CONTRIBUTION OF PLANT CANOPIES TO SOIL ORGANIC CARBON ALONG AN ELEVATION GRADIENT

By

Phoebe Ly

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University of California, Riverside

APPROVED

Dr. Samantha Ying

Department of Environmental Science

Dr. Richard Cardullo, Howard H Hays Jr. Chair

University Honors

Abstract

H.F. Birch was the first to characterize the phenomenon, known as the Birch Effect, that describes how carbon dioxide (CO_2) emissions pulse when dry soils wet up. While researchers have observed this effect on a myriad of soil types over the past few decades, the mechanisms that affect these fluxes are still poorly understood. What previous literature lack is information on the soil composition, which impacts how carbon (C) is stored and its accessibility to the microbial community. Our research objective poses to characterize and compare compositional differences between soils where there is plant growth and where there is no plant growth, with respect to elevation, to better understand the processes of microbial respiration and C cycling. We test the hypothesis that soils at the highest elevation where precipitation rate is heaviest, soil C content will also increase due to greater plant growth compared to the lower elevations. In addition, we expect the distribution of C to be more homogenous at the highest elevation due to soil mixing caused by precipitation. Soil samples were collected across four field sites ranging from the dry desert landscape to the thick, shrubbery forest to allow us to analyze the interactions of plant growth and soil moisture. Our observations do support our hypotheses and show that plant canopies are clear hotspots for microbial activity, which allow C to be sequestered, while also potentially increasing C flux from respiration.

Acknowledgments

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Introduction/Background

Carbon dioxide (CO_2) has been rapidly increasing since the start of the Industrial Revolution in 1750. One key natural mechanism for reducing CO_2 in the atmosphere is to increase the global storage of carbon (C) in soils, also known as carbon sequestration (ESA 2012). To understand how much C can be stored in soil organic matter (SOM), it is important to study the biological, chemical, and physical mechanisms that allow C to be sequestered in soils and released into the atmosphere. Past research has found that when soils are dry, less CO_2 is emitted due to inhibited microbial respiration (Manzoni et al., 2012; Carnarini et al., 2017); however, once wetting occurs and soils become more saturated, the microbial community is then able to access the C and pulse CO_2 into the atmosphere. This phenomenon is known as the "Birch Effect" (Birch, 1958), where the introduction of moisture into the soil catalyzes microbial respiration. Previous research on the Birch Effect has been more focused on gas flux responses to wetting and drying events, while research into understanding the soil properties, dynamics, and microbial response to soil moisture fluctuations has been less developed. Better understanding of the mechanisms contributing to this phenomenon is particularly timely as climate shifts across the globe due to global warming, which will inherently change the rates of CO_2 flux in nearly all soils.

Soil composition varies greatly across different environments and ecosystems, with different parent material, vegetation, and climatic factors contributing to high soil diversity. Soils also vary significantly at a micro-scale, with small, topographical and faunal variations contributing to significant compositional differences between soils in close proximity to one another. Soils underneath plant canopies tend to have higher fertility, moisture, and organic matter due to plant debris decomposing into the soil directly underneath the plant in comparison to the "interspaces" defined as areas where there is no plant growth. Due to these micro-topographical differences in composition between the soils underneath plant canopies and interspace soils, investigations into soil carbon sequestration processes should take this landscape heterogeneity into account.

Our research objective aimed to quantitatively characterize and compare compositional differences between plant canopy and interspace soils to better inform how much microbial activity and C cycling are dependent on soil moisture. The three factors that are evaluated in this study are elevation (as a proxy for soil moisture), plant growth, and depth below soil surface. Aside from insight into differences in C distribution between plant canopies and interspace soils, this information will give us insight into the macronutrients and metals that should be further explored as being potential controls of C gas fluxes, which will also contribute to better understanding which environments are most vulnerable to climate change.

In this study, we test the hypothesis that soils at the lowest, driest elevation would have the lowest soil C concentration overall, regardless of the presence of plant islands. Correspondingly, we hypothesize that as we move to higher elevations where precipitation rate increases both in total volume and frequency, soil carbon content will also increase due to greater plant growth. Additionally, we expect to see the distribution of C to be more homogenous at the highest elevation compared to the lowest due to greater contribution of litterfall within interspace soils. Overall, because great precipitation occurs at the highest elevations, we expect soils to have lower concentration of soluble salts (e.g. sodium, calcium, magnesium), and lower silicon from greater weathering (removal) of silicate minerals, and higher concentration of secondary minerals relative to the drier lower elevation sites.

Materials and Methods

Site description

Soils were sampled across four sites along an elevation gradient at the Santa Rosa Mountain in the San Jacinto Mountains of Southern California. This area of California has a semi-arid climate characterized by cold-wet winters and hot-dry summers. The four sites in order from lowest to highest elevations are Boyd Deep Canyon (FS-1), Pinyon Flats Observatory (FS-2), Santa Rosa Mountain at 6000 ft (FS-3), and Santa Rosa Mountain at 8000 ft (FS-4). Annual precipitation also varies significantly with elevation, with FS-1 having significantly lower rainfall than FS-4. This elevation transect crosses through a variety of ecosystems, each with unique soil types and vegetation. The dominant vegetation of field sites range from desert shrubs such as *Larrea tridentata* (creosote bush) and chaparral communities at FS-1, chaparral and junipers at FS-2, to Jeffrey pine and White fir forests dominating at FS-3 and FS-4. The density of vegetation and the amount of organic matter significantly increases as elevation increases, which influences the diversity of the vegetation and heterogeneity of the chemical composition. Soils from each site can be described by their USDA soil taxonomy as described by the Web Soil Survey (https://websoilsurvey.sc.egov.usda.gov/; Table 1).

Table 1. USDA Soil Taxonomy. The field site ranges from lowest to highest elevation.

Field Site	**Site Code**	**Soil Taxonomy**
Boyd Center, Deep Canyon	FS-1	Typic Torriorthents
Pinyon Flat Observatory	FS-2	Typic Xerorthents
Santa Rosa Mountain (6000 ft)	FS-3	Lithic Xerorthents
Santa Rosa Mountain (8000 ft)	FS-4	Typic Xeropsamments

Soil sampling and analysis

At each field site, twenty total soil samples were collected to compare soil elemental composition; ten were sampled under plant canopies and the other ten sampled within interspaces between plants. Two depth profiles were sampled at each elevation with one depth profile located under a plant canopy and another sampled within the interspace soils. Depth profile soils were dug to a total depth of 40 cm with samples taken from 0-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm (total of eight soil samples). Depth profiles sampled under plant canopies were taken to examine whether organic matter produced by plants is translocated into the subsurface and to different depths depending on the elevation and soil type. The depth profiles within interspaces is expected to show chemistry that varies less with depth. Twelve samples were taken from six other locations at the near surface from 0 to 10 cm, including three plant canopy soils and three interspace soils. Interspace samples were randomly selected at points furthest from shrubs and trees in order to examine soil carbon without plants in proximity. Samples were dried, ground, and sieved before conducting lab experiments.

Table 2. Experimental setup shows soil samples from four elevations, subjected to whether or not there is plant growth and depth level. The values in the table represent the number of replications taken.

Elevation	**Plant Canopy**					**Interspace**				
	Surface	0-10 cm	10-20 cm	20-30 cm	30-40 cm	Surface	0-10 cm	10-20 cm	20-30 cm	30-40 cm
FS-1	3	4	1	1	1	3	4	1	1	1
FS-2	3	4	1	1	1	3	4	1	1	1
FS-3	3	4	1	1	1	3	4	1	1	1

FS-4	3	4	1	1	1	3	4	1	1	1

To determine the elemental composition of the soil samples, energy dispersive X-ray fluorescence (XRF) spectroscopy (Spectro XEPOS XE) was used. XRF is a technique used to determine elemental concentrations within solid materials, such as soils, without chemically altering it. Plastic cups are filled with approximately 2 grams of ground soil and covered with polypropylene film (Chemplex). A 50-watt X-ray tube generates X-rays through each of the samples and are detected by five energy targets that can determine the concentration of elements with masses ranging from sodium to uranium. The analysis chamber is continuously purged with helium gas to minimize X-ray attenuation by other heavier elements found in ambient air. Elemental abundance is then calculated and presented as a percentage based on the X-ray fluorescence intensity produced as a spectra. Elements that are too small to be effectively written as a percentage is recorded in units of $\mu g\ g^{-1}$ (parts per million). Total carbon and nitrogen content of samples were determined using elemental analysis.

Statistical Analyses

XRF data was stratified by field site and further categorized by 'plant' and 'interspace' soils. Due to the small sample size after stratification, nonparametric comparisons were performed to produce significant results when making conclusions on the different field sites. The Wilcoxon Rank Sum analysis was performed to statistically test whether amounts of solid organic C were different between field sites ($\alpha = 0.05$). Furthermore, the same analysis was applied to test whether there was a significant difference between chemical composition of plant canopy soils and interspace soils at each field site. The data consisted of a random sample of observations: $P_1, P_2, \ldots, P_{40}$ from the plant population and $I_1, I_2, \ldots, I_{40}$ from the interspace population. Outliers were omitted from the test as well as figures to compensate for errors in XRF process. Wilcoxon Rank Sum analysis hypotheses tests used in this study include the following:

$$H_o: E(P) = E(I) \quad (1)$$

$$H_a: E(P) \neq E(I) \quad (2)$$

$$H_a: E(P) > E(I) \quad (3)$$

$$H_a: E(P) < E(I) \quad (4)$$

The null hypothesis (1) states that the two centers of the plant and interspace group are the same. The alternative hypotheses (2, 3, 4) state that the plant group is not equal to, greater than, or less than the interspace group, respectively. Tukey's Multiple Comparisons test, also referred to as Tukey's HSD, was performed to identify which mean among a set of means differs from the rest.

To determine whether depth has an effect on chemical composition, we further stratified the plant canopy soils and interspace soils by their respective depth category then plotted the data. The depth categories include the "surface", 0-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm. The concentration of each element was then averaged and plotted as a line graph. It is important to note that the stratified groups have low and unequal sample sizes (refer to Table 2). The x-axis represents the value of concentration (%) of the element and the y-axis represents the cm below the ground surface at which each sample was taken. All data analyses performed for this project was done in the statistical programming language, R (R Core Team, 2020).

Results and Discussion

Soil Carbon Analyses

Total C analysis shows that soil C concentrations increase with increasing elevation using averaged values across all samples collected at each site (Figure 1). Results show a wide range of soil carbon contents, with medians of 0.1694% C at the lowest elevation and 2.280% C at the highest elevation. While a trend can be observed, a statistically significant difference in soil C content was calculated for FS-4 compared to all other sites (Table 3). This increase in solid phase carbon with elevation is likely due to an increase in precipitation along the transect. Though both FS-3 and FS-4 are located within the Santa Rosa Mountains, the forest vegetation is visibly denser along with a thicker O-horizon of forest litter at FS-4 compared to FS-3. This observation is the most likely explanation for the significant difference (greater total soil C content) seen in FS-4 compared to other sites.

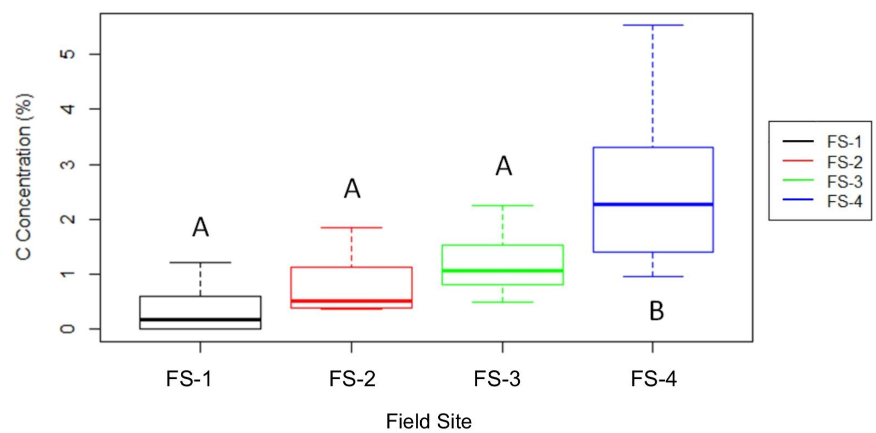

Figure 1. An overview of soil C concentrations (total carbon in solid phase) at each elevation. The box plots labeled 'A' show no significant difference in average C concentrations, while the box plot labeled 'B' does show a significant difference. Outliers are omitted from the figure.

Table 3. Pairwise Comparisons. The highlighted cells represent the field sites that are significantly different from each other (α = 0.05). The "diff" column on the table contains the mean difference between the two groups. The columns "lwr" and "upr" give the 95% confidence

interval of the differences. The "p adj" column gives the p-value of the test after it is adjusted for multiple comparisons.

Pairs	diff	lwr	upr	p adj
FS-2 - FS-1	0.3959132	-0.7369084	1.528735	0.7952902
FS-3 - FS-1	0.7742230	-0.3585987	1.907045	0.2835808
FS-4 - FS-1	2.3930793	1.2602576	3.525901	0.0000024
FS-3 - FS-2	0.3783098	-0.7545119	1.511131	0.8166206
FS-4- FS-2	1.9971661	0.8643444	3.129988	0.0000858
FS-4 - FS-3	1.6188563	0.4860346	2.751678	0.0018872

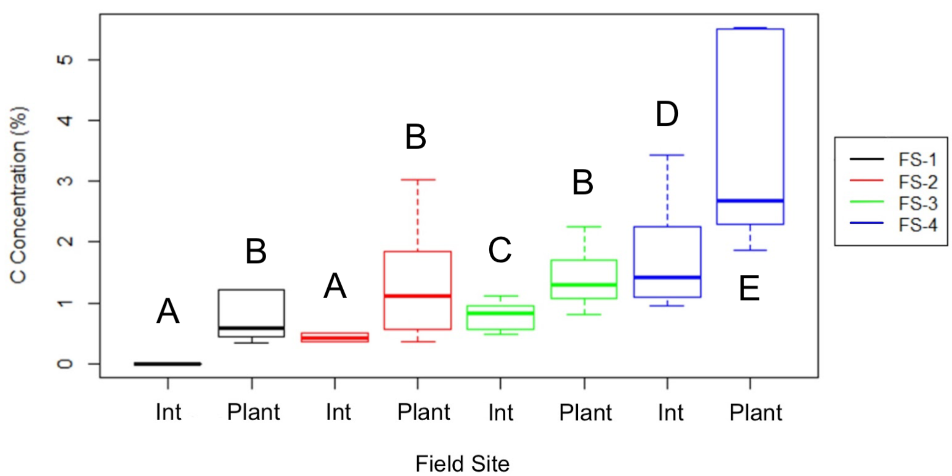

Figure 2. An overview of C concentrations (total carbon in solid phase) in plant canopies (Plant) and interspace (Int) soils at each of the four elevations. Outliers are omitted from the figure. No C data was reported for interspace soils at FS-1 due to C being below the detection limit. For statistical analysis, near zero concentration of C was assumed for FS-1 interspace soils.

When soils are separated between plant and interspace categories, it becomes apparent that average soil C content in bulk soils is clearly driven by higher concentrations found in plant canopy soils. At each elevation, all plant canopy samples contained significantly higher concentrations of C than their interspace counterparts. Interspace soils still show a clear increasing trend with elevation, but is consistently lower than C content in plant canopy soils. Results also show that the source of organic matter distribution is highly spatially heterogeneous at the low elevation desert site (FS-1) where soil carbon is constrained to only contribution from plant materials under plant canopies with a near complete absence of carbon in interspace soils. At FS-1, the soil texture is sandy in interspace soils which has a high infiltration rate. The soils are poorly developed and have poor structure that are not amenable to soil moisture retention. These features lead to high soil infiltration rates that cause the surface soils to remain dry and uninhabitable for microbial communities. These aspects of the lower elevation desert site explain the below detection limit carbon concentrations throughout the interspace soils. With increasing elevation, the contrast between plant canopy and interspace soil carbon content is smaller, showing slightly more homogenous distribution of carbon. This is likely due to litterfall that scatter organic matter more evenly across the forest floor and more developed soils that are of finer texture that can retain the rainfall contributed soil moisture more evenly in spaces between plants.

Pairwise comparison of plant canopy soil carbon content shows that only the highest elevation had a significantly different concentration (Table 3). This result demonstrates that regardless of precipitation rate and type of vegetation type, a comparable concentration of carbon can be accumulated under plant canopies. As mentioned above, the significantly different (higher) concentration of C found at the highest elevation is likely due to higher litter contribution and finer soil texture. Interestingly, pairwise comparison of interspace soils across sites shows the same result (i.e. highest elevation site FS-4 has significantly higher concentration of carbon than interspace soils at other sites) with the addition of a significant difference in C content between FS-1 and FS-3 (Table 4). This likely due to the large contrast in contribution of soil C from the surrounding vegetation; FS-3 is the first of the two higher elevation forest sites where forest litter begins to contribute to the interspace soil carbon. Therefore, we interpret this result to reveal the difference in plant type which is able to disperse plant-derived organic matter in different ways, namely a smaller radius around shorter desert shrubs at FS-1 versus higher radius of litter distribution from trees at FS-3 (and FS-4).

Plant derived organic matter provides nutrients that fuel microbial growth. Both plant root and microbial exudates have been shown to increase soil aggregation by acting as "glue" that adhere particles together. Greater soil aggregation increases soil moisture retention which in turn further supports microbial growth. This feedback effect leads to localized accumulation of organic matter which likely explains the significantly higher concentrations of C under plant canopies consistently across all sites.

Table 4. **Plant Canopy Pairwise Comparisons.** The highlighted cells represent the plant canopy samples that are significantly different from each other at each field site ($\alpha = 0.05$).

Pairs	diff	lwr	upr	p adj
FS-2 - FS-1	0.3299284	-1.5863469	2.246204	0.9664716
FS-3 - FS-1	0.5345293	-1.3817461	2.450805	0.8755273
FS-4 - FS-1	2.8711587	0.9548833	4.787434	0.001488
FS-3 - FS-2	0.2046009	-1.7116745	2.120876	0.9915699
FS-4- FS-2	2.5412302	0.6249549	4.457506	0.0054415
FS-4 - FS-3	2.3366294	0.420354	4.252905	0.0117072

Table 5. Interspace Pairwise Comparisons. The highlighted cells represent the interspace samples that are significantly different from each other at each field site (α = 0.05).

Pairs	diff	lwr	upr	p adj
FS-2 - FS-1	0.4618981	-0.39976973	1.323566	0.4812449
FS-3- FS-1	1.0139167	0.15224892	1.875585	0.0157455
FS-4 - FS-1	1.915	1.0533322	2.776668	0.0000042
FS-3- FS-2	0.5520187	-0.30964915	1.413686	0.3257885
FS-4- FS-2	1.4531019	0.59143413	2.31477	0.0003389
FS-4 - FS-3	0.9010833	0.03941548	1.762751	0.037525

Soil Elemental composition and chemical extractions

Table 6 displays the strength of variation in soil elemental composition (elements aside from carbon) between plant canopy and interspace soils at each elevation, as well as the aggregated data regardless of elevation. Smaller p-values indicate stronger evidence that our hypotheses are correct. As predicted, a clear trend can be seen in the C concentration across sites; each sampling site shows that C concentrations in plant canopy soils are significantly greater than interspace soils, and as elevation increases from FS-1, the disparity decreases. Because of the low p-values, we can be more confident that there is a significant difference between the distributions of plant canopy and interspace soils. At FS-1, the p-value for C is 6.39E-05, indicating a very strong difference between plant and interspace. These values support our previous figures that show a greater carbon content surrounding plant islands versus where there is not one.

Table 6 . *p*-values indicate a significant difference in the distribution of each macroelement listed between the plant canopy soils and interspace soils at each elevation. The "All" column represents the aggregated data of all the samples collected from each field site. Significant p-values are ones that are < α= 0.05. P-values highlighted yellow indicate that the median of plant canopy soils are less than that of interspace soils. Values highlighted green indicate that the median of plant canopy soils are greater than that of interspace soils. Blank cells indicate that there was insufficient evidence to support there to be a significant difference between the plant canopy and interspace soils.

Element	FS-1	FS-2	FS-3	FS-4	All
Na	0.0147			0.0442	
Mg	0.0115	0.0446			
Al	0.0052	0.0147			0.031
Si	0.0376	0.0147			
P		0.0376			
S	1.08E-05	0.0001	0.0115	0.0262	1.56E-09
Cl	0.0262	0.0446		0.0446	0.0395
Ca	0.0446	0.0052			
Sc	7.58E-05				0.0095
Fe				0.0444	0.0257
Ni		0.0443			
Cu	0.0444				
Zn				0.0185	
Br	0.0007	0.0245			0.0047
C	6.39E-05	0.009	0.0115	0.0101	5.91E-05
N	6.39E-05		0.0005	0.0288	1.49E-05

Similarly, when comparing elemental composition between soils from the two sites at lower elevations, we can see that there are more contrasts compared to the higher elevations. Magnesium (Mg), aluminum (Al), and silicon (Si) for example are more concentrated in the interspace regions than under plant canopies at FS-1 and FS-2; however, there is no evidence to show that there is such a difference at FS-3 and FS-4, with the exception of Al concentrations being greater in the plant canopy soils at FS-4. The relatively higher concentration of Al at the high elevations is likely due to higher weathering and acid contribution to soils from litter deposition which facilitates Si removal from primary silicates. Overall, these results support our hypothesis of greater homogeneity in soil composition between the plant canopy and interspace soils at higher elevations. As briefly mentioned above, elemental distribution at higher elevations is facilitated by several factors like rainfall, snowmelt, pine root systems, nutrient uptake, and organic matter scattered evenly over the soil surface as pine needles.

Interaction between depth and elevation

The depth profiles show a similar pattern of C accumulation in near surface soils as elevation increases compared to previous figures. The Figure 3 shows that there is little variation in C content with depth at FS-1, FS-2, and FS-3. At FS-4, however, C concentrations are highest in surface soils and decrease rapidly with depth. This observation can be attributed to two factors: 1) forest litter contributes significantly to the top O-horizon and part of A-horizon carbon concentrations whereas no such source is available at other sites and 2) water infiltration is inhibited more so at FS-4 because of more clayey soil texture, which restricts movement of C from the surface to deeper layers.

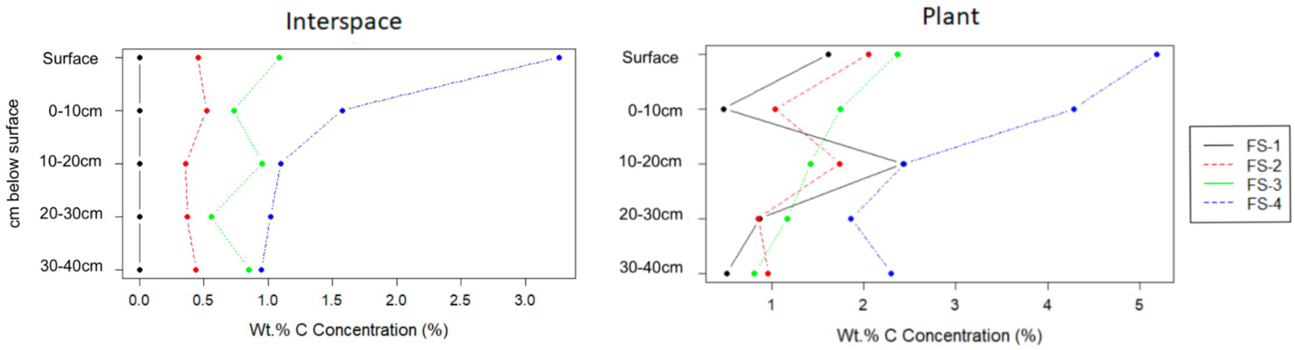

Figure 3. Each point represents the average concentration of C wt% in the soil at each depth from the surface at each sample site. Sites are indicated by the following colors: FS-1 (black), FS-2 (red), FS-3 (green), and FS-4 (blue). Samples analyzed at each depth varies as indicated in Table 2. Near zero concentration of C was assumed for FS-1 interspace soils.

Due to the lack of data when assessing the effects of the depth factor, no statistically significant results can be concluded; however, based on the results shown in Figure 3, further investigation is warranted. We can qualitatively assess that there appears to be little difference in C concentrations with depth at the three lower elevation sites. This is likely because entisols are the dominant soil order in the region, which is characterized by poor development and lack of differentiation between horizons. The poor development is due to low precipitation and organic matter input in the region. There is a general trend of greater noise with depth in C concentrations measured under plant canopies across all elevations. This may be due to variation in infiltration rate across the sites influenced by soil aggregation, plant species, and organic matter composition.

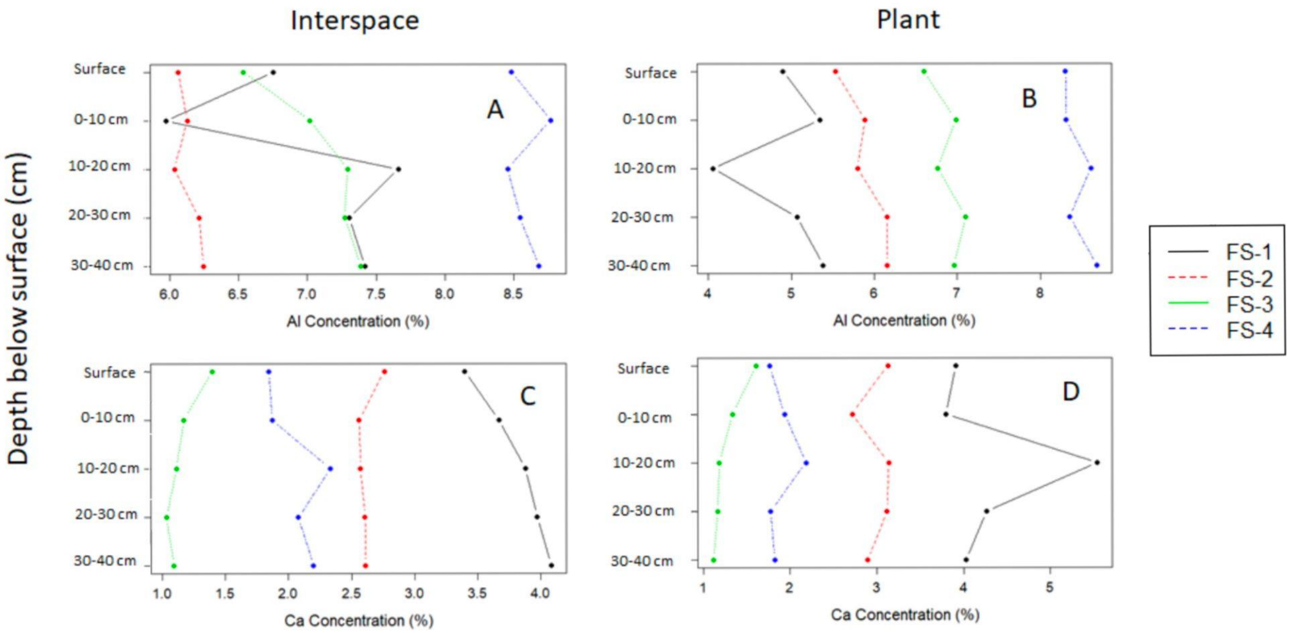

Figure 4. Each point represents the average concentration (%) of Al and Ca in the soil at each depth from the surface at each sample site. Sites are indicated by the following colors: FS-1 (black), FS-2 (red), FS-3 (green), and FS-4 (blue). Samples analyzed at each depth varies as indicated in Table 2.

In Figures 4B through 4D, there is a clear distinction of elemental concentration between each of the four sites shown by the isolated line segments. And because each of those line segments are more notably vertical, it indicates that there is a low variation in soil concentrations with depth. Figure 4A shows a similar pattern with the exception of the FS-1 line segment. It is also notable that the third highest elevation, FS-3, has a consistently lower concentration of Ca than the rest of the elevation sites. There were a number of other chemical elements that showed the same consistently lower concentration at FS-3 relative to other sites. Further investigation is required to understand why FS-3 had particularly distinct chemistry that did not follow the trend of the other elevations.

We chose to focus on displaying the results from Ca and Al analysis because of their known interactions with C sequestration. Ca ions can contribute to C sequestration through a mechanism known as ion bridging where positively charged divalent ions such as Ca^{2+} and Mg^{2+} can contribute to C stabilization in the form of SOM. This stabilization of C as SOM can prevent microbes from being able to easily remove the carbon from SOM for respiration, inhibiting C flux into the atmosphere as CO_2. Therefore, possible implications of the higher Ca and Al concentrations at these sites would be that more C can be sequestered. Lastly, Ca concentrations are highest at the lowest elevation site due to low precipitation which leads to salt accumulation. At FS-1, because of the low carbon content measured in those soils, it is unlikely the Ca in those soils are playing a significant role in ion bridging and rather has accumulated due to desiccation.

Poorly crystalline alumino-silicates, particularly allophane, form under highly weathered conditions (Al/Si = 2) and can contribute to carbon sequestration through co-precipitation, where dissolved Al^{3+} ions undergoing hydrolysis incorporate organic carbon molecules into the mineral structure of the resultant oxide precipitate. The Al oxides then acts as a shell around the SOM that physically prevents microbes from accessing the organic carbon needed for microbial respiration. This is another possible pathway for C sequestration.

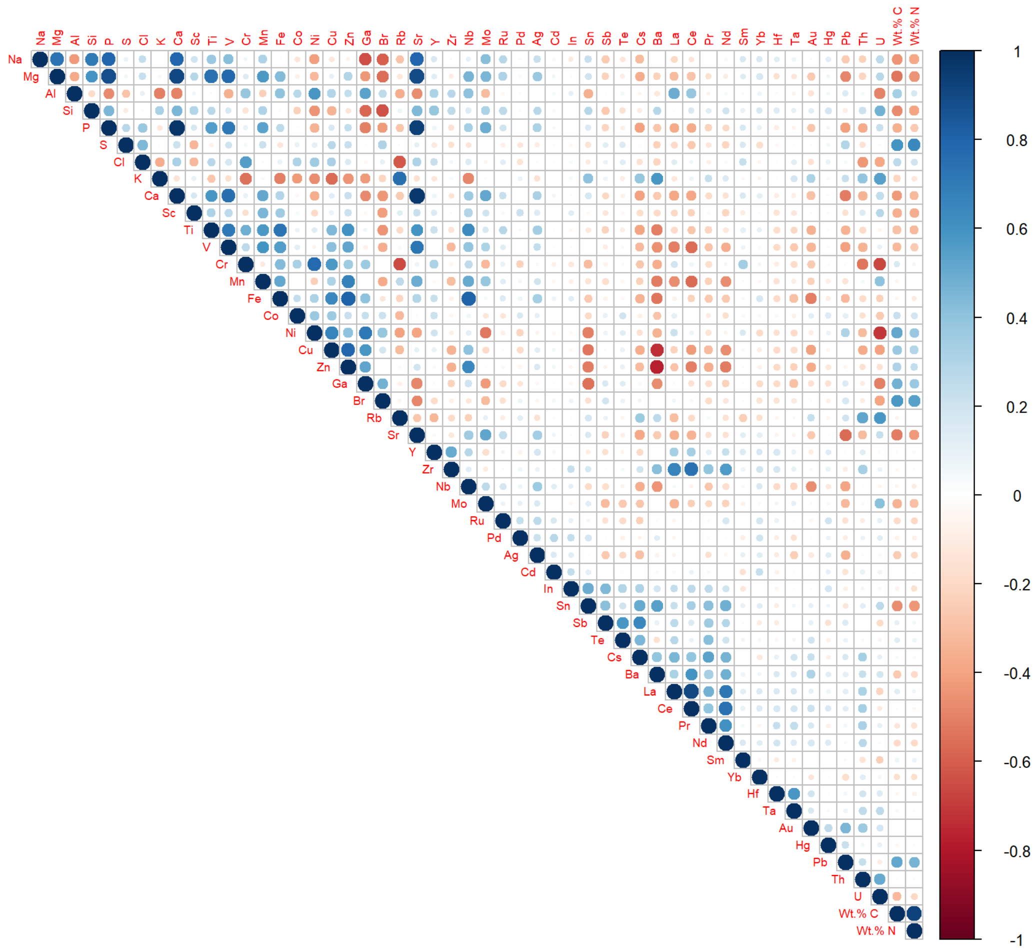

Figure 5. The concentration of each element in the soil samples were compared to each other. The strength of the Spearman correlation coefficients (ρ) are given by the color scale ranging from -1 to 1. A (1) on the scale (dark blue) shows a perfectly linear relationship and a (-1) on the scale (red dots) shows a perfectly negative relationship.

Figure 5 shows the correlation of all elemental concentrations measured through XRF from samples across all sides. This analysis provides an exploratory method to discover whether other elements may have an influence on C and metals cycling through the various ecosystems. The darker the color on the correlation matrix the stronger relationship between the two elements along the mountain transect. Calcium and strontium (Sr), for example, have a strong positive correlation with $\rho = 0.96$. Because we know that Ca has potential to contribute to C sequestration in soils, further research would be helpful to know if this relationship is significant.

Conclusions

The work completed over the past two years involved gathering clean and manageable data from a range of different soils, to explore the effects of precipitation, plant growth, depth, topography, and other climate factors that affect C dynamics, which therefore affect climate change. Our results clearly show that plants contribute to localized organic matter heterogeneity, which leads us to support that plant canopy soils are hotspots for microbial activity that both helps accumulate C while also increasing C flux from respiration. It would be interesting to investigate these two fighting mechanisms to see which direction the net change is facing. That way we can have better insight to help us predict how soils and C cycling will change in certain conditions over time, especially during the rapid increase of global warming.

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