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Resource Amendments Influence Density and Competitive Phenotypes of *Streptomyces* in Soil

Daniel Schlatter · Alfred Fubuh · Kun Xiao · Dan Hernandez · Sarah Hobbie · Linda Kinkel

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Abstract Carbon from plant rhizospheres is a source of energy for soil microbial communities in native habitats. Soil amendments have been used as a means for deliberately altering soil community composition in agricultural soils to enhance plant health. However, little information is available in agricultural or natural soils on how specific carbon compounds or quantities influence soil microbial communities. *Streptomyces* are important soil saprophytes noted for their ability to produce antibiotics and influence plant health. To explore how specific types and amounts of carbon compounds influence *Streptomyces* in soil, glucose, cellulose, and lignin were added alone and in combination with six other carbon substrates of varying complexity to mesocosms of native prairie soil for 9 months at amounts equivalent to natural inputs from plants. Estimated culturable population densities, antibiotic inhibitory phenotypes, and resource utilization profiles were examined for *Streptomyces* communities from each treatment. The type and quantity of carbon compounds influenced densities, proportions, antibiotic phenotypes, and substrate utilization profiles of *Streptomyces*. Cellulose and lignin inputs produced the largest *Streptomyces* densities. Also, *Streptomyces* communities receiving high-resource inputs were more inhibitory whereas those receiving low-resource inputs used substrates more efficiently. Knowledge of how the availability and quantity of particular carbon compounds influences *Streptomyces* communities and their function, specifically resource use and inhibitory phenotypes, may be helpful in understanding the roles of resource availability in *Streptomyces* community dynamics and the potential of *Streptomyces* to suppress pathogens and enhance plant fitness in native and agricultural soils.

D. Schlatter · A. Fubuh · L. Kinkel (✉)
Deparment of Plant Pathology, University of Minnesota,
495 Borlaug Hall, 1991 Upper Buford Circle,
St Paul, MN 55108, USA
e-mail: kinkel@umn.edu

K. Xiao
USDA-ARS Cereal Disease Laboratory, University of Minnesota,
1551 Lindig Street,
St. Paul, MN 55108, USA

D. Hernandez · S. Hobbie
Department of Ecology, Evolution, and Behavior,
University of Minnesota,
100 Ecology Building, 1987 Upper Buford Circle,
St. Paul, MN 55108, USA

Introduction

Soil microbes play significant roles in plant health as pathogens, pathogen antagonists, symbionts, and saprophytes [1, 3, 5, 12, 15, 32, 33]. Plant roots, in turn, are critical to soil microbes as a source of carbon compounds from root exudates, root cells, and mucigel [2, 8, 9, 20, 21, 25, 40]. Carbon inputs from plant rhizospheres are hypothesized to influence the surrounding microbial community size, composition, and function [30, 31], with consequent effects on nutrient cycling [4], pathogen inhibition [22, 27], and microbial diversity [18]. In agricultural systems, a diverse array of soil nutrient amendments including green manures, compost, and animal manures have been used in attempts to deliberately alter soil community composition [27]. However, little is known of the direct effects of specific carbon compounds on the phenotype of soilborne microbes.

Streptomyces are gram positive filamentous bacteria that are ubiquitous in soil, important as plant saprophytes, and are noted as prolific producers of a broad range of antibiotics. In agricultural systems, *Streptomyces* species

have been shown to suppress diverse plant pathogens including fungi, bacteria, and nematodes [35, 44]. The disease-suppressive activity of *Streptomyces* in soil is hypothesized to arise via antibiosis or resource competition, both of which are likely to be influenced in part by resource availability [6, 16, 22, 23]. Furthermore, nutrient augmentation of soil microbial communities via green manures has been shown to enhance the density and inhibitory activities of antibiotic-producing *Streptomyces* [7, 11, 42, 43]. These findings suggest that both the quality and quantity of resources available are important in influencing the size and phenotypic composition of soil microbial communities. Moreover, these results suggest that resource quality and quantity are critical to determining the potential for *Streptomyces* populations to effectively suppress plant diseases in the rhizosphere.

The objectives of this work were to explore the impacts of resource additions on the density and phenotypes of soilborne *Streptomyces*. Specifically, we compared culturable *Streptomyces* communities in field soils following 9 months of glucose, cellulose, or lignin additions, alone or in combination with six other substrates of varying complexity, at high or at low doses. In addition, we evaluated resource utilization profiles and inhibitory activities of *Streptomyces* isolates from each treatment. In total, these results shed light on the influence of individual carbon compounds on the population and phenotypic dynamics of *Streptomyces* in soil and the importance of carbon resources as selective agents for phenotypic shifts.

Materials and Methods

Soil collection and processing Five hundred grams of soil was collected from an unburned prairie site at Cedar Creek Natural History Area (CCNHA), a National Science Foundation Long Term Ecological Research site in east-central Minnesota. Soil was sieved (2 mm mesh), homogenized with a cement mixer, placed into jars sealed with polyethylene to prevent water loss, and incubated in the dark at room temperature. The moisture content of each soil jar was adjusted to 10% by weight. After 1 month of incubation to allow residual labile carbon to be respired, lignin, glucose, cellulose, or a combination of these with six other substrates of varying complexities (xylose, alanine, starch, pectin, chitin, and tannic acid) was added to each soil jar weekly at low and high doses for 9 months (four resource inputs—glucose, cellulose, lignin, or a combination, and five replicates per resource-dose treatment). Jars were gently rotated once a month to incorporate substrates into the soil. Low-dose resource inputs were equivalent to 100 g C/m^2/yr, approximating the inputs from prairie plants to soil in nature based on old field sites at CCNHA [24]. High-dose inputs were equivalent to 250 g C/m^2/yr. For the combination treatment, each of the nine nutrients was added so as to comprise an equal fraction of the total added C in that treatment (Hernandez, unpublished). To calculate the amount of carbon (C) input/g of soil, the soil depth productively used by plants was considered to be 20 cm and the bulk density of the sandy soils at CCNHA was assumed to be 1.8 g soil/cm^3 (J. West, personal communication). All insoluble resources were added in powder form followed by the addition of 1 ml deionized H_2O. Soluble resources were added in a 1 ml solution of deionized H_2O.

After a 9-month incubation period, 5 g soil samples were taken from each replicate and dried overnight in a fume hood under two layers of sterile cheesecloth. Individual samples were placed in 50 ml of sterile water and shaken on an orbital shaker at 175 rpm for 1 h at 4 °C. Soil suspensions were dilution plated (100 µl/plate) onto oatmeal agar (OA) and starch casein agar (SCA) and incubated at 28 °C for 7 days [44].

Microbial community assessment Bacterial and *Streptomyces* colonies were counted on both OA and SCA plates. OA is a high-nutrient medium that supports growth of many genera of the bacterial community, while SCA plates provide a semi-selective medium resulting in the growth of predominantly *Streptomyces*. In combination, these media provide a means for estimating *Streptomyces* in relation to total aerobic heterotrophic bacterial densities (colony forming units/g soil) for each soil sample. *Streptomyces* colonies from each treatment were randomly collected using sterile toothpicks to transfer spores from each colony onto SCA amended with cycloheximide and penicillin for purification. Isolates from each treatment were subsequently transferred onto OA plates with a cotton swab and grown for further study. *Streptomyces* isolates from the glucose and lignin treatments were characterized further as described below. Isolates from the glucose and lignin treatments were chosen for further characterization because these treatments showed the greatest differences in bacterial and *Streptomyces* densities in preliminary analyses and microbial densities can be an important correlate for inhibitory phenotypes.

Streptomyces antibiotic assays Nine randomly selected *Streptomyces* isolates from the lignin and glucose treatments (high and low) were evaluated for their antibiotic inhibitory activities using a modification of a method described by [39]. Each of the 36 isolates was evaluated for the ability to inhibit each of five well-characterized *Streptomyces* test strains DL87, LK2-12, LK6-14, LK4-16, and LK4-2 [13]. These strains represent diverse resistance phenotypes and provide a means for quantifying antibiotic inhibitory phenotypes for *Streptomyces* isolates. Moreover,

previous work has also shown that inhibition of *Streptomyces* isolates is significantly positively correlated with inhibition of important soilborne plant pathogens, including *Rhizoctonia*, *Fusarium*, *Verticillium*, and *Phytophthora* [42, 43]. Thus, these assays also provide insight into the pathogen-suppressive potential of *Streptomyces* communities following distinct resource inputs.

For each prairie soil isolate, 10 µl of spore suspension in 20% glycerol was dotted onto SCA (15 ml/plate) and grown for 3 days at 28 °C. The resulting *Streptomyces* colonies were killed by inverting the plate over a watch glass containing 4 ml chloroform for 1 h. Plates were aerated in a fume hood for 30 min to evaporate any remaining chloroform. Plates were subsequently overlaid with 15 ml of 1% water agar (WA). After the WA solidified, 100 µl of a test isolate were spread evenly over each plate and incubated at 28 °C for 3 d. Presence or absence of inhibition was evaluated for every soil isolate–test strain combination and resulting inhibition zones were measured from the edge of the colony to the edge of the clear inhibition zone.

Streptomyces resource utilization assays Resource utilization profiles were determined for the subset of 36 *Streptomyces* described above using Biolog SF-P2 plates (Biolog, Inc. Hayward, CA). SF-P2 microplates™ measure the growth of an isolate on single carbon sources by comparing the turbidity of each well to a water control well. Spore suspensions of each isolate were made by swabbing spores from a pure culture grown on OA for 7 day at 28 °C into 1.5 ml of 0.2% carrageenan. Suspensions were adjusted to an optical density of 0.20–0.24 at 590 nm then diluted in 13.5 ml of 0.2% carrageenan. One hundred microliters of the new suspension were pipetted into each well of the Biolog plate and incubated at 28 °C for 3 d. A Multiskan EX microplate reader (Labsystems, Helsinki, Finland) was used to measure the absorbance of each well at 590 nm. For each plate, the absorbance of the well containing only water was subtracted from the absorbance of every other well to standardize absorbance values. Negative absorbance values were set to zero for subsequent analyses. Utilized substrates, substrate richness, substrate use efficiency, and substrate use intensity were calculated for each isolate. Utilized substrates were defined as those which had an absorbance value greater than 0.005. Niche width for an isolate was defined as the total number of substrates utilized. For each substrate, substrate use intensity for an isolate was defined as the absorbance at 590 nm for that substrate. Substrate use efficiency for an isolate was defined as the mean of the standardized absorbances for the substrates that the isolate used. Niche overlap[1] was determined for each pair of isolates. Mean niche overlap within or among communities was determined as the mean of all pairwise niche overlap values for the target set of isolates. Similarity matrices for substrate utilization among isolates were constructed based on utilized substrates with a utilized substrate designated as 1 and a non-utilized substrate designated as 0. Simple matching criteria [37] were used to generate similarity matrices (NT-SYS) [34].

[1] Niche overlap=[{(N_{share}/N_1)+(N_{share}/N_2}/2)], where N_1 and N_2 are the total numbers of substrates used for two isolates, and N_{share} is the number of substrates used by both isolates.

Results

Bacterial and Streptomyces communities in soil Both resource type and dose-influenced culturable bacterial community size (Fig. 1; 2-way ANOVA, F=4.13; p=0.00025). Overall, glucose-treated soils supported significantly lower density bacterial communities than soils treated with cellulose, lignin, or the combination of resources. Soil microbial communities treated with high-resource doses had higher culturable densities than communities treated with low-resource doses (F=3.99; p=0.054). However, for individual resources the effect of resource dose on total community size was significant only for lignin-treated soils (F=15.88; p=0.004).

Densities of *Streptomyces* also varied significantly among soil communities treated with different resources (Fig. 2; F=10.25; p<0.0001). Soils treated with either glucose or the combination of resources supported significantly smaller *Streptomyces* densities at both high- and low-resource doses than soils treated with lignin or cellulose (Fig. 2). *Streptomyces* densities were not influenced significantly by resource dose overall (F=0.05; p=0.8293), or by resource dose for lignin and glucose individually (data not shown).

Resource type, but not dose, influenced the proportion of the soil bacterial community comprised of *Streptomyces* (Fig. 3; F=3.25, p=0.08; F=1.70, p=0.19, for resource type and resource dose, respectively). Cellulose-treated

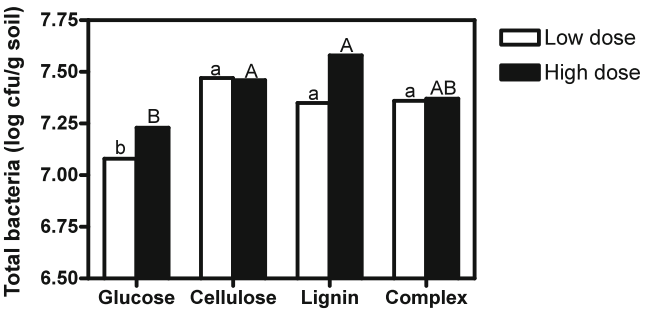

Figure 1 Total culturable densities of bacteria from prairie soils amended with high- and low-resource doses. Significant differences in bacterial densities among resources at high- (*upper case*) or low- (*lower case*) doses are indicated by different letters (Fisher's LSD, p< 0.05)

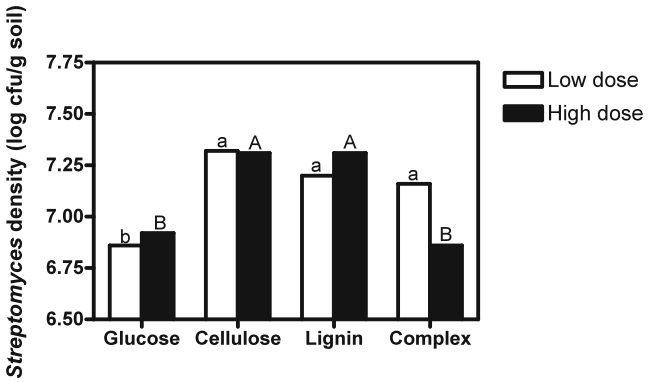

Figure 2 Culturable *Streptomyces* densities of prairie soils amended with high- and low-resource doses. Significant differences in *Streptomyces* densities among resources at high (*upper case*) and low (*lower case*) doses are indicated by different letters above the bars (Fisher's LSD, $p<0.05$)

soils supported significantly higher proportions of *Streptomyces* than soils treated with the resource combination; remaining resources supported intermediate proportions of *Streptomyces*. For the complex resource treatment, the proportion of the community comprised of *Streptomyces* was greater at low-resource than at high-resource doses (Fig. 3; $F=5.48$, $p=0.0474$).

Antibiotic inhibitory phenotypes among Streptomyces Inhibitory phenotypes among *Streptomyces* were studied in glucose- and lignin-treated soil communities. There were no significant differences in the mean inhibitory activity between communities receiving glucose or lignin (mean inhibition zone 4.3 vs. 3.7 mm, respectively; $F=0.10$, $p=0.75$). Likewise, mean inhibitory activity did not differ significantly among communities receiving high- vs. low-resource doses (4.65 vs. 3.35 mm, respectively; $F=0.59$, $p=0.46$). However, considering inhibition of individual *Streptomyces* standards, communities treated with high-resource doses had consistently greater inhibition zone sizes against individual standards than communities treated with low-resource doses (Fig. 4.) Specifically, five of five standards were inhibited more by *Streptomyces* from high-glucose than low-glucose communities, four of five standards were inhibited more by *Streptomyces* from high-lignin than from low-lignin communities (binomial, $p=0.03125$), though individual contrasts were not statistically significant. Likewise, the number of standards inhibited per *Streptomyces* isolate was greater at high than at low-resource doses (Fig. 5).

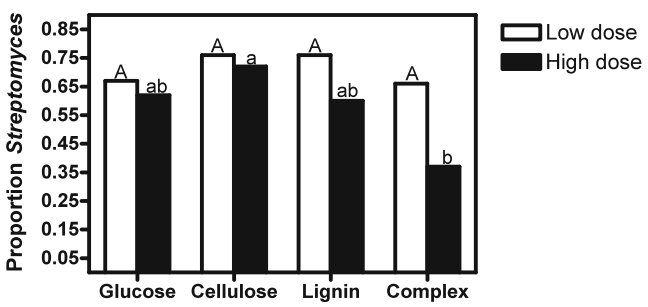

Figure 3 Proportion of culturable *Streptomyces* in bacterial communities from prairie soils amended with high- and low-resource doses. Significant differences among resources at low (*upper case*) and high (*lower case*) doses are indicated by different letters above the bars (Fisher's LSD, $p<0.05$)

Overall, a significantly greater frequency of interactions between *Streptomyces* isolates and standards were inhibitory for isolates from the high-lignin treatment than from the low-lignin treatment (Chi-square=6.76; $p=0.0093$). In contrast, there was no significant difference in the frequency of interactions that were inhibitory among *Streptomyces* from the high- vs. low-glucose treatments (Chi-square=0.649; $p=0.42$). The frequency of inhibitory interactions did not differ between glucose- and lignin-treated communities (data not shown).

Substrate utilization among Streptomyces Individual *Streptomyces* isolates used from 42 to 95 of the 95 substrates tested. Average niche widths did not vary significantly among resource types or doses. Among all isolates, there was substantial variation in substrate utilization. Among the 36 isolates (nine from each of the four treatments), no two isolates clustered at 95% similarity. However, there were nine clusters of two or more isolates at 75% similarity. Seven of these clusters contained only isolates from soils

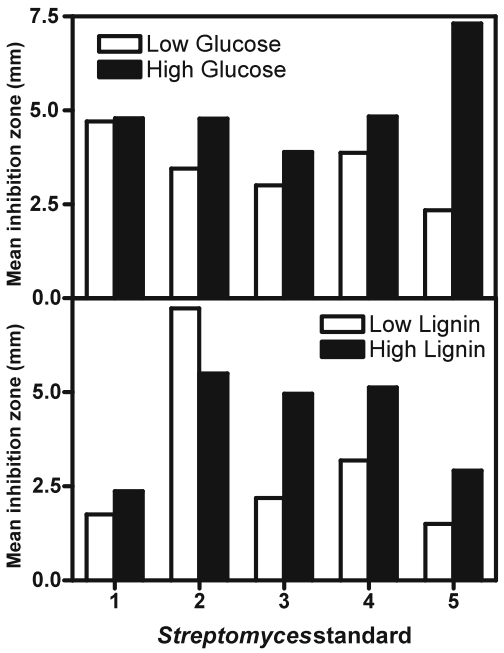

Figure 4 Mean inhibition zone sizes for *Streptomyces* isolates from prairie soils treated with different resources ($n=9$ for each resource/dose combination) against five *Streptomyces* standard isolates

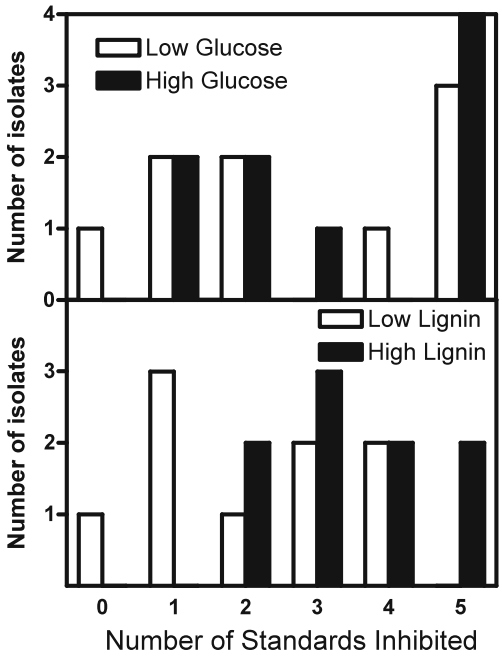

Figure 5 Number of *Streptomyces* isolates from prairie soils treated with different resources (n=9) from each resource/dose combination that inhibited from 0–5 of the five standard *Streptomyces* isolates

treated with the same resource type, and six of these seven clusters contained isolates from different samples, suggesting that treatment with a particular resource may repeatedly select for a specific substrate utilization profile among *Streptomyces* isolates. Among the five most-used substrates, the most commonly used was uridine (32 of 36 isolates), followed by D-melibiose (21 of 36 isolates).

Niche overlap among isolates from communities treated with the same resource varied significantly depending on the carbon input. *Streptomyces* isolates from lignin-treated communities had higher niche overlap (less niche differentiation) on average as compared to those from glucose-treated communities (Fisher's LSD, $p<0.05$). There were no significant differences in niche overlap among isolates

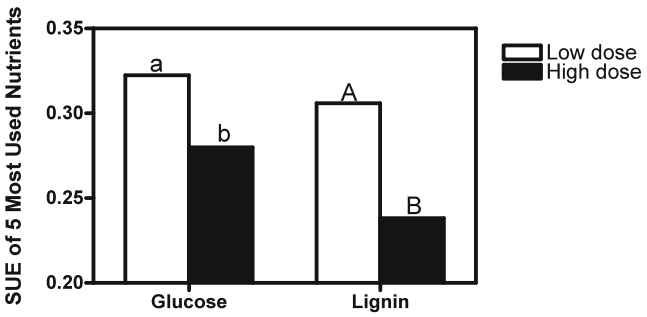

Figure 6 Average substrate use efficiency (*SUE*) for the five preferred substrates (nutrients with the greatest growth for the isolate) among *Streptomyces* from nutrient-amended prairie soils. *Different letters above bars* represent significant differences (Fisher's LSD, $p<0.05$) between low and high doses for each resource

from the high- vs. low-lignin communities. In contrast, isolates from the low-glucose community had significantly greater niche overlap than those from the high-glucose community (data not shown).

Streptomyces communities from lignin- vs. glucose-treated soils did not vary significantly in their mean substrate use efficiency, (mean=0.091 vs. 0.079 for glucose and lignin, respectively; F=2.85, p=0.117). Likewise, there were no differences in substrate use efficiency between *Streptomyces* communities treated with low- vs. high-resource doses (mean=0.095 vs. 0.078 for low and high, respectively; F=1.90; p=0.193). However, when considering the substrate use efficiency of only the five preferred substrates for each isolate (five substrates on which most growth occurred), isolates from low-resource-input soils were marginally more efficient than isolates from high-resource-input soils (Fig. 6; p=0.062).

Relationships between Streptomyces densities and frequencies and competitive phenotypes Among all isolates, there was a significant positive correlation between the proportion of *Streptomyces* in the community from which the isolate was collected and the mean inhibitory activity of the isolate against other *Streptomyces* (Table 1; R=0.45333; p=0.0048). *Streptomyces* from communities that had a high proportion of *Streptomyces* were more inhibitory than *Streptomyces* from communities with a low proportion of *Streptomyces*. Furthermore, communities that supported a higher density of *Streptomyces* had isolates that were better inhibitors than communities with low densities of *Streptomyces* (Table 1; R=0.31639; p=0.0564). Both the density and the relative frequency of *Streptomyces* in the soil community were important correlates of inhibitory ability among *Streptomyces* isolates from all treatments. Density was also a predictor of substrate use efficiency. Among *Streptomyces* isolates from all treatments, there was a

Table 1 Correlation between the proportion of *Streptomyces* in the community or the population density (Log) of *Streptomyces* and the mean inhibition zone or substrate use efficiency (SUE) among individual *Streptomyces* isolates from resource-amended prairie soil

Resource Treatment	Zone and Proportion	Zone and Density	SUE and Proportion	SUE and Density
Overall	R=0.45	R=0.33	R=−0.22	R=−0.38
	$p<0.01$	p=0.06	p=0.19	p=0.02
Glucose	R=0.41	R=0.30	R=−0.33	R=−0.22
	p=0.08	p=0.22	p=0.18	p=0.37
Lignin	R=0.52	R=0.24	R=−0.21	R=−0.49
	p=0.27	p=0.33	p=0.41	p=0.04
High	R=0.50	R=0.34	R=−0.21	R=−0.42
	p=0.03	p=0.15	p=0.41	p=0.08
Low	R=0.32	R=0.41	R=−0.42	R=−0.27
	p=0.21	p=0.10	p=0.08	p=0.28

significant negative correlation between substrate use efficiency and *Streptomyces* density in soil (Table 1; $R=-0.37600$; $p=0.0238$). High *Streptomyces* density communities supported isolates that had, on average, lower substrate use efficiencies than low-density communities

Relationships among competitive phenotypes Among all *Streptomyces* isolates, there was a significant positive correlation ($R=0.59014$; $p=0.0001$) between the mean inhibitory activity (zone size) and the number of standards inhibited by an isolate: isolates that inhibited more standards were also better at inhibiting each of those standards. Relationships between the inhibitory activity and the number of standards inhibited by an isolate varied among *Streptomyces* from different resource treatments (Fig. 7). *Streptomyces* from high-glucose, low-glucose, and high-lignin communities all showed increasing inhibitory activities with increasing frequencies of inhibition, though the specific pattern of increase varied. There was no significant relationship between inhibition frequency and mean inhibitory activity for *Streptomyces* from low-lignin communities ($R=-0.13274$; $p=0.7540$).

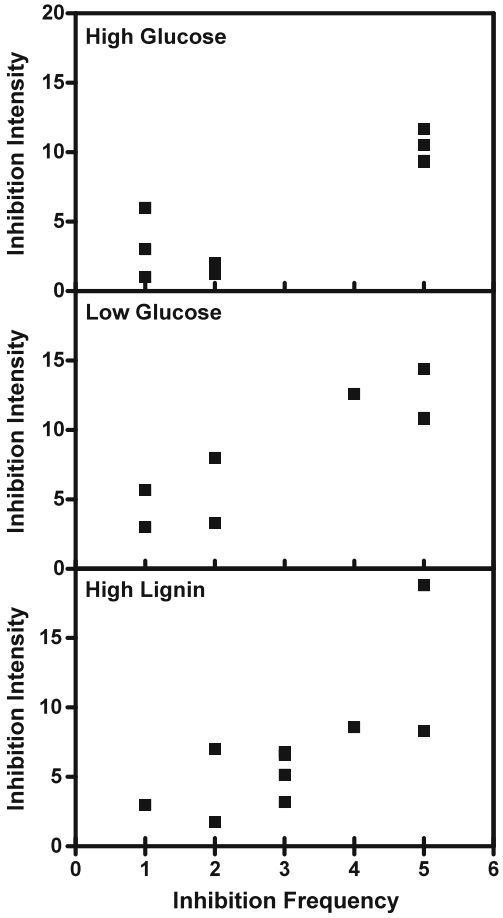

Figure 7 Relationships between the frequency (number of *Streptomyces* standards inhibited by each prairie soil isolate) and intensity (mean inhibition zone produced by each prairie soil isolate against the five standards) of inhibition among *Streptomyces* isolated from resource-amended prairie soils

Substrate use and inhibitory activity were related among isolates in some treatments but not others. Mean inhibition zone size and substrate use efficiency were positively correlated within the low-lignin treatment ($R=0.73151$; $p=0.0251$). Thus, good inhibitors tended to use substrates more efficiently than poor inhibitors in the low-lignin community. In contrast, within the low-glucose communities, the mean inhibition zones and substrate use efficiency were negatively correlated ($R=-0.60371$; $p=0.0852$). In low-glucose communities the strong inhibitors used substrates less efficiently than poor inhibitors. There was no significant correlation between substrate use and inhibitory phenotypes within the high-lignin or high-glucose communities.

Discussion

Previous studies have reported significant effects of soil resource amendments on microbial community structure and function [8, 14, 20, 31, 36]. [31] found that carbon substrates differ significantly in their effects on microbial community function, but not community structure.

Resource amendments generally are reported to have broad impacts on subsequent nutrient utilization activities within soil microbial communities, whether the nutrients are added as simple carbon substrates or as a function of root exudates produced by different plant species [20, 36]. Our work extends prior studies by documenting shifts in microbial interaction phenotypes, including both antibiotic inhibitory phenotypes and resource use, among individual microbial isolates within the genus *Streptomyces* following repeated soil amendments with varying nutrient doses. In particular, this work shows that higher nutrient inputs resulted in *Streptomyces* communities that had greater antibiotic inhibitory activity than low inputs, and greater resource use efficiency following low- vs. high-nutrient inputs.

Antibiotics are traditionally thought to be important in mediating microbial interactions as inhibitory compounds, though recent work suggests they may also be important as signaling molecules in natural habitats [19, 45, 46]. Our data are consistent with the idea that antibiotics are critical to microbial interactions in soil. Specifically, the greater frequency of inhibitory interactions and greater inhibitory activity among *Streptomyces* from high-nutrient-input communities suggests that, as the soil microbial communities increased in density in response to added nutrients, there was positive selection for antibiotic-producing isolates. At higher densities, both the frequency and diversity of species interactions would be expected to increase in soil, which would impose selection on those traits that are critical to

mediating species interactions. Our data suggest that antibiotics are important to mediating these interactions, either as inhibitors or as signaling molecules, based upon the enhanced antibiotic phenotypes observed in the high-nutrient vs. low-nutrient communities.

In contrast to the enhanced antibiotic activities observed in the high-nutrient communities, *Streptomyces* from the low-input communities were more efficient in utilizing nutrients, especially preferred nutrients, than isolates from the high-input communities. When nutrient availability is low, and when local microbial densities are relatively smaller, microbes that are most efficient in utilizing available nutrients will be most fit. Overall, the data are consistent with the prediction that both soil nutrient availability and microbial population densities are likely to be key determinants of phenotypic composition among *Streptomyces* communities in soil. More specifically, these data suggest that enrichment for antibiotic-producing *Streptomyces* is most likely in nutrient-enriched habitats in soil, including plant rhizospheres.

Nutrient enrichment, specifically via addition of organic amendments to soil, has been used broadly as a means for enhancing the suppression of diverse soilborne plant pathogens [17, 26, 28, 29, 38, 41–43,47]. In particular, differences in density and antibiotic inhibitory activity among soilborne *Streptomyces* communities following organic matter incorporation have been shown by many researchers to correspond with significant differences in pathogen suppression and plant disease intensity, though possible mechanisms of suppression include nutrient competition, inhibition, parasitism, or systemic induced resistance [6, 10, 11, 42, 43]. Unfortunately, the use of organic amendments to manage soil microbial communities has often been inconsistent [28]. This reflects the complexity of nutrient quantity and quality among organic amendments (green manures, compost, agricultural and wood processing waste). The use of single purified nutrient sources, as in the present study, may offer an important means for characterizing the specific nutrients and nutrient quantities necessary for attaining desired shifts in microbial community phenotypes necessary to suppress plant pathogens, and for understanding the potential effects of particular nutrient doses on the evolution of communities in different soils.

Though *Streptomyces* isolates from low-input communities were generally poorer inhibitors than isolates from high-input communities, the relationships between inhibition (mean zone size) and nutrient-use efficiency differed within the low-lignin vs. low-glucose communities (positive correlation in low-lignin community, negative correlation in low-glucose community). When lignin was the added nutrient, efficient isolates were best at inhibiting other *Streptomyces*; while when glucose was added, the most efficient isolates were poorest at inhibiting other *Streptomyces*. The data suggest that fitness tradeoffs between growth efficiency and antibiotic inhibition phenotype differ in lignin- vs. glucose-amended soils. Such differences may be important to understanding the effectiveness of different nutrient inputs in generating a highly inhibitory soil microbial community.

Understanding how specific nutrient inputs influence *Streptomyces* inhibitory and nutrient-use phenotypes is necessary for active management of soil microbial communities to promote disease-suppressive soils. In order to achieve practical and broadly useful management strategies, we must first understand the complex interactions within soil microbial communities and the primary drivers of competitive phenotypes. Further research is needed to better understand how nutrient inputs affect microbial interactions and disease suppression in soil.

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