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Shrub invasion and bacterial community pattern in Swedish pasture soil

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Abstract

In arid environments, soil resources accumulate around shrubs to form resource islands. These islands are accompanied by increased bacterial counts and/or increases in microbe mediated processes. The present study investigates the universality of resource islands by measuring bacterial numbers and soil nutrients under and between shrubs invading a Swedish pasture. Substrate utilization patterns were also compared. Neither bacterial count patterns nor soil nutrient measurements supported resource island formation. Analysis of the substrate utilization patterns indicated metabolic differences comparing under- and between-plant communities. The results of this study suggest that resource island formation is not an intrinsic property of shrub invasions but rather may be related to the water harvesting or hydraulic lift associated with shrubs in arid environments.

Keywords: Resource island; Substrate utilization profile; Bacterial population

1. Introduction

The distribution of microorganisms in soil is under complex control. Soil nutrient resource distribution patterns appear to be an important factor in the control of microbe distribution in soil [1,2]. Resources implicated include organic matter [2–8], nitrogen [2,3,5,9], and soil moisture or soil water potential [2,5,10,11]. In arid environments, shrub invasion into grasslands is often accompanied by the redistribution of these resources to form resource islands with water, organic matter and mineral nutrients accumulating around shrubs at the expense of the between-shrub areas [12–14]. These shrub-focused resource islands form by trapping organic matter making it available for mineralization. In addition, they are foci where the biological community modifies the water status of the island soils, concentrating water around the shrub by a combination of funnel-shaped canopies which concentrate water at the plant stem via stem flow and/or hydraulic lift [15–19]. Once shrubs invade grasslands, these processes produce a positive feed-back loop reinforcing the resource island around the shrub and diminishing resources in the inter-plant spaces [13].

The resource redistribution apparent in resource island formation appears to exert a strong influence on the distribution of bacterial numbers in arid soils. Total heterotrophic bacteria and nitrogen efficient

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guild members (NEG, organisms that can fix atmospheric N or are effective scavengers of soil N) were 5–40 times more numerous adjacent to shrubs than in the inter-shrub spaces in the Chihuahuan desert. In contrast, at and between plant populations in undisturbed Chihuahuan grasslands never differed by more than 2.5-fold [20].

In order to test the universality of the resource island control of microbial populations, a study was initiated to compare juniper invasion into a cool-temperate pasture grassland at Lövstalöt, Sweden to patterns observed in the Chihuahuan desert [20]. The Lövstalöt grassland is not under the same water stress as the Chihuahuan desert system and the juniper canopy morphology does not exhibit the same funnel-shaped, water-harvesting morphology as the tar bush, creosote bush or mesquite found in the Chihuahuan desert. If water stress/water harvesting is a major factor in the generation of resource islands, the Lövstalöt site would be expected to have little or no resource island development and no concentration of bacterial populations under shrubs. Similar bacterial population and nutrient distributions in both the desert and temperate shrub invasions would suggest that the resource island hypothesis has universal applicability, probably driven by litter accumulation and mineralization.

2. Materials and methods

2.1. Site characteristics

Field samples were collected at the Swedish University of Agricultural Sciences Lövstalöt Research area located 12 km north of Uppsala, Sweden (17°36′30″ E, 59°56′30″ N). The area has been used as pasture for the last 300 years and has been the site of a variety of research projects since the 1940s. The site is on the western slope of the Uppsala Ridge. The soil is comprised of well sorted materials with sandier soils up-slope and soils with higher clay content down slope. Major vegetative cover is grassy (*Agrostis capillaris*, *Festuca rubra*, *Poa pratensis* and *Festuca ovina*) with forbs such as *Alchemillia vulgaris*, *Taraxicum vulgare*, *Trifolium repens* and *Geranium sylvaticum* common. The pasture has scattered woody vegetation comprised largely of juniper (*Juniperus communis*), birch (*Betula pendula*) and patches of rose (*Rosa majalis*). Soils are characteristically about pH 5.5 with organic carbon and total nitrogen 3.6% and 0.3% respectively [21].

2.2. Sample collection

Four juniper bushes located at mid slope and isolated from large trees were selected. Soil cores were collected under the canopy and 1–1.5 m from the canopy using a 45 mm diameter cylindrical sampler which could be pounded with a sledge. Soil between a depth of 5 and 10 cm was chosen for microbiological analysis for a variety of reasons. Preliminary sampling demonstrated that this zone had large and consistent numbers of microorganisms. Samples closer to the surface were initially collected in an attempt to maximize the likelihood of observing the influence of secondary chemicals from the junipers. Unfortunately, preliminary analysis demonstrated extremely high variability in sub-samples taken from single cores and between cores taken at the same location, making between-site comparisons much more difficult than with samples from 5–10 cm which showed much higher within core and within site consistency. Samples of 0–5 cm depth were collected for chemical analysis. The soil was transferred from the sampler to plastic bags and brought back to the laboratory for analysis. Samples were thawed if necessary, broken manually in the bags and aseptically sieved through a 2.0 mm sieve. A 1 g sample was aseptically transferred to a dilution bottle containing 99 ml of sterile tap water. The bottles were shaken for 30 min at 225 rpm and dilution series made to NF/MM (nearly nitrogen free/mannitol malic acid) plates or MPN (most probable number) tubes. Soil samples were weighed and dried for 24 h at 105°C and reweighed to calculate percent moisture. All values are reported as the means ± S.E.M. of the four cores in each treatment.

2.3. Media and enumeration

Total heterotrophic counts were carried out using MPN tubes containing broth with the following composition (g l^{-1}) yeast extract, 1.0; tryptone, 1.0; peptone, 1.0; acid hydrolyzed casein, 1.0; L-malic acid, 0.5; sodium succinate, 0.5; soluble

starch, 0.5; K_2HPO_4, 0.5. The medium was adjusted to pH 7.1 with KOH prior to autoclaving. This medium consistently recovered the highest number of counts of the six media tested in preliminary experiments. MPN was estimated using 3-tube series tables from Harrington and Chance [22] on dilutions of $1:1\times10^4$ to $1:1\times10^8$ after 92 h incubation at room temperature ($\sim$20°C). NEG members were isolated and enumerated on NF/MM plates [23] containing (g l^{-1}) KH_2PO_4, 0.4; K_2HPO_4, 0.1; $MgSO_4$, 0.097; NaCl, 0.1; $CaCl_2$, 0.0196; $FeCl_3{\cdot}6H_2O$, 0.017; $NaMoO_4{\cdot}H_2O$, 0.002; yeast extract, 0.001; L-malic acid, 3.58; mannitol, 5.0; and agar, 15. The medium was adjusted to pH 7.0 with KOH prior to autoclaving. Known added nitrogen is less than 1 μM with agar impurities adding unknown quantities of additional N. Dilutions of $1:1\times10^4$ and $1:1\times10^5$ were plated and counted after 96 h growth at room temperature. Total bacteria were estimated by the fluorescein isothiocyanate (FITC) method modified from Babuik and Paul [24]. Briefly 90 ml of 1:100 dilutions of soil were preserved with the addition of 10 ml concentrated formaldehyde solution containing 0.1 g Tween 20 (final concentration 3.67% formaldehyde, 0.1% Tween 20). The preserved samples were shaken 30 min at 225 rpm and 0.5 ml (5 mg wet weight soil) removed and mixed with 3.5 ml of freshly prepared, filtered FITC stain (0.4 mg/ml FITC in 50 mM NaH_2PO_4, 0.85% NaCl, pH 9.0 buffer). The sample was allowed to stain for 10 min and vacuum filtered over pre-washed 0.20 μm black polycarbonate filters (Poretics Inc.). The staining tubes were rinsed with an additional 5 ml buffer which was added to the filters. The filters were mounted and 10 randomly selected fields per filter were counted. All MPN, NEG and FITC counts were log transformed and analyzed by ANOVA or MANOVA by SAS general linear models procedures [25]. Groups were considered different when P was <0.05.

2.4. Substrate utilization potential

Substrate utilization potential was assessed on two near and two far samples at each of six collection times by inoculating Gram-positive and Gram-negative Biolog plates with 150 μl of the 1:1000 dilutions (3000–3500 'viable' cells). Wells were scored after 72 h incubation at room temperature. Shorter incubations did not allow full color development, while fungal growth obscured some wells with longer incubations. Wells were scored using the following scale: no change, 0; pale but perceptible purple, 1; obviously purple, 2; very strong purple, 3. The data were further reduced by combining substrates which occurred on both plates and entering the higher value to give a matrix of 135 unique substrates. The samples were grouped using cluster analysis (Euclidean distance, Ward's method) and by principal components analysis using SAS. Group substrate utilization means were compared by Student's t-test.

2.5. Soil analysis

Soils were analyzed for total C, Kjeldahl N, NO_3-N, NH_4-N and total P in solids by the Soil, Water and Air Testing Laboratory at New Mexico State University.

3. Results

FITC total direct counts, total heterotrophic counts and NEG numbers were estimated under juniper canopies and between juniper plants during the period September 1995 through June 1996. Fig. 1 shows FITC total direct counts from under-plant and between-plant samples. Counts were significantly higher between plants for samples taken between 3 October 1995 and 18 March 1996. Samples collected in April, May and June showed no significant difference in total counts. Fig. 2 displays the most probable number of heterotrophs from under-plant and between-plant samples. The estimated number of heterotrophs was significantly higher between plants for five of eight sampling dates between October and March with no significant differences observed in April, May or June. NEG member populations are plotted in Fig. 3. There were no significant differences in NEG numbers at any time during the year comparing under-plant and between-plant samples.

In order to determine if resource islands were formed, a number of physiochemical parameters were measured in duplicate for each of the under- and between-plant sites. Soil nitrogen (total, NH_4

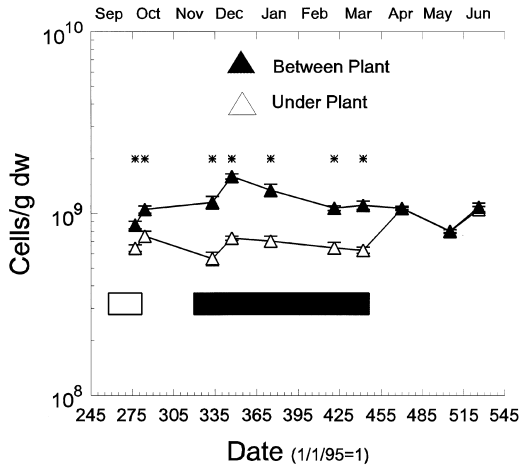

Fig. 1. FITC direct counts over time in Lövstalöt soils. Day 1 is 1 January 1995. Approximate month reference is on the second abscissa. All points are the mean of four determinations ± S.E.M. Samples where between-plant sample populations were significantly greater than under-plant sample populations are marked with an asterisk. The bars represents periods when the between-plant soils were significantly moister than under-plant samples. The open portion of the bar represents periods of unfrozen soils while the filled bar represents frozen periods.

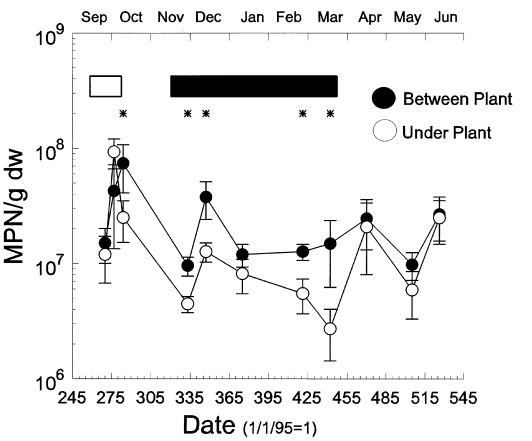

Fig. 2. MPN total heterotrophic counts over time in Lövstalöt soils. Day 1 is 1 January 1995. Approximate month reference is on the second abscissa. All points are the mean of four determinations ± S.E.M. Samples where between-plant sample populations were significantly greater than under-plant sample populations are marked with an asterisk. The bars represents periods when the between-plant soils were significantly moister than under-plant samples. The open portion of the bar represents periods of unfrozen soils while the filled bar represents frozen periods.

and NO_3), phosphorus and total soil carbon were assayed for each site. Mean soil nutrient values for under-plant and between-plant sites are presented in Table 1. Whether mean values were higher for the under-shrub samples was about evenly divided in both the 5–10 cm and 0–5 cm samples. Nitrate nitrogen was the only nutrient higher under shrubs and then only in the 0–5 cm sample. In general, the 0–5 cm samples were higher in nutrients than the 5–10 cm samples. The lack of significant differences in total N, ammonia N, P and C levels comparing between- and under-plant samples would indicate weak or non-existent resource island development. Soil moisture was determined for all samples taken (Fig. 4). Soil moisture levels were significantly higher between plants for two of three fall (September/October) samples and for all winter (November–March) samples. There were no significant differences between under-plant and between-plant soil moisture in the spring/summer (April–June) samples. The ground was frozen for all samples taken during November–March. The open bars in Figs. 1–4 indicate samples where soil moisture was greater in the between-plant samples while the black bar indicates

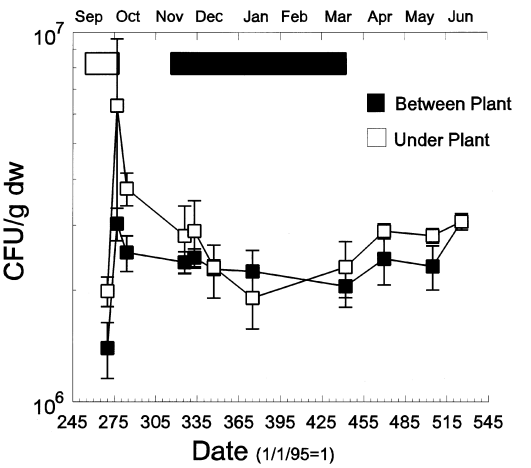

Fig. 3. Plate counts of NEG members over time in Lövstalöt soils. Day 1 is 1 January 1995. Approximate month reference is on the second abscissa. All points are the mean of four determinations ± S.E.M. There were no samples where between-plant populations were significantly greater than under-plant populations. The bars represents periods when the between-plant soils were significantly moister than under-plant samples. The open portion of the bar represents periods of unfrozen soils while the filled bar represents frozen periods.

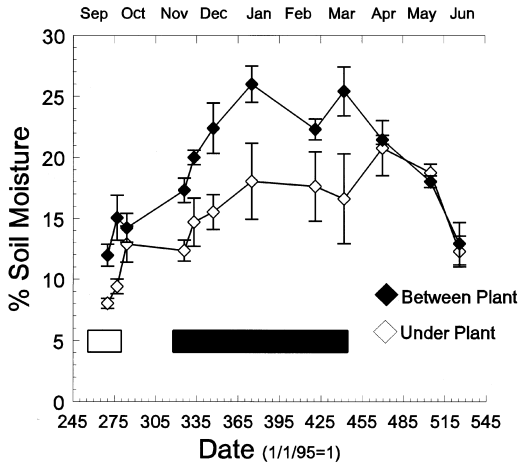

Fig. 4. Soil moisture content over time in Lövstalöt soils. Day 1 is 1 January 1995. Approximate month reference is on the second abscissa. All points are the mean of four determinations ± S.E.M. The bars represents periods when the between-plant soils were significantly moister than under-plant samples with. The open portion of the bar represents periods of unfrozen soils while the filled bar represents frozen periods.

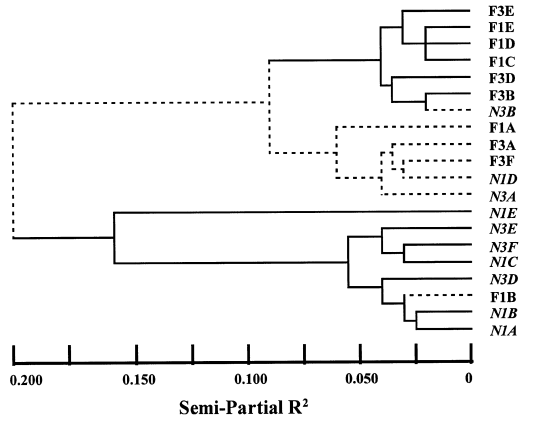

Fig. 5. Cluster diagram of Biolog plate substrate utilization pattern from under-plant (N1 and N3) and between-plant (F1 and F3) samples at six sampling periods (A–F). Solid lines connect similar sample types, dotted lines connect dissimilar sample types.

that the ground was frozen and soil moisture was greater in the between-plant samples. The ground was frozen during the majority of sampling periods where there were differences in FITC or heterotrophic counts comparing under-shrub and between-shrub samples. In all samplings but one where population differences were observed, the higher populations between shrubs were accompanied by higher soil moisture levels between shrubs.

The substrate utilization potential, often referred to as 'functional diversity' [26] of communities, was estimated by the pattern of substrate utilization on Biolog® plates. Substrate utilization patterns were compared at six times from February 1996 to March 1997 (A–F) in samples taken from two under-plant sites (N1 and N3) and two between-plant sites (F1 and F3). Fig. 5 presents a cluster diagram generated using Ward's method to cluster samples. Samples grouped into three clusters. The upper cluster consisted of six between-plant samples and one under-plant sample. The lower cluster contained seven under-plant samples and one between-plant sample. The middle cluster contained two between-plant and three under-plant samples. Within the main clusters, there was some tendency for samples to group by collection location. When the data were subjected to principal components analysis, the first four principal components accounted for 27.10%, 18.16%, 8.22% and 5.97% of the variance respectively. The P values for the hypothesis that between- and under-plant samples were not randomly distributed along the principal components axes were 0.058,

Table 1
Selected nutrients measured under plant canopies and between plants

	Under canopy 5–10 cm	Between plants 5–10 cm	P	Under canopy 0–5 cm	Between plants 0–5 cm	P
Total C (%)	3.49 ± 0.21	4.16 ± 0.30	0.15	4.58* ± 0.39	5.04* ± 0.31	0.35
Kjeldahl N (mg/kg)	2413 ± 281	2630 ± 295	0.69	3380 ± 260	3806* ± 223	0.11
Nitrate N (mg/kg)	4.7 ± 1.2	2.0 ± 0.12	0.13	5.5 ± 0.72	2.8 ± 0.50	0.04
Ammonia N (mg/kg)	88.6 ± 46.6	35.6 ± 5.6	0.29	139.5* ± 49.4	117.1* ± 12.4	0.63
Phosphorus (mg/kg)	456 ± 60	472 ± 34	0.66	497 ± 50	534* ± 27	0.41

*The value is significantly higher ($P < 0.05$) than the value for the 5–10 cm samples.

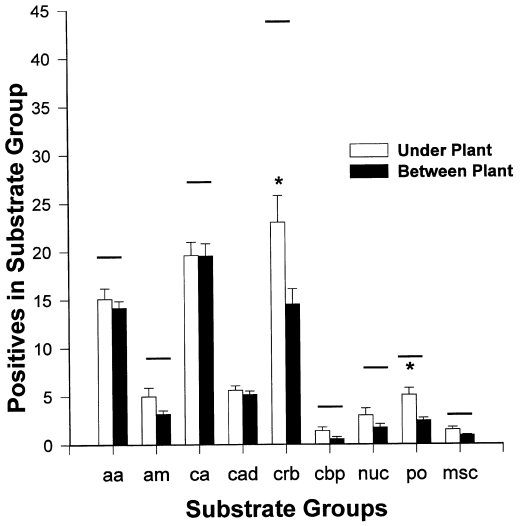

Fig. 6. Mean number of substrates used from different substrate groups by communities isolated from soil between plants and under plants. Substrate groups were: aa = amino acids, am = amines and amides, ca = carboxylic acids, cad = carboxylic acid derivatives, cb = carbohydrates and related compounds, cbp = phosphorylated carbohydrates, nuc = nucleotides and nucleotide derivatives, po = polymers, msc = miscellaneous. The line over each bar indicates the total number of substrates in the group. Groups with significantly greater substrate utilization by under-shrub samples are marked with an asterisk.

0.357, 0.539 and 0.173 for the first four axes respectively. While not significant, under-plant samples tended to have high values for the first principal component while between-plant samples tended to have low values.

Biolog plate substrates can be grouped according to substrate type [26]. Fig. 6 shows the average number of substrates in each substrate group utilized by the between-shrub and under-shrub samples. The under-plant samples used significantly more substrates overall (79.18 ± 6.76 vs. 62.27 ± 4.27, $P = 0.047$). Among individual substrate groups higher numbers of carbohydrates ($P = 0.014$) and polymers ($P = 0.002$) were used by under-plant samples. There were no differences in utilization between the two sample sites for the other seven substrate groups.

4. Discussion

Arid shrublands in western North America show resource island development with an accumulation of biologically important nutrients in patches the sizes of which approximate shrub canopy size [12,14]. This resource island formation occurs as an autogenic process as shrubs invade and grasslands [12,13]. In the northern Chihuahuan desert, these resource islands are accompanied by increased populations of heterotrophic and nitrogen efficient bacteria [20]. If the formation of resource islands is generated by the accumulation of litter under shrub canopies trapping nutrients and making them available for recycling by detritovores, then resource islands should occur wherever shrubs invade grasslands. On the other hand, if the island formation is primarily generated by water harvesting shrub canopies and/or hydraulic lift, the phenomenon should be prominent in arid environments and should be absent or weak in environments where water is not strongly limiting.

It was clear that resources were not strongly concentrated under juniper shrub canopies in the temperate Swedish pasture grassland studied (Table 1). This is in clear contrast to the situation which prevails in the southwestern United States where nutrients such as total nitrogen and phosphorus were strongly concentrated around shrubs [12,20]

Total direct counts (Fig. 1), total heterotrophic counts (Fig. 2) and counts of NEG members (Fig. 3) fluctuated over the course of the study, with the total counts showing the least fluctuation on a proportional basis. Bacterial populations in the 5–10 cm zone were either not different (NEG members, Fig. 3) or higher in the between-shrub samples. This contrasts sharply with previous, directly comparable population studies in the Chihuahuan desert where differences always favored the at-shrub samples [20]. It also contrasts with a variety of studies which show that surrogates of microbial populations such as microbial biomass [14] or microbial processes [14,19,27,28] were higher near shrubs than between shrubs in arid settings. It is not possible to say that bacteria found in the top 5 cm would not exhibit a different pattern, however, the similar pattern of soil resources at both depths reduces this likelihood.

In general, the higher populations of total bacteria and heterotrophs in the between-shrub samples in the present study were associated with higher soil moisture levels in the samples. These data are consistent with many other studies showing a correlation

of bacterial numbers, biomass or processes with soil water potential [2,5,10,11,29]. It does not appear that the fact that the soil was frozen had a strong effect on the recovery of total or viable organisms. This is reflected both in the population trends shown in Figs. 1–3 and by the fact that freezing soil samples, holding them frozen for a week and slowly thawing them did not result in a significant reduction in the number of viable counts (data not shown). Interestingly, higher NEG counts were not correlated with higher soil water levels in the Swedish pasture soils as they were in the desert [29].

Biolog plates provide a convenient way to expose microbial communities to a wide variety of carbon sources. The resulting patterns of substrate utilization can be used to group similar samples and to follow differences in communities over space or time [26,30–34]. Based on substrate utilization, bacterial populations under shrubs and between shrubs tended to cluster by site type (Fig. 5). Despite the fact that there were often fewer organisms in the under-shrub samples, they used a wider variety of substrates (Fig. 6). It is possible that the under-shrub communities show this broader substrate use because these sites receive a wider variety of polymers and carbohydrates in the incoming litter derived from both the juniper shrubs and the surrounding grass/herbaceous community.

The results of the present study show neither a microbe nor nutrient distribution pattern consistent with resource island formation by junipers invading pasture soils. This suggests that resource island formation is more likely due to some factor associated with arid environments, perhaps the soil water dynamics that are influenced by the water harvesting canopy morphology of desert shrubs. The response of bacterial populations to increased soil water levels would suggest that resource island formation is not a universal phenomenon as shrubs invade grasses and may be due to soil processes more strongly influenced by water dynamics than litter dynamics.

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