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Abstract

The Pacific Northwest, a region known for mesic coniferous forests, is also home to scattered prairies, which have been maintained by a combination of xeric site conditions and anthropogenic fires. These prairies, which existed for thousands of years, have been reduced to 2-4% of their historical extent over the past two centuries due to urban development, agriculture, and forest encroachment. We used soil properties, including organic matter concentration, black carbon concentration, proportion of large black carbon particles and moist color, to determine the historical location of prairie-forest ecotones at Mima Mounds and American Camp prairies. Based on these parameters, we conclude that Mima prairie historically extended 50 m north and 300 m east of the current ecotone. In contrast, at American Camp all sampled areas that are currently forested appear to have been grassland at some time in the past. Soils can provide an effective means of determining historical prairie boundaries.

Introduction

The Pacific Northwest, a region known for mesic coniferous forests, is also home to prairies that occur sporadically throughout the area. These prairie ecosystems have been maintained by a combination of xeric site conditions and anthropogenic fires (Norton 1979, Boyd 1999). These unique ecosystems began forming on excessively well-drained soils derived from glacial outwash approximately 10,000 years ago (Ugolini and Schlichte 1973). This climatic transition took place at approximately the same time the first human inhabitants arrived in the region (White 1980, Kehoe 1992). These first people came to rely on various prairie species for food, basketry materials, and medicines (Wray and Anderson 2003).

Roughly 6000 years ago, the climate of the Pacific Northwest became more mesic, encouraging the growth of coniferous forests (Hansen 1947, Barnosky 1983, Hebda and Mathewes 1984, Brubaker 1986, Franklin and Dyrness 1988, Gavin et al. 2001). The first people regularly burnt open areas to maintain them as prairies, preventing the forest from encroaching (Norton 1979, White 1980, Boyd 1999). Despite human maintenance of the prairies, the forest/prairie ecotone may have fluctuated over time with changes in climate, resulting

in a broad boundary over which the prairie may have expanded and contracted (Neilson 1993, Risser 1995, Loehle 2000). However, fluctuations in the ecotone due to climate shifts are thought to have been less drastic due to human efforts to maintain the extent of the prairie (Arabas 2000, Foster and Shaff 2003).

Over the past two centuries, prairies in the Puget Sound region have been reduced to 2-4% of their historical extent due to urban development, agriculture, and fire suppression (Crawford and Hall 1997). A number of plant and animal species are threatened by the drastic reduction in prairie ecosystem extent. For example, golden paintbrush (*Castilleja levisecta* Greenm.), a species endemic to these prairies, has declined to 11 remaining populations in Washington and British Columbia (Arnett and Thomas 2008). To restore the historical extent of these prairies, it is important to identify the former prairie-forest interface. Historical accounts, historical photographs, and tree ages can be used to solve this problem in some areas (Wray and Anderson 2003, Peter and Shebitz 2006). However, these approaches are not effective for these sites as there are no photographs, few accounts of the area prior to European settlement, and because many of the adjacent forests have been disturbed or harvested since European settlement.

Soils are silent recorders of site history through pedogenic processes. They are continuously being

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altered in distinct but predictable ways by the soil forming factors: climate, organisms, topography, parent materials, and time. For example, vegetation type and frequent anthropogenic burning can leave distinct impacts on soil profiles by changing the horizon type, abundance of charcoal, and charcoal type. However, it may take many decades to hundreds of years to produce noticeable changes in soil characteristics (Dahlman and Kucera 1965). Therefore, when a soil forming factor changes, such as a shift from prairie to forest vegetation, pedogenic inertia will prevent soil properties from rapidly changing, and prairie soil characteristics will persist under a forest (Barton and Wallenstein 1997).

Grasslands and oak savannahs with abundant grass understory have soils characterized by a deep, dark-colored upper layer, or A horizon. This is caused by frequent dieback and rapid decomposition of fine roots and foliage from herbaceous vegetation or litter from deciduous trees. This contrasts with soils of coniferous forests in which belowground litter inputs and decomposition rates are lower and aboveground litterfall forms an O horizon, or a litter layer above the mineral soil (Bottner et al. 1998). Additionally, coniferous foliage can acidify the soil, helping to weather minerals and develop a distinct B horizon, or mineral soil layer that lacks the dark coloration of the A horizon. Furthermore, areas that experience regular fires are often marked by deposits of black carbon (incompletely combusted carbon) in the soil. The quantity of black carbon is generally positively correlated with the frequency of the fire regime (Wooller et al. 2000).

In this study, we utilized the distinct pedogenic effects of prairie vegetation and the measurable effects of regular, frequent and long-term burning to determine the historical ecotone between prairie and coniferous forest at two Puget Sound prairies. Many soil variables could be measured; we chose a suite that were relatively easy and cost effective to measure and likely to indicate the dominant vegetation during the development of the soil: organic matter concentration, black carbon concentration, and proportion of large black carbon particles. We also considered moist soil color and microtopography. These variables were measured across several prairie-forest ecotones.

We expected that soils that primarily developed beneath historical prairies would contain higher concentrations of organic matter and black carbon than those that developed beneath coniferous forest. In addition, we expected fewer large black carbon particles in grassland soils because the herbaceous prairie vegetation is smaller in size and because woody material generally

deposits larger black carbon fragments. Although size of black carbon particles is not a definitive indication of vegetation type (Tinner and Hu 2003), we believe that it can be used to indicate whether soil black carbon was the result of burning herbaceous prairie or woody forest vegetation. We also expected the increased organic matter and black carbon concentrations within grassland soils to provide soils with a darker moist color.

Methods

Site Description and Sampling

We sampled prairies at two locations, American Camp prairie and Mima prairie (Figure 1). The American Camp prairie, located on San Juan Island north of Puget Sound, is part of the San Juan Island National Historical Park. The American Camp fort was established in 1859 as a U.S. Army post and inhabited through 1874. Early reports depict 'open doug fir' to the north of the fort, and 'mixed pine/fir' on the northern slope of the bluff, which slopes between 15-30% to the NNE as reviewed in Gilbert (1987). Mima prairie, located 20 km southwest of Olympia, Washington, is managed by the Washington Department of Natural Resources as part of the Mima Mounds Natural Area Preserve.

Soil surveys have been conducted at both sites, but the coarse scale of these surveys places the boundary between prairie and forest soils at the current ecotone (Franzen et al. 2002). As described here, we found that prairie soils may extend well into areas that are currently surveyed as forest soils. Prairie soils at American Camp are mapped as the San Juan series, a coarse sandy loam that is well drained with a dark colored 48 cm deep A horizon; this is one of the most common series associated with prairies in western Washington (Schlots 1962). Forest soils at American Camp are mapped as the Hoypus series, a gravelly sandy loam with a relatively thin (13 cm) A horizon. Prairie soils at Mima Prairie are typically the Spanaway series, which is also a gravelly sandy loam that is well drained with a deep (45 cm) A horizon (Ness and Glassey 1958). Forest soils at this site are mapped as the Everett series, which is a gravelly sandy loam with a thin A horizon (5 cm) that is typically associated with coniferous forests.

At each prairie, sampling transects were positioned perpendicular to the current prairie-forest ecotone and extended up to 500 m directly into the forest and prairie. In establishing the starting point at the current ecotone, an effort was made to direct the linear transect such that it went into the forest that appeared to be the most mature while the opposite direction of the transect ex-

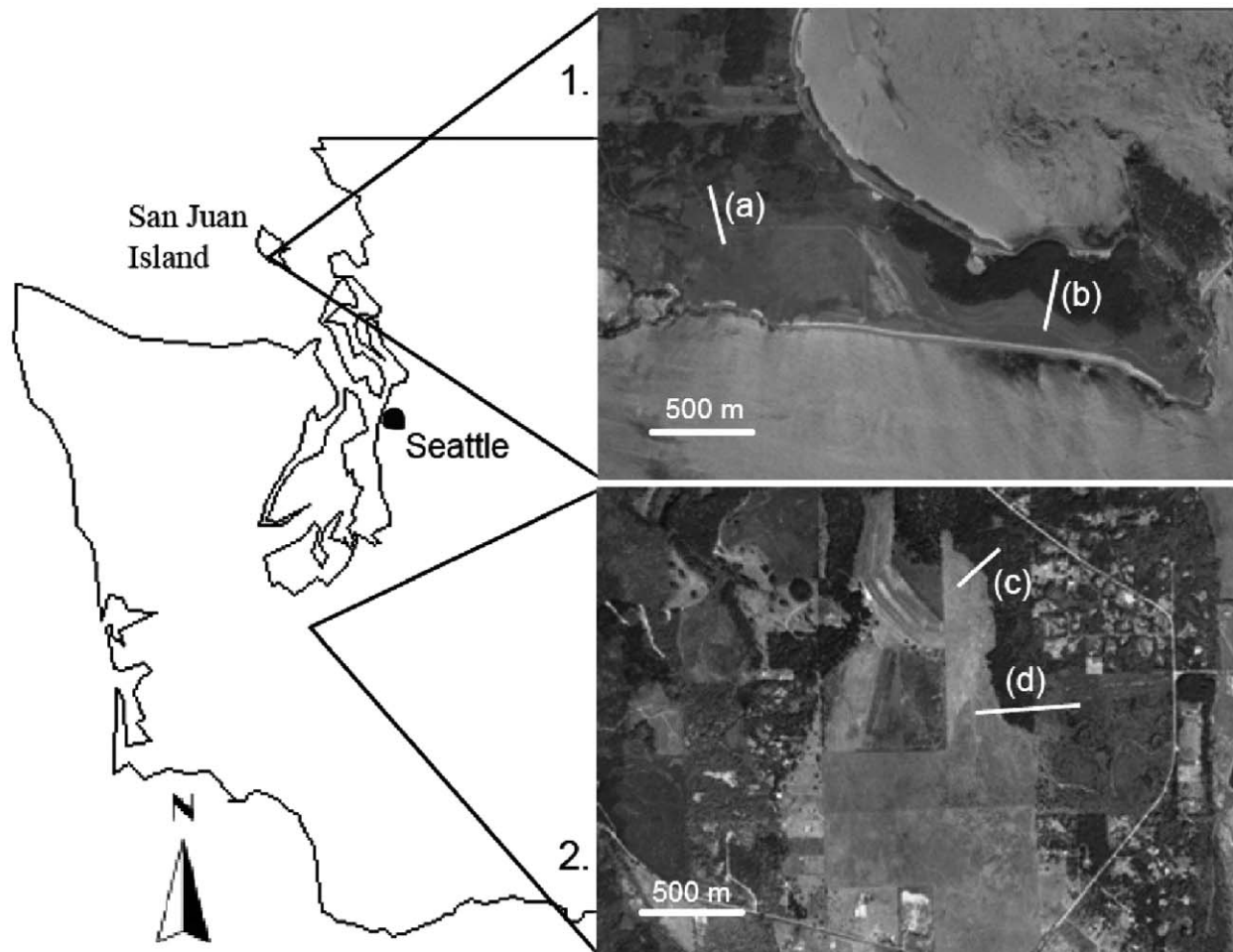


Figure 1. Location of (1) American Camp prairie, and (2) Mima prairie in western Washington, and transect locations (a) Fort, (b) Bluff, (c) north Mima, and (d) east Mima.

tended towards the center of the prairie. This resulted in linear transects with one end in mature forest and the other in the middle of the prairie. Sampling points along each transect were approximately 50 m apart, with additional samples near the current ecotone to increase resolution. Each sampling point along a transect was selected to be representative of that location, avoiding areas of obvious disturbance or standing water.

At American Camp, two transects were positioned at the forest interface on the bluff at the east side of the park, and two north of the fort, in the western portion of the park (Figure 1). Transects at each of these locations were combined because they were close together (~ 50 m), resulting in a dataset for the bluff and another for the fort. At Mima prairie, one transect was positioned at the north end of the prairie and another at the eastern boundary.

Soil samples were collected to a depth of 20 cm with a 2 cm diameter soil sampling probe (American

Camp) or a narrow trowel (Mima prairie). If present, the O horizon was carefully removed before sampling, leaving only mineral soil. In instances where the sampling site was obviously heterogeneous, multiple samples were taken at the same location and the replicates averaged together. Each sample was air dried and sieved to 2 mm, removing stones and root fragments, and then divided using a sample splitter, to give approximately 10 g of a homogenized sample for subsequent analyses. Moist color was determined in the laboratory using a Munsell soil color chart. Between analyses, the air-dried samples were stored in a refrigerator at 3 °C.

Organic Matter and Black Carbon Analyses

A loss on ignition (LOI) method adapted from Ball (1964) was used to quantify total organic matter and total black carbon. The LOI method is known to overestimate organic matter in fine-textured soils due to a loss of structural water and carbonates (Wang et

al. 1996). However, for the purposes of this study the LOI methodology was appropriate because it gives consistent results and because we were comparing samples of closely related soils (Beaudoin 2003). Total black carbon is gravimetrically determined as the difference between organic matter that combusts at 375 °C and black carbon that combusts at 550 °C (Skjemstad and Taylor 1999). Approximately 1 g of each homogenized sample was placed in a porcelain crucible, dried at 100 °C for 8 hr and weighed to the nearest 0.0001 g. Each sample was then heated at 375 °C for 24 hr to ignite the humified carbon, reweighed, heated at 550 °C for 6 hr to ignite the black carbon, and weighed again. Organic matter (OM) concentration was calculated as the difference between the dry mass and the mass after heating to 375 °C, with the black carbon (BC) concentration as the difference between the mass after heating to 375 °C and the mass after heating to 550 °C (Skjemstad and Taylor 1999). These data are reported as weight relative to total dry mass of soil.

Black Carbon Size and Structure

Four to eight samples per transect were selected for analysis of black carbon particle size. Samples were cleaned for microscopy following Rhodes (1998). Initial observations showed two distinct and easily distinguishable size classes of particles, one between 5 µm and 20 µm and the other greater than 35 µm. Scanning electron micrographs indicated that larger

particles were typically woody while smaller particles were herbaceous charcoal (Figure 2).

To verify that particles in the larger size class were woody, we photographed them with an FEI Sirion Scanning Electron Microscope (SEM). While the charred fragments of plants can be identified to the genus level based on morphological features observable with an SEM (Wooller et al. 2000, Skjemstad et al. 2002, Wooller 2002, Di Pasquale et al. 2008), for our purposes it was only necessary to determine that these larger particles were typically woody while the smaller particles were not woody. To aid in identification of the fragments as woody or herbaceous, samples of vegetation common in prairie and forest ecosystems (bracken fern [*Pteridium aquilinum*], fescue grass [*Festuca* sp.] and wild rye [*Elymus* sp.] for prairie vegetation, and Douglas fir [*Pseudotsuga menziesii*] for woody forest vegetation) were heated at 375 °C in an oxygen limited environment, resulting in an incomplete combustion (Di Pasquale et al. 2008). Key defining characteristics for each species were identified such as size and architecture of vascular tissue (Wheeler et al. 1989).

For scanning electron microscopy, cleaned samples were also prepared according to Rhodes (1998), and the black carbon particles were separated from the cleaned, dried samples by floating in deionized water. Particles were then mounted on SEM stubs with carbon paste and coated with gold. The structure of particles larger than 35 µm were compared to the structure of the standards and determined to have a distinctly woody

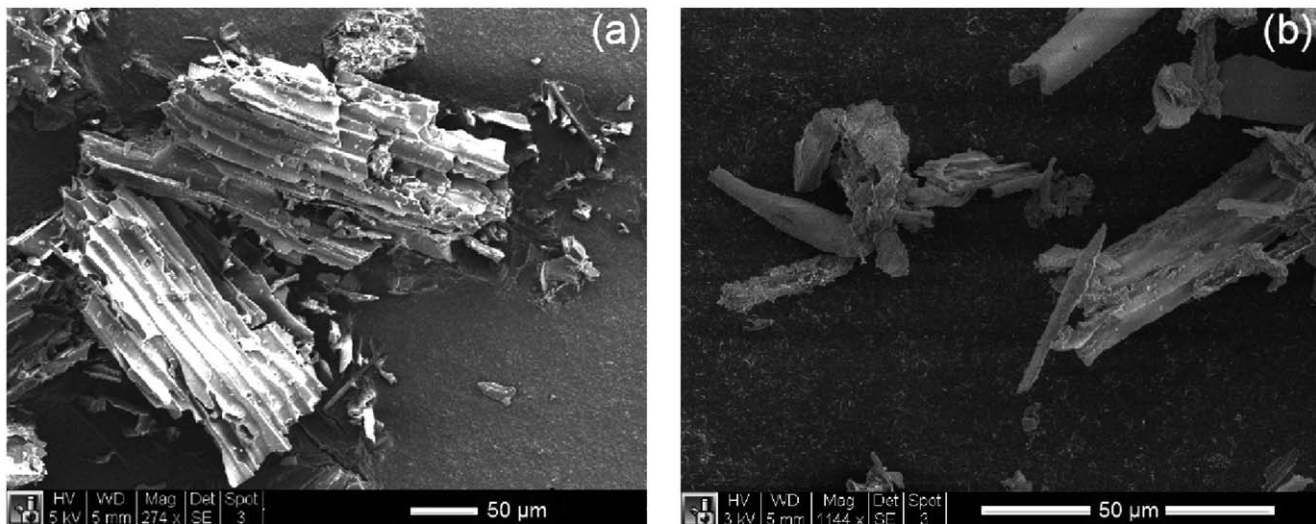


Figure 2. Scanning electron micrographs of reference samples of (a) Douglas-fir [*Pseudotsuga menziesii*], and (b) bracken fern [*Pteridium aquilinum*], fescue grass [*Festuca* sp.] and wild rye [*Elymus* sp.]. Note size and structure difference between woody and prairie vegetation. A 50 µm scale bar is included at the lower right for comparison.

structure; particles less than 20 μm were similar to the herbaceous standards.

Once we verified that the micrographs of large particles had a woody structure, we felt confident using 30 μm as the boundary between small (herbaceous) and large (woody) size classes. The sample was then prepared for light microscopy and viewed under a dissecting microscope at 95x zoom. Black carbon particles that touched a randomly selected printed line under the dish were tallied into the two size classes (Clark 1982, MacDonald 1991). The proportion of large particles relative to the total number of particles was calculated for each sample.

Statistics

We used multiple lines of evidence to infer the locations of the historical prairie-forest ecotones, analyzing each transect separately (Thevenon et al. 2003). We began by conducting cluster analyses of the organic matter and black carbon data to visualize the patterns. The calculations in this analysis require that each sample have a value for each variable, which resulted in the exclusion of charcoal-size ratio as this was not done at each distance. We assumed that if an historical ecotone was present, it would be evident as a strong separation into two groups in a dendrogram. We relativized each variable by its range and calculated the dissimilarity matrix using Euclidean distance. Dendrograms were constructed using the complete linkage method as coded in the `hclust` function within R (version 2.10.0), which illustrate how closely related each of the samples is based on the soil parameters. The lower linkages that separate at a low height indicate more closely related samples. The strongest difference between soil samples would appear in these diagrams as two primary groupings that branch from each other high in the diagram with closely linked samples within each group. Next, we determined which distance had the strongest support for being the ecotone as determined by the correlation between the soil data (organic matter and black carbon) and the coding of samples as prairie or forest. We began with the prairie-forest ecotone at its current position and systematically moved it deeper into the forest, increasing the number of samples coded as being from prairie. At each step, the correlation between the soil data and the coding of samples as prairie or forest was assessed for significance using a Mantel test function in the `vegan` package within R (Legendre and Legendre 1998) with $\alpha = 0.05$. The distance at which the correlation was strongest was identified as the one that most accurately indicated the historical ecotone. Finally, we qualitatively compared samples in terms

of the proportion of large black carbon particles, moist soil color, and microtopography.

Results

Mima Prairie

Along the east and north transects at Mima prairie there were significant changes in soil properties; we discuss them separately because they suggest different historical prairie boundaries. Along the east transect, black carbon and organic matter concentrations decreased steadily from approximately 0.009 g BC g^{-1} and 0.22 g OM g^{-1} at 40 m in the prairie to approximately 0.006 g BC g^{-1} and 0.11 g OM g^{-1} at 350 m into the current forest (Figure 3). The cluster analysis identified two major groups, one from the prairie to 150 m into the forest, and the other from 250 to 450 m in the forest (Figure 4). However, the strongest correlation ($r = 0.494$, $P = 0.011$, $n = 9$) occurred when the proposed ecotone was 300 m into the current forest. The proportion of large (>30 μm) black carbon particles was between 0.2 and 0.3 for samples from the prairie through 250 m into the forest. The proportions for the remaining samples from 300 to 450 m into the forest ranged between 0.3 and 0.4. In addition, the moist soil color of samples at 250 m and more into the forest were brownish black (10YR 3/1), whereas samples closer to the boundary and into the prairie were black (10YR 2/1). The mounded topography that is characteristic of Mima prairie (Dalquest and Scheffer 1942) was observed approximately 250 m into the forest, beyond which the ground flattened out.

A cluster analysis of the north transect data at Mima prairie indicated two distinct groups, one containing the prairie samples and extending 40 m into the forest, and the other containing the samples 60 m and further into the forest (Figure 4). This grouping also had the most support in a Mantel test ($r = 0.507$, $P = 0.001$, $n = 17$). The prairie group had 0.005 to 0.012 g BC g^{-1} and 0.02 to 0.32 g OM g^{-1} , while the forest group had 0.002 to 0.004 g BC g^{-1} and 0.02 to 0.24 g OM g^{-1} (Figure 3). The moist color was black (10YR 2/1) in the prairie and shifted after 80 m into the forest to brownish black (10YR 3/1). Additionally, mounded topography occurred approximately 100 m into the forest.

American Camp Prairie

Soils of both transects at American Camp prairie had similar contents of black carbon and organic matter and a similar proportion of large charcoal particles. Throughout the lengths of both transect sites these levels were relatively constant. This is reflected in the

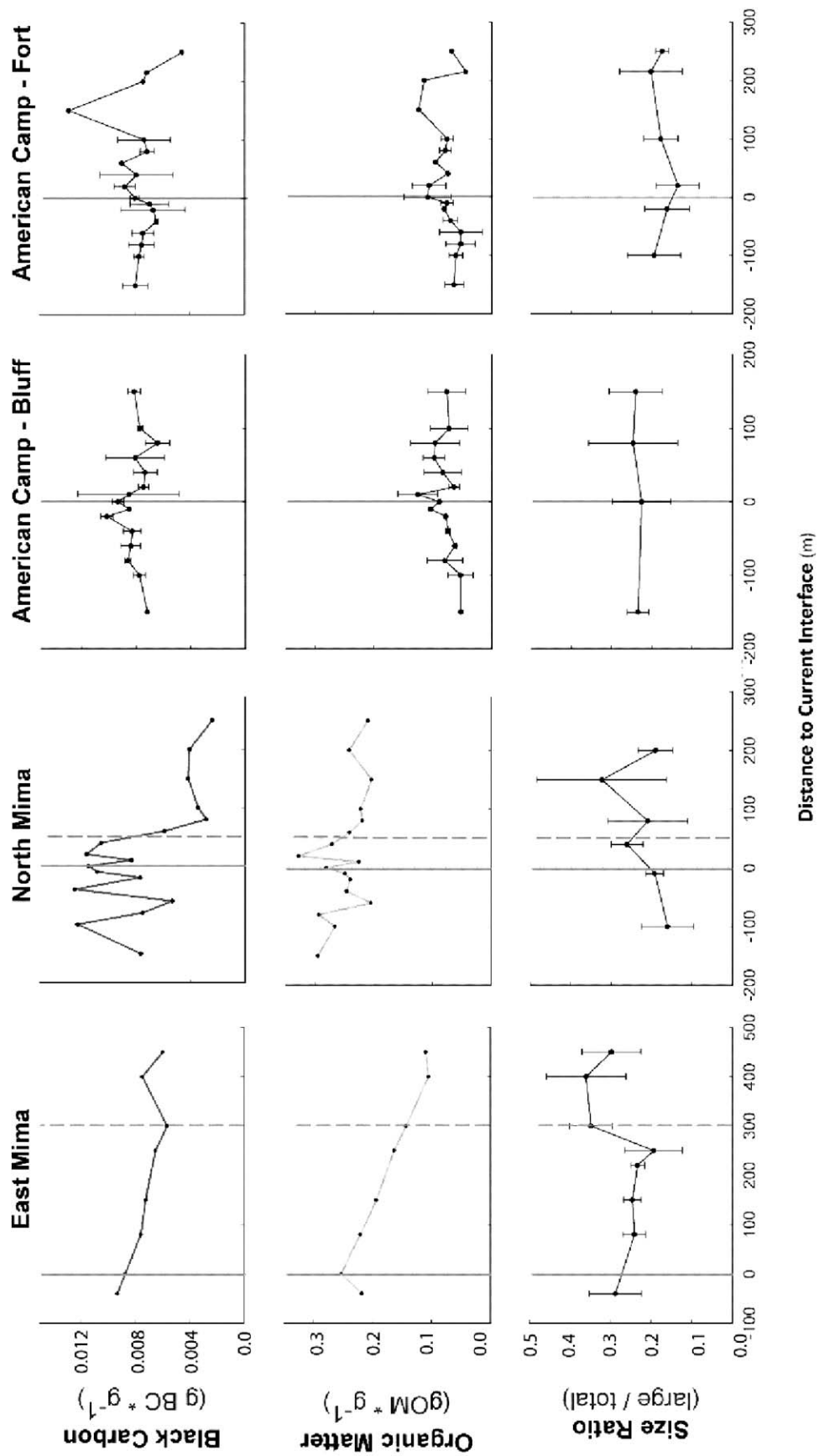


Figure 3. Total black carbon, organic matter and ratio of large black carbon particles to the total number of particles along each transect. Standard deviations are shown where multiple samples were taken at a given distance. The solid vertical lines depict the current prairie-forest ecotone, and the dashed lines represent the proposed historical ecotone. Samples in the current prairie are at negative distances from the current ecotone, while samples in the forest are at positive distances.

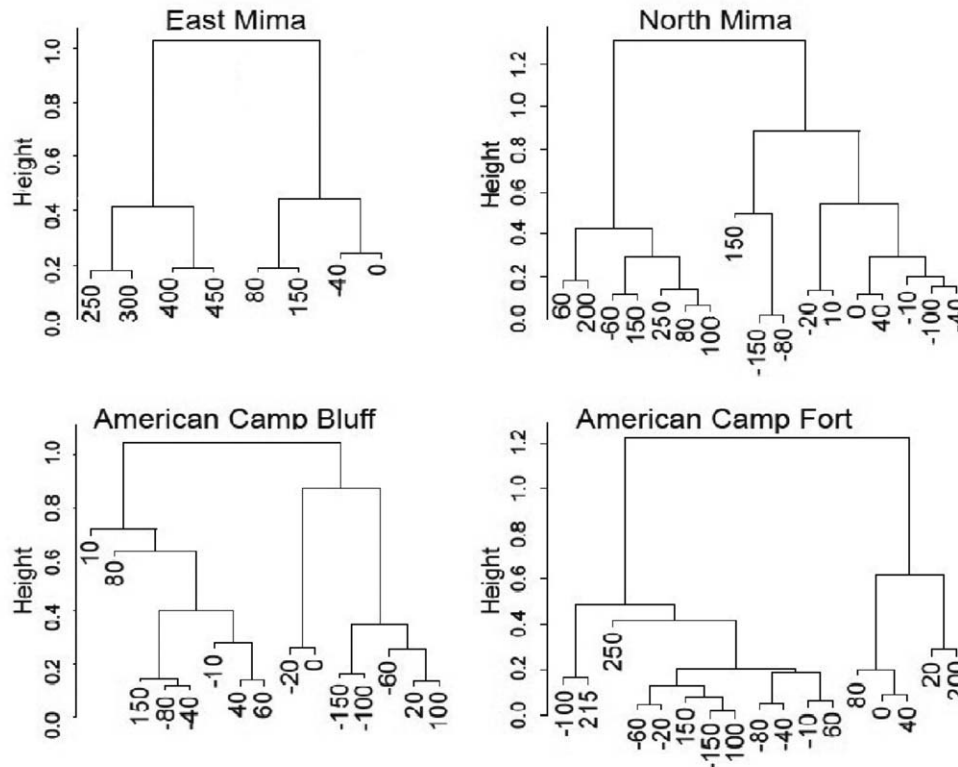


Figure 4. Dendrograms based on black carbon and organic matter concentrations of soil samples along each transect. The vertical axis (height) in each dendrogram is related to the distance among samples or groups of samples; groups that are connected at higher heights differ more strongly than those connected at lower heights. Each sample is listed as a distance from the ecotone; negative distances are within the current prairie while positive distances are within the current forest.

cluster analyses, which did not show a clear separation into prairie and forest groups (Figure 4) and by the low confidence of the Mantel tests, which indicated strongest support for a historical ecotone 150 m into the forest ($r = 0.446$, $P = 0.024$, $n = 17$) along the fort transect, and weak support for the current ecotone ($r = 0.125$, $P = 0.08$, $n = 15$) along the bluff transect. In addition, the moist soil color varied inconsistently throughout these transects between black (10YR 2/1) and dark brown (10YR 3/3). This site does not have mounded microtopography.

Discussion

Soil variables differ in sensitivity to changes in soil forming factors and to disturbances such as timber harvesting. Nonetheless, the different analyses of soil characteristics agree in broad terms and provide some conclusions about the location of past prairie-coniferous forest boundaries.

Along Mima prairie's eastern boundary, for example, samples taken from the prairie to 300 m into the forest had higher concentrations of black carbon

and organic matter, as is characteristic of prairie soils that experienced regular fires. In addition, the cluster analysis suggested a division 150 to 250 m into the forest. Finally, a dark soil color and mounded microtopography characteristic of Mima prairie were observed approximately 250 m into the forest. Overall, these data suggest that the eastern boundary of Mima prairie, with its herbaceous vegetation and regular fires, historically extended approximately 300 m into what is now forest. At greater than 300 m into the forest, the lower soil organic matter and black carbon concentrations together with a higher proportion of large charcoal particles and a lighter soil color are all more characteristic of coniferous forest soil indicating persistent forest over a long time period.

The north transect at Mima prairie similarly shows soil characteristics changing to indicate an historical ecotone at 40 to 60 m into the current forest. This is not only supported by distinct declines in black carbon and organic matter concentrations, but is statistically the most significant distance. These changes in black carbon and organic matter concentrations are our best

indicators of a change of vegetation and fire regime. Both of the proposed ecotones at Mima prairie are also consistent with the observation of oaks in the current coniferous forest to the east of the Mima prairie. The presence of these oaks suggests that the transition from prairie-oak ecosystem to coniferous forest is relatively recent.

Some discrepancies in the historical boundaries are evident among the different analyses. Cluster analyses indicated the eastern boundary occurred after 300 m, and the black carbon size data indicated that the ecotone was after 250 m into the current forest. These differences can be attributed to the natural variation in the ecotone over time and the disturbance caused by timber harvesting in the current forests. However, it is clear that at the eastern boundary the historical ecotone was approximately 250 to 300 m farther into the current forest and the northern boundary was historically between 40 to 60 m farther into the current forest.

In contrast, transects at American Camp prairie show little evidence of an historical prairie-coniferous forest ecotone; we observed little change in soil characteristics along our transects. We interpret these results to mean that the historical ecotones at American Camp either were not static or were not encompassed by our sampling transects. Furthermore, spatially separate samples were grouped together in the cluster analyses and the moist soil color ranged from black to dark brown across both transects. This heterogeneity could suggest that past forest/prairie vegetation types were interspersed, or could be a reflection of localized human disturbances associated with the nearby fort. However, organic matter concentrations along both transects suggest that the soil developed primarily under herbaceous prairie type vegetation. Furthermore, the black carbon concentrations across both transects are similar to those in soils beneath prairie vegetation at Mima prairie, suggesting that a regular fire regime was experienced throughout this area. The proportions of large charcoal particles are low and suggest that the same type of vegetation was historically burned along these transects, unlike at the East Mima prairie, where a shift to a larger proportion of large woody particles was observed. We suggest, therefore, that the areas near our transects at American Camp were largely prairie historically, although grouped or scattered trees may have been present.

The dark, deep A horizons, soil organic matter concentrations, and black carbon indicate that fire-adapted prairies must have persisted within their current extent and within parts of the adjacent forest for hundreds

of years prior to forest encroachment. Climatic data show a period of more mesic conditions during the Little Ice Age from approximately AD 1601 – 1850 (Graumlich and Brubaker 1986, Helama et al. 2009). This cooler and wetter period could have supported the initial encroachment of coniferous forests into prairies (Greenwald and Brubaker 2001). Adjacent coniferous forests at both prairies may have been approaching their present boundaries since this time aided by fire suppression. This would be consistent with the early accounts from the American Camp fort that describe open forest to the north of the fort, and on the north slope of the bluff (Gilbert 1987). Pedogenic inertia could retain prairie soil characteristics over this time period.

Conclusions

At both sites, it appears that fire suppression, along with climatic changes, has aided coniferous forest encroachment and loss of historical prairie. At Mima prairie, we conclude that the historical prairie extended approximately 50 m north and 300 m east of the current prairie-coniferous forest ecotone. At American Camp, we conclude that forests either did not exist, were much less dominant or were sparsely forested at our transect locations hundreds of years ago than they are at present.

This study shows that soils can be used effectively to create detailed maps of the historical extent of fire-adapted prairie ecosystems. While using a variety of measures can provide a more compelling argument, given the general consistency of the conclusions drawn from the different soil measures in this study, future investigations may not need to include the relatively time consuming study of black carbon particle size and structure (Lepofsky et al. 2003) and focus on organic matter concentration, black carbon concentration, and moist soil color as indicators for locating historical ecotones. Changes in the depth of the A horizon would be a simple additional parameter we would recommend for future studies. Other measures such as carbon isotope discrimination of black carbon particles or the study of opal phytoliths could also be used, but are much more costly or labor intensive (Fisher et al. 1995). The approach used in this study presents a cost effective means of determining where these ecotones developed and could be a powerful tool to guide land managers in restoration of prairie ecosystems and the species they support.

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