in nurse plant inoculation, facilitating the return and spread of advantageous taxa following invasive plant eradication. Emerging evidence suggests AM fungal communities recovered within two years at tallgrass prairie sites previously disturbed by row crop agriculture (van der Heyde *et al.* 2018); however, similar chronosequence assessments have not been conducted following invasion by non-native grasses. To determine the time required to re-establish native AM fungi in grasslands following invasion by non-native grasses will require the assessment of AM fungi in native grass roots from undisturbed adjacent native prairie. This can then be compared with the AM fungi associated with roots established during the restoration process. This future research my help us gain a better understanding of soil microbial community dynamics following the initiation of tallgrass restoration. Improved knowledge of soil processes will facilitate the recovery of ecosystems degraded by invasion of non-native invasive plant species. Understanding how mycorrhizal associations are affected by plant invasions may be a critical aspect of the conservation and restoration of native ecosystems. Determination of highly beneficial AM taxa, specifically selected for optimal benefit of key forb

species will improve survivorship, and therefore success, of establishing diverse species in restored ecosystems.

Conclusion: My research will improve our understanding of the ecosystem-level consequences of invasion by a non-native invasive grass species. Understanding how mycorrhizal associations are affected by plant invasions may be a critical aspect of the conservation and restoration of native ecosystems and aid restoration management practices. Knowledge gained from my study may allow selection of effective inoculums, with fewer disturbances to native grassland soils through propagation of selected AM taxa as inoculum.

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Table 1: Post-solarization extraradical AM hyphae (m g^{-1} soil) assessment. Samples collected from the belowground plot experiment at Konza Prairie Biological Station (KPBS) and adjacent non-disturbed native prairie. Data presented as means. Means that share a letter are not significantly different ($p < 0.05$).

	Native Prairie*	Solarized *B. bladhii*
Extramatrical AM hyphae (m g^{-1} soil)	7.3[a]	2.6[b]
Total microbial biomass (nmol g^{-1} soil)	148.1[a]	77.8[b]
Soil temperature °C at 5cm	33.4[b]	46.8[a]
Soil temperature °C at 10cm	31.3[b]	42.1[a]
Soil moisture at 5cm (%)	26.1[a]	23.9[b]
Soil moisture at 10cm (%)	54.9[a]	54.1[a]

*No solarization treatment

Table 2: Soil and plant biomass baseline measurements. Assessments include extraradical AM hyphae (as determined by PLFA) and storage structures (e.g. spores, determined by NLFA), saprophytic fungal biomass, intraradical AM fungal colonization, water-stable aggregates (macro- and microaggregates), root biomass and aboveground biomass. Samples collected from the belowground plot experiment at Konza Prairie Biological Station (KPBS) or adjacent undisturbed native prairie. Data represented as means. Means that do not share a letter are significantly different ($p < 0.05$).

	Native Prairie	*B. bladhii*
Soil organic matter (%)	7.0[a]	6.1[b]
NH_4^+ (mg kg^{-1})	11.4[a]	10.5[a]
NO_3^-N (mg kg^{-1})	1.3[a]	1.0[a]
AM Fungal Assessments		
Extraradical hypha (nmol g^{-1} soil)	7.3[a]	3.3[b]
Extraradical fungal storage (nmol g^{-1})	68.7[a]	33.4[b]
Intraradical fungal colonization (%)	35.6[a]	27.6[a]
Saprophytic fungal biomass (nmol g^{-1} soil)	8.6[a]	3.6[b]
Gram positive bacteria	9.3[a]	8.5[a]
Gram negative bacteria	6.4[a]	4.2[b]
Total microbial biomass (nmol g^{-1} soil)	148.1[a]	135.0[b]
Water-stable aggregates (%)		
Macroaggregate (proportion)		
> 2000 μm	31[a]	36[a]
250-2000 μm	36[a]	32[a]
Microaggregate (proportion)		
53-250 μm	21[a]	21[a]
20-53 μm	12[a]	11[a]
Plant Biomass Assessments		
Aboveground biomass (g m^{-2})	241.7[a]	300.3[a]
Belowground biomass (g m^{-2})	260.0[a]	127.7[b]

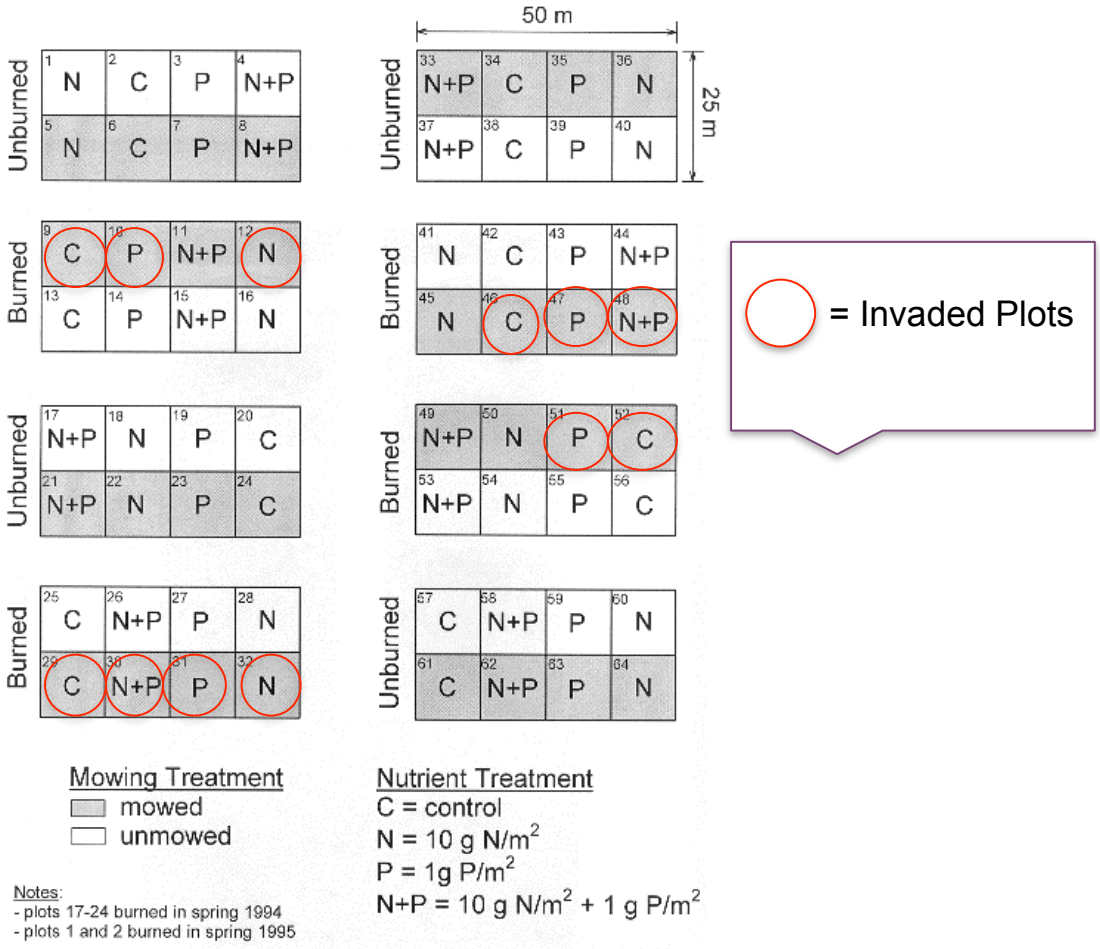

Figure 1: Belowground plot experiment located at Konza Prairie Biological Station, Manhattan, KS. Plots are arranged in a split-split plot with burning as the whole plot treatment, mowing as the subplot treatment, and N and P amendments as factorial sub-subplot treatments. Red circles indicate plots used in this experiment invaded with >75% *B. bladhii*.

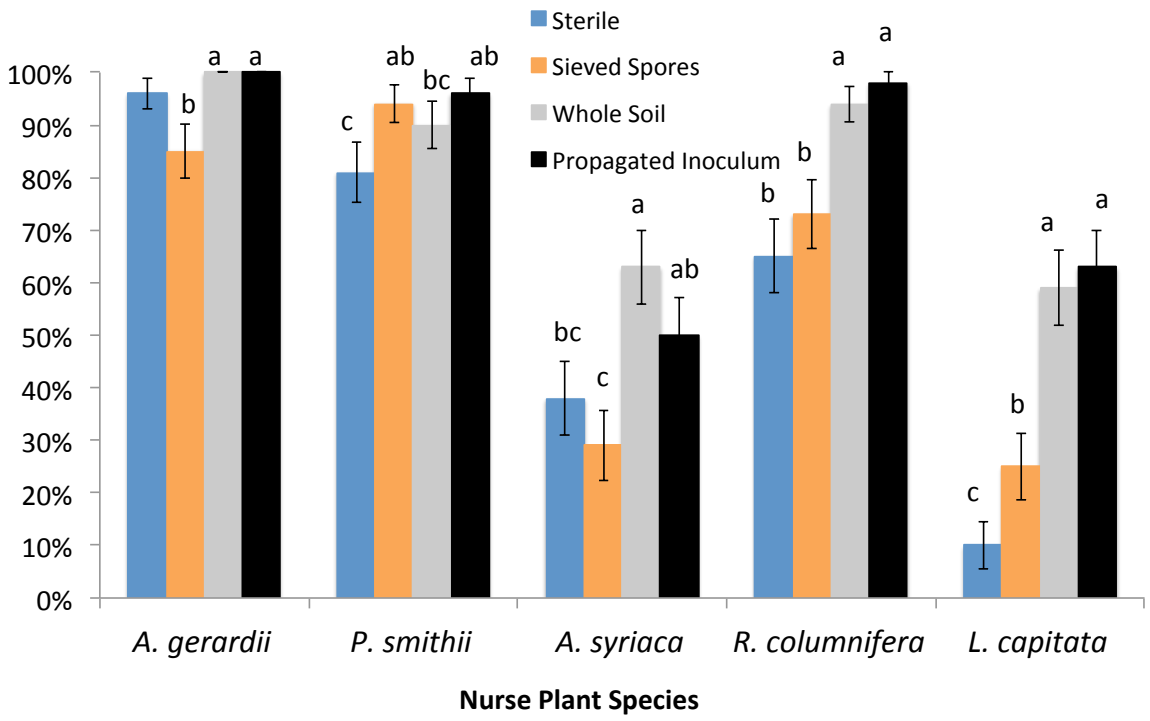

Figure 2: Nurse plant survival (%) at year two. Nurse plant species include: *Andropogon gerardii*, *Pascopyrum smithii*, *Asclepias syriaca*, *Ratibida columnifera*, *Lespedeza capitata*. Nurse plants were either non-amended or spores isolated from Konza Prairie Biological Research Station (KPBS), amended with whole soil collected from KPBS, or spores of selected arbuscular mycorrhizal fungal taxa found in KPBS soil. Data presented as means + SE, and bars that do not share a letter are significantly different ($p < 0.05$).

VITA

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Master of Science

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