Succession and soil development of Pleistocene glacial remnants in a sagebrush steppe

Sophie Borison¹, Charlotte Bruggeman², and Sam Steuart³

¹University of California, Davis; ²University of California, San Diego; ³University of California, Santa Barbara

ABSTRACT

Following glacial retreat, soils and plant communities often undergo drastic changes as succession occurs. As bare soil is colonized, the plant community shifts and drives future succession patterns. The aim of this study was to assess the modern stage of succession on different-aged glaciated areas by sampling a Tahoe-era glaciation (130 to 70 ka) lateral moraine, a Tioga-era glaciation (28 to 13 ka) lateral moraine, a flat which the Tahoe-era glacier covered, and a flat that remained unglaciated during the most recent glacial cycles. The physical and chemical soil properties were assessed along with the vegetation community and the phenological differences of a common indicator species, rabbitbrush. There were more coarse particles, soil organic matter, and rock cover on the Tioga-era moraine than the Tahoe-era moraine, as well as more grass cover on the Tioga-era moraine than any other test site. Additionally, rabbitbrush was smaller on the moraines compared to the flats and smaller on the Tioga-era moraine than the Tahoe-era moraine. We attribute these findings to the time spent since glaciation undergoing physical changes, such as weathering and erosion, and the ongoing changes in modern succession patterns as the shifting vegetation community continues to impact and shape the soil properties. The unpredictable variation in these patterns today, thousands of years after glacial retreat, reflect the long-lasting complexity of changing disturbed landscapes.

Keywords: post-glacial retreat, succession, soil formation, soil organic matter, lateral moraine

INTRODUCTION

As glaciers retreat over time, the rocky terrain they leave behind undergoes ecological succession, as it is progressively colonized by changing plant communities. The development of different dominant vegetation types through time is driven by more than just the amount of time the rocks have weathered into soils; the establishing plants often drive changes as well (Crocker and Dickson 1957). Their unique characteristics and functions change the physical and chemical properties of the soil. This can improve soil properties such as the nutrient content and water retention,
thereby facilitating the establishment of different types of plants over time and driving the classic primary succession patterns (Crocker and Dickson 1957). The vegetation community is further influenced by the physical characteristics of an area. For example, the presence of large rocks and boulders can promote the growth of plants by providing sheltered locations for seedlings during recruitment and establishment stages (Frenot et al. 1998, Jumpponen 1999, Niederfriniger Schlag and Erschbamer 2000, Raffl et al. 2006). Initially, plant community succession occurs rapidly, and diversity increases quickly (Raffl et al., 2006). However, local diversity typically plateaus after approximately 40–50 years, a trend observed across different ecosystems and continents (Raffl et al., 2006, Helm et al. 1999). These patterns of succession are well-studied, especially on short-term time scales on glaciers that are currently melting or have recently vanished. However, fewer studies have been done examining the plant communities on the glacial landforms created during older glacial retreats (Raffl et al. 2006).

Workers recently found that the rates of soil organic matter (SOM) accretion accelerated through the early stages of succession (Vilmundardóttir et al. 2014). SOM is composed of organic molecules, including those released from living plant and microbial cells (such as extracellular enzymes) and more complex debris from plant, animal and microbial remains in various states of decomposition due to biotic and abiotic processes (Kleber et al. 2007). These compounds play important roles as plant nutrients, soil stabilizers, and in the exchange of greenhouse gases at the soil surface-atmosphere interface (Grandy and Neff 2008). Soils are the largest terrestrial carbon pool, containing an estimated 1,500–2,000 Pg of carbon globally (Grandy and Neff 2008). This is more than double the size of the atmospheric carbon pool of approximately 770 Pg, leading to speculation that anthropogenic climate change may be mitigated through relatively small increases in the global soil carbon storage (Grandy and Neff 2008). Our study is tangent but related to this emerging field.

In this study, we examined the process of soil formation including SOM accumulation in relation to plant succession in two lateral moraines and two flats of Tahoe and Tioga glaciers in the Eastern Sierra Nevada sagebrush steppe. The aim of this study was to examine the physical and chemical properties of glacial remnants of different ages along with their corresponding plant communities and an indicator species to better understand the modern stage of succession reached in these areas on both the biotic and abiotic levels. In doing so we sought to unify the more physical fields of geology/soil science with the biological field of plant ecology. The primary objectives were to 1) determine the differences in physical soil structure, 2) determine the differences in the chemical properties of soil, and 3) examine the differences in the vegetation community across different areas previously impacted by glaciation, especially through the lens of our indicator species, rabbitbrush. We expected that the Tioga-era moraine would have the highest percentage of coarse particles due to shorter exposure to weathering and erosion (Sharp 1969). We also expected the Tioga-era moraine to have the lowest percent SOM due to plants having been established there more recently. We predicted that the pH of the soil on the Tahoe-era moraine
would be lower than on the Tioga-era moraine as a result of increased SOM. Lastly, we expected to see a difference in the plant community due to the changes predicted to be observed in the soil. Specifically, we expected to see a greater proportion of exposed soil, rock, and grasses on the Tioga-era moraine due to lower soil quality associated with coarse particle size, and a more diverse community of plants on the Tahoe-era moraine due to aspects of higher soil quality, such as increased water retention associated with finer particles.

METHODS

2.1 Study site

Our study was undertaken during the end of July through the beginning of August of 2019 at the Sierra Nevada Aquatic Research Laboratory (SNARL), located at the base of the Eastern Sierra near Mammoth Lakes, California. The area is located at an elevation of ~2100 m and is characterized by a Great Basin sagebrush steppe habitat and a desert climate with high levels of precipitation in the winter and low levels in the summer. Specifically, our four study areas consisted of a lateral moraine belonging to a Tahoe-era (130–70 ka) glacier (hereafter referred to as the old moraine, 37°36'27"N 118°49'11"W), a lateral moraine belonging to a Tioga-era (28–13 ka) glacier (hereafter referred to as the young moraine, 37°36'04"N 118°50'39"W), a flat area where the Tahoe-era glacier sat (Tobacco Flats, 37°36'48"N 118°48'59"W), and a non-glaciated flat area (37°36'48"N 118°48'59"W) used for comparison (Figure 1). We will refer to these sites by the order in which soil was exposed: young moraine, old moraine, Tobacco Flats, and flat non-glaciated area.

![Figure 1: Study site locations.](image)

Sites studied were the old moraine (37°36'27"N 118°49'11"W), young moraine (37°36'04"N 118°50'39"W), Tobacco Flat (37°36'48"N 118°48'59"W), and a flat non-glaciated area (37°36'48"N 118°48'59"W).
2.2 Transects

In order to test our hypotheses, we set up four 50 m transects at each of our sites. We began our transects by taking a number of steps from our last transect, generated using a random number generator. We placed our transects at similar elevations at the top of the moraines in order to account for differences in slope. Along each of our transects we collected soil and vegetation data.

2.3 Soil particle size relationships

We took soil samples at ten-meter intervals along four randomly selected 50 m transects per site for a total of 24 samples. Using a hand trowel, we dug small holes approximately 10 cm in diameter until we reached the depth to refusal (DTR). We imposed a cutoff maximum depth of 20 cm in order to keep our samples to a manageable size and allow comparison between similar soil horizons. Further, we excluded rocks greater than 0.25 kg from our samples. We sieved the soil samples into three fractions; coarse (>4 mm), medium (4 mm–0.5 mm), and fine (<0.5 mm). We chose these size categories to facilitate comparison to Sharp (1969), who used three similar fractions; coarse (>5 mm), medium (5 mm–0.8 mm), and fine (<0.8 mm) at the same study site. We then weighed each fraction.

All statistical tests were performed using JMP v14.0. We conducted ANOVAs and Tukey Kramer tests on the effect of location on DTR, and percent coarse, medium and fine particle sizes.

2.4 pH

To measure pH, we consolidated the fine (<63 μm) fractions from the six sampling sites along each transect into one sample which we thoroughly mixed to get one representative pH for the entire transect (Sharp 1969). Then we mixed these samples with water in a 1:1 ratio and measured the pH using an Oakton® pH Benchtop pH Meter. We conducted an ANOVA on the effect of location on pH.

2.5 Soil organic matter

We sieved all six soil samples from each transect through a 2 mm screen to exclude gravel and larger particles following the methods of Rowell and Coetzee (2003). Then we combined them to make a single sample per transect. We thoroughly mixed the samples together and then took a smaller sample of approximately 20 g (mean=19.71 g) which we dried overnight at 60±5 °C. We had already removed the finest fraction of the soil (<63 μm) for the pH measurement. This particle size contributes most to the binding of water (Wang et al., 2011). Furthermore, the proportion of particles less than 63 microns was between 1–2 percent per transect on average and did not differ between the moraines nor between the flats, thereby allowing confidence in comparing our results between the two site types.

Next, we took the mass of the soil and then combusted it in a kiln at moderate temperatures between 360 °C and 450 °C for three hours, again based closely on the methods of Rowell and Coetzee (2003). We took the mass of the burned soil to determine how much of the original mass was SOM which combusted. Finally, we
performed an ANOVA and a Tukey Kramer test on the effect of location on the percent SOM.

2.6 Vegetation sampling

We sampled ground cover at the four transect locations. At each study location, we surveyed the same four, randomly placed 50 m transects used in the soil survey. We surveyed 44 points in each area for a total of 176 vegetation surveys across the entire study. Every 5 m, we determined the percent ground cover in a 0.25 m² quadrat, based on the following categories: exposed soil, exposed rock, bitterbrush (*Purshia tridentata*), sagebrush, horsebrush (*Tetradymia canescens*), rabbitbrush (*Chrysothammus viscidiflorus*), grasses, forbs, shrubs, and dead vegetation. We used a one-way ANOVA and Tukey Kramer post-hoc analysis to test for differences in percent ground cover among the four different areas. Data was log transformed in order to meet the normal assumption for the ANOVA test.

2.7 Rabbitbrush sampling

In order to hone in on the specific effects of soil properties on vegetation, we chose rabbitbrush (*Chrysothammus viscidiflorus*), one of the three dominant shrubs in the sagebrush steppe, as an indicator species. Soil moisture and nitrogen content are co-limiting factors for shrub species in the sagebrush steppe, suggesting that this shrub can serve as an indicator of soil quality and SOM (Inouye 2006). Additionally, rabbitbrush reaches peak growth before flowering in mid-August, meaning we can use its size to gain insight into soil properties (Young and Evans 1974).

In order to test our hypotheses, we sampled 12 rabbitbrush plants at each of our four sites, separate from the transects. We used a random number generator to decide the number of steps to take before we selected a rabbitbrush plant to sample. We measured height, length, and width of each plant using a meter stick in order to calculate volume. We performed two t-tests to test the difference in the volume of individual rabbitbrush plants between the flats and moraines and between the young and old moraine sites.

RESULTS

3.1 Soil particle size relationships

The DTR is very different from site to site (*n*=96, *F*=30.9, *p*=0.0001, Figure 2). Tobacco Flat had the deepest soils, the flat non-glaciated site had the second deepest; the young moraine had the shallowest soil, and the old moraine overlapped with the flat non-glaciated site and the young moraine.

There was a significant difference in the coarse fraction among sites (*n*=96, *F*=3.5, *p*=0.012) mostly driven by differences between the old and young moraines (Figure 3A). There was also a difference in the medium fraction among sites (*n*=96, *F*=13.8, *p*=0.0001) as the old moraine had a greater fraction than the young moraine (Figure 3A). The fraction of fine material did not vary between old and young moraines or between the flats, but the old moraine did have a higher percent of fine particles than Tobacco Flat (*n*=96, *F*=3.7, *p*=0.014, Figure 3). In contrast, for the flat sites, neither the percent coarse nor fine particle sizes differed, but the percent of medium particles was far greater at Tobacco Flat (*n*=96, *F*=13.8, *p*=0.0001, Figure 3B).
Figure 2: Soil depths at each site. We dug holes until refusal, or the point at which large rocks prevented us from digging further. We dug six holes per transect, or 24 holes per site. We imposed a maximum cutoff depth of 20 cm. The young moraine had the shallowest soil, the flat non-glaciated site was intermediate in depth, and Tobacco Flat had the deepest soils (*n*=96, *F*=30.9, *p*=0.0001). The old moraine was intermediate between the young moraine and the flat non-glaciated site but did not differ significantly from either.

Figure 3: Proportion of coarse, medium, and fine particles per site for A) the moraines and B) the flats. We sieved the soil samples into three different fractions: coarse (>4 mm), medium (0.5–4 mm), and fine (<0.5 mm). There was a significant difference in coarse fraction among sites (*n*=96, *F*=3.5, *p*=0.012), mostly driven by differences between the young and old moraines. We also found a difference in the ratios of the medium particle size between sites (*n*=96, *F*=13.8, *p*=0.0001). The largest fraction of medium sized particles was at Tobacco Flat, an intermediate amount on the old moraine, and the least on the young moraine. The flat non-glaciated site overlapped with the two moraines. Lastly, we detected a difference in the ratios of fine particle sizes (*n*=96, *F*=3.7, *p*=0.014). The old moraine had the highest percentage of fine particles, Tobacco Flat the least, and the other sites overlapped with both.

Figure 4: Proportion of soil organic matter per site. We used a loss on ignition method to determine %SOM per transect. We combined all 6 samples from each transect and excluded particles greater than 2 mm based on the methods of Rowell and Coetzee (2003). Particles less than 0.63 mm were used to determine pH and not included in the SOM value, but consisted of only 1–2% of the total sample. We thoroughly mixed the samples together, took a subsample of approximately 20 g (mean=19.71 g), and dried it overnight at 60±5 °C. Next, we took the mass of the soil and then combusted it in a kiln between 360°C and 450°C for three hours (Rowell and Coetzee 2003). We took the mass of the burned soil to determine how much of the original mass was SOM. The %SOM was far greater on the new moraine than it was at any other site (*n*=16, *F*=42.4, *p*=0.0001). Other sites did not differ statistically.
Table 1: One-way ANOVA statistics for the effect of site on percent ground cover type. Variables were log transformed in order to meet the ANOVA assumption of normality. Asterisks represent significant effects of site. Asterisks indicate significant treatment effects (*p<0.10; **p<0.05; ***p<0.001).

<table>
<thead>
<tr>
<th>Ground Cover Type</th>
<th>N</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil</td>
<td>147</td>
<td>1.30</td>
</tr>
<tr>
<td>Forbes</td>
<td>19</td>
<td>0.87</td>
</tr>
<tr>
<td>Horsebrush</td>
<td>15</td>
<td>0.11</td>
</tr>
<tr>
<td>Rabbitbrush</td>
<td>5</td>
<td>0.56</td>
</tr>
<tr>
<td>Dead vegetation</td>
<td>80</td>
<td>10.66**</td>
</tr>
<tr>
<td>Rock</td>
<td>48</td>
<td>4.15**</td>
</tr>
<tr>
<td>Bitterbrush</td>
<td>68</td>
<td>7.15***</td>
</tr>
<tr>
<td>Grass</td>
<td>101</td>
<td>2.36*</td>
</tr>
<tr>
<td>Sagebrush</td>
<td>69</td>
<td>3.08*</td>
</tr>
<tr>
<td>Shrubs</td>
<td>14</td>
<td></td>
</tr>
</tbody>
</table>

3.2 pH

Soil pH did not differ among the four sites (n=16, F=1.8, p=0.2). However, the range of the pH was greatest at Tobacco Flat (5.86–6.51) and least at the old moraine (6.12–6.27). The flat non-glaciated site (6.20–6.51) and the young moraine (6.16–6.55) were intermediate in terms of pH variation as expressed by the range.

3.3 Soil organic matter

SOM on the new moraine was greater than the SOM at the other three sites (n=16, F=42.4, p=0.0001, Figure 4). The mean %SOM on the young moraine was 17.4%, while on the old moraine, Tobacco Flat and the flat non-glaciated site it was 7.0%, 5.6% and 5.1%, respectively.

Figure 5: Effect of site on percent rock cover. The young moraine had more rock cover than the young moraine (n=48, F=10.86, p=0.0019). Percent grass as ground cover was determined by using a quadrat at each sampling site. Error bars represent ±1 S.E.

Figure 6: Effect of site on percent grass cover. The young moraine had more grass cover than any of the other sites (n=101, F=7.15, p=0.0002). Percent rock as ground cover was determined by using a quadrat at each sampling site. Error bars represent ±1 S.E.
3.5 Rabbitbrush

After binning moraine sites and flat sites, we found rabbitbrush volume was smaller in the moraines than the flats (n=48, F=17.41, p=0.0001, Figure 7A). Furthermore, when analyzing individual sites, we found rabbitbrush volume was smaller on the young moraine than the old moraine (n=24, F=4.58, p=0.0436, Figure 7B).

![Chart showing rabbitbrush volume comparison between flat and moraine sites](chart.png)

**Figure 7:** Effect of site A) and site type B) on rabbitbrush volume. We measured the width, height, and length in order to calculate the volume of 12 rabbitbrush plants at each of our 4 sites. Rabbitbrush had less volume in the moraines than the flats (n=48, F=17.41 p=0.0001). Rabbitbrush had less volume in the young moraine than the old moraine (n=24, F=4.58 p=0.0436). Error bars represent ± 1 S.E.

DISCUSSION

4.1 Soil particle size relationships

As predicted, we found the largest soil particles on the young moraine, matching the pattern reported by Sharp (1969). However, our differences were not as dramatic, especially with regards to the coarse fraction. He reported a coarse fraction of 78% for the young moraine, and an average coarse fraction of 36% for the old moraine. Despite our cutoff for the coarse fraction being one millimeter less than his, (4 mm as opposed to 5 mm), we found that the coarse fraction for the young and old moraine, respectively, were 31.8% and 21.2%. This discrepancy is likely due to methodological differences; Sharp dug 13–15 cm wide holes to a depth of 30 cm, while we dug holes about 10 cm in diameter to a cutoff of 20 cm deep. He mentions having avoided large rocks, but there is no indication of his having excluded rocks above a certain size. Furthermore, he only dug one sample hole on the young moraine, which brings this data into question, particularly since we found the highest variability in soil composition on the young moraine (Figure 3A).

We anticipated that the flat non-glaciated area could be used as a control against Tobacco Flat, which was glaciated during the Tahoe glaciation, creating the old moraine. However, though we found a greater percentage of medium sized particles at Tobacco Flat, our results do not indicate a clear cause of this difference. There are too many confounding factors influencing the soils and vegetation at these sites to allow for a clear comparison. It is likely that the far larger percentage of medium particle size found at Tobacco Flat is due to erosion from McGee Mountain and the old moraine, which flank Tobacco Flat on both sides. The erosion probably explains why the DTR is much greater at Tobacco Flat than at the other sites. In addition, based on our observations there seems to be considerably more grazing impact at Tobacco Flat as compared to the
non-glaciated flat site. Furthermore, Tobacco Flat has a steeper gradient, and the close proximity to the slopes of McGee and the old moraine could lead to increased runoff transporting out fine sediments. Soils weathered from glacial till on flat areas tend to be highly variable and spatially heterogenous, making it difficult to make conclusions about soil composition. Similarly, a study on a glacial retreat in Iceland found areas ranging from fine silts and clays on the sandur plains to areas with larger fluvioglacial sands and gravels all interspersed with glacial till on the same outwash plain between the glacier and the sea (Boulton and Dent 1974).

4.2 pH

We predicted that the old moraine would have more acidic soils based on Sharp’s (1969) observations. However, we did not find a difference in pH between any of our sites. We may have found different results from Sharp (1969) because we homogenized the soil samples from each transect by mixing them together instead of testing each sample individually. A recent study found that manure from cattle grazing led to increased acidity in the absence of inorganic nitrogen fertilizer application (Clegg 2006). The greater variability in pH at Tobacco Flat may thus have been caused by the manure from the cows, which seem to be more prevalent at this site.

4.3 Soil organic matter

Our hypothesis that SOM would be greater in the older soils was not supported by our data. Instead, the youngest soil (which has only been exposed approximately 20,000 years—a short period of time for soil formation), had by far the highest percent SOM by mass. Soil from the young moraine had around three times as much SOM relative to the older moraine. This finding is supported by a recent study which found that soil organic carbon, which is intimately coupled to SOM, decreased with increasing soil depth (Liu et al. 2015). We believe that this pattern is best explained by the observation that there is less soil on the young moraine, as shown by lower DTR values, but that the plant density is the same between moraines. It takes only around 40–50 years for local plant diversity to stabilize, which has been observed across different continents, climates and ecosystems (Raffl et al. 2006). Thus, there is less soil, but the same amount of plants dropping detritus such as dead leaves on the young moraine. Further, the percent cover by grasses on the young moraine is higher, and grasses increase SOM by seasonal root die back (Marshall et al. 2016).

4.4 Vegetation and ground cover

The differences in rock, bitterbrush, and grass ground cover between our sites, supports our hypothesis that there would be differences in vegetation communities between areas of different ages. Overall, we found that the density of the vegetation did not differ among these areas, nor were there many differences in the community compositions. Only some vegetation types (i.e. grass) differed between sites. The finding that the young moraine had more grass cover than any of the other sites brings forward an intriguing relationship between the plant community and the SOM of the site. Although further studies would need to be done at these sites, it is possible
that the increased presence of grass drives the increase in SOM. Studies have shown that both annual and perennial grasses increase SOM and moisture retention on both short and long-term scales (Ekwue 1990, Low 1954, Williams and Cooke 1961). This could explain the observed increases in both SOM and grass cover on the young moraine. This increase in SOM may also be driving changes in the composition of the soil horizons, which could be further studied in the future (Leinweber et al. 1996). In terms of rock cover, we found more exposed rock on the young moraine compared to the old moraine. This makes sense in terms of weathering and erosion, which has had little time to progress since the Tioga-era (Blackwelder 1929). However, a study by Birkeland (1964) concluded that weathering in Tahoe-era and Tioga-era moraines is approximately the same. Although, this may be due to differences in the landscape and environment, as these findings were found in the North Lake Tahoe area, which differs notably from the Eastern Sierra in that the former is characterized by a coniferous forest habitat versus the sagebrush steppe (Birkeland 1964).

4.5 Rabbitbrush

We expected rabbitbrush to be more voluminous in the young moraine because it had the most soil organic matter, which is a major source of nitrogen (Inouye 2006). However, rabbitbrush was actually least voluminous there, so soil moisture, which covaries with particle size, may be the main driver of rabbitbrush volume on the moraines (Cosby et. al 1984).

The difference in rabbitbrush size between moraine and flat areas can be attributed to differences in drainage properties between the flats and moraines (Burt and Butcher 1985). However, because rabbitbrush size also differs between the young moraine and old moraine, where drainage properties are relatively the same, these differences in size cannot solely be attributed to differences in topography. Instead, the differences in rabbitbrush size between the young and old moraines can be attributed to differences in soil particle size. This is corroborated by the results of our soil research. The young moraine had the most coarse particles, meaning it has the least ability to hold water. Coarse particles drain water faster, and rabbitbrush size is largely determined by soil moisture, so these coarse particles might mean drier soil, and smaller rabbitbrush (Craul 1985, Inouye 2006).

While succession can take tens of thousands of years, we still see differences in the physical soil properties and vegetation communities today. Even so many years later, the succession patterns remain unpredictable across different aged glacial remnants, which invites further studies into modern vegetation and soil changes on previously disturbed landscapes.

ACKNOWLEDGMENTS

We would like to thank Pralada Papper, Krikor Andonian and Tim Miller for their insightful edits. This work was performed at the University of California Natural Reserve System’s Sierra Nevada Aquatic Research Laboratory, doi:10.21973/N3966F. Lastly, thanks to Josh Schimel for taking the time to advise us.
REFERENCES


Niederfriniger Schlag, R., and B. Erschbamer. 2000. Germination and establishment of seedlings on a...


