Invasive Plants Affect Prairie Soil Biology

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Sericea lespedeza may have long-term effects on microbial structure and processes beneath the prairie

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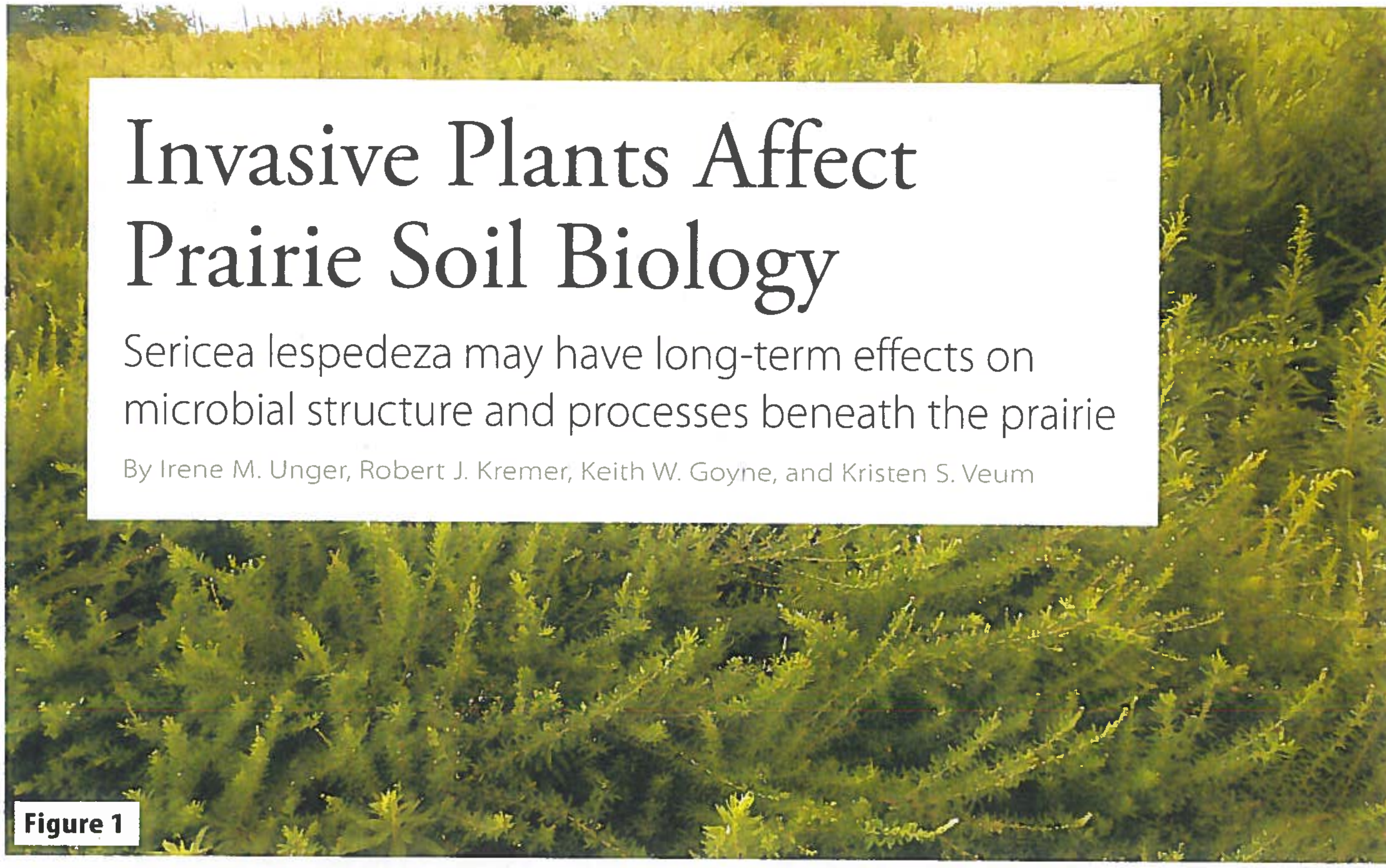


Figure 1

Dense stand of sericea lespedeza at Green Conservation Area.

Invasive Plants and the Prairie Ecosystem

Non-native or exotic plants often cause ecological and environmental damage in ecosystems where they invade and become established. After outright habitat conversion, these invasive plants may be the most serious threat to plant diversity in prairies. Particularly vulnerable are scattered remnant prairies, which may be subject to rapid invasion from agricultural fields, woodlots, and other disturbed sites bordering prairies within the same landscape. Invasive plants may reduce plant community diversity by adversely affecting survival, growth, and reproductive capacity of native prairie plants by releasing deleterious plant growth substances (i.e., allelochemicals) and altering light regimes, soil temperatures, moisture conditions, and vegetative litter constituents, thereby disrupting decomposition patterns and soil nutrient cycling.

Interactions of invasive plants with native prairie species have been examined in depth with the aim of developing strategies to minimize or eliminate their impacts on plant diversity and biological functioning in the prairie ecosystem. The relationships of invasive plants with the soil microbial community in prairie ecosystems, however, have received considerably less attention and are often overlooked in management planning.

It is well known that the soil microbial community responds to changes in vegetation that occur in many ecosystems. However, less information is available for specific impacts of invasive plants. Substances released from roots of invasive species may stimulate selected soil microorganisms to increase nutrient cycling for their preferential uptake. On the other hand, the soil's native microbial community may alter allelopathic chemicals released by an invasive plant to either more or less toxic forms that affect adjacent vegetation. Also, invasive plants escape growth-restricting factors (including associations with growth-regulating soil microorganisms) found in their native habitat, which may allow them to thrive in new environments.

When invasive plants become established in prairies and sites undergoing prairie restoration or reconstruction, drastic management strategies requiring additional resources must be devised to effectively manage or eradicate the invading species (Helzer 2010, Smith et al. 2010). Eradication by killing or removing top growth may not eliminate effects of the invasive plant on the soil microbial community. Belowground effects of invasive plants may linger for a period of time after removal, a so-called "legacy effect." Legacy effects may hinder native plant re-establishment during restoration efforts due to detrimental effects on soil microorganisms beneficial for native plant growth. Thus, the presence of invasive plants and the methods used for control or eradication may degrade the native microbial community and make prairie management, reconstruction, or restoration very difficult.

We evaluated invasive plant species impacts by characterizing soil biological properties in a remnant prairie, two reconstructed prairies, and an unmanaged old-field site in central Missouri. Sericea lespedeza (*Lespedeza cuneata*) was chosen as a representative invasive plant under which to evaluate soil biological properties in prairie ecosystems (Figure 1). Sericea lespedeza is a persistent perennial herbaceous plant originally introduced into the U.S. as a forage crop. However, it has spread into grasslands, abandoned fields, and prairies partly due to high seed production, competitiveness, and ability to tolerate a range of environmental conditions. Sericea lespedeza is particularly difficult to control in prairies because it releases allelochemicals into the soil that may suppress native plant growth. Most management strategies, including herbicide treatment and prescribed burning, provide inconsistent control or may even encourage invasiveness (Wong et al. 2012).

Soil Biological Characteristics

We measured selected soil properties that influence the biological characteristics of soil health, which were also expected to be sensitive to invasive plant species impacts in prairie ecosystems. As noted previously in *Missouri Prairie Journal* articles (Kremer 2014; Kremer and Veum 2015), describing a set of soil biological, chemical, and physical properties based on a soil health assessment approach can quantify the extent of degradation occurring on prairie soils due to management or other external factors such as invasion by non-native plants.

Overall biology of soil, including composition of microbial communities, biodiversity, and biological functions, are often considered synonymous with soil health. Soil health is the capacity of a living soil to function, within natural or managed ecosystem boundaries, to sustain plant and animal productivity, maintain or enhance water and air quality, and promote plant and animal health. Optimal soil health depends upon a balance of soil productivity, environmental quality, and plant and animal health—all factors that must be considered with management and land-use decisions. Understanding how specific factors such as invasive plant species affect soil health is very difficult to comprehend because comparative assessments with intact prairie ecosystems are practically non-existent. The work presented here is one of the few that documents impacts of an invasive plant on soil health in invaded sites relative to a non-invaded prairie situated on similar landscapes and soils.

We evaluated selected soil health indicators including bulk density and water-stable aggregates (physical properties), nutrient contents, carbon and soluble phenolic contents (chemical properties), and soil microbial components using phospholipid fatty acid (PLFA) analysis and biological activity by assaying for activity of the enzymes β-glucosidase and β-glucosaminidase (biological properties). The PLFA analysis of soil, detailed previously (Kremer and Veum 2015), allows for identification of specific functional groups of microorganisms (bacteria, actinobacteria, fungi [including mycorrhizae], protists) based on the PLFA patterns unique to each group. The total PLFA content is considered an estimate of the viable microbial biomass present in soil. The enzymes β-glucosidase and β-glucosaminidase were selected because they indicate the level of organic carbon- and nitrogen-cycling activities, respectively, in soil. Soils at sampling sites were collected from the claypan region in northeastern Missouri. The major feature of these soils is the subsoil layer or horizon with a high clay content of 40 to 50% at relatively shallow depths ranging from 4 to 20 inches beneath the soil surface.

Soils were collected from the following four sites. ① A native prairie remnant, **Tucker Prairie Natural Area** (Figure 2), is a "hardpan prairie" natural plant community as described by Nelson (2005). Grasses make up a full 50% of herbaceous cover with four dominant species: big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and prairie dropseed (*Sporobolus heterolepis*). While not completely undisturbed, (e.g., it has been grazed and mowed in the past and is currently managed with periodic prescribed burns) this area has never been plowed. ② and ③ **Two reconstructed prairies at Prairie Fork Conservation Area** (PFCA; Figure 3) that have been under active reconstruction within the past four to six years following a corn-soybean rotation system to obtain clean seedbeds before broadcast seeding with local native plant ecotypes. These sites were under intensive crop production until 1997 when the Missouri Department of Conservation (MDC) undertook management for subsequent prairie reconstruction. ④ The **Charles W. Green Conservation Area** served as our unrestored/invaded site (Figure 4). This 342-acre area—donated to MDC in 1956—was once part of a large pre-civil war plantation. A variety of crops including wheat, corn, rye, and oats were cultivated and a variety of livestock including horses, milk cows, sheep, and swine pastured on the fields. The area is no longer under cultivation and mixed native and non-native vegetation, including dense stands of sericea lespedeza, occur in the abandoned fields that have not been subject to prairie reconstruction attempts. Soils were intentionally collected from within the rooting zone of sericea lespedeza at the Green CA site, while at

Figure 2

Landscape and vegetation features at Tucker Prairie Natural Area, which served as the native prairie site for the study.

Figure 3

Landscape and vegetation features at one sampling site at Prairie Fork Conservation Area.

Figure 4

Landscape view of sampling site at Green Conservation Area. Note infestation of sericea lespedeza in foreground.

the other sites any sericea lespedeza stands were intentionally avoided.

Interestingly, results for all soil health indicators showed that the native prairie (Tucker Prairie) differed from the other three sites and that the reconstructed prairies without sericea lespedeza did not differ from the old field site invaded by sericea lespedeza (Green CA). Soils at Tucker Prairie were about 40% lower in bulk density and up to twice as high in water stable aggregates than soils at all other sites. Green CA soils were more compacted.

For chemical indicators, Tucker Prairie also differed with 40–45% higher organic carbon, and 35–38% higher total nitrogen than soils at the Green CA or PFCA sites. Water-soluble phenolic carbon was lower in Tucker Prairie soil relative to the other sites, suggesting this class of allelochemicals might be associated with existing or prior sericea lespedeza stands. However, these differences were not significant, and future evaluation of allelopathic potential should focus on isolation of specific phenolic compounds rather than using a general indicator chemical to confirm involvement of allelochemical exudates in the persistence of sericea lespedeza.

Assessment of soil microbial community function revealed few differences (Figure 5). No clear trends were discernable for carbon metabolism and cycling indicated by β-glucosidase activity. However, organic nitrogen metabolism, indicated by β-glucosaminidase activity, was highest at Tucker Prairie. Interestingly, the specific mineralization of nitrogen from β-glucosamine, a subunit of naturally occurring chitin, coincided with a similar pattern of results for potential mineralization of nitrogen, which represents total organic nitrogen mineralization by the soil microbial community. This suggests Tucker Prairie soils support a highly diverse community of nitrogen-mineralizing microorganisms and previous management and/or invasive species at the other sites have suppressed or decreased the diversity of this microbial group.

Our PLFA analysis showed that Tucker Prairie soil had 45% more microbial biomass than the Green CA or the PFCA sites (Figure 6A). The considerable reduction in total PLFA found in the old-field and reconstructed prairie sites is likely due to previous disruptive factors including intensive tillage, use of fertilizers and pesticides, and invasion of non-native plants. Total PLFA represents the living microbial biomass in soil and indicates the potential of greater biodiversity relative to soils with lower PLFA. Microbial biomass is constantly recycled through decomposition of dead microorganisms, known as microbial turnover. Most of the decomposed biomass is then incorporated into organic matter that helps to maintain overall soil carbon content. For Tucker Prairie soil, the high PLFA content, or microbial biomass, correlates well with the high soil carbon content and explains higher aggregate stability that is built with soil carbon. High PLFA content also explains the higher total nitrogen because microbial biomass is about 50% nitrogen, much of which is released during microbial turnover.

Tucker Prairie had a more robust soil microbial community than soils of the reconstructed prairies or the invaded site (Figure 6 B and C). Initial analysis revealed 33% more mycorrhizae, 40% more saprophytic fungi, 46% more actinobacteria, 49% more Gram-negative bacteria, and 50% more Gram-positive bacteria in Tucker Prairie soil relative to the other sites. As documented previously, mycorrhizae are abundant in prairie ecosystems, which is due to proliferation of these symbiotic fungi on extensive root systems established by perennial vegetation (Kremer and Veum 2015, Tipton 2017). The lower detection of mycorrhizae in both reconstructed and old-field sites suggests that either root density or vegetative diversity, which accommodates high mycorrhizal populations, is lower relative to native prairie.

This finding may be a result of previous or current infestations of invasive plants. Mycorrhizae are critical to growth and vigor of prairie ecosystems as they account for nutrient and water uptake for the host plant, protect the plant by suppressing root pathogens, and aid in aggregation of soil particles to improve soil structure. As evident in Figure 6B and validated by a recent study (Tipton 2017), previous soil disturbance associated with cultivated systems and possibly invasion by sericea lespedeza prior to initiating prairie reconstruction or cessation of agricultural production greatly disrupt the mycorrhizal community, which require considerable time to re-establish to pre-agricultural levels.

Total fungal PLFA (Figure 6B) was highest in the Tucker Prairie ecosystem due to the continuous accumulation of organic materials from both vegetation and roots from perennial prairie plants that stimulates development of a large fungal community responsible for the primary decomposition of vegetative and root residues. Previous tillage and continuous row-crop production led to reduced soil organic matter in sites under prairie reconstruction as well as the old-field site and seemingly delayed a buildup of fungal community biomass.

We found similar trends for the bacterial components (Figure 6C) that were highest in Tucker Prairie soil. This suggests a well-balanced soil food web in which a proportionally high fungal community is able to break down complex organic materials into simpler compounds at rates sufficient to support highly active bacterial communities resulting in an efficiently functional carbon cycle. The reconstructed and old-field sites with lower bacterial communities apparently

Figure 5

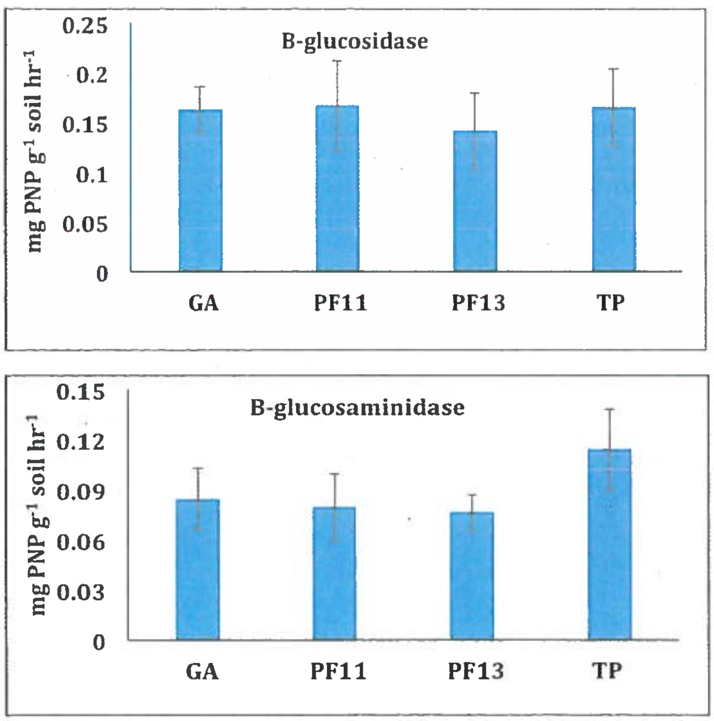
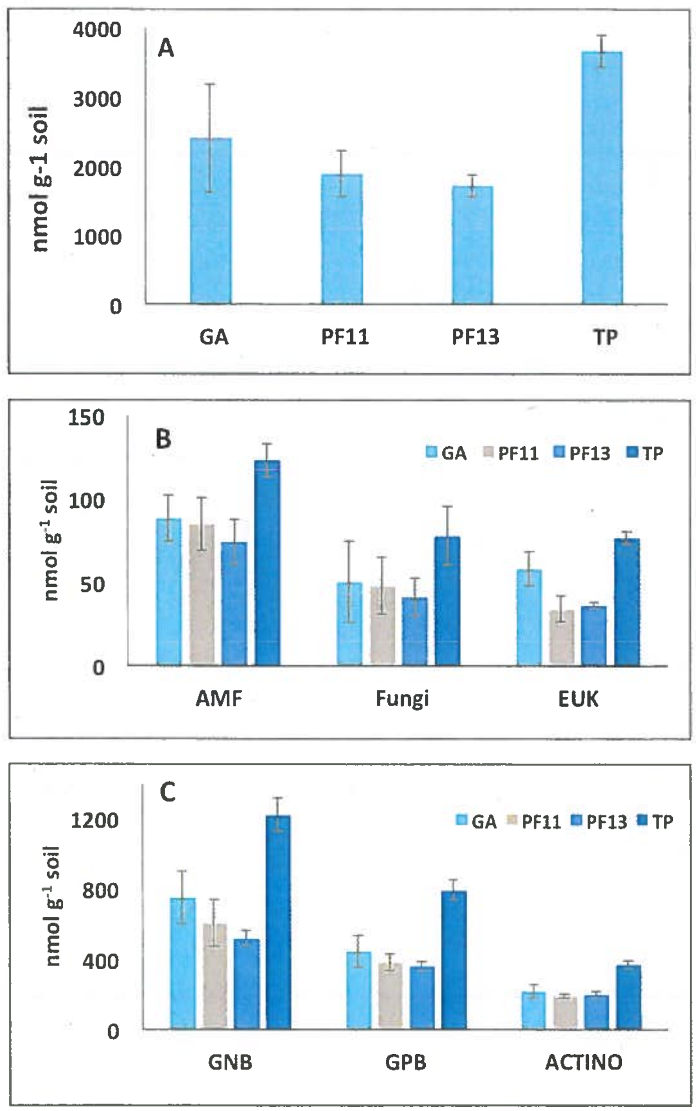


Figure 6



Above, soil enzyme activity of glucosidase and glucosaminidase in soils collected from four sites used in the study. Activity results are expressed as mg para-nitrophenol produced by each enzyme using an assay with surrogate substrates for glucosides and N-acetyl glucosamine. Vertical lines on each bar indicate standard error.

At right, PLFA soil microbial community response for prairie, reconstructed prairie, and old-field sites. Results are expressed in nanomoles per gram of dry soil to quantify total microbial biomass and each community component at each site. GA, Green CA; PF11, PFCA site 1; PF13, PFCA site 2; TP, Tucker Prairie; AMF, arbuscular mycorrhizal fungi; EUK, protists; GNB, Gram-negative bacteria; GPB, Gram-positive bacteria; ACTINO, actinobacteria. Vertical lines on each bar indicate standard error.

have not yet reached fungi-bacteria balance for optimum carbon cycling. Both Gram-negative and -positive bacteria are important root-colonizing microorganisms that transform many nutrients taken up by plants, synthesize plant growth regulating substances that promote plant cell growth and root development, and produce antibiotic-like substances to protect plants from attack or infection by plant pathogenic microorganisms.

Furthermore, a profuse Gram-negative bacterial community assures that all nitrogen transformation steps (mineralization, nitrification, denitrification, nitrogen-fixation) are functional because this is the only group capable of mediating all steps in this important cycle. Actinobacteria degrade complex organic compounds and synthesize many antibiotics that suppress plant pathogens and protect plants from potential disease. The lower amounts of soil organic matter, poorer soil structure, and possible detrimental effects of sericea lespedeza appear to contribute to lower bacterial components in the reconstructed and old-field sites. We also detected a higher component of protists (or "protozoa"), the predators of the other microbial groups that cycle nutrients from the microbial biomass for uptake by plants and living microorganisms, in the Tucker Prairie soil (Figure 6B).

Implications of this Study

The native prairie exceeded other sites on claypan soils in supporting diverse soil microbial communities based on PLFA characterization and in higher soil health indicator values. As we suggested in earlier studies (Kremer 2015, Kremer and Veum, 2015), continuous presence of vegetation, lack of soil disturbance, and greater organic inputs point to the differences between soil microbial communities of the prairie site and the reconstructed and old-field sites. Despite the apparent successful aboveground reconstruction of native plants at the PFCA sites, belowground restoration of the soil microbial community and other soil properties is only in initial stages.

Other researchers suggest that the soil microbial community and certain soil edaphic (physicochemical) factors in restored or reconstructed sites require decades to recover to values similar to those in native prairie soils (Jangid et al. 2010, Tekiela and Barney 2017). The additional impact of the invasive sericea lespedeza to soil properties was evident at Green CA, however, it is not clear how it affected soil properties at PFCA. We know that PFCA sites previously hosted scattered sericea lespedeza stands and it is possible that legacy effects on the soil microbial community may continue after these stands have been weakened or eradicated, thus prolonging time to successful belowground restoration.

Based on our results and other studies, the old established sericea lespedeza stands at Green CA likely pose challenges to soil health restoration efforts if the site is renovated for prairie reconstruction. However, knowledge of legacy effects due specifically to sericea lespedeza invasions is practically non-existent, and we suggest studies should be undertaken to fill this information gap to help assure effective management of prairie sites affected by this invasive plant. Also, interactions of soil edaphic factors including soil temperature and moisture, pH, texture, and nutrient contents with invasive plants should be evaluated more in depth, as these factors may influence soil biology as much or more than the plant (Bainard et al. 2016).

Overall, our study emphasized the importance of monitoring soil health indicators in prairies and sites undergoing restoration or reconstruction that have diverse histories including present or previous stands of invasive plants. Such information would be valuable in guiding management decisions and could be applied in restorations on various soils. The rich information to be mined from original prairie soils is yet another compelling reason to protect the unplowed original prairie that remains.

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