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Variation of key elements in soils and plant tissues in subalpine forests of the northern Rocky Mountains, U.S.A.

David P. Pompeani[1], Kendra K. McLauchlan[1], Barrie V. Chileen[1], Kyra D. Wolf[2], Philip E. Higuera[2,3]

[1]Department of Geography, Kansas State University, Manhattan, KS 66506
[2]Systems Ecology Intercollegiate Graduate Program, University of Montana, Missoula, MT 59812
[3]Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812

Abstract

The essential elements for the structure and function of forest ecosystems are found in relatively predictable proportions in living tissues and soils; however, both the degree of spatial variability in elemental concentrations and their relationship with wildfire history are unclear. Quantifying the association between nutrient concentrations in living plant tissue and surface soils within fire-affected forests can help determine how these elements contribute to biogeochemical resilience. Here, we present elemental concentration data (C, N, P, K, Ca, Mg, S, Fe, Mn, Zn) from 72 foliar and 44 soil samples from a network of 15 sites located in the fire-prone subalpine forests of the northern Rocky Mountains, U.S.A. Plant functional type is strongly correlated with carbon (C) and nitrogen (N)— C concentrations are highest in coniferous needles, and N concentrations are highest in broadleaved plant species. The average N/P ratio of foliage among samples is 9.8 ± 0.6 (μ ± 95% confidence). This suggests that N is the limiting nutrient for these plants, however several factors can complicate the use of N/P ratios to evaluate nutrient status. Average C concentrations in organic soil horizons that were burned in regionally extensive fires in 1910 or 1918 CE are lower than those from sites that burned prior to 1901 CE ($p<0.05$). This difference suggests that wildfires reduced the pool of soil C and that the legacy of these fires can be measured a century later. Our results help aid in modeling how changing wildfire regimes will influence biogeochemical cycling in subalpine forests.

1. Introduction

Although living plant tissue is primarily composed of carbon (C), there are approximately 20 other elements that are necessary for biochemical reactions and growth. These other key elements—including nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (in the form of SO_4)— play important roles in regulating terrestrial ecosystem processes. The quantities of these elements are controlled by a number of factors including bedrock parent material, soil composition (Kramer et al., 2017), vegetation type (Hu et al., 2001), and climate (Campbell et al., 2009). It is generally thought that plant tissue and soil nutrient concentrations can provide information about element limitation to growth (Wardle et al., 2004;Boerner, 1984;Schreeg et al., 2014). However, relatively few studies have analyzed the concentrations of a large suite of elements in both plant and soil samples from one region.

Plant traits, such as biochemical, physiological, and anatomical features measured at the individual level (Violle et al., 2007), reflect the outcome of evolutionary processes responding to environmental constraints (Valladares et al., 2007). Traits determine how primary producers respond to abiotic and biotic environmental factors and influence a host of other ecosystem services (Kattge et al., 2011). Plant functional type (PFT) models capture a substantial fraction of the observed trait variation across plant species. A relatively small number of PFTs (5-20) have been used to represent the functional diversity of >300,000 documented plant species on Earth in global vegetation models (Kattge et al., 2011). Growth-limiting elements in foliar material derived from soils, such as phosphorus, make nutrient concentrations among the most plastic of plant traits (Wright et al., 2004) because the availability of these nutrients varies spatially as a result of parent bedrock composition. Nutrient concentrations in plants are influenced by a number of other factors, including the age of the tissue and overall age of the plant (Turner et al., 1977;Reich et al., 1992;Schreeg et al., 2014;Luo et al., 2017). Additionally, sunlight and location on a tree branch can also affect nutrient concentration in leaves (Schreeg et al., 2014), and weather-related factors such as precipitation and temperatures can affect nutrient levels on a seasonal basis (Turner et al., 1977). Therefore, samples of plant tissues taken over a short time period for several species across one region are particularly useful for differentiating factors that influence foliar nutrient concentrations and subsequent bioavailability of nutrients in leaf litter and upper soil horizons (Qualls and Haines, 1991;Taylor et al., 1989).

High severity fires can profoundly impact the cycling of C, N, and other nutrients in plants and soils (Chen et al., 2017;Fletcher et al., 2014;Certini, 2005;Dunnette et al., 2014), and could therefore affect the ability of the forest to regenerate to pre-fire conditions (Smithwick, 2011;McLauchlan et al., 2014). Several mechanisms determine how forests respond to fire, and how cycling of C, N, and other elements subsequently change (Pellegrini et al., 2018;Certini, 2005). For example, combustion of vegetation and soils from frequent, low-intensity burning can lead to the loss of C and N to the atmosphere (Pellegrini et al., 2014;Reich et al., 2001;Deluca and Sala, 2006;Yelenik et al., 2013). Fires also release nutrients from plant tissues as ash, which can potentially increase post-fire vegetation growth through soil nutrient enrichment (Boerner et al., 2009;Hurteau and Brooks, 2011). Over longer time scales of centuries to millennia, ecosystem modeling informed with paleofire history records suggest that changing fire regimes can have substantial and long-lasting impacts on C and nutrient cycling (Hudiburg et al., 2017;Kelly et al., 2016).

Here we provide data from 72 leaf and 44 soil samples from a network of 15 sites in the coniferous subalpine forests of the northern Rocky Mountains, U.S.A. (Fig. 1, Table 1). The samples were collected during the middle of the growing season from sites with similar elevation, climate, and bedrock geology, but with varying fire histories over the 20th century. Our approach isolates local plant and soil forming processes that affect the distribution of key elements, and compares sites that are reported to have burned in extensive fires in 1910 and 1918 CE to those that have not burned since before 1901 CE (Morgan et al., 2014). We evaluate nutrient status and characterize patterns of element distribution within and among the leaves of several tree and shrub species in the context of associated bioavailable nutrient data from upper soil horizons. We use statistical methods to infer the transfer and distribution of key elements in soil and vegetation.

2. Methods

2.1 Study area

The study sites are located between 1623-2011 m above sea level in the northern Bitterroot Mountains along the border of Idaho and Montana, U.S.A. (Fig. 1). The vegetation at all sites is subalpine forest dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and mountain hemlock (*Tsuga mertensiana*). Of the 14 sites, seven experienced wildfire in 1910 or 1918 CE, while the other seven have no indication of fire activity back to 1901 CE (Morgan et al., 2014)(Table 1). The regional climate is classified as modified maritime with warm, dry summers and cool, wet winters. The study region is underlain with partially metamorphosed argillites of the Belt Basin Supergroup, known as Belt meta-sedimentary rocks. Glacial till and shallow entisols overlay the bedrock (Sasich and Lamotte-Hagen, 1989).

2.2 Fieldwork

Soil cores, approximately 2 cm in diameter and 25 cm deep, and foliage samples were collected at 15 sites along a 100-km northwest to southeast transect (46.78°-47.36° N; 114.76°-115.57° W) from 12 July to 25 August, 2017 CE (Fig. 1). At each soil core site, except for Hoodoo, associated leaf samples were collected from nearby trees and shrubs, avoiding new growth and juvenile trees. The majority of the foliar samples consist of coniferous needles from eight species (n=68): *Abies lasiocarpa*, *Larix occidentalis*, *Pinus albicaulis*, *Pinus contorta*, *Picea engelmannii*, *Taxus brevifolia*, *Thuja plicata*, and *Tsuga mertensiana*. We also collected two samples each of the broadleaf species green alder (*Alnus viridis*; n=2) and false huckleberry (*Menziesia ferruginea;* n=2). Foliar samples were taken directly from living vegetation located approximately 2 m above the soil surface. Soil cores were sampled by horizons: 'litter' was unconsolidated plant material from the surface; 'organic' soil was identified visually and sampled at a depth between approximately 0-10 cm; the 'mineral' soil layer was sampled between 10-25 cm below the surface depending on overall soil depth. Samples were stored in airtight plastic containers for transport back to the laboratory.

2.3 Laboratory analyses

Samples were dried, homogenized, and sent to the Department of Agronomy Soil Testing Lab at Kansas State University. Foliar samples were weighed into 50 ml Kimax digestion tubes for elemental analysis. Boiling chips and 5 ml of nitric acid at 50% strength were added to the tubes, which were covered with plastic wrap to react overnight. The following day, 5 ml of perchloric acid was added to predigested plant material and tubes were then placed on a cold techator digestion block. Temperatures were set to 200°C and digests were heated for approximately three hours or until white fumes appeared and the acid was clear (and colorless when cooled to room temperature) (Gieseking et al., 1935). Tubes were diluted to 25 or 50 ml with deionized water and mixed by inverting twice. Each digested sub-sample was then analyzed for P, Mg, K, Ca, iron (Fe), manganese (Mn), zinc (Zn), and SO_4 using a Varian Model 720-ES ICP Optical Emission Spectrometer. Analytical precision (σ) for element analysis was <0.0001%.

Base cations (Ca, Mg, K, and Na) were extracted from soil sub-samples using 1 M ammonium acetate (pH 7.0). The resulting supernatant was then analyzed using a Varian Model 720-ES ICP Optical Emission Spectrometer. Trace elements (e.g. Mn, Zn, etc.) were not measured on soil sub-samples. Soils were not analyzed for P.

Total carbon and nitrogen concentrations (weight %) in both plant and soil sub-samples were measured using a LECO CN 2000 combustion analyzer. Analytical precision (σ) was approximately 0.06% for carbon and 0.006% for nitrogen.

2.4 Statistics

To compare elemental concentrations among different sample sites, we used box plots, unpaired t-tests (assuming unequal variance), principal components analysis (PCA), and Pearson correlation coefficients. We calculated principal components using the ade4 package in R (Dray and Dufour, 2007). Correlation tables were calculated using the R base stats package (R Core Team).

3. Results and discussion

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3.1 Patterns in soil and foliar elements

Soil C and N concentrations were highest on average (34.94% and 1.32%, respectively) within litter material and declined with depth through organic (18.30% and 0.84%) and mineral (6.05% and 0.29%) soil horizons (Table S1, Fig. 2). The concentration of other nutrients such as K, Ca, and Mg were highest on average within the litter (0.016%, 0.115%, and 0.012%, respectively) and organic soil horizons (0.019%, 0.104%, and 0.013%), and decreased in the mineral soil horizon (0.009%, 0.046%, 0.007%). Na concentrations displayed the opposite pattern and increased from litter (<0.001%) to mineral (0.001%) soil horizon.

The pattern of five elements in the soil— C, N, Ca, K, and Mg—correspond with the dominant role of decomposing plant material controlling the concentration of nutrients in forested soils (Aerts and Chapin, 1999). These results are consistent with a global compilation of 10,000 soil profiles that indicate ranking of nutrient concentrations from shallow to deep (Jobbagy and Jackson, 2001) (Fig. 2, Fig. S1). The decline in the bioavailable K, Ca, and Mg in the mineral horizon suggests removal by mineralization or microbial immobilization (Qualls et al., 1991;Qualls, 2000).

Foliage contained C concentrations between 47-52%, with the exception of *Larix occidentalis*, *Alnus viridis,* and *Menziesia ferruginea,* which had slightly lower concentrations of C between 43-47% (Fig. 3, Table S2). N concentrations were generally low (0.75-1.89%) in coniferous needles, and high in leaves of the broadleaved species *Alnus viridis* and *Menziesia ferruginea* (2.5-3.5%). P, K, and Ca concentrations were variable within and between tree and shrub species, with no clear pattern differentiating needle and broadleaf species (Fig. 3).

There was considerable variability in trace element concentrations among samples of foliar material (Fig. 3). Mg was below 0.20% in all leaf material, except for *Alnus viridis* (0.35%) and *Menziesia ferruginea* (0.50%). Fe, Mn, and Zn concentrations were highly variable within and between species. *Menziesia ferruginea* contained high concentrations of Mn (0.48%) and Zn (0.01%). SO_4 concentrations ranged between 0.01-0.15% for all foliar material, except for higher values found in *Alnus viridis* (0.18%).

Element concentrations did not vary with site latitude or elevation likely as a result of the constricted latitude and elevation range of the study sites. Soil and foliar N, K, and Mg were all positively correlated ($p<0.001$) with each other ($r=0.42-0.75$) (Figs. S1, S2, S3, and S4). In soils, Ca was positively correlated ($p<0.01$) with Mg (0.74), K (0.54), N (0.47), and C (0.39), whereas in plant tissues Ca was poorly correlated ($p>0.05$) with P (-0.21), K (-0.21), and Mg (0.15), C (0.05), and N (0.02). Foliar C was negatively correlated ($p<0.05$) with Mg (-0.53), N (-0.41), P (-0.38), and K (-0.30). In soils, Na was inversely related ($p<0.05$) to both C (-0.52) and N (-0.42). In vegetation, Zn was correlated ($p<0.05$) with Mn (0.54), K (0.33), and C (-0.26). Trace elements Fe and Mn were weakly correlated ($p>0.05$) with C, N, P, K, and Mg in plant tissues.

A multivariate analysis of elemental concentrations clearly separated foliar (n=72) from litter/soil samples (n= 44) (principal component analysis [PCA]; Fig. 4). Axis 1 of the PCA explained 58.7% of total variation in the soil and foliar elements. The concentrations of several elements were negatively loaded on Axis 1: C (-0.905), K (-0.809), Ca (-0.791), Mg (-0.799), and N (-0.706). C/N was correlated to Axis 1 (-0.535) but more weakly than C, N, and the base nutrients. Axis 2 explained 22.4% of the variation and was primarily driven by N and Mg (0.577, 0.381, respectively), and was strongly influenced by the high foliar N concentrations of *Alnus viridis* (n=2). Foliage samples from different plant species were dispersed along Axis 2.

Leaf carbon, nitrogen, and phosphorus content are considered important biochemical traits in PFT modeling, as seen in the TRY plant database (Kattge et al., 2011). We measured additional elemental concentrations to understand inter- and intra-species variation in biogeochemical traits. In live vegetation, N, P, K, Mg, and SO_4 are all positively correlated (Fig. S2), indicating that leaf tissues are built in predictable stoichiometric ratios, but the variation in the concentration of those nutrients among sampling sites suggests that the availability of these elements in soils and bedrock likewise varied. Ca was weakly correlated with N, P, K, Mg, and SO_4 in leaves. Ca concentration is strongly affected by foliage age (Turner et al., 1977), which represents another source of variation in the sampled foliage not controlled for in this study.

We found substantial differences in the foliar nutrient concentrations between evergreen and deciduous plant types (Fig. 3). N, Mg, and SO_4 were found at higher concentrations in broadleaf material relative to evergreen needles, probably due to higher rates of metabolic activity and photosynthesis in broadleaf material during the summer (Linzon et al., 1979). Leaves from *Alnus,* a nitrogen-fixing plant, contained greater N (2.55-3.56%) relative to non-fixing species (Taylor et al., 1989). Leaf N concentrations ranged from 0.75 to 1.89% in the evergreen conifer species (i.e., excluding *Larix occidentalis*) (n=63) —which is slightly lower but consistent with (1.15±0.24%) a previously reported global average of 1.21±0.01% N for needleleaf evergreens (n= 5558)(Kattge et al., 2011). These data suggest that nutrient variation between plant functional types (i.e. evergreen needleleaf versus deciduous) is much greater than inter- or intra- specific variation within PFTs. This supports the use of broadly-defined PFTs in biogeochemical models of ecosystem processes.

3.2 Fire legacies on nutrient availability

We compared average elemental concentrations (i.e. C, N, Ca, K, and Mg) in organic soil horizons taken from sample sites burned in 1910 or 1918 CE with sites that were burned prior to 1901 CE (i.e., the start of the Fire Atlas published by Morgan et al. (2014))(Fig. 1,Table 1) to investigate the long-term effects of wildfires on soil nutrient availability. Soil samples from the organic horizon that were burned in the early 20th century contained significantly less C on average than samples from sites that burned prior to 1901 CE ($t = -2.26$, df= 9.60, p= 0.0484). In contrast, N ($t = -1.46$, df= 10.54, p= 0.1731) and other soil nutrient concentrations (Fig. 5; Ca, K, Mg not shown) did not significantly differ between these two populations.

The significant difference in soil C suggests that a single fire event in the early 20th century at several sites reduced the pool of soil C, and that the legacies of those fires are still detectable today (Fig. 5). These results are consistent with ecosystem modeling experiments, which find that both fire frequency and severity are the dominant drivers of C dynamics in sub-alpine coniferous forests over centennial to millennial timescales (Hudiburg et al., 2017). Furthermore, the greater variance in C concentrations observed in soils burned in the early 20th century (σ^2=37.31) versus soils not burned (σ^2=12.44)(Fig. 5) may also reflect aspects of fire history, and specifically high spatial variability in fire severity and post-fire recovery.

The results from this study are broadly consistent with ecosystem model simulations suggesting that changing fire regimes under climate change scenarios have the potential to alter C stored in forested ecosystems by changing the frequency and intensity of wildfire events (Hudiburg et al., 2017;Kelly et al., 2016). We show that even in a relatively small region of subalpine forests in the Rocky Mountains, an assumption of a single value for C stocks would not hold, and are instead highly dependent on a spatially heterogeneous fire history extending back for a least a century. The importance of this variability in determining post-fire C dynamics implies that equilibrium scenarios extrapolated from a single fire event in one location are a poor assumption when simulating fire regimes in Earth System models at spatial scales larger than an individual site (Hudiburg et al., 2017).

3.3 Evaluating nutrient limitations

The process whereby forest vegetation typically returns to pre-fire conditions after several years or decades following wildfire events is referred to as biogeochemical resilience (McLauchlan et al., 2014;Smithwick, 2011). This resilience is determined, in part, by the availability of growth limiting nutrients, such as N and P (Güsewell, 2004;Schreeg et al., 2014). In non-N_2-fixing plant species, foliar N and P concentrations reflect soil N and P availability (Reich and Oleksyn, 2004). Previous studies have shown that a N/P mass ratio in foliar material of about 10-20 is optimal for plant growth (Aerts and Chapin, 1999;Ingestad and Lund, 1979). N/P ratios >16 can indicate P-limited biomass productions, whereas N/P ratios <14 are suggestive of N-limited plant growth (Aerts and Chapin, 1999;Koerselman and Meuleman, 1996).

The average (± 95% confidence intervals) N/P values for sampled foliage (n=72) was 9.8 ± 0.6. This suggests a N-limited growing environment. Although N/P ratios of leaves are often used to evaluate nutrient status in plants, several factors could complicate this interpretation: (1) N/P ratios of old leaves may be different than new foliage growth (Schreeg et al., 2014). When plants are older, nutrients are reallocated to active meristems (e.g., young leaves, shoot tips) (Güsewell, 2004). We did not account for foliage or plant age during sampling. (2) All foliage was recovered in the summer, therefore N/P ratios could be low because samples were taken during the period of active growth (Méndez and Karlsson, 2005;Rivas-Ubach et al., 2012). (3) As a result of N limitation, biomass allocation to roots can increase at the expense of foliage (Andrews et al., 1999;De Groot et al., 2003). (4) P uptake can be enhanced in response to deficiencies through several mechanisms, such as exudation of enzymes or acids (Dakora and Phillips, 2002) and association with mycorrhizal fungi (Colpaert et al., 1999). (5) Productivity might also be limited by other elements (van Duren and Pegtel, 2000), solar irradiance, and/or climatic factors (Spink et al., 1998).

To assess potential nutrient limitations resulting from wildfire, we compared average N and P concentrations in foliar material from plants grown in soils that were burned in 1910 and 1918 CE (n= 29) with sites not burned (n= 43) since the start of the Fire Atlas (Morgan et al., 2014). We found no significant difference in average N (t = -0.13, df= 47.76, p= 0.8948) or P (t= 0.99, df= 53.48, p= 0.3258) concentrations between the two sample groups. Likewise, average C (t= -0.40, df= 65.96, p= 0.6901) concentrations did not significantly differ between foliar samples taken from burned versus unburned locations. This indicates that, although past wildfires reduced the pool of soil C, they did not affect the concentration of growth limiting nutrients measured in vegetation a century later.

4. Conclusions

Analyses of foliar and soil samples from a network of sites located in the northern U.S. Rocky Mountains indicate the spatial distribution of key elements in subalpine forested ecosystems. The concentration of C and nutrients (N, K, Mg, Ca) in soils is highest in the upper litter and organic horizons and decreases at depth in the mineral soil, consistent with previous studies. Comparing the two plant functional types, needle leaf plants contain higher concentrations of C, while broadleaf material is enriched in N and other trace elements (Mg, SO_4). Sites that were burned in a regionally extensive wildfire in the early 20th century contained significantly lower C on average in the organic soil horizon, compared with sites that burned prior to the 20th century. This highlights the important role of wildfires as a dominant driver of soil C dynamics in sub-alpine forests, with legacies that can last for more than a century (Hudiburg et al., 2017). Furthermore, the high degree of variance in soil C concentrations among burned soils is consistent with the inherent spatial heterogeneity in fire severity seen in contemporary fires. This spatial heterogeneity adds to additional complexity Earth Systems Modeling efforts to represent fire across space and time. The low average values of foliar N/P ratios (9.8 ± 0.6) suggest that N may be in low supply to plants. Therefore N availability in soils may play an important role in understanding the biogeochemical resilience of coniferous forests to wildfires. Finally, these data contribute empirical data to efforts to model the biogeochemical consequences of wildfires in the subalpine forests of western North America.

Data Availability

Foliar data are available in the TRY Plant Trait Database.

Supplemental information

Supplementary information is available online.

Author contribution

DPP and KKM designed the study, analyzed the data, and prepared the paper with contributions from BC, KW, and PEH. KW and PEH selected study sites. KW, PEH, and KKM collected the samples. BC conducted laboratory analyses to acquire data and assisted with data analysis.

Competing interests

The authors declare that they have no conflict of interest.

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Table 1. Study sites

Site name	Elevation m asl	Latitude	Longitude	Year of last major fire (CE)[1]
Cliff	1810	47.1390	-115.1919	1910
Heart	1682	47.2856	-115.4529	unknown
Hoodoo	1817	46.9789	-115.0012	unknown
Hub	1819	47.2756	-115.3757	unknown
Kid	1909	46.7782	-114.8146	1910
Little Montana	2011	46.8151	-114.7652	unknown
Lost Lake	1840	47.1047	-115.1274	1910
Lower Bonanza	1922	47.0916	-115.1330	1910
Lower Oregon	1811	47.0554	-115.0913	unknown
Missoula	1807	47.0671	-115.1162	1910
Moore	1629	47.1818	-115.2521	unknown
Silver	1623	47.3596	-115.5659	1918
Surveyor	1831	46.8241	-114.7585	unknown
Upper Bonanza	1922	47.0916	-115.1330	1910
Upper Oregon	1811	47.0554	-115.0913	unknown

[1] This coverage includes fire perimeters recorded from 1901-2008 CE (Morgan et al., 2014).

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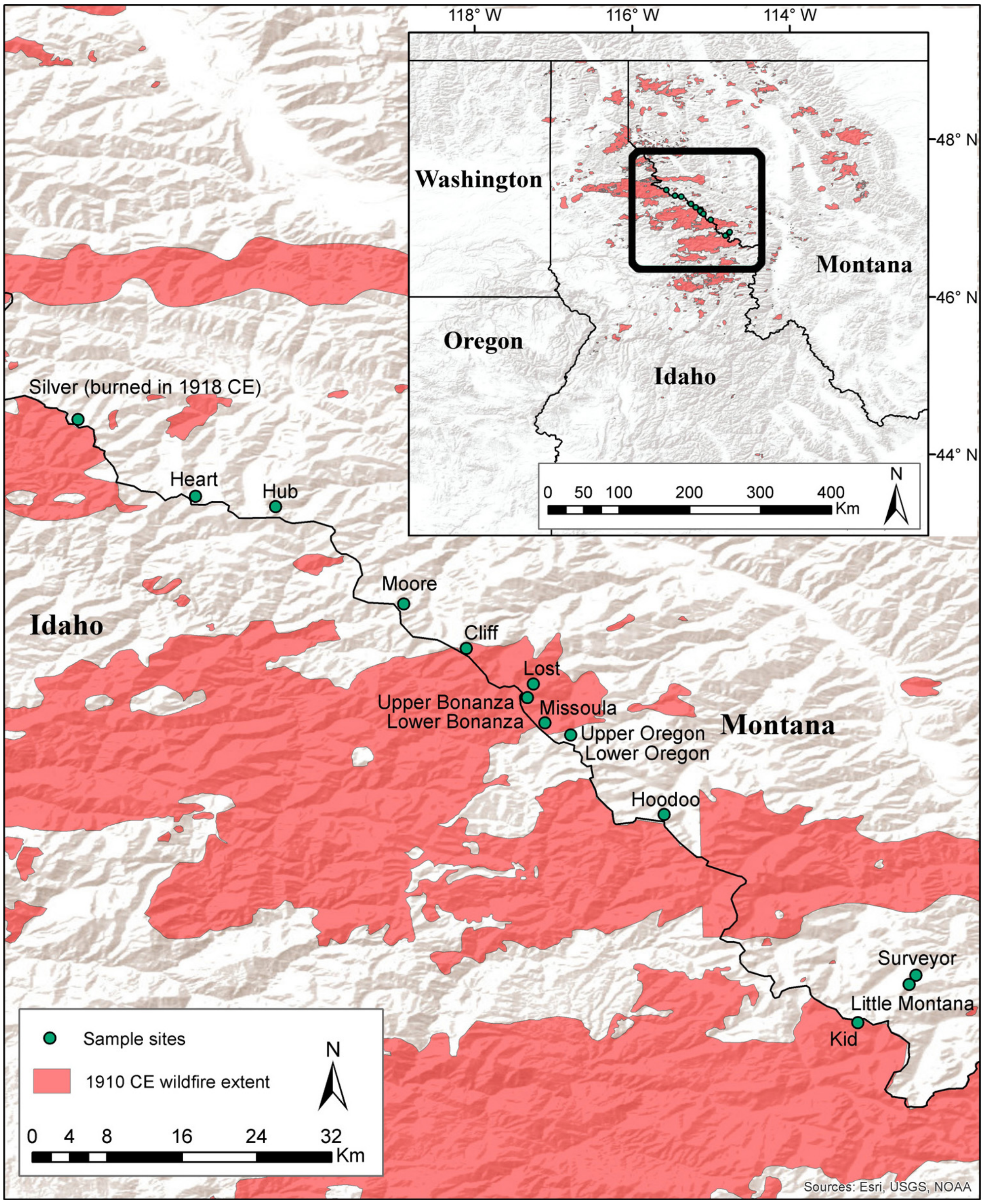
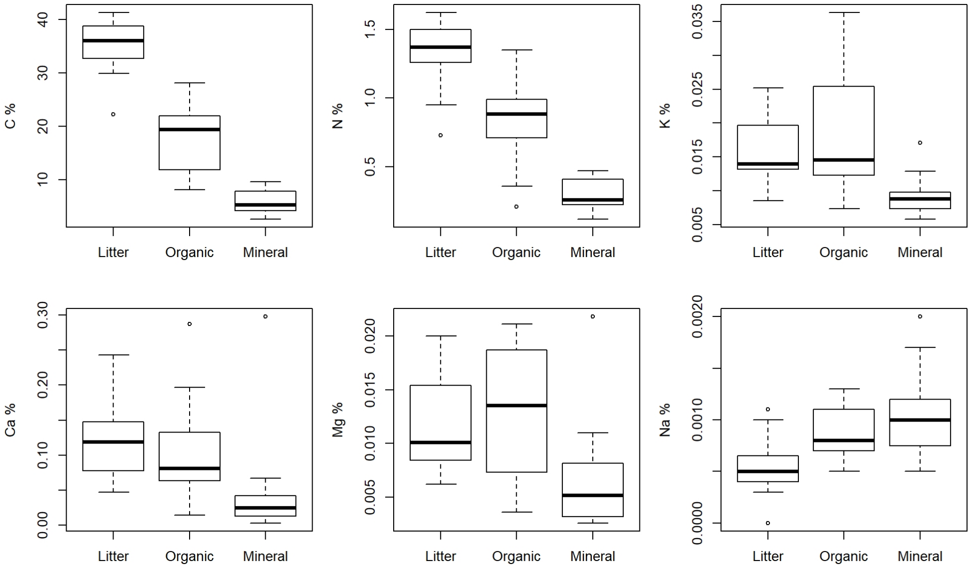
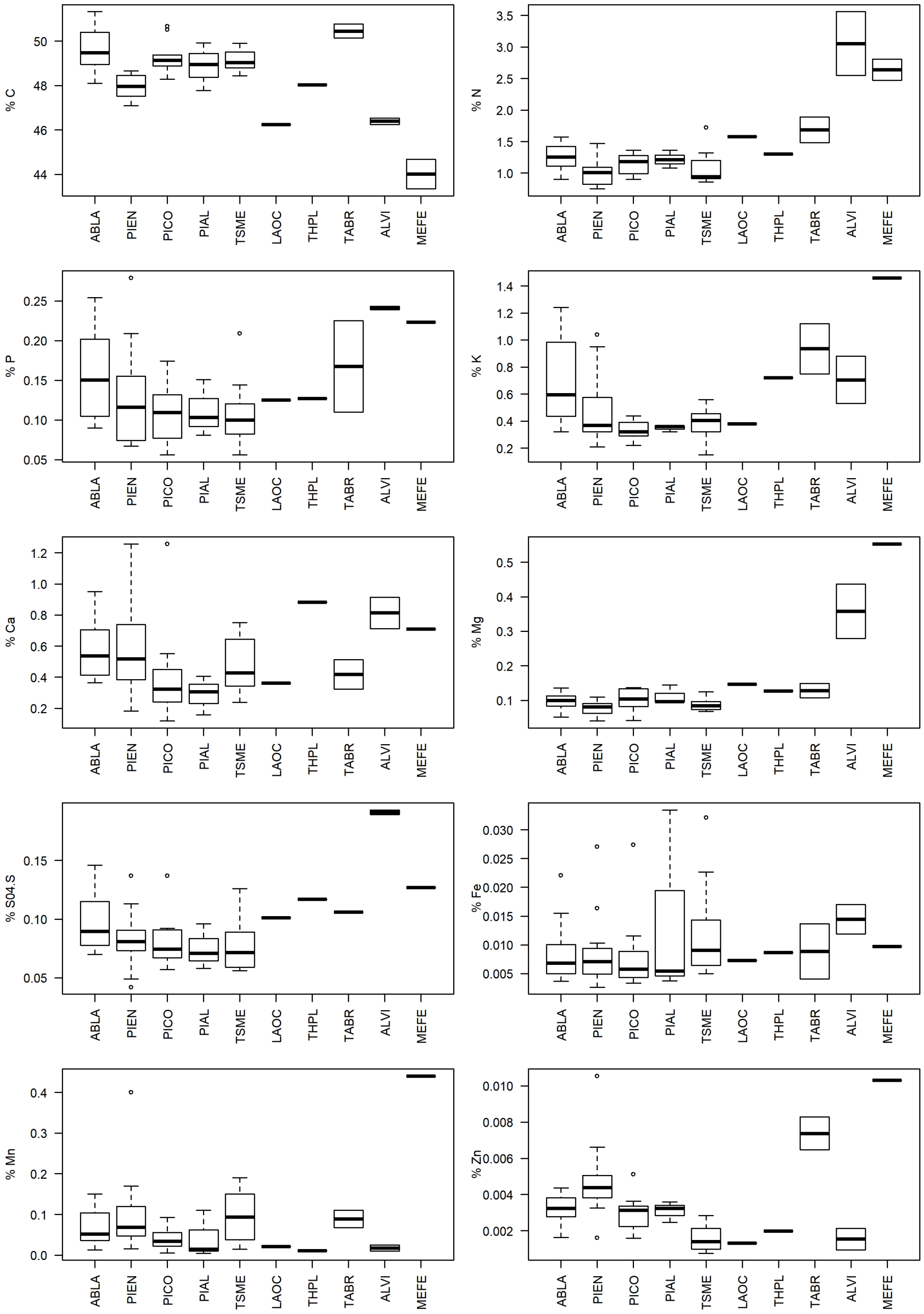


Fig. 1) (Bottom) Map of the study area with 1910 CE fire extent polygons (Morgan et al., 2014). (Upper right) Regional map of the study region.



375
376 Fig. 2) Boxplots displaying element concentrations in soil samples.
377



378
379 Fig. 3) Boxplots displaying element concentrations in foliar samples. Subtypes are *Abies*
380 *lasiocarpa* (ABLA), *Alnus viridis* (ALVI), *Larix occidentalis* (LAOC), *Menziesia*

ferruginea (MEFE), *Pinus albicaulis* (PIAL), *Pinus contorta* (PICO), *Picea engelmannii* (PIEN), *Taxus brevifolia* (TABR), *Thuja plicata* (THPL), and *Tsuga mertensiana* (TSME).

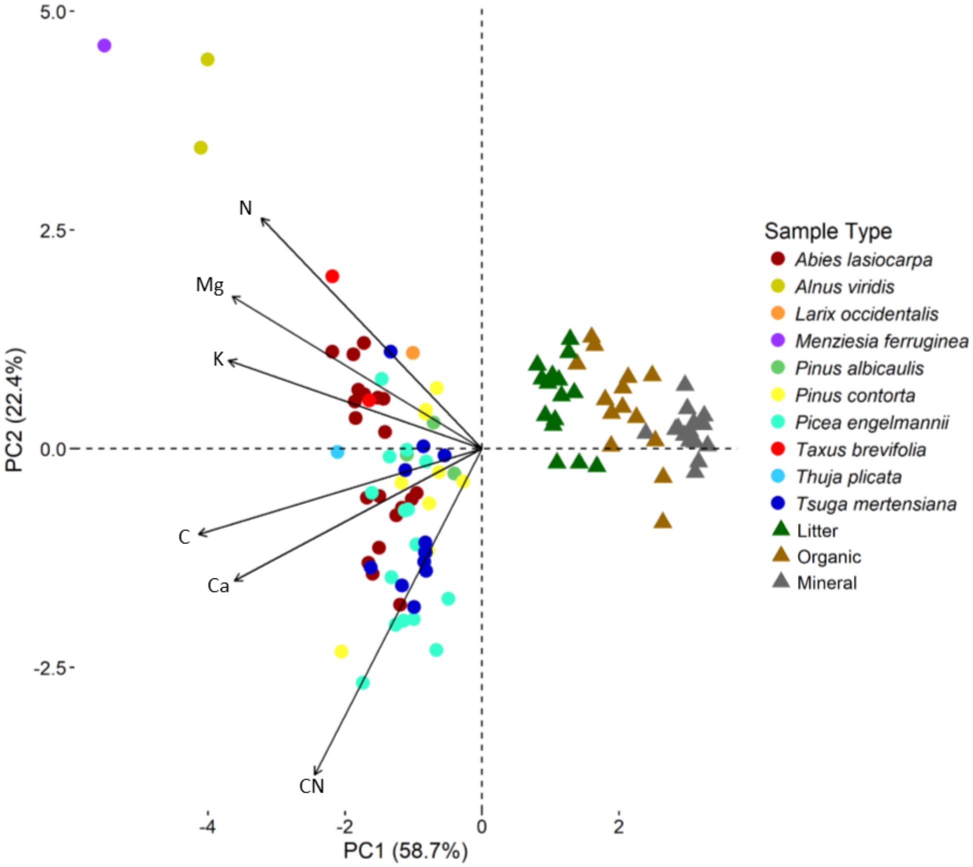


Fig. 4) Principal component analysis of soil and vegetation element concentrations.

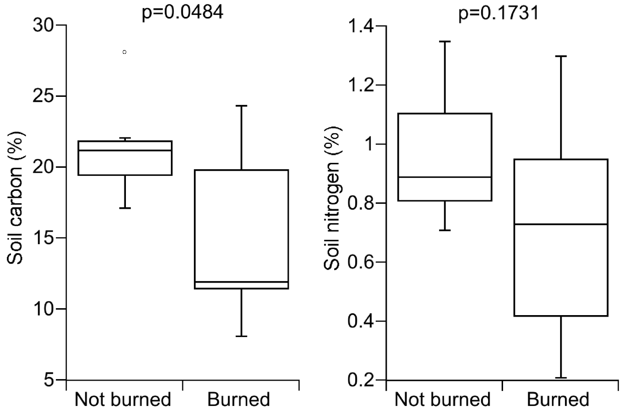


Fig. 5) Boxplots of C and N from the organic soil horizon burned (n= 7) in 1910 CE and 1918 CE versus sites not burned (n= 7) during the historical record (Morgan et al., 2014). An unpaired t-test indicates that soil C concentrations are significantly (p=0.0484) lower in burned sites.

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