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Soil Organic Carbon Storage and Aggregate Stability in an Arid Mountain Range, White Mountains, CA

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Soil Organic Carbon Storage and Aggregate Stability in an Arid Mountain Range, White Mountains, CA

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in

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by

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DEDICATION

This thesis is dedicated to my mom, Valerie.

You are my inspiration.

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1. INTRODUCTION

Soil organic carbon (SOC) has significant potential to influence the global carbon cycle. Soils contain three times as much carbon as is contained in plant biomass and the atmosphere combined, and can act as a net sink or a net source of carbon dioxide, depending on environmental conditions. While the net primary productivity (NPP) of an ecosystem dictates how much carbon enters a soil system (Baldock, 2007), site specific factors such as soil mineralogy (Torn et al., 1997; Baldock and Skjemstad, 2000), clay content (Torn et al., 1997; Huang and Schnitzer, 1986), and redox status (Reddy and Patrick, 1975; DeLuane et al., 1981), as well as external factors such as climate, have been shown to influence the storage of carbon as SOC (Sollins et al., 1996). However, responses of SOC to climate change, especially temperature and precipitation, remain unclear (Dungait et al., 2012; Wu et al., 2011; Schmidt et al., 2011). Attempts to elucidate soil carbon responses to varying temperatures and respiration rates alone have had conflicting results, illustrating the uncertainties in SOC response to climate change (Knorr et al., 2005; Giardina and Ryan, 2007; Davidson et al., 2000; Trumbore et al., 1996).

Soil structure and soil organic carbon are intimately associated; organic inputs encourage the formation of aggregates, which when considered in conjunction with soil pores, make up the three-dimensional arrangement of soil structure. Soil aggregates protect organic inputs from decomposition by creating a physical barrier to heterotrophic microbes, which in turn influences SOC storage and retention (Schmidt et al., 2011; Blanco-Canqui and Lal, 2003). Because of the intimate association between SOC and aggregate stability, any changes in one parameter will likely have effects on the other.

Desertification is projected to be one consequence of climate change (IPCC, 2007). In the United States, one third of the land area is affected by desertification, and according to the United Nations Environment Program (UNEP) (1975), the rate of desertification is accelerating. In the southwestern United States, desertification is exemplified by replacement of arid and semiarid grasslands by desert shrubs (York and Dick-Peddie, 1969; Schlesinger et al., 1990; Bahre and Shelton, 1993), which causes landscape-scale redistribution of soil resources such as carbon and nitrogen, where accumulation occurs under shrubs and depletion occur under shrub-interspaces (Tromble, 1988; Mauchamp and Janeau, 1993; Rostagno, 1989; Takar et al., 1990). The heterogeneity of these systems confounds the spatial understanding of their SOC distribution, and this heterogeneity must be considered in any inventories of SOC storage and aggregate stability to accurately depict soil resource availability and landscape stability (Bird et al., 2002). Assessments of SOC inventories and the spatial distribution of stable aggregates in arid and semiarid ecosystems, as well as their potential for change, is critical to understanding how a warming climate may impact SOC and soil functioning on a global scale. Although soil organic carbon content in arid systems is lower than in their more humid counterparts, their contribution to terrestrial carbon inventories is significant; the global distribution of arid systems is greater than that of tropical, temperate and boreal forests combined, and more than twice that of tropical savannas and grasslands (IPCC, 2000). The areal distribution of arid systems is also actively increasing (UNEP, 2000). Arid and semiarid environments are of vital importance, as these systems are fragile and susceptible to landscape-scale change with relatively small system perturbations (Reynolds et al., 1999; Schlesinger et al, 1990). Furthermore, these systems lend insight into understanding how microscale changes in soil properties, such as organic matter, moisture, and nutrient status, affect soil functioning at the landscape scale.

Elevation transects have been an important tool used to investigate the relationship between SOC and a dynamic climate at the regional scale. Increases in altitude are accompanied by increases in precipitation and decreases in temperature, which in turn influence the type and amount of SOC input, metabolic activity of decomposer organisms, and carbon mineralization rates. Consequently, elevation transects can be used to investigate the effects of climate change on SOC dynamics and associated processes, as changes in temperature and precipitation with elevation may serve as a proxy for future climate conditions and, by association, any climate-driven changes in SOC and related processes. Indeed, one climate change scenario assumes shifts from Mediterranean climate zones to semiarid and arid zones, characterized by higher temperatures and lower precipitation amounts (Lavee et al., 1998).

The overall goal of this research is to assess how a warming climate may impact SOC and aggregate stability in high elevation arid systems at the landscape and regional scale. This is accomplished by integrating landscape heterogeneity in our inventory of SOC (Chapter 1), and evaluating aggregate stability under the different landscape components that frequently result as a product of a warming climate (Chapter 2). In addition, this research aims to assess the impact of regional climatic changes on SOC storage and distribution (Chapter 1), as well as aggregate stability (Chapter 2), by using a climatological transect in a high- elevation, arid mountain range to simulate changes in temperature and precipitation induced by a warming climate.

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2. THE EFFECT OF SPATIAL VARIATION AND CLIMATE ON SOC STORAGE AND DISTRIBUTION IN A HIGH ELEVATION ARID MOUNTAIN RANGE, WHITE MOUNTAINS, CA, USA

Introduction

Soil organic carbon (SOC) has significant potential to influence the global carbon cycle. Soils contain three times as much carbon as is contained in plant biomass and the atmosphere combined (Ågren and Bosatta, 2002), and can act as a net sink or a net source of carbon dioxide, depending on environmental conditions (Jastrow et al., 2007). Soil organic carbon is formed as atmospheric CO_2 enters terrestrial ecosystems via photosynthesis, whereby carbon is transformed from inorganic to organic forms. Temporary storage in plant biomass occurs initially, but eventually this carbon becomes deposited in the soil by plant and microbial secretion or death. Upon entering the soil system, organic carbon can either be mineralized through microbial respiration or stored within the soil. Soil organic carbon (SOC) storage is a function of the difference between the net primary productivity (NPP) and decomposition rate (Baldock, 2007; Janzen, 2004; Lutzow et al., 2006). While the NPP of an ecosystem dictates how much carbon enters a soil system (Baldock, 2007), site specific factors such as soil mineralogy (Torn et al., 1997; Baldock and Skjemstad, 2000); clay content (Torn et al., 1997; Huang and Schnitzer, 1986); and redox status (Reddy and Patrick, 1975; DeLuane et al., 1981) have been shown to influence the stability of carbon inputs (Sollins et al., 1996).

Soil organic carbon (SOC) and soil carbon dynamics have been extensively studied, traditionally in terms of their effects on agricultural productivity and viability. Soil organic carbon has been shown to increase water retention (Rawls et al., 2003), positively influence soil fertility (Tiessen et al., 1994), and improve soil aggregation and structure (Jastrow et al., 1996;

Paustian et al., 2000; Tisdall and Oades, 1982), attributes that enhance agricultural productivity. More recently, SOC has been investigated to understand its role in a changing climate, and how it can be used to sequester atmospheric carbon as a climate change mitigation tool. However, SOC dynamics are not completely understood (Blanco-Canqui and Lal, 2004; Sollins et al., 1996; Wang and Hsieh, 2002), and responses of SOC to climate change, especially temperature and precipitation, remain unclear (Dungait et al., 2012; Wu et al., 2011). Attempts at elucidating soil carbon response to varying temperatures and respiration rates alone have had conflicting results, illustrating the uncertainties in SOC response to climate change (Knorr et al., 2005; Giardina and Ryan, 2007; Davidson et al., 2000; Trumbore et al., 1996).

Desertification is projected to be one consequence of climate change (IPCC, 2007). In the United States, one third of the land area is affected by desertification, and ccording to the United Nations Environment Program (UNEP) (1975), the rate of desertification is accelerating. In the southwestern United States, desertification is exemplified by replacement of arid and semiarid grasslands by desert shrubs (York and Dick-Peddie, 1969; Schlesinger et al., 1990; Bahre and Shelton, 1993). Replacement of arid and semiarid grasslands by desert shrubs causes landscape-scale redistribution of soil resources such as carbon and nitrogen, where accumulation occurs under shrubs and depletion occur under shrub-interspaces (Tromble, 1988; Mauchamp and Janeau, 1993; Rostagno, 1989; Takar et al., 1990). This results in landscape heterogeneity which confounds our spatial understanding of SOC distribution in these ecosystems at the landscape-scale, and must be considered in any inventories to accurately depict soil resource availability (Bird et al., 2002). Assessments of SOC inventories in arid and semiarid ecosystems, as well as their potential for change is critical to understanding how a warming climate may impact SOC on a global scale. Although soil organic carbon content in arid systems is lower than in their more humid counterparts, their contribution to terrestrial carbon inventories is significant; the global distribution of arid systems is greater than that of tropical, temperate and boreal forests combined, and more than twice that of tropical savannas and grasslands (IPCC, 2000). Furthermore, arid soils are a massive repository for carbonate-carbon which is less vulnerable to impacts of climate change than soil organic carbon (Batjes, 1996). The areal distribution of arid systems is actively increasing (UNEP, 2000).

Elevation transects have been an important tool for investigating the relationship between SOC and a dynamic climate at the regional scale. Increases in altitude are accompanied by increases in precipitation and decreases in temperature, which in turn influence the type and amount of SOC input, metabolic activity of decomposer organisms, and carbon mineralization rates. Consequently, elevation transects can be used to investigate the effects of climate change on SOC dynamics, as changes in temperature and precipitation with elevation may serve as a proxy for future climate conditions and, by association, any climate-driven carbon gains or losses. Indeed, one climate change scenario assumes shifts from Mediterranean climate zones to semiarid and arid zones, characterized by higher temperatures and lower precipitation amounts (Lavee et al., 1998).

The objectives of this research were to assess how a warming climate may impact SOC in arid systems at the landscape scale by integrating landscape heterogeneity in our inventory of SOC, as well as at the regional scale using an elevation transect along an arid mountain range to simulate changes in temperature and precipitation induced by a warming climate. In addition, an investigation was made of the extent of soil resource heterogeneity, and how this heterogeneity changes under a warming climate.

Materials and Methods

Environmental setting

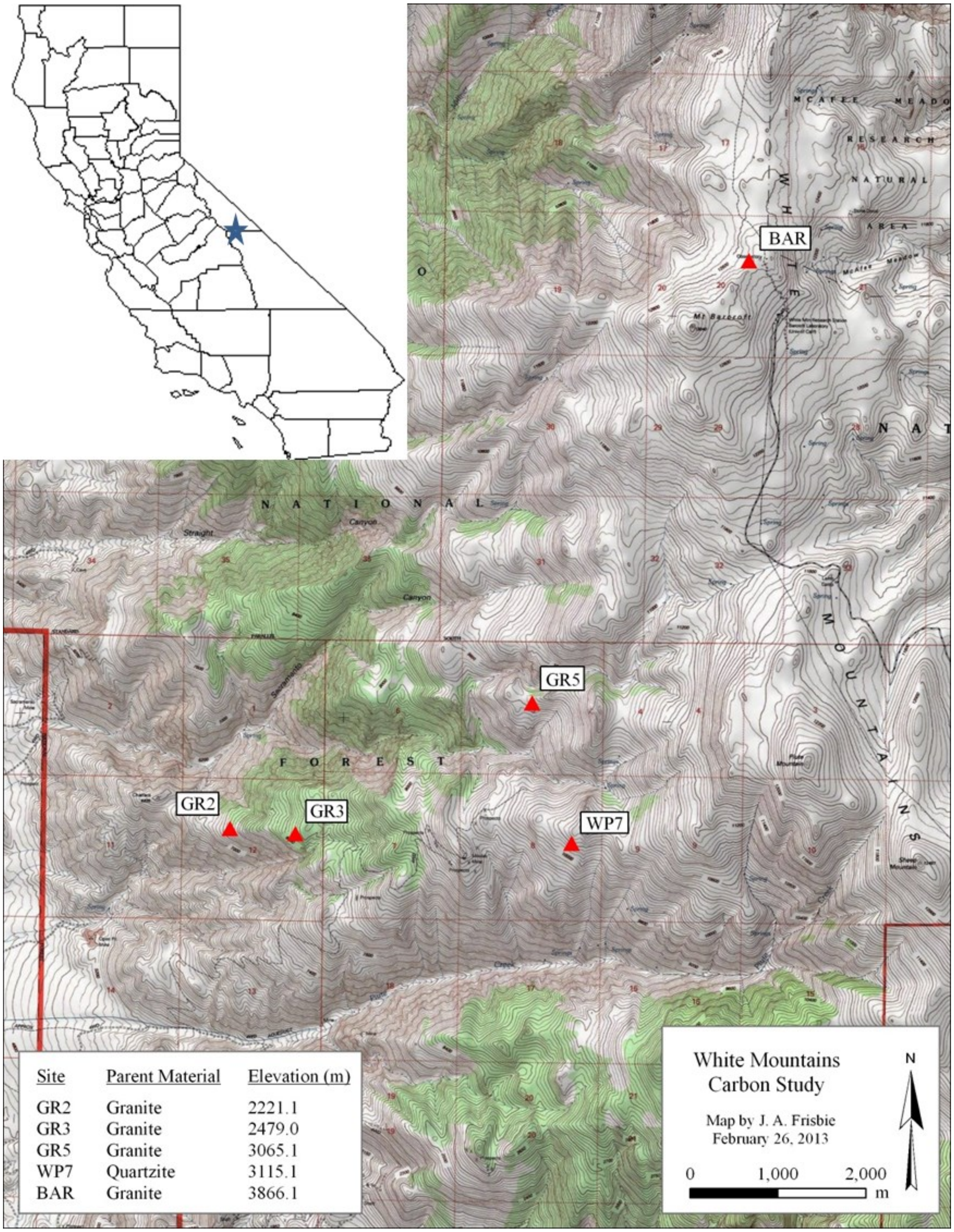
This study was conducted along an elevation gradient in the White Mountains, Mono County, California. The White Mountains are a fault-block mountain range located within the eastern section of Inyo National Forest, and on the western margin of the Basin and Range Province. The White Mountains face westward toward the Sierra Nevada across the upper Owens Valley. The Inyo Mountains lie to the south, where the two ranges are separated by Deep Springs Valley and Westgard Pass. To the east lies Fish Lake Valley, and the northern end of the White Mountains is bounded by Montgomery Pass. The towns of Bishop, Big Pine, and Independence lie to the west and southwest. Five elevations were chosen for the study (2221, 2479, 3065, 3115, and 3866 m) (Figure 1), encompassing Pinyon-Juniper woodland (PJW), subalpine, and alpine ecosystems. Mean annual temperature (MAT) along the elevation gradient was obtained by interpolation of data obtained from three meteorological stations located within and below the White Mountain range. Within the range, the White Mountain Research Station (WMRS) operates two weather stations, one in the valley of Crooked Creek (White Mountain I) at 3095 m, and one on the eastern slope of Mt. Barcroft (White Mountain II) at 3800 m. Climate data from these stations are from 1956 to 1985. Outside of the range, the National Weather Service operates a weather station on the valley floor in Bishop, CA at 1250 m, and data are from 1947 to present. MAT decreases from 7.1 ^{o}C at 2221 m to -2.7 ^{o}C at 3866 m. Mean annual precipitation (MAP) data was also obtained by interpolation, and increases from 23.8 cm at 2221 m to 44.6 cm at 3866 m. Soil moisture regime (SMR) along the elevation gradient is aridic, and soil temperature regimes (STR) grade from mesic and frigid at 2221 and 2479 m, to cryic at 3065, 3115 and 3866 m. All soils along the elevation transect were formed on granite except site WP7 at 3115 m, which was formed on quartzite and is included in the study for comparison of soil characteristics across parent materials. The soils are on mountain backslopes with slopes ranging 10 to 39 percent. Site and soil characteristics are summarized in Table 1.

Table 1. Summary of site characteristics

Site	Elevation (m)	[1]MAT (°C)	[2]MAP (cm)	[3]SMR	[4] STR	Geology	Ecosystem	Slope (%)	*Rock Fragment (%)	Aspect	Great Group
GR2	2221	7.1	23.8	Aridic	Mesic	Granite	PJW	39	31	W	Calciargid
GR3	2479	5.5	27.1	Aridic	Frigid	Granite	PJW	30	23	S	Haplargid
GR5	3065	2.1	34.5	Aridic	Cryic	Granite	Subalpine	27	42	W	Argicryid
WP7	3115	0.2	35.1	Aridic	Cryic	Quartzite	Subalpine	35	35	S	Argicryid
BAR	3866	-2.7	44.6	Aridic	Cryic	Granite	Alpine	10	72	W	Haplocryid

*Average soil rock fragment content of all pedons sampled at the site.

[1] MAT= mean annual temperature; [2]MAP= mean annual precipitation; [3]SMR= soil moisture regime; [4]STR= soil temperature regime.



Site	Parent Material	Elevation (m)
GR2	Granite	2221.1
GR3	Granite	2479.0
GR5	Granite	3065.1
WP7	Quartzite	3115.1
BAR	Granite	3866.1

Figure 1. Location of study sites.

Field sampling

At each elevation, a 600 m^2 sampling macroplot was established by distributing a 10 m line upslope and downslope from a chosen center point (total length of 20 m), and 15 m across-slope in both directions from the center point (total length of 30 m) (Figure 2). One to three pedons were selected for sampling and description at both ends of each line, depending on the type of vegetation present at each elevation. For shrub-dominated sites (GR2, GR5 and WP7), two pedons were selected for description at each end point. One pedon was chosen under mature representatives of mountain big sagebrush (*Artemisia tridentata)* or low sagebrush (*Artemesia arbuscula*)*,* and the second pedon was selected in the bare interspace between shrubs, outside of the canopy projection. At site GR3, the presence of trees in addition to shrubs and interspace made it necessary to sample three pedons at each end point, and pedons were sampled directly under singleleaf pinyon pine (*Pinus monophylla)* in addition to under shrubs and interspaces. At the highest elevation BAR site, a homogenous vegetative distribution including prairie Junegrass (*Koeleria macrantha*) and associated low-growing herbs and forbs, made only one pedon at each end point appropriate for sampling and description. This resulted in four replicate pedons for each microsite type (shrub, interspace, tree, and grass) present. One representative interspace pedon at GR2, GR3, GR5 and WP7, and one main grass pedon at BAR, was chosen for detailed physical and chemical analysis by the National Soil Survey Laboratory (NSSL) in Lincoln, Nebraska. All pedons were sampled to a depth of approximately 50 cm (or shallower if bedrock was encountered first), and pedons chosen for analysis by NSSL were sampled to two meters or bedrock if shallower. Rock fragment content of the main pedon was determined by weighing in the field, and rock fragments of all other pedons were visually estimated. The morphology of each pedon was described in the field, and samples were collected by morphologic horizon from each pedon and brought back to the laboratory for analysis.

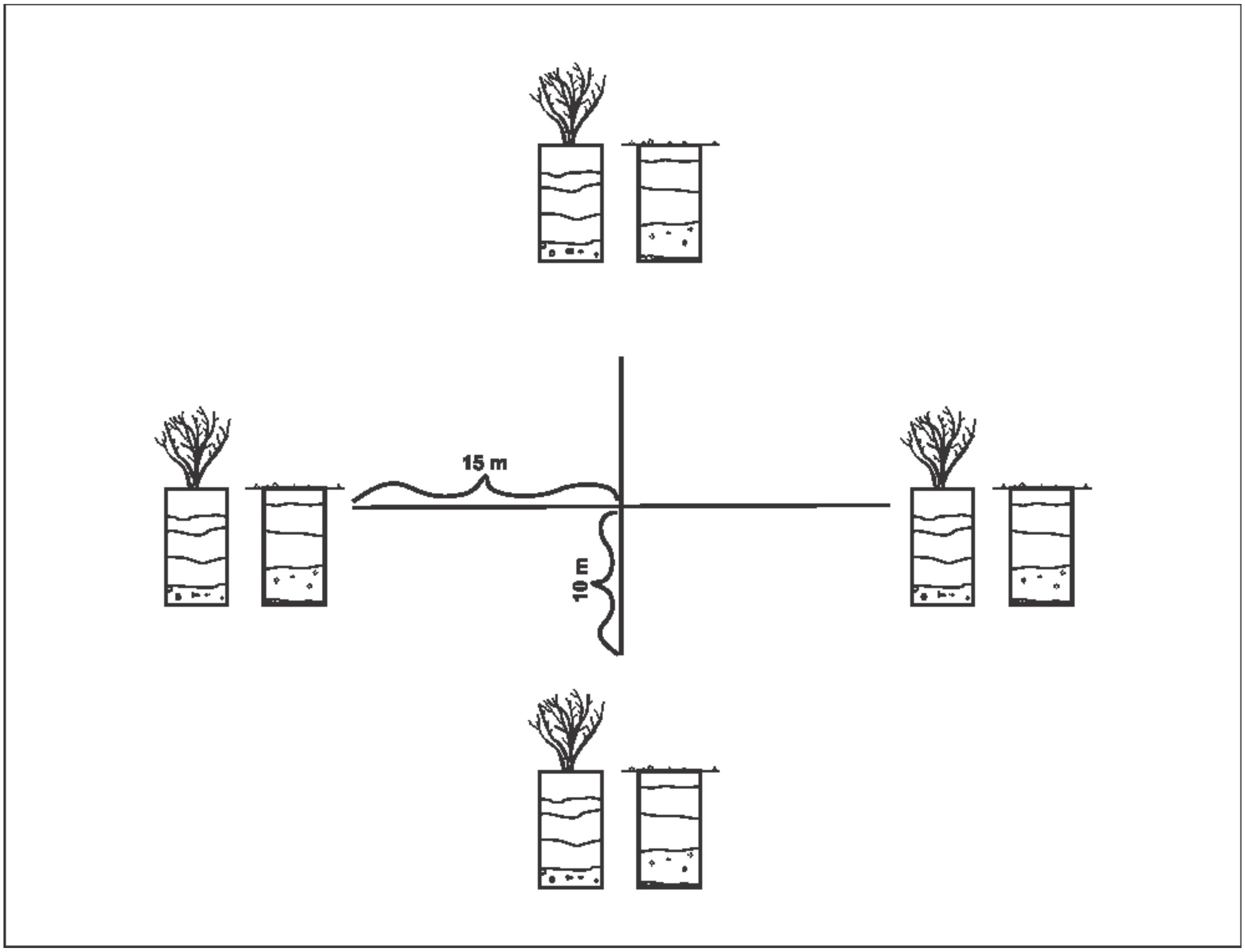


Figure 2. Field sampling diagram. Sampling plots were established from a center point, where one line was taken 10 m upslope and downslope from the center point and another line 15 m across slope in each direction from the center point. Microsite pedons were hand-dug, described, and sampled at each end point.

Figure 3. (a) Shrub and interspace distribution over landscape at site GR5; (b) grassland vegetation distribution over landscape at site BAR; (c) interspace pedon at site GR5; (c) shrub pedon at site GR5.

Vegetation

A variety of ecosystems is present along the elevation transect, and reflects the variation in climate that occurs with significant increases in elevation. All vegetation discussed here occurs in the sampling macroplot, and makes up the plant census at each elevation.

Pinyon-Juniper Woodland Ecosystem

Sites GR2 and GR3 are characterized as Pinyon-Juniper Woodland ecosystems (Hall, 1991). However, at site GR2 no trees were present in the sampling macroplot, and were not included in the plant census. At GR2, the dominant woody shrub species are mountain big sagebrush (*Artemisia tridentata* ssp*. vaseyana*) and Douglas rabbitbrush (*Chrysothamnus viscidiflorus*), with Mormon tea (*Ephedra nevadensis*) and spiny hopsage (*Grayia spinosa*) occurring as the sub-dominant shrub species. The dominant grass species is desert needlegrass (*Achanterum speciosus*), with a sparse occurrence of James galleta (*Pleuraphis jamesii*). No herbs or forbs were documented in the plant census at GR2. At site GR3 (2479 m) the woody shrub species mountain big sagebrush (*Artemesia tridentata* ssp. *vaseyana*) and Douglas rabbitbrush (*Chrysothamnus viscidiflorus*) dominate the landscape. Sub dominant woody shrub species are black sagebrush (*Artemesia nova*) and Mormon tea (Ephedra viridus). Singleleaf pinyon pine (*Pinus monophylla* Torr.) is the only tree. Milkvetch (*Astragalus lentinginous*) and granite prickly phlox (*Linanthus pungens*) are the dominant herb/forb on the landscape, and a sparse population of grizzlybear pricklypear (*Opuntia polycantha* var*. erinacea*) is also present. No grasses were documented in the plant census.

Subalpine Ecosystem

Sites GR5 (3065 m) and WP7 (3115 m) are characterized as subalpine ecosystems (Hall, 1991). The sites occur at similar elevations but differ in geologic substrate, resulting in different species composition. Site GR5 is dominated by the woody species mountain big sagebrush (*Artemisia tridentata* ssp*. vaseyana*) and Douglas rabbitbrush (*Chrysothamnus viscidiflorus*), with mountain snowberry (*Symphoricarpos rotundifolius*) and Mormom tea (*Ephedra viridis*) occurring as sub-dominant shrubs. Dominant grasses are pine needlegrass (*Achnatherum pinetorum*), starwort (*Arenaria sp*.), and squirreltail (*Elymus elymoides*), with a sparse population of Indian ricegrass (*Achnatherum hymenoides*) and prairie Junegrass (*Koeleria macrantha*). Dominant forbs/herbs are thorn skeletonweed (*Pleiacanthus spinosus*), cushion buckwheat (*Eriogonum ovalifolium*) and granite prickly phlox (*Linanthus pungens*), with milkvetch (*Astragalus lentinginous*), MacDougal's biscuitroot (*Lomatium foeniculaceum* ssp*. macdougalii*), compact phacelia (*Phacelia hastate* spp*. compacta*) and hoary tansyaster (*Machaeranthera canescens*) occurring in sparse populations.

Site WP7, on quartzite, is dominated by the woody shrub species low sagebrush (*Artemesia arbuscula*), with mountain big sagebrush and slender buckwheat (*Eriogonum microthecum*) occurring as sub-dominant shrub species. Sparse populations of Mormon tea (*Ephedra viridis*), spineless horsebrush (*Tetradymia canescens*) and rock spirea (*Holodiscus dumosus*) are also present. The dominant grass species is squirreltail (*Elymus elymoides*), with Sandberg bluegrass (*Poa secunda*) and needlegrass (*Achatherum* sp.) occurring as sub-dominant grasses. A sparse population of Ross' sedge (*Carex rossii*) is also present. The dominant forb/herb is bastardsage (*Eriogonum wrightii*), with cushion buckwheat (*Eriogonum ovalifolium*), matted buckwheat (*Eriogonum caespitosum*), granite prickly phlox (*Linanthus pungens*), mountain monardella (*Monardella odoratissima*), Clokey's fleabane (*Erigeron clokeyi*), desert parsley (*Lomatium* sp.), catchfly (*Silene* sp.), spreading groundsmoke (*Gayophytum diffusum*) and Indian paintbrush (*Castilleja* sp.) occurring as sub-dominant forbs/herbs. Also present is a sparse population of Douglas dustymaiden (*Chaenactis douglasii*).

Alpine Grassland Ecosystem

Site BAR is located in the alpine zone, which in the White Mountains is characterized as a high altitude desert with intense solar radiation, high wind speeds, and significant evaporative water loss (Hall, 1991). The landscape is dominated by the graminoid species prairie junegrass (*Koeleria macrantha*), Douglas sedge (*Carex douglasii*), and fiveleaf clover (*Trifolium andersonii*), with squirreltail (*Elymus elymoides*) and timberline bluegrass (*Poa glauca* ssp*. rupicola*) occurring as sub-dominant grasses. Dominant forbs/herbs are Watson's spikemoss (*Selaginella watsonii*), dwarf phlox (*Phlox condensate*), fewseed draba (*Draba oligosperma*), and cushion buckwheat (*Eriogonum ovalifolium* var*. nivale*). Also present are sparse populations of Sierra beardtongue (*Penstemon heterodoxus*), Mason's Jacob's-ladder (*Polemonium chartaceum*) and clubmoss mousetail (*Ivesia lycopodioides*).

Site Characterization

The geomorphology of all sampling sites from 2221 to 3115 m is broad ridgeline slopes separated by deep canyons. The highest elevation site located at 3866 m is on a mountain backslope. Percent interspace, shrub cover, and surface litter cover were determined using two

45.7 m line transects that intersected at their centers, one trending NE-SW and one trending NW-SE. These transects were used to measure the proportion of line occupied by the various components. Plant production was calculated by establishing five representative 3.7 x 7.3 m plots, and sampling and weighing all aboveground vegetation within the plot. A correction for water content was used to express vegetation weight on an air-dry basis. Air-dry vegetation weight was then converted to a mass per area basis using the plot areas. Surface site characteristics are summarized in Table 2.

Table 2. Surface site characteristics

Site	Interspace (%)	Shrub Cover (%)	Tree Cover (%)	Standing Biomass (lbs/acre)	Litter Cover (%)	Lichen Crusts (%)	Rock Fragments (%)	†Clay (%)	Profile Depth (cm)
GR2	28.5	71.5		141	17.6	20.6	56.9	17.7	80
GR3	71.7	9.3	19.0	880	44.5	30.6	36.6	22.4	55
GR5	57.0	43.0		312	23.5	33.7	37.6	15.8	45
WP7	83.2	16.9		1683	35.0	16.8	60.0	7.2	110
BAR	0	100.0		433	28.0	20.6	46.0	3.6	152

†All values listed are surface characteristics except clay, which is the weighted average of clay in the control section of the representative pedon sent to NSSL.

Soil samples

Bulk density measurements were made in the field using the plaster cast method (Frisbie et al., 2014, *in press*). All samples brought back to the laboratory were air dried and sieved to <2 mm. Subsamples from each morphologic horizon were oven-dried and ground for total carbon (TC) and nitrogen analysis. Total carbon and nitrogen concentrations of morphologic horizons were measured after combustion with an elemental analyzer (Thermo Scientific Flash EA 1112 Series, Massachusetts, USA). Soil samples reacting to introduction of 4N HCl (Nelson, 1982) were measured for carbonates. Soil organic carbon storage in pedons was calculated by multiplying SOC concentration (%) in a given horizon by the horizon bulk density, horizon thickness, and fraction soil volume (1-Rock $\text{Fragment}_{\text{horizon}}$), using conversions to obtain values on a mass per area basis (kg m^{-2}). Horizon SOC values were then summed to the 50-cm depth to get SOC at the pedon scale. Representative pedons sent to the NSSL were sampled to greater depth than the other replicate pedons at each site. For these pedons, SOC was determined to the 2 m depth (or bedrock). SOC found at depths greater than 50 cm was added to the other replicate pedons to that same depth. Replicate microsite pedon SOC values were then averaged, and multiplied by their respective microsite surface cover (Table 2) to obtain microsite SOC values. For example, at GR2 the pedons under shrubs averaged 5.04 kg m^{-2} SOC, and shrub cover at the site is 71.7%, so the total SOC storage under shrubs at GR2 was 3.6 kg m^{-2}. To obtain total SOC storage for a given elevation, averaged microsite SOC values were summed (e.g., interspace + shrub values). An example calculation of SOC storage is presented in Appendix B. Soil organic carbon of surface horizons was calculated using the same method, and includes any A or V horizons described in the field.

Statistical analysis

Differences in storage values between elevations were investigated using a one-way analysis of variance (ANOVA) and Tukey's Highly Significant Difference (HSD) Test.

Results

Soil organic carbon storage

Interspace SOC Storage

Storage in soil interspaces averaged between 0.80 and 1.16 kg C m^{-2} (Figure 4). No significant differences among interspace storage values were detected between elevations.

Shrub SOC Storage

Shrub SOC storage values averaged between 0.20 and 3.60 kg C m^{-2} (Figure 4). Significant differences in storage means were tested with Tukey's HSD. Results indicate significantly higher ($p<0.05$) SOC storage at site GR2 than GR3 and GR5.

Storage of Vegetated Sites

Three types of vegetation were present along the elevation transect, and include shrub, tree and grass. Considering all sampled elevations, average SOC storage under vegetated sites ranged from 1.54 kg C m^{-2} under shrubs to 3.84 kg C m^{-2} under grass. SOC storage under trees was the lowest of all vegetation types, with an average of 0.43 kg C m^{-2}. Soils under grass had significantly higher ($p<0.05$) SOC storage than under both shrubs and trees, and soils under shrubs had significantly higher ($p<0.05$) storage than found under trees (Figure 5).

Shrub and Interspace Storage

Differences in SOC storage between interspace and shrub microsites at each elevation were tested with Tukey's HSD, and show significant differences between SOC storage at sites GR2 and GR3 (Figure 4).

Total SOC Storage

Total SOC storage along the elevation transect ranged between 1.61 and 4.54 kg C m^{-2}, with highest total storage occurring at the lowest and highest elevations (Figure 6). No significant differences in total SOC storage values were observed between sites GR2 and BAR, which occur at the lowest and highest elevations; however, sites GR2 and BAR had significantly higher ($p<0.05$) total storage than GR2 and GR3.

A Horizon SOC Storage

Total SOC storage in the surface horizons (A and V horizons to the depth they were encountered) ranged between 0.13 and 3.08 kg C m^{-2} (Figure 7). Tukey's HSD determined site BAR had significantly higher storage amounts ($p<0.05$) in surface horizons than the other sites along the transect.

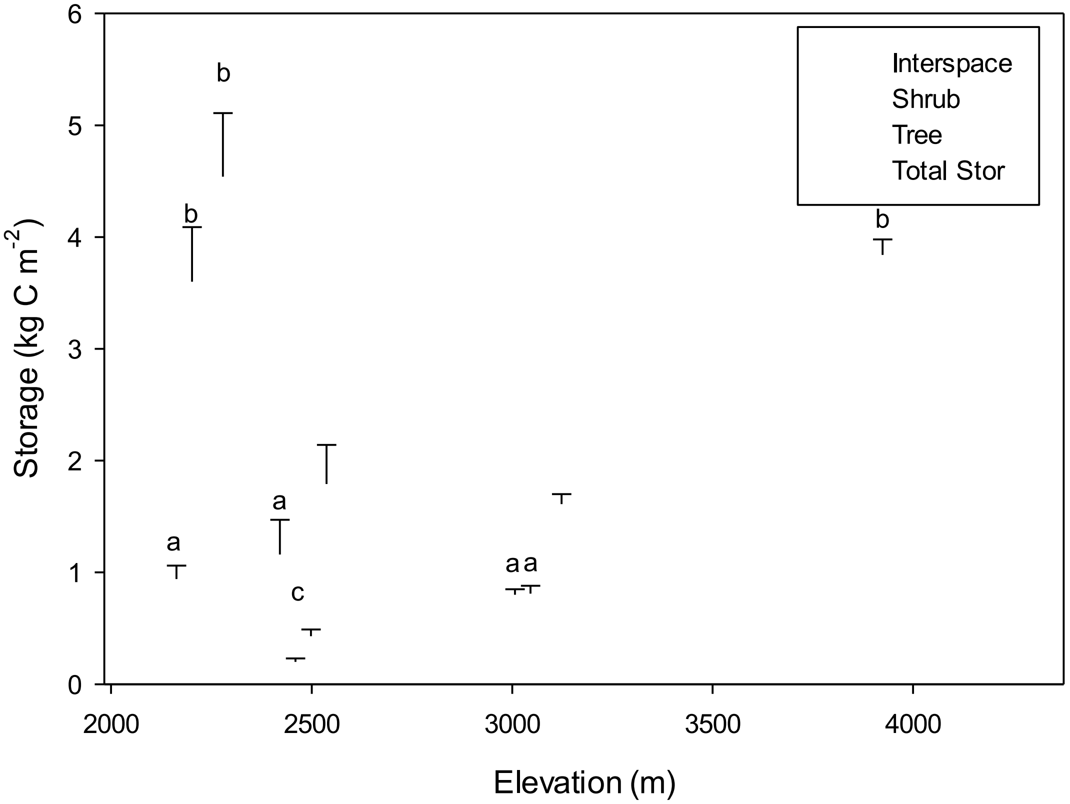


Figure 4. Total and microsite SOC storage (1 SE) grouped by elevation for soils on granite. Different letters indicate significant differences ($p<0.05$). Storage was calculated to profile depths indicated in Table 2.

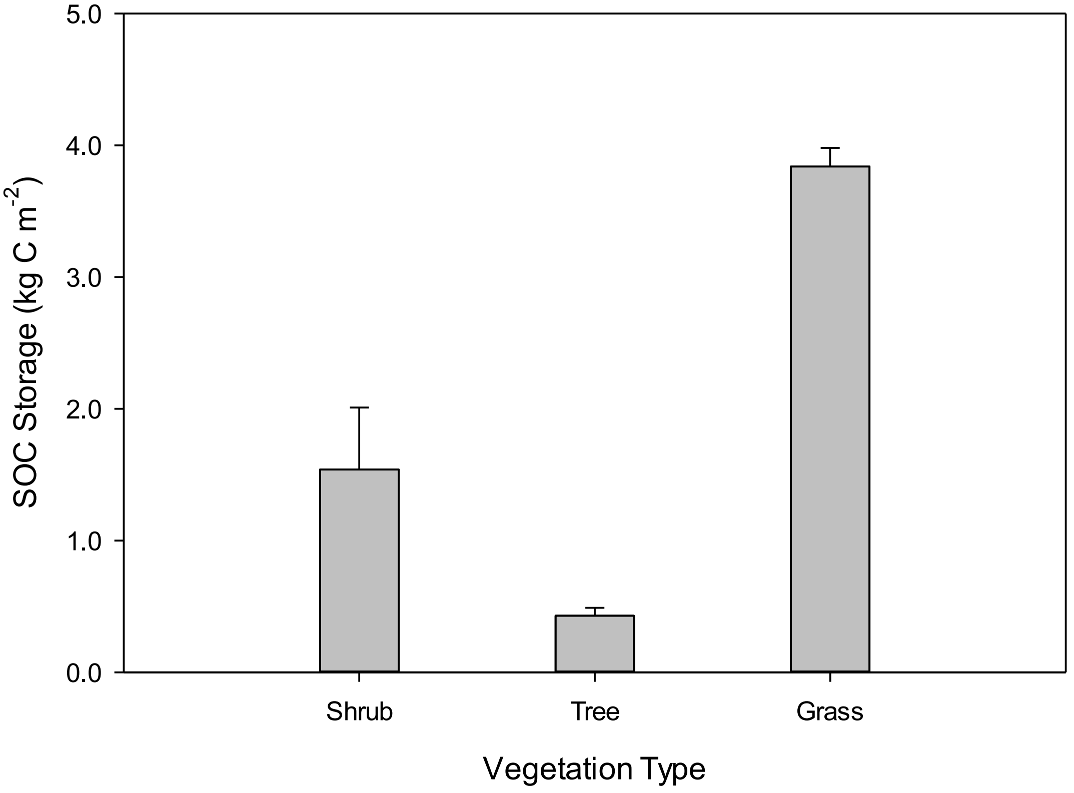


Figure 5. SOC storage under the various vegetation types present along the elevation transect.

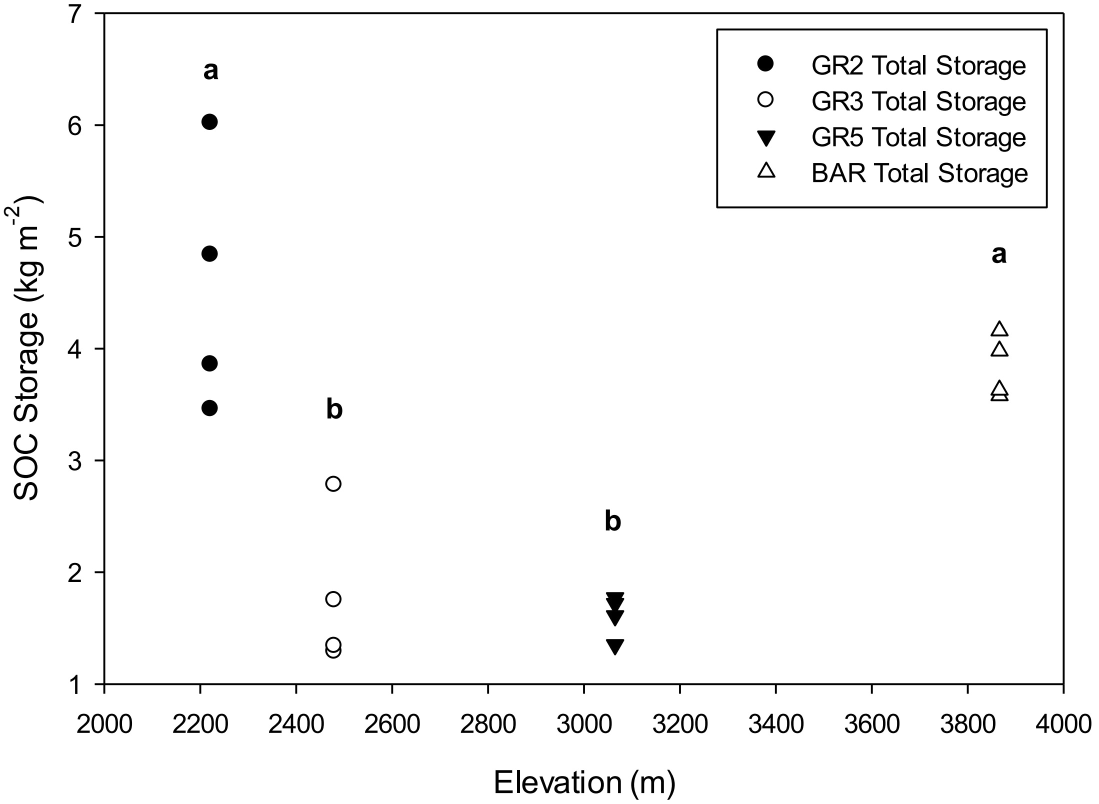


Figure 6. Total SOC storage as a function of elevation for soils on granite. Different letters indicate significant differences ($p<0.05$). At each elevation, SOC (kg m^{-2}) for each replicate microsite pedon (i.e., GR2-1I, 21, 31, 41; and GR2-1S, 2S, 3S 4S) was multiplied by its respective % cover. Each replicate microsite pedon set (i.e., GR2-1I and GR2-1S) was then summed to get total replicate SOC (kg m^{-2}). This was done for each of the 4 replicate pedon sets at each elevation, and represents the four data points in the graph. Storage was calculated to profile depths indicated in Table 2.

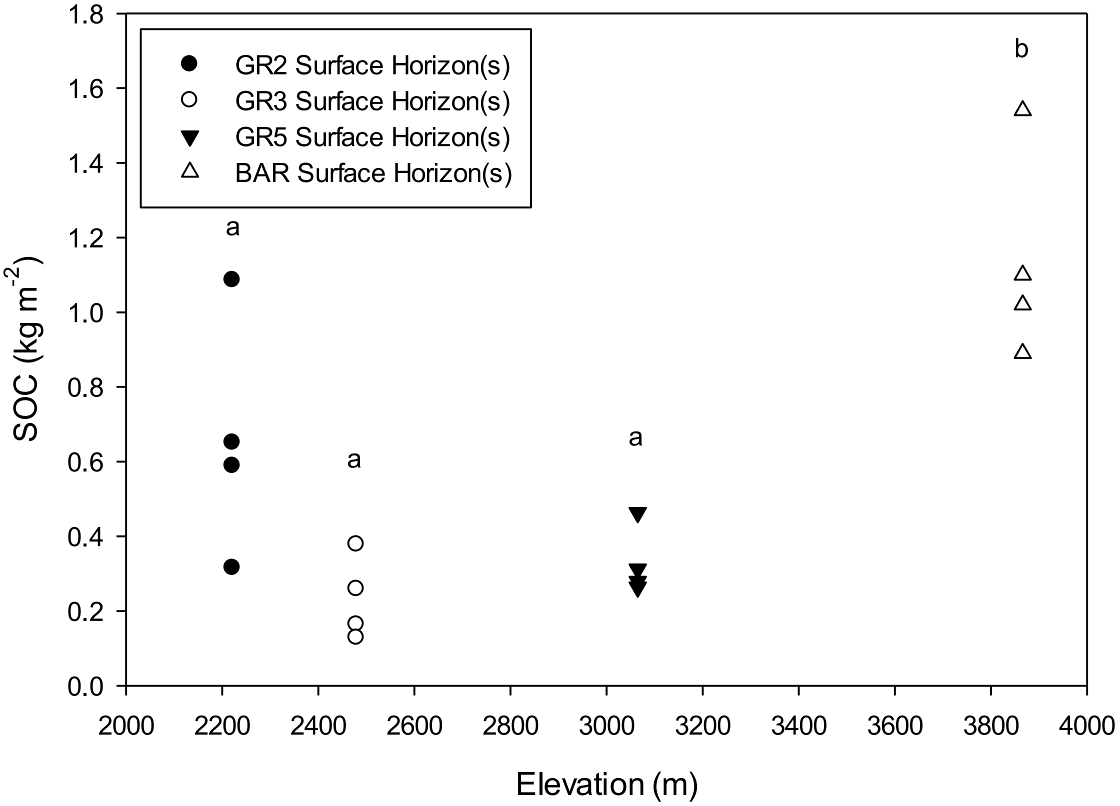


Figure 7. SOC storage in surface horizons as a function of elevation for soils on granite. Surface horizons include all morphologic horizons above the B horizon(s) to whatever depth they occur, under both shrub and interspace. At each elevation, SOC (kg m^{-2}) for the surface horizons of each replicate microsite pedon (i.e., GR2-1I, 21, 31, 41; and GR2-1S, 2S, 3S 4S) was multiplied by its respective % cover. SOC (kg m^{-2}) in surface horizons for each replicate microsite pedon set (i.e., GR2-1I and GR2-1S) was then summed to get total replicate SOC (kg m^{-2}) for surface horizons. This was done for each of the 4 replicate pedon sets at each elevation, and represents the four data points in the graph. Different letters indicate significant differences ($p<0.05$).

Effects of parent material on SOC storage

Results of Holm-Sidak pairwise comparison of both total and interspace SOC storage between granite (GR5) and quartzite (WP7) parent materials shows significantly higher ($p<0.001$) storage in soils developed on quartzite than in granitic-derived soils. (Figure 8). No significant differences were detected in SOC shrub storage values between parent materials. Comparison of surface horizon SOC storage between parent materials shows significantly higher ($p<0.05$) storage on quartzite parent material.

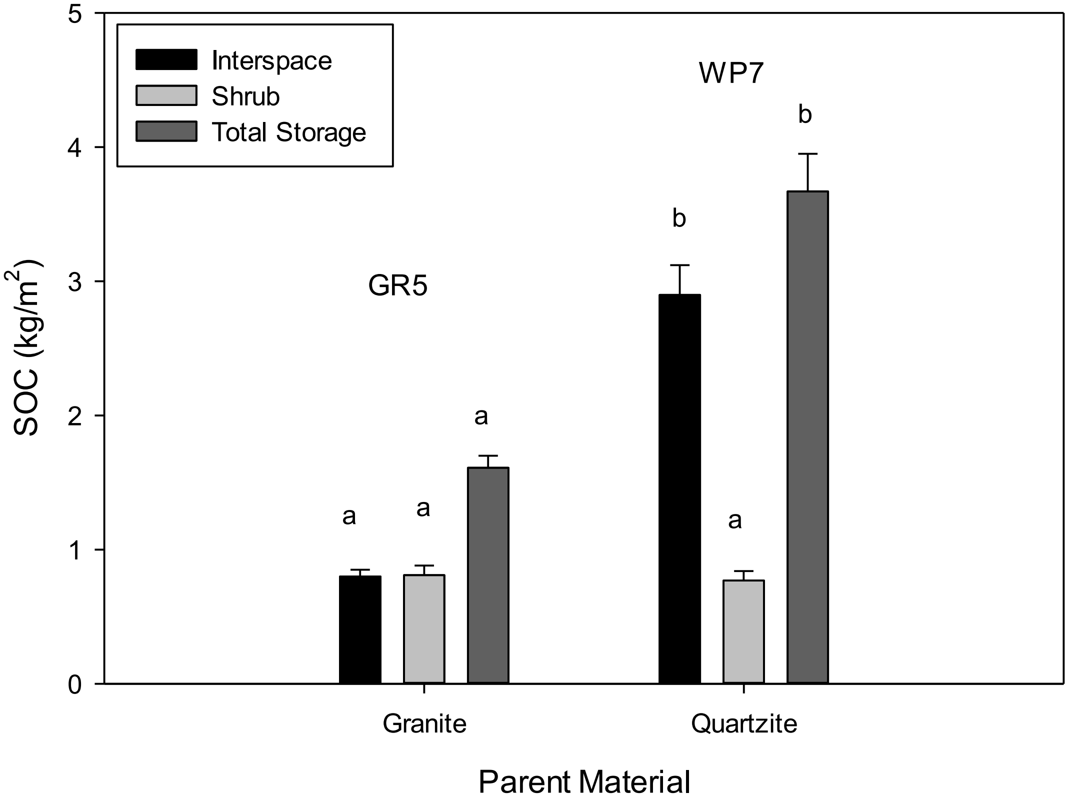


Figure 8. Comparison of total and microsite SOC storage on granite (GR5) and quartzite (WP7). Different letters indicate significant differences ($p<0.001$).

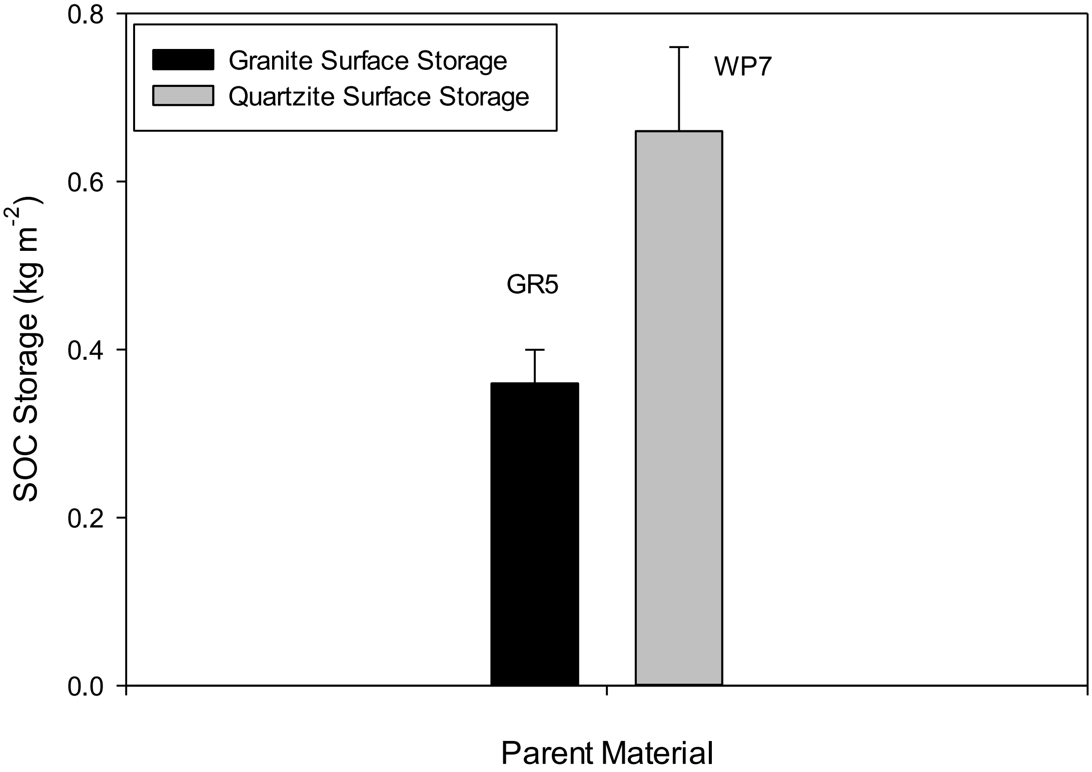


Figure 9. Comparison of SOC stored in the surface A and V horizons of granite and quartzite parent materials.

Table 3. Comparisons of particle-size distribution under desert pavement on granite terrain (GR5) and quartzite (WP7). Data are from a single interspace pedon at each site: GR5-2I on granite and WP7-2I on quartzite.

Site	Horizon	Depth (cm)	% SOC	% Clay	†% F Silt	†% C Silt	†% VF Sand	% F Sand	†% M Sand	% C Sand	% VC Sand
GR5	A	0-1	0.06	4.4	8.1	6.2	12.5	10.6	11.0	18.2	29.0
	AV	1-6	0.30	9.2	22.6	13.1	14.5	11.2	10.0	10.0	9.4
WP7	A	0-4	0.45	5.3	11.3	15.4	25.4	16.0	7.1	8.5	11.0
	AV	4-14	0.87	7.3	15.1	17.3	22.5	15.6	7.5	7.0	7.7

†F= fine; C= coarse; VF= very fine; M= medium.

Discussion

Results of ANOVA demonstrate that climate significantly affects carbon storage for the portions of the landscape dominated by vegetation. Climate did not, however, affect SOC storage within plant interspaces. Climate significantly affected shrub SOC storage, total SOC storage, and storage within soil surface horizons. It can be posited that landscape heterogeneity and associated vegetative density, as well as plant litter quality may be factors controlling SOC storage in this ecosystem.

Interspace SOC Storage

SOC storage in soil interspaces was not significantly affected by changes in climate in this study, which is not completely surprising. Subsurface carbon inputs are mediated by surface degradation and incorporation of plant litter, as well as soil respiration, which includes respiration by soil organisms, roots and mycorrhizae (Raich and Schlesinger, 1992). Plant litter is virtually absent from the interspace regions of the landscape, resulting in negligible contributions from this SOC pool. Interspaces in this study are not completely devoid of vegetation influence, as they contain laterally encroaching roots from adjacent shrubs. Decomposition of these roots contributes to SOC production.

Vesicular horizons are a ubiquitous soil surface horizon in the Great Basin. They are associated with decreased infiltration rates, in some cases as much as four times less than that found under shrubs (Blackburn, 1975). This reduces soil moisture in these portions of the landscape, a factor that has been observed to reduce root respiration in other arid ecosystems (Liu et al., 2009). Furthermore, decreases in soil moisture are often accompanied by decreases in microbial biomass, activity, and respiration (Liu et al., 2009), which contributes much to belowground SOC storage and retention (Tisdall and Oades, 1982; Bronick and Lal, 2005; Amezkéta, 1999).

Elevation transect studies that have observed increases in SOC storage with elevation have also observed concomitant increases in vegetation density and associated below-ground carbon inputs prompted by increases in precipitation (Amundson et al., 1988; Amundson et al., 1989a, 1989b). Increases in SOC storage are also influenced by decreases in temperature, which limits microbial activity and respiration in soils (Bunnell et al., 1977; Barja et al., 1997). However, consistently low SOC contents seem to negate the generally positive association between increased precipitation and carbon storage in the White Mountains, and suggests that carbon storage under this landscape type is sparse, and not enough for differences in temperature caused by elevation changes to have observable effects.

Shrub and total SOC storage

Results of ANOVA show that climate exerts significant control on shrub and total SOC storage in the White Mountains. Since no significant differences in SOC storage were detected in plant interspace sites, variation in total SOC storage can be attributed to variation in shrub SOC storage. Other elevation transect studies of granitic-derived soils in the Sierra Nevada range have observed positive linear relationships between elevation and SOC storage (Table 4) (Harradine, 1954; Dahlgren, 1997), where overall SOC storage increases with elevation. In this study, however, the lowest elevation site (GR2) stores 0.71 kg m^{-2} more total SOC than the highest elevation grassland site, despite receiving lower amounts of precipitation and having higher temperatures (Table 1), and having the lowest standing biomass of all sites (Table 2). In the Sierran soils, maximum SOC carbon storage is accompanied by maxima in clay concentration and primary productivity, suggesting that these parameters are climate-associated controls of carbon storage in the Sierra. However, it is apparent that other factors are influencing carbon storage and retention in the White Mountains.

Table 4. SOC values for a selection of elevation transect studies for comparison.

	Site	**Elevation (m)**	**Ecosystem**	**Total SOC (kg/m^2)**
White Mountains, CA	GR2	2221	PJW	4.5
	GR3	2479	PJW	1.8
	GR5	3065	Subalpine	1.6
	BAR	3866	Alpine	3.8
Sierra Nevada Mountains, CA *Dahlgren et al, 1997*	Vista	†211	Oak Woodland	*4.9
	Ahwahnee	427	Oak Woodland	4.8
	Auberry	802	Oak Woodland	5.7
	Musick	1348	Oak/mixed-conifer forest	12.6
	Shaver	1869	Mixed-conifer forest	14.7
	Sirretta	2338	Mixed-conifer forest	12.5
	Chiquito	2943	Subalpine mixed-conifer forest	10.5
Central Ethiopian Rift Valley *Lemenih and Itanna, 2004*	‡AW	†1625	Acacia Woodland	4.0
	DTW	1925	Dry transitional woodland	9.8 13.4
	SHA	2200	Mixed forest	23.5
	CSA	2475	Montane Woodland Thickets	15.7

†Median elevations calculated by elevation range given in study.
*Values are for solum carbon contents given in study.
‡Site names were assigned by abbreviation of eco-climatic zones.

Comparisons of soil profile depth, vegetation density, and litter quality lend some insight into the observed differences in storage under shrubs between sites GR2, GR3 and GR5. GR2 has relatively deep soil profiles when compared to GR3 and GR5 (Figure 10), with depth to bedrock reaching 80 cm compared to only 55 cm at GR3 (Figure 11), and 45 cm at GR5 (Figure 12). This equates to 1.5 and 1.8 times more soil volume contributing to SOC storage at this lower elevation site. GR2 also has the highest vegetation cover of all heterogeneous landscape sites in this study, where shrubs account for 71 percent of the surface landscape (Table 2). Shrub SOC decreases with concomitant decreases in vegetative density along the transect, illustrating the significant role of plant density in SOC storage in this region.

Vegetative density affects below-ground carbon inputs through root respiration and decomposition, and addition of organic substrates via rhizodeposition of root exudates and cell sloughing (Clark and Paul, 1970; Dahlman and Kucera, 1965; Barber and Martin, 1976), which increases subsurface carbon inputs. Vegetative density also affects surface plant-litter inputs, which contributes to the SOC pool. However, estimates of SOC contributions from roots compared to above-ground litter show that roots contribute significantly more to the organic carbon content of soils than above-ground plant litter (Campbell et al, 1991; Reicosky et al., 2002), with observed SOC contributions consistently greater than 1.5 times, and in some cases, almost 4 times that of the above-ground plant litter (Boone, 1994; Balesdent and Balabame, 1996; Scheu and Schauermann, 1994; Puget and Drinkwater, 2001). Moreover, root-derived carbon inputs have been observed to be significantly more aromatic and chemically recalcitrant than litter-derived carbon within a given species (Rasse et al., 2005), with an average of two times greater lignin and three times greater lignin:N than that of plant litter for a suite of different species (Goering and Van Soest, 1970; de Neergarard et al., 2002; Moretto et al., 2001; Vanlauwe et al., 1996). These observations suggest that vegetative density may be more important than above-ground standing biomass in contributing to SOC storage in this region, and may explain why despite having six and two times less standing biomass than GR3 and GR5 (Table 2), GR2 stores significantly more SOC.

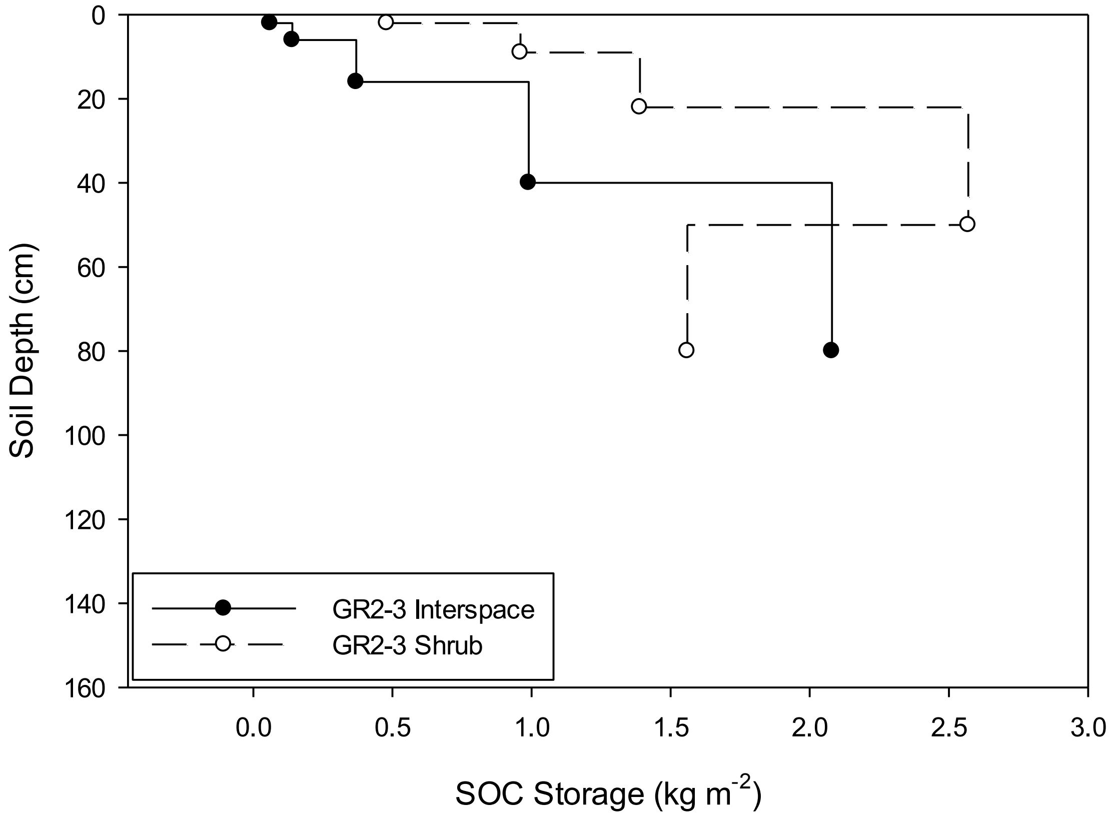


Figure 10. GR2-3 interspace and shrub SOC storage with depth. Each step in the graph represents the top and bottom of a horizon.

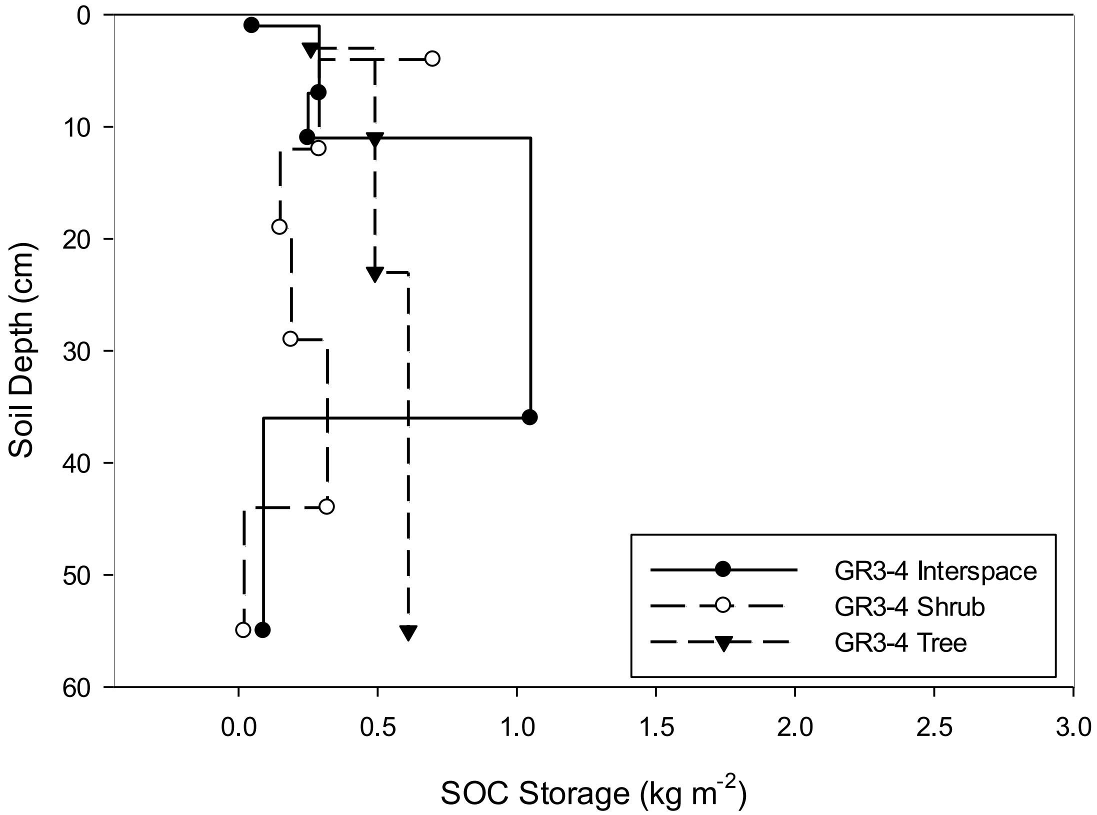


Figure 11. GR3-4 interspace, shrub and tree SOC storage with depth. Each step in the graph represents the top and bottom of a horizon.

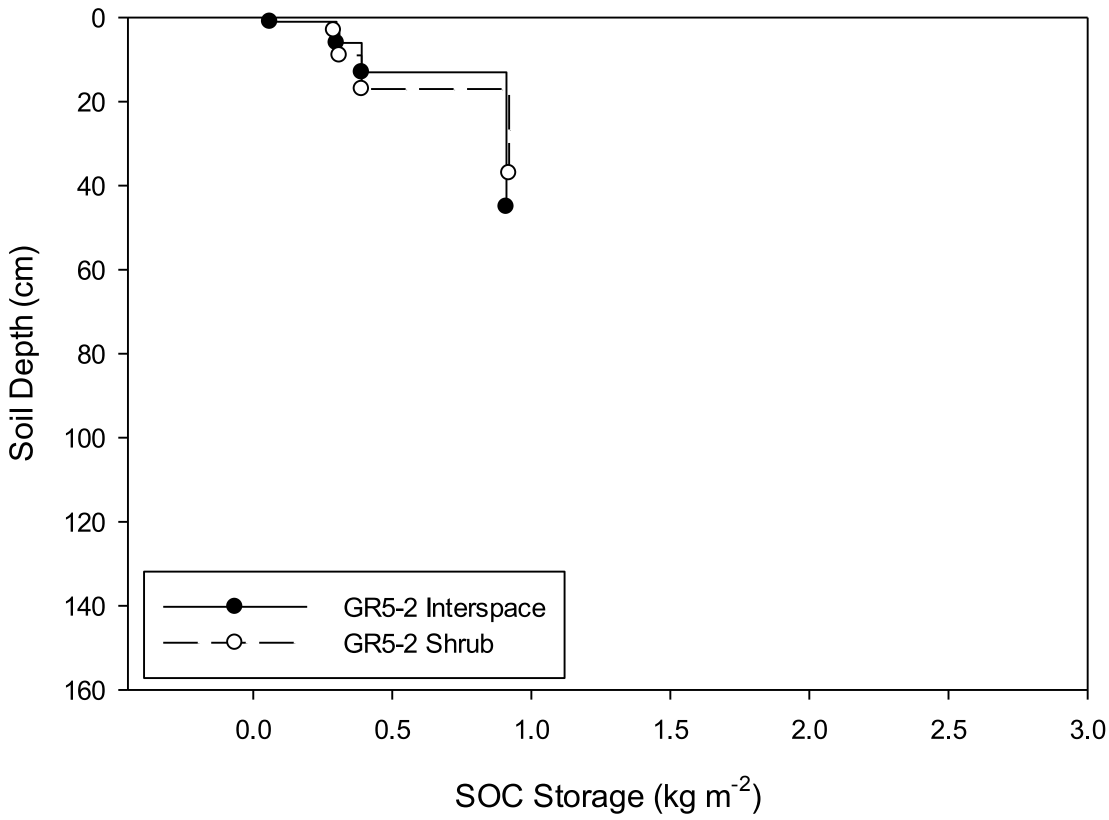


Figure 12. GR5-2 interspace and shrub SOC storage with depth. Each step in the graph represents the top and bottom of a horizon.

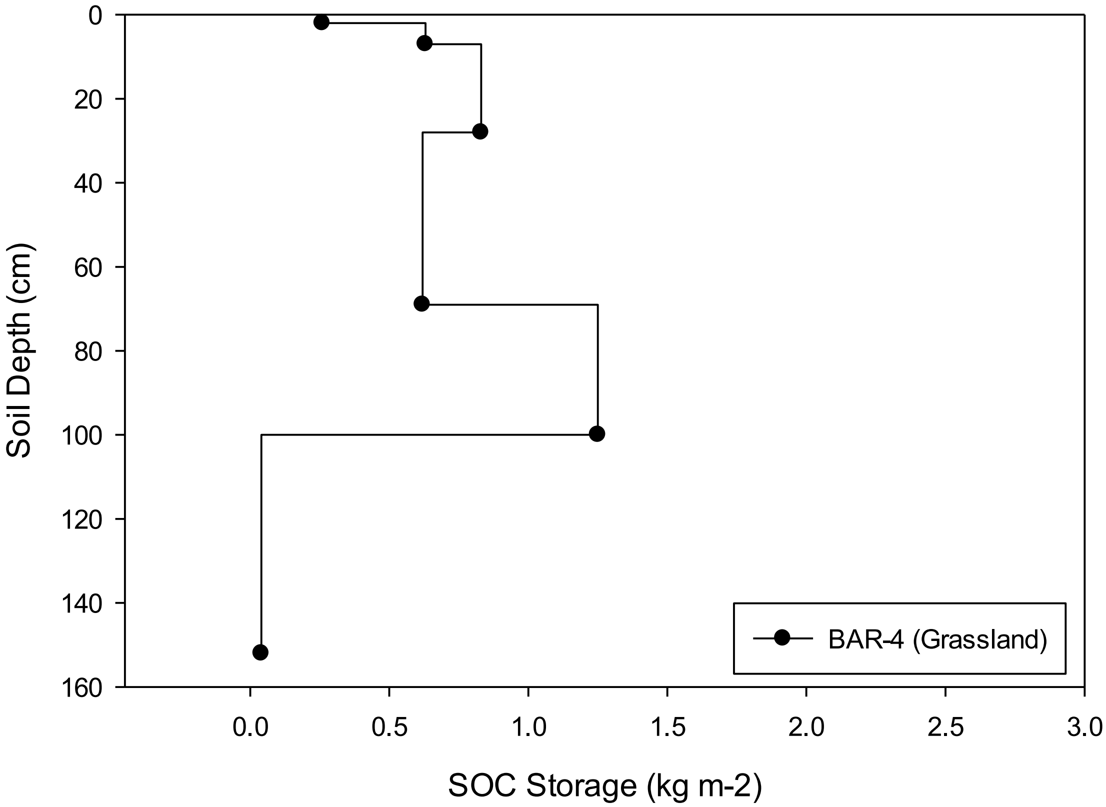


Figure 13. BAR-4 SOC storage with depth. Each step in the graph represents the top and bottom of a horizon.

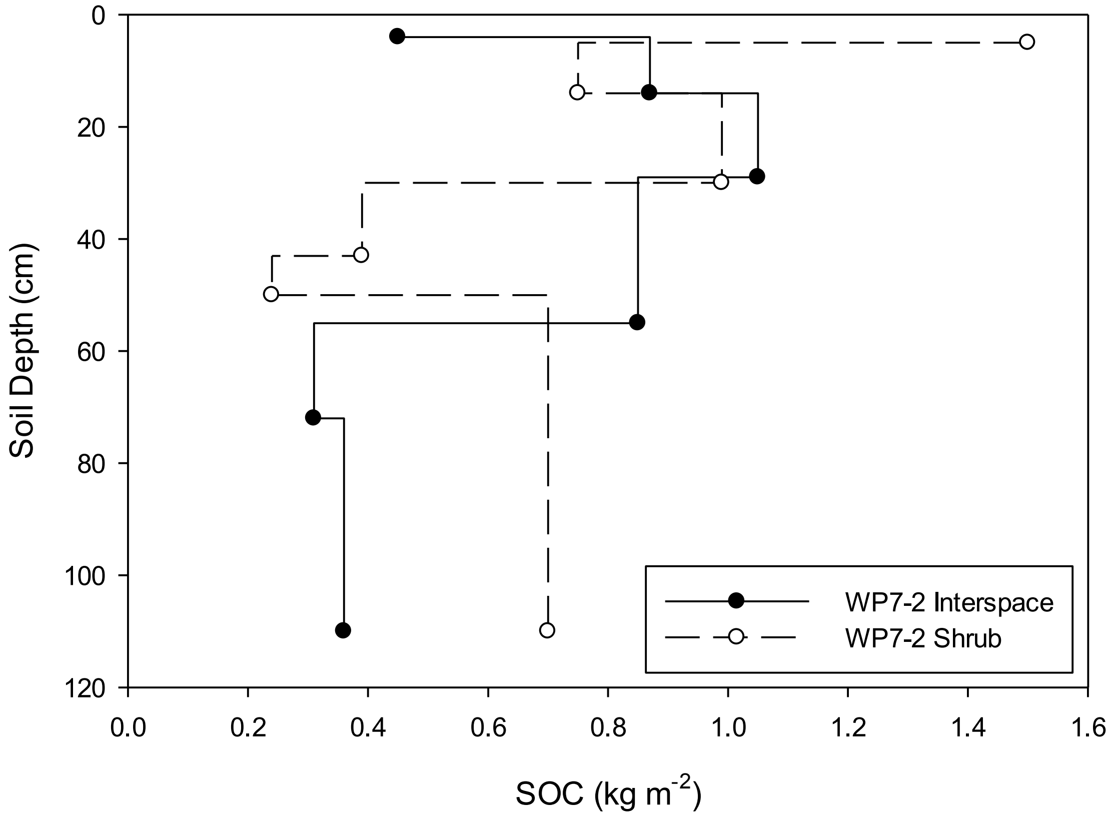


Figure 14. WP7-2 interspace and shrub SOC storage with depth. Each step in the graph represents the top and bottom of a horizon.

An additional important factor that might be affecting carbon decomposition dynamics between these sites is plant community composition. Herbs and forbs were absent during the plant census at GR2, but increased in occurrence and density with increases in elevation at sites GR3 and GR5. Vegetation species composition is known to affect organic matter decomposition dynamics by producing variations in bulk litter quality (Quideau et al., 2001; Shaw and Harte, 2001), and sagebrush litter contains higher lignin:N ratios than herbs and forbs which results in a more recalcitrant substrate affecting decomposition (Gupta and Singh, 1981; Shaw and Harte, 2011; Perfors et al., 2003).

It can only be speculated upon as to why GR2 has a higher vegetative density than its higher-elevation counterparts, but temperature and precipitation might be a factor. It has been documented that warming encourages expansion of sagebrush species (Sturges, 1989; Harte and Shaw, 1995), and warming experiments have shown sagebrush expansion with temperature increases of ~1.5 °C , which falls within the temperature range between GR2 and GR3 (Table 2) (Perfors et al., 2003). Pollen records corroborate these observations, and indicate expansion has indeed occurred in other mountainous regions, such as the Rocky Mountains, in the past (Whitlock and Bartlein, 1993). Furthermore, drying has been observed to decrease rates of soil respiration and decomposition, leading to relatively high SOC contents in other arid systems (Grunzweig et al., 2003). Given that GR2 is the warmest and driest of all sites included in this study, sagebrush expansion and moisture limits on decomposition may be a logical explanation for the high vegetation density observed at GR2 relative to GR3 and GR5.

No significant differences were detected between GR2 and BAR despite GR2 having less vegetative cover and higher temperatures, and receiving less precipitation. One important factor affecting carbon storage at these two sites is rock fragment content within the soil profile. GR2 contains an average rock fragment content of 31 percent compared to 72 percent at BAR (Table 1). Rock fragment content affects the storage capacity of soil by decreasing the volume of soil available for carbon storage.

Another important consideration when comparing carbon dynamics between these two sites is location of soil organic carbon within the soil profile, which may impact decomposer accessibility to organic substrates (Jobbagy and Jackson, 2000). While pedons at BAR contain more SOC in surface horizons than GR2 on average (Figure 13), GR2 contains significantly more SOC in the 20-50 cm region (Figure 10). These differences may be attributed to differences in root distribution between sites, as BAR vegetation is composed of grasses and forbs whose roots are generally more dense in surface horizons, and do not penetrate as deep nor spread out as wide as shrub root systems (Lee and Lauenroth, 1994). Comparisons of root distributions and subsurface SOC storage with depth in the soil profile confirm this observation. Soil profile descriptions of BAR show decreasing root quantities with depth (Table 5) when compared to GR2, and GR2 also stores a greater amount of carbon in the soil subsurface per given depth than BAR: a total of 1.56 kg m^{-2} from 50 to 80 cm compared with 0.73 kg m^{-2} for the same depth at BAR. Reduced decomposer accessibility to SOC at greater soil depths may explain the variation in estimates of SOC between these sites.

Table 5. Root descriptions of representative GR2 and BAR shrub microsite pedons by horizon depth for comparison. Visual estimates were made in the field at time of sampling.

Microsite and Depth (cm)	*Root Description
GR2- 1S	
0-8	2 VF, 2 F, 1 VC
8-14	2 VF, 1 M, 1 C
14-32	2 VF, 1 F, 1 C
32-50	2 VF, 2 F, 1 M
BAR-4	
0-3	3 VF
3-7	2 VF, 2 F
7-28	2 VF, 1 F
28-69	1 VF, 1 F

*1= few; 2= common; 3= many
C= coarse; F= fine; M= medium; VF= very fine; VC= very coarse

Differences in landscape heterogeneity with elevation

Differences in shrub and interspace storage were found to be significant with elevation. Generally speaking, the magnitude of differences between shrub and interspace storage decreases with increased elevation (Figure 4). However, since there is no general trend of increasing/decreasing landscape heterogeneity with elevation, it cannot be speculated how future changes in climate may alter soil carbon storage and dynamics in this system. It is generally thought that increases in precipitation are associated with increases in vegetation density; however, this general trend is not observed in the White Mountains. Shrub cover is highest (71%) and bare interspace is lowest (28.5%) at the lowest elevation site (2221 m). At GR3 (2479 m), bare interspace reaches a maximum of all sites at 71%, and then decreases to 57% at GR5 (3065 m) (Table 2). If we exclude GR2 from consideration, it may be possible to say that increases in elevation are accompanied by decreases in landscape heterogeneity; however the difference in landscape heterogeneity between GR3 and GR5 was not found to be significant. If future changes in climate do affect soil carbon storage as postulated (Davidson and Janssens, 2006; Kirschbaum, 1995; Davidson et al., 2000), initial decreases in SOC may be offset by increases in SOC gained at lower elevations in similar systems as a result of increased drying, shrub expansion, or both.

Surface horizon SOC storage

Results of ANOVA show that SOC storage in surface horizons is strongly influenced by climate. Similar to total storage and storage under shrubs, GR2 surface horizon SOC storage is greater than that of GR3 and GR5; however, in contrast to the estimates of total and shrub SOC storage, GR2 contains significantly less ($p<0.05$) surface SOC than BAR (Figure 7). Surface depositional processes, such as slopewash, are common in the White Mountains, and could explain the observed differences between surface SOC storage between GR2 and BAR, as slopewash tends to dilute SOC concentrations which affect SOC storage calculations. Furthermore, BAR vegetation composition is dominated by grasses and forbs whose root systems tend to be concentrated near the surface (Lee and Lauenroth, 1994), resulting in most of the SOC being produced and stored in this zone. BAR stores on average greater than 50 percent of its total SOC in the top 14 cm compared to only 17 percent in the same depth at GR2. Evidence suggests that soils dominated by particulate organic matter (POM) are more sensitive to environmental perturbations than minerally-associated or occluded organic matter (Cambardella and Elliot, 1992). Furthermore, SOC in surface horizons is impacted by climate significantly more than SOC in the subsurface (Wang et al., 2005; Jobbagy and Jackson, 2000). Since most of the SOC at BAR occurs in the surface, this may result in significant SOC loss with the onset of climate change.

Effects of parent material on SOC storage

To test for effects of parent material on soil carbon storage in the White Mountains, soils from granite (GR5) and quartzite (WP7) were compared at similar elevations (3065 and 3115 m) (Table 1). No significant difference in carbon storage under shrubs was observed, which suggests that differences in standing biomass, vegetation density, and community structure are not significantly affecting carbon storage between sites. The source of variation between sites originates from storage in interspaces. While the interspaces of both sites do contain laterally encroaching roots which could be contributing to some SOC inputs, vegetation density is nearly identical at both sites (Table 2), suggesting some factor unrelated to vegetation and associated carbon inputs may be controlling differences in storage between sites.

Depth to bedrock is much greater at WP7 than GR5 (Table 2), which obviously affects calculations of soil carbon storage. WP7 stores an average of 0.70 kg C m^{-2} more SOC in the interspaces than GR5 due to its greater depth (115 cm at WP7 compared to approximately 50 at GR5) (Figure 14). However, it is the variation in SOC contents of surface horizons between the two sites that accounts for the observed significant differences. WP7 has almost 3.5 times more SOC stored in surface horizons of interspaces than GR5 (Figure 9). Visual comparisons of surface rock fragments between sites (Figure 15) show that both landscape surfaces have partial desert pavement development, with more strongly developed desert pavement at WP7. Data from the

NSSL in Lincoln, Nebraska (Table 3) show that the particle-size distribution of interspace soils is affected by eolian inputs, most likely from nearby arid valleys: both pedons contain a vesicular horizon, a feature ubiquitous in other desert pavement systems (McFadden et al., 1987). Particle size analysis of the surface A and V horizons corroborates enrichment of eolian inputs (Table 3), as 31 percent of GR5, and 56 percent of WP7 surface horizons falls into particle sizes attributable to eolian deposition (0.02-0.25 mm) (Hirmas and Graham, 2010). Furthermore, X-ray diffraction results of surface horizons indicate the presence of mica, and microscopic analysis of fine sand grains reveals the presence of volcanic glass (data not shown). Although mica is a mineralogical component of granite, it is not a component of quartzite, and volcanic glass does not occur in either granite nor quartzite. These data indicate surface features such as desert pavement and dust enrichment have a strong influence on the morphology of these soils, and may lend insight into the observed differences in SOC storage between the two parent materials.

WP7 contains > 12 % more silt in the surface horizon than GR5, likely due to the more developed desert pavement acting as an intercept for eolian dust (McFadden, 1987). Desert pavement is known to inhibit soil erosion by wind and water (Cooke et al., 1993), and provide a matrix for the capture of eolian inputs (Wood, et al., 2005), perhaps some of which are enriched in organic carbon. Dust deposition studies in the region bordering California and Southern Nevada west of the White Mountains observed influx rates of 11.1 g m^{-2} yr^{-1} at the Cima fans near Cima Volcanic Field (Reheis et al., 1955), and 7.5 g m^{-2} yr^{-1} at the southern tip of Death Valley (Reheis and Kihl, 1995). While the authors did not publish organic carbon data for the dust collected in the study, other researchers have reported organic carbon concentrations of

3.2 to 18.4 % in dust originating from San Joaquin Valley (Chow et al., 2003), 6.7 to 8.3 % in the Argentinian Pampas (Rampsberger et al., 1998), and 11.6% in dust from Tempe, Arizona (Péwé et al., 1981). It could be speculated that dusts enriched in organic carbon may be being trapped in the desert pavement at WP7, while the sparse desert pavement formation at GR5 is contributing little toward protection of the surface soil, resulting in wind or water erosion, and subsequent depletion rather than accretion of organic carbon.

Figure 15. Comparison of desert pavement development between sites GR5 (left) and WP7 (right).

Conclusions

The objectives of this research were to inventory SOC storage in the White Mountains as a function of elevation, and assess how future changes in climate may impact SOC storage in arid systems at the landscape and regional scale. Observations indicate spatial heterogeneity exerts a strong influence on SOC storage at the landscape scale, as sites with the greatest spatial heterogeneity were also observed to have the greatest differences in microsite SOC storage. Climate is a strong control on SOC at the regional scale, but does not exhibit the linear relationship observed between SOC and climate in other studies. There was no observed trend between interspace SOC storage and elevation, presumably due to reduced infiltration of vesicular horizons which reduces subsoil moisture, and limits soil respiration. SOC storage under shrubs decreased with elevation. SOC storage under vegetation also decreased with elevation until approximately 3800 m, where it showed a significant increase in SOC storage at the highest elevation site. Parent material was observed to significantly affect SOC storage between granite and quartzite, as quartzite has developed a strong desert pavement, which captures eolian dust likely to be enriched in organic carbon. Under future warming scenarios, initial decreases in SOC caused by microbial-induced mineralization of organic matter at higher elevations may be offset by gains as a result of shrub expansion at warmer elevations.

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3. THE EFFECT OF SPATIAL VARIATION AND CLIMATE ON AGGREGATE STABILITY IN A HIGH-ELEVATION ARID MOUNTAIN RANGE, WHITE MOUNTAINS, CA, USA

Introduction

Soil structure is an important physical characteristic that affects many soil processes, including water infiltration and erosion (Barthés and Roose 2002), root penetration and crop yield (Wiersum, 1957), organic matter content (Tisdall and Oades, 1982; Balesdent, 2000) and nutrient cycling (Bronick and Lal, 2005). Soil structure is an essential component of agricultural sustainability and overall environmental quality (Amezkéta, 1999), and is the product of complex, intimate associations between primary particles and binding agents that bind soil particles together into larger secondary units called aggregates (Six et al., 2000). Various binding agents have been observed to play a role in soil aggregation, and can be organic (microbial, fungal, and plant debris and products) or inorganic (clays, polyvalent cations, Fe- and Al-oxides, $CaCO_3$, and gypsum) (Six et al., 2000; Amezkéta, 1999), and vary depending on soil and ecosystem type. Soil aggregate stability and structure are empirically related, as the stability of aggregates under various disintegrating forces such as wind and water is often used as a metric to infer the degree of soil structure (Bronick and Lal, 2002), and can serve as an indicator of overall soil quality (Arshad and Coen, 1992).

The binding agents that promote soil aggregation differ by region, and the extent of their influence on aggregation depends on the interactive chemistry between the binding agents and internal soil factors such as electrolyte concentration (electrical conductivity and sodium adsorption ratio), pH, organic matter and organic matter form, clay mineralogy and charge, and the presence and size of $CaCO_3$ particles (Amezkéta, 1999; Le Bissonais, 1996). The complexity of the natural soil environment prevents clean behavioral predictions for every soil constituent influencing soil aggregate stability in every possible environment, resulting in variable behavior for a wide range of aggregate stability predictors across studies (Amezkéta, 1999). However, several studies have confirmed the positive contributions of soil organic matter, clay, glomalin, and soil moisture in aggregate stability of non-calcareous soils in arid and semiarid environments (Goldberg et al., 1988; Haynes and Swift, 1990; Cantón et al., 2009). Likewise, strong evidence suggests both microclimate and regional climate exert significant influence on the stability of soil aggregates in arid and semiarid regions (Lavee et al., 1991, 1996; Imeson et al., 1998; Pariente, 2002).

Organic matter and clay

In a general sense, clay and organic matter enhance soil aggregation by virtue of their electrochemistry. Commonly negatively charged due to isomorphic substitution, phyllosilicate clays such as smectites, vermiculites, micas, and chlorites can form cation bridges with other clay particles, typically via polyvalent cations to accomplish complexation (Tisdall and Oades, 1982). Cation bridging prevents the swelling of clays and flocculates the constituents bound to it, resulting in significant stability (Oades, 1988). Clays can also form cation bridges with organic matter. While organic matter content in arid systems is relatively low compared to more humid environments, studies have shown that organic carbon plays a significant role in aggregate formation, which greatly reduces erosion via runoff, a major form of soil degradation in arid systems (Barthes and Roose, 2002; Cantón et al; 2009; Boix-Fayos et al., 2001). Organic matter serves as a nucleus in the formation of aggregates by contributing carbon for heterotrophic organisms that produce mucilages and bacterial metabolites as a byproduct of decomposition (Oades, 1988; Six et al., 2000). This partially decomposed organic matter and its metabolic products become physically encrusted with clay particles, resulting in aggregate formation (Tisdall and Oades, 1982; Six et al., 2000). Furthermore, organic matter has a tendency to sorb clays because of the high reactivity of ionizable functional groups that make up a significant portion of the organic matter structure (Johnston and Tombacz, 2002), resulting in the mineral encapsulation of organic matter, and concomitant formation of soil aggregates (Oades, 1984). Being that both organic materials and clays are polyanions, they can be bridged by polyvalent cations (Edwards and Bremner, 1967; Muneer and Oades, 1989), also resulting in aggregate formation.

Glomalin and glomalin related soil proteins (GRSP)

In addition to the synergistic exchanges between clay particles, organic matter, and bacteria, soil fungi, especially arbuscular mychorrizal fungi (AMF), also play an important role in soil aggregation. AMF are obligate symbionts that inoculate the roots of over 80 percent of higher terrestrial plants, greatly improving their nutrition, growth, and resistance to disease (Rillig, 2004; Bago et al., 2008). They have intraradical mycelia that penetrate the plant root where it obtains carbon from the host plant, and extraradical mycelia that inhabit the soil matrix (Allen, 2007). The primary function of the extraradical mycelia is to colonize new regions within the soil to extract water and soil nutrients (Allen, 2007; Wright and Upadhyaya, 1998), but they also act to stabilize the soil by enmeshing and entangling soil particles, organics and microaggregates in a fashion similar to plant roots (Rillig and Mummey, 2006). AMF have been linked to the production of glomalin and glomalin-related soil proteins (GRSP), which have been hypothesized to promote soil aggregation by acting as a hydrophobic glue upon fungal senescence (Rillig and Mummey, 2006). This glue interacts with primary soil particles and results in aggregation (Tisdall and Oades, 1982). Furthermore, AMF are of considerable value to arid and semiarid plants, as they increase water uptake by minimizing the capillary length and tortuosity of pore flow paths within the soil matrix, which increases plant root access to vital water sources (Allen, 2007). AMF are able to extract soil water inaccessible to roots, such as in micropores where soil water is held at very low potentials (Allen, 1986). This is a critical factor for plant survival in arid and semiarid environments.

Climate

Researchers attempting to elucidate the effects of climate on soil aggregate stability have observed variable results (Soulides and Allison, 1961; Tisdall et al., 1978; Utomo and Dexter, 1982; Barzegar et al., 1995), but this may be, at least in part, attributed to differences in site specific soil factors such as texture and mineralogy, and/or differences in experimental conditions (Amezkéta, 1999). However, the limited aggregate stability studies of arid and semiarid systems have had generally consistent results; namely, that aggregate stability decreases with increasing aridity, and that microclimatic differences such as shading and moisture differences induced by shrubs increase aggregate stability (Bird et al., 2002, 2007; Shinjo et al., 2000; Pariente, 2002; Cantón et al., 2009).

Aggregate stability studies of arid and semiarid environments are of vital importance, as these systems are fragile and susceptible to landscape-scale change with relatively small system perturbations (Reynolds et al., 1999; Schlesinger et al, 1990). Furthermore, these systems lend insight into understanding how microscale changes in soil properties, such as organic matter, moisture, and nutrient status, affect soil functioning at the landscape scale. It is well documented that desertification of arid and semiarid systems is exemplified by the replacement of arid grasses by desert shrubs, resulting in redistribution of soil resources where selective depletion of organic matter and soil nutrients occurs in the interspaces between shrubs, and accumulation occurs underneath shrubs (Charley and West, 1975; Reynolds et al., 1999; Schlesinger et al., 1996). This redistribution results in the spatial heterogeneity of these constituents, many of which have been shown to positively influence aggregate stability. While these studies have focused on relatively low-elevation arid systems, very few studies have been conducted in high-elevation arid systems, even though evidence suggests soils influenced by cold or freezing temperatures may be particularly susceptible to changes in climate (Schmidt et al., 2011).

Objectives

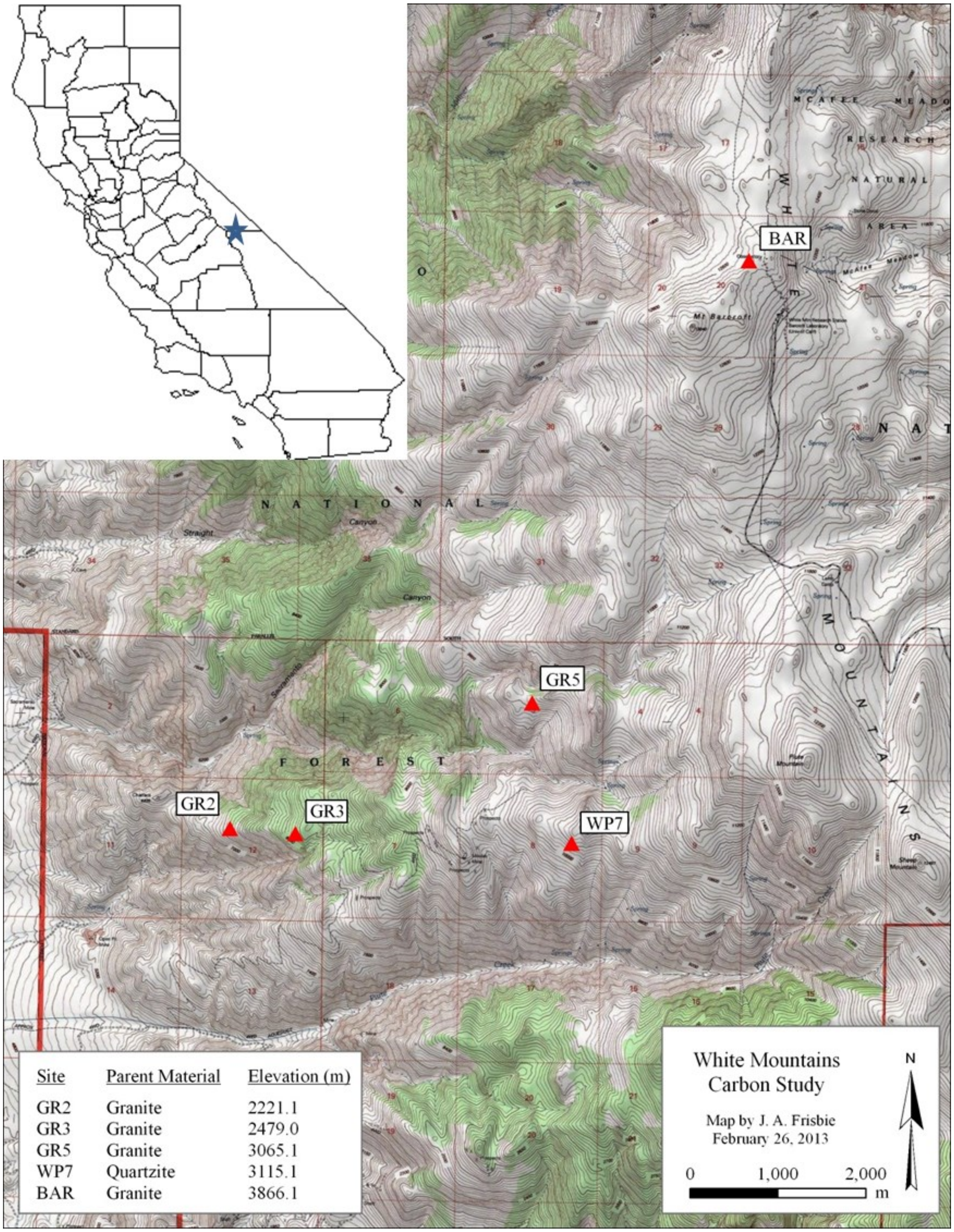
The objectives of this research are to assess how changes in soil properties, such as organic carbon and glomalin, induced by desertification affect aggregate stability in high elevation soils at the landscape scale by testing for differences in these parameters between vegetated and interspace microsites. In addition, the effects of climate on aggregate stability will be evaluated by testing for differences in these parameters along a climatological transect, using elevation as a proxy for differences in temperature and precipitation.

Materials and Methods

Environmental Setting

The study was conducted along an elevation gradient in the White Mountains, Mono County, California. The White Mountains are a fault-block mountain range located within the eastern section of Inyo National Forest, and on the western margin of the Basin and Range Province. The White Mountains are situated between the Sierra Nevada and the Inyo Mountains which lie to the west and south, and are separated by the upper Owens Valley and Deep Springs Valley. The towns of Bishop, Big Pine and Independence lie to the west and southwest. Five elevations were chosen for the study (Figure 1), encompassing Pinyon-Juniper woodland (PJW), subalpine and alpine ecosystems. The soil moisture regime along the transect is aridic, and soil temperature regimes are mesic at 2221, frigid at 2479, and cryic at 3065, 3115 and 3866 m. Mean annual temperature (MAT) along the elevation gradient was obtained by interpolation of data obtained from three meteorological stations located within and below the White Mountain range. Within the range, the White Mountain Research Station (WMRS) operates two weather stations, one in the valley of Crooked Creek (White Mountain I) at 3095 m, and one on the eastern slope of Mt. Barcroft (White Mountain II) at 3800 m. Climate data from these stations are from 1956 to 1985. Outside of the range, the National Weather Service operates a weather station on the valley floor in Bishop, CA at 1250 m, and data are from 1947 to present. MAT decreases from 7.1 ^{o}C at 2221 m to -2.7 ^{o}C at 3866 m. Mean annual precipitation (MAP) data was also obtained by interpolation, and increases from 23.8 cm at 2221 m to to 44.6 cm at 3866

m. The soils included in the study were formed on granite, except the quartzite site at 3115 m which was included for comparison of soil characteristics across parent materials. The soils were formed on slopes ranging from 10 to 39 percent. Site and soil characteristics are presented in Table 6.



Site	Parent Material	Elevation (m)
GR2	Granite	2221.1
GR3	Granite	2479.0
GR5	Granite	3065.1
WP7	Quartzite	3115.1
BAR	Granite	3866.1

White Mountains
Carbon Study

Map by J. A. Frisbie
February 26, 2013

Figure 1. Location of study sites.

Table 1. Summary of site characteristics

Site	Elevation (m)	MAT (°C)	MAP (cm)	SMR	STR	Geology	Ecosystem	Slope (%)	*Rock Fragment (%)	Aspect	Great Group
GR2	2221	7.1	23.8	Aridic	Mesic	Granite	PJW	39	31	W	Calciargid
GR3	2479	5.5	27.1	Aridic	Frigid	Granite	PJW	30	23	S	Haplargid
GR5	3065	2.1	34.5	Aridic	Cryic	Granite	Subalpine	27	42	W	Argicryid
WP7	3115	0.2	35.1	Aridic	Cryic	Quartzite	Subalpine	35	35	S	Argicryid
BAR	3866	-2.7	44.6	Aridic	Cryic	Granite	Alpine	10	72	W	Haplocryid

*Average rock fragment content of all replicate pedons.

Field Sampling

At each elevation, a 600 m^2 sampling plot was established by distributing a 10 m line upslope and downslope from a central point, and 15 m across-slope in both directions from the central point (Figure 2). At each endpoint, one to three pedons were selected for soil sampling and description, depending on vegetation type. For sites dominated by shrubs (GR2 and WP7) two pedons were selected for soil sampling and description at each endpoint: one under a shrub and one in the interspace. At site GR2, one pedon was chosen under mature representatives of mountain big sagebrush (*Artemesia tridentata*), and the second pedon was selected in the bare interspace between shrubs. At site WP7, one pedon was selected under low sagebrush (*Artemesia arbuscula),* and the second pedon in the bare interspace. At GR3, the presence of trees made it necessary to sample and describe three pedons at each endpoint, one each under mature representatives of singleleaf pinyon pine (*Pinus monophylla Torr*.) and mountain big sagebrush, and another in the bare interspace between vegetation. The homogenous vegetation (mostly alpine grasses) at site BAR made it necessary to sample only one pedon at each endpoint. This sampling scheme resulted in four replicate pedons for each microsite (shrub, tree, and interspace) at each elevation. The morphology of each pedon was described in the field, and samples were collected by morphologic horizon from each pedon and brought back to the laboratory for analysis. All values included in the analyses were weighted to 0-10 cm and 10-20 cm depths using the morphologic depths from each horizon, up to and including, the 20 cm depth for comparison across sites. A detailed vegetation census for each site is provided in Table 7, and images of landscape vegetation and interspace and shrub pedons are provided in Figure 3.

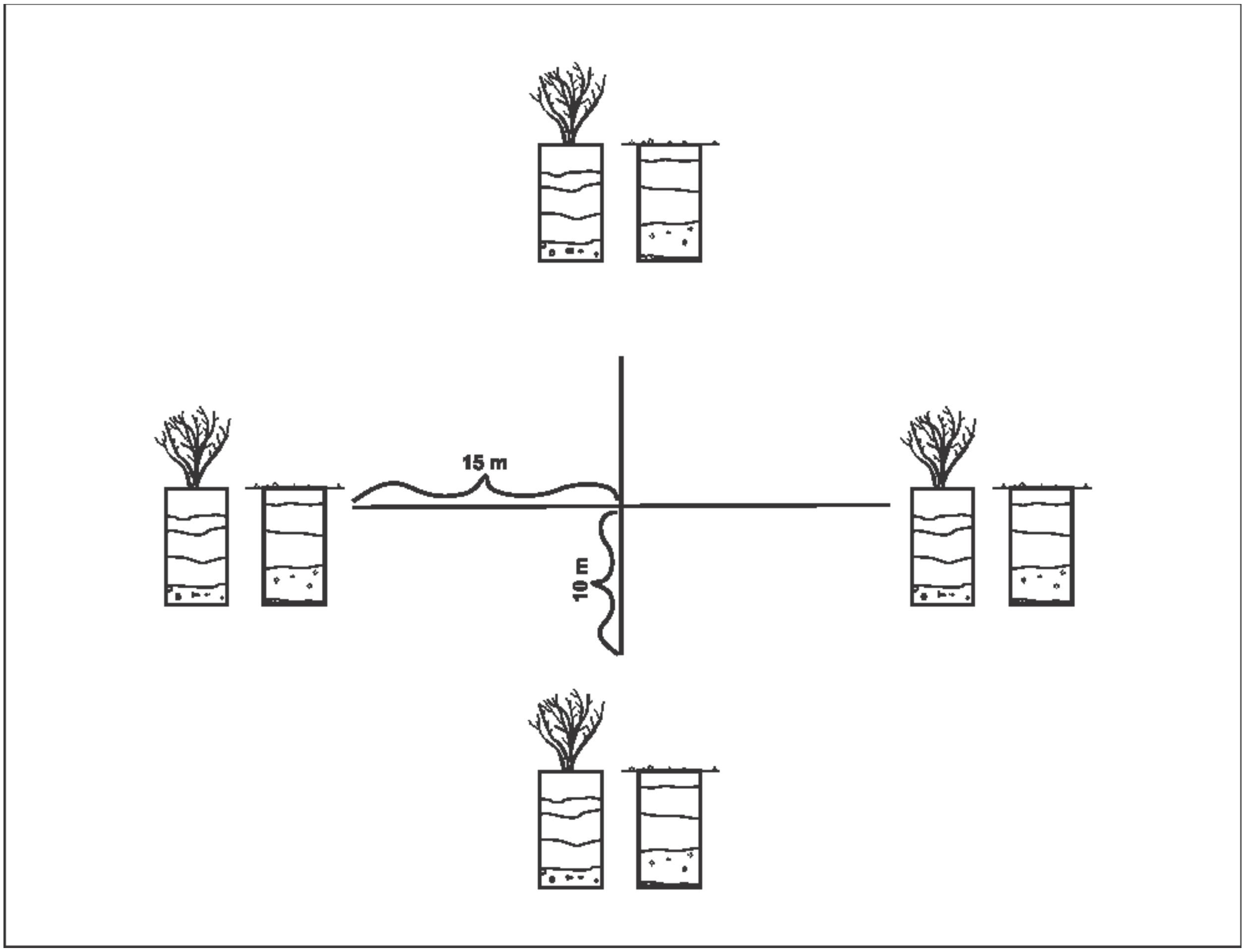


Figure 17. Field sampling diagram. Sampling plots were established from a center point, where one line was taken 15 m upslope and downslope from the center point and another line 10 m across slope from the center point. Microsite pedons were hand-dug, described and sampled at each end point.

Table 7. Vegetation census listed by predominance at each site. All vegetation listed occured in the sampling macroplot.

Site	Woody Species	Grass	Herbs/Forbs
GR2	Mountain big sagebrush Douglass rabbitbrush Mormon tea Spiny hopsage	Desert needglegrass James galleta	n/a
GR3	Singleleaf pinyon pine Mountain big sagebrush Douglas rabbitbrush Black sagebrush Mormon tea	Milkvetch Granite prickly phlox	n/a
GR5	Mountain big sagebrush Douglas rabbitbrush Mountain snowberry Mormon tea	Pine needlegrass Starwort Squirreltail Indian ricegrass Prairie Junegrass	Skeletonweed Cushion buckwheat Granite prickly phlox Milkvetch MacDougal's biscuitroot Compact phacelia Hoary tansyaster
WP7	Low sagebrush Mountain big sagebrush Slender buckwheat Mormon tea Spineless horsebrush Rock spirea	Squirreltail Sandberg bluegrass Needlegrass Ross' sedge	Bastardsage Cushion buckwheat Matted buckwheat Granite prickly phlox Mountain monardella Clokey's fleabane Desert parsley Catchfly Spreading groundsmoke Indian paintbrush Douglas dustymaiden
BAR	n/a	Prairie Junegrass Douglas sedge Fiveleaf clover Squirreltail Timberline bluegrass	Watson's spikemoss Dwarf phlox Fewseed draba Cushion buckwheat Sierra beardtongue Mason's Jacob's Ladder Clubmoss mousetail

Figure 18. (a) Shrub and interspace distribution over landscape at site GR5; (b) grassland vegetation distribution over landscape at site BAR; (c) interspace pedon; (c) shrub pedon.

Site Characterization

The geomorphology of all sampling sites except BAR is broad ridgeline slopes separated by deep canyons. The geomorphology of site BAR is a mountain backslope. Percentage of shrub, interspace and tree distribution over the landscape was determined using two 45.7 m line transects that intersected at their centers, one trending NE-SW and one trending NW-SE. These transects were used to measure the proportion of line occupied by the land surface components. Standing biomass was calculated by establishing five representative 3.7 x 3.7 m plots, and sampling and weighing all above ground vegetation within the plot. A correction for water content was used to express vegetation weight on an air-dry basis. Air-dry vegetation weight was then converted to a mass per area basis using the plot areas. Surface site characteristics are summarized in Table 8.

Table 8. Surface site characteristics, soil clay concentration and profile depth.

Site	**Interspace (%)**	**Shrub Cover (%)**	**Tree Cover (%)**	**Standing biomass (lbs/acre)**	**Litter Cover (%)**	**Lichen Crusts (%)**	**Surface Rock Fragments (%)**	**†Clay (%)**	**Profile Depth (cm)**
GR2	29	72		141	18	20.6	57	14	80
GR3	72	9	19	880	45	30.6	37	15	48*
GR5	57	43		312	24	33.7	38	12	44*
WP7	83	17		1683	35	16.8	60	7	110
BAR	0	100		433	28	20.6	46	5	152

*Average values of replicate pedon depth to bedrock. †Averaged weighted values for 0-10 and 10-20 cm depths from a single interspace pedon.

Soil samples

All analyses were performed on the <2mm fraction of morphologic horizons in triplicate, and were weighted and averaged to obtain values for 0-10 and 10-20 cm depths for comparison between microsites and across elevations. Percent clay was determined on a single interspace pedon at each site by the NSSL in Lincoln, Nebraska.

Wet aggregate stability

Water stable aggregates were determined using the method of Kemper and Rosenau (1986). Four grams of 1 to 2 mm soil material was placed onto a 24-mesh (0.71 mm) sieve. The material was wetted by capillary action by placing a sponge in a basin filled with 6 cm of deionized water, and allowing the sponge to reach saturation. Sieves were then placed on top of a layer of dry paper towels situated atop the saturated sponge to allow for slow wetting. Each sample was immersed in aluminum cans containing deionized water and sieved for three minutes on a motorized platform that generated 1.5 cm of vertical movement, which was adjusted to ensure submersion of aggregates on sieving upstroke. Sieving stroke frequency was 35 cycles per minute. Any remaining aggregates were then sieved for an additional 5 minutes in 100 ml of 2 M sodium hexametaphosphate to disintegrate water stable aggregates. Aluminum cans containing water-unstable and water stable aggregates were placed in an oven and dried at 105 °C.

Organic carbon

Total carbon and nitrogen concentrations of morphologic horizons were measured after combustion of samples with a combustion analyzer (Thermo Scientific Flash EA 1112 Series, Massachusetts, USA). Calcium carbonate equivalent was measured manometrically using the method described by Nelson and Sommers (1986), and organic carbon was obtained by taking the difference in total and inorganic carbon values.

Glomalin

Total glomalin was determined according to the method described by Wright and Upadhyaya (1996). Extraction was performed on 1.5 g samples mixed with 8 ml of sodium citrate at pH 8.0, and autoclaved for 60 min at 121 °C. Two milliliter subsamples of solubilized glomalin were transferred to Eppendorf tubes and centrifuged at 10,000x*g* for 5 minutes. A 1 ml aliquot was transferred to a cuvette, and protein in the supernatant was determined by the Bradford dye-binding assay with bovine serum albumin as the standard (Wright and Upadhyaya, 1996). Assay values were extrapolated to mg/g glomalin using the total volume of liquid and mass of soil containing total solubilized glomalin.

Statistics

All statistical analyses were performed using SAS (JMP, Pasadena, CA). The effect of elevation, clay, organic carbon, and glomalin on aggregate stability in the surface (0-10 cm) and subsurface (10-20 cm) depths for all vegetated and interspace microsites was analyzed using linear regression. Differences in aggregate stability between vegetated and interspace microsites at a given elevation due to differences in these parameters were tested using Tukeys Highly Significant Difference (HSD) test. The effect of climate on aggregate stability was investigated by analyzing for differences between sites with elevation using ANOVA, and testing differences with Tukey's (HSD) test.

Results

Aggregate stability

Aggregate stability under vegetated sites was consistently higher than in the plant interspaces at all elevations at both depths, except at site GR5, which had essentially equal aggregate stabilities in the subsurface of interspaces and vegetation (Figure 4). Surface (0-10 cm) aggregate stability under vegetation was significantly higher ($P<0.05$) than in the interspaces at sites GR3 and GR5. Surface interspace aggregate stability was maximum at the lowest elevation site GR2, and decreased significantly ($p<0.05$) with increasing elevation at sites GR3 and GR5. There was no observable trend in surface aggregate stability for vegetated sites, but GR5 had significantly higher ($P<0.05$) values than at BAR in both the surface and subsurface depths, where maximum and minimum vegetated soil aggregate stabilities along the transect occur. In the subsurface, interspace aggregate stability increased with elevation, but not significantly. Vegetated soil aggregate stabilities at this depth also increased with elevation, but significantly decreased ($p<0.05$) once reaching the highest elevation site BAR. Subsurface aggregate stability was higher than in the surface at all sites and microsites along the elevation transect (Figure 19). However, no significant differences in aggregate stability were observed between interspace and shrub values at any elevation in the subsurface.

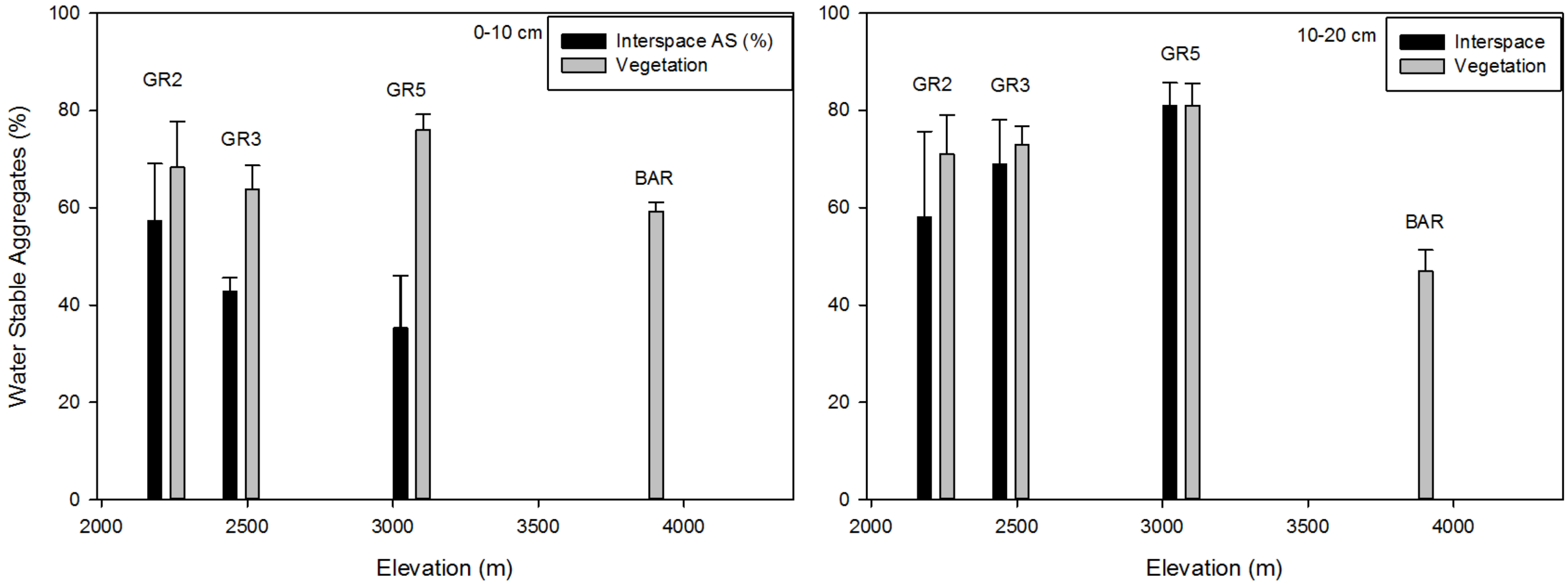


Figure 19. Aggregate stability of the surface 0-10 and subsurface 10-20 cm depths for all sites along the transect.

Organic carbon

Organic carbon was consistently higher under vegetated sites than in the interspaces, and significant differences between microsites were observed in surface SOC at site GR5 ($p<0.05$) (Figure 20). Interspace SOC values were similar in the surface and subsurface. SOC values under vegetation were almost 50 percent greater in the surface than in the subsurface at all elevations except BAR, where values in the surface were more than three times higher than in the subsurface (Figure 20). At GR3, both interspace surface and subsurface SOC values were lowest among all sites. No observable trends in interspace SOC were evident with elevation, and no significant differences were observed between interspace microsites as a function of elevation. Significant differences ($p<0.05$) in vegetated microsites as a function of elevation were observed between BAR and all other sites.

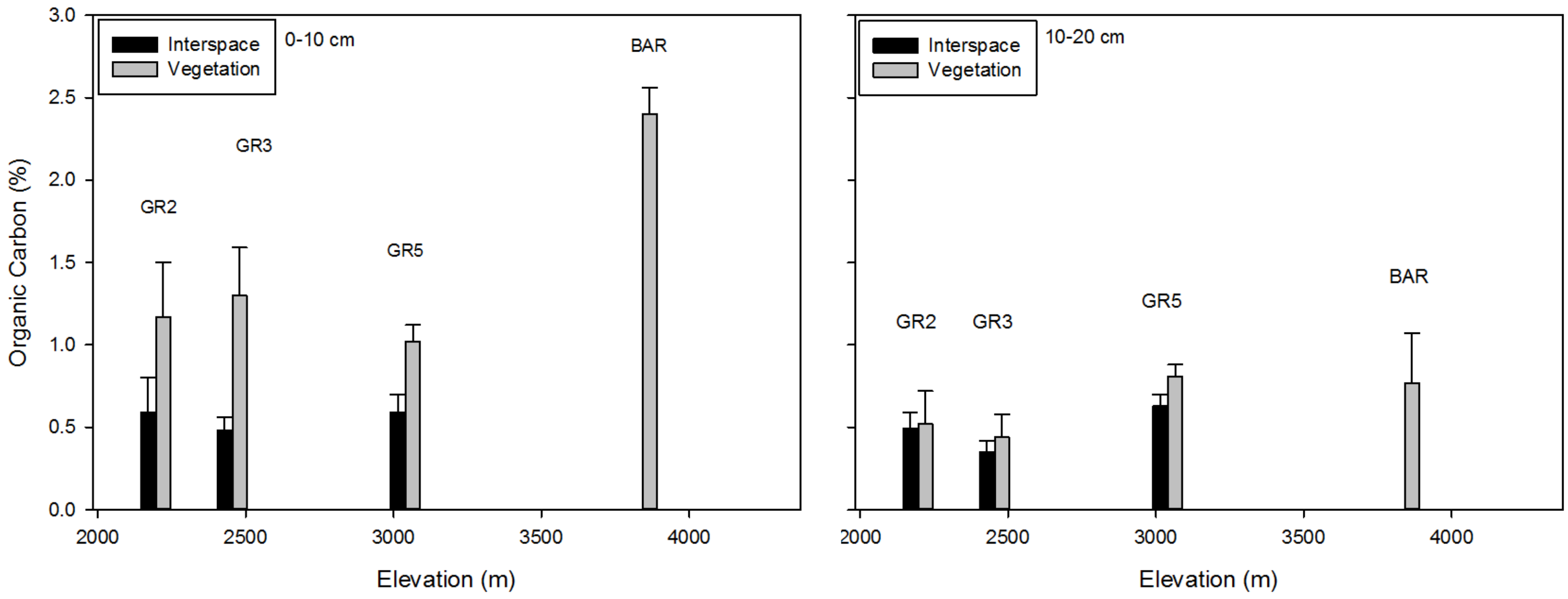


Figure 20. Organic carbon concentration of the surface 0-10 and subsurface 10-20 cm depths for all sites along the transect.

Glomalin

Glomalin was substantially higher under vegetation than in the interspaces for both depths and at all sites along the elevation transect (Figure 21). Significant differences in glomalin values between vegetated and interspace microsites in surface horizons were observed at GR2 and GR5 and (Figure 21). Glomalin values in surface horizons of interspaces increased significantly ($P<0.05$) from GR2 to GR3, but no further significant increases in interspace glomalin values were observed. Under vegetated sites, glomalin values in surface horizons were almost identical with elevation at sites GR2, GR3 and GR5, and then significantly increased ($P<0.05$) at site BAR (Figure 21). In the subsurface horizons, glomalin increased with elevation in both interspace and vegetated microsites, reaching a maximum at site BAR. However, the increases were slight, and were not significant.

Effect of Parent Material on Aggregate Stability

No significant differences in aggregate stability were observed between granite (GR5) and quartzite (WP7) parent materials in either shrub or interspace microsites, nor at any depth (0-10 or 10-20 cm) (Figure 22).

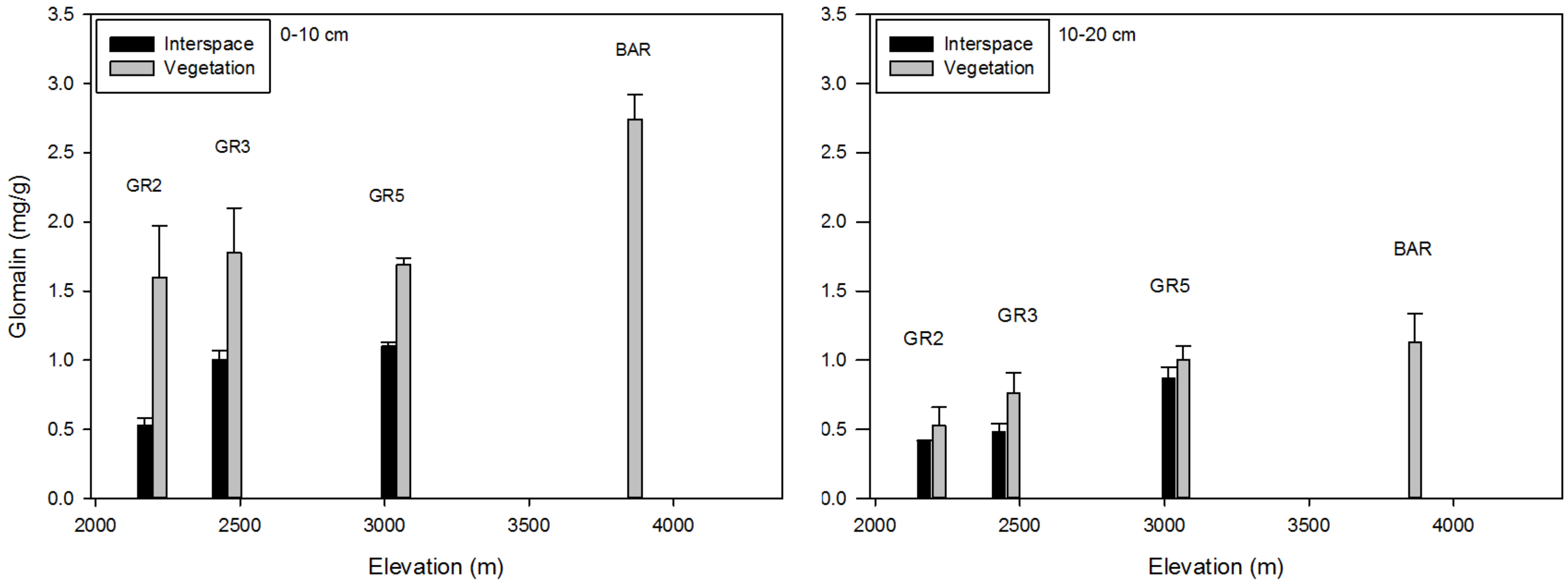


Figure 21. Glomalin concentration of the surface 0-10 and subsurface 10-20 cm depths for all sites along the transect.

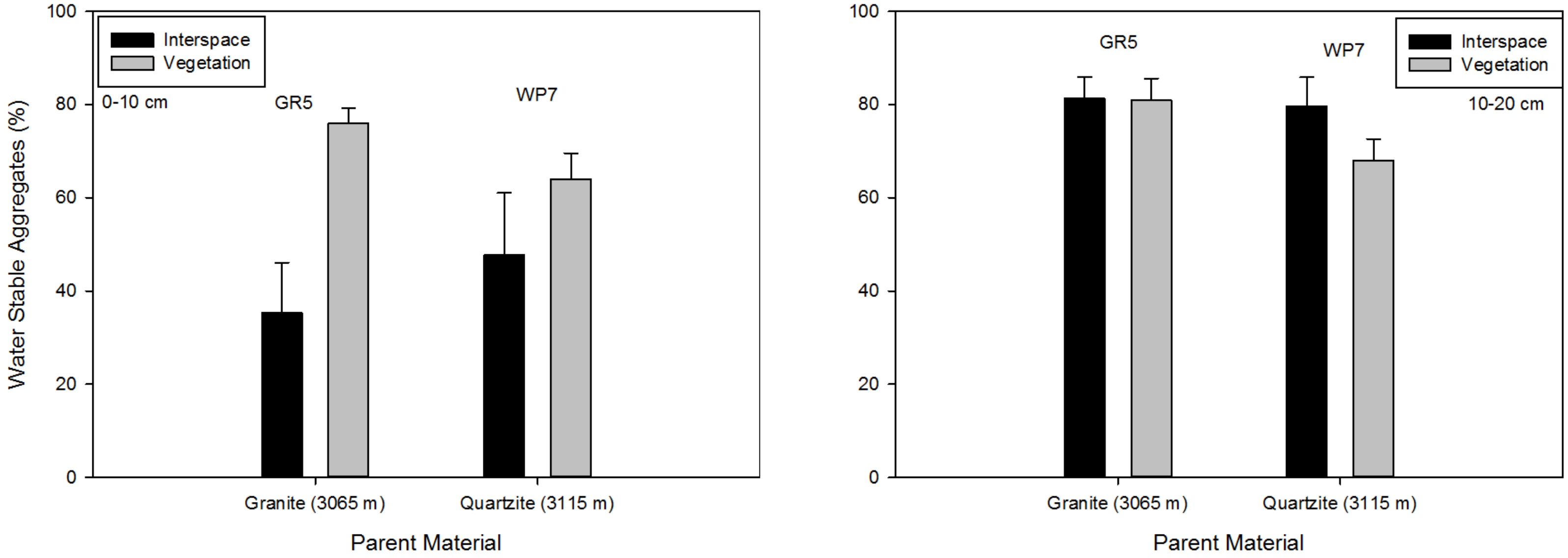


Figure 22. Comparison of aggregate stability of the surface 0-10 and subsurface 10-20 cm depths between granite and quartzite parent materials.

Discussion

Glomalin and percent clay were found to be significant predictors of aggregate stability in the surface (0-10 cm) ($p<0.05$; $r^2=0.33$). No significant predictors of aggregate stability were observed in the subsurface 10 to 20 cm depth; however, OC and clay were observed to be significant predictors of the combined 0 to 20 cm depth ($p<0.05$; $r^2=0.20$). The observed higher values in aggregate stability under vegetated sites than in plant interspaces are consistent with observations by other studies (Bird et al., 2002, 2007). Plant roots and associated fungal hyphae promote aggregation by enmeshing soil particles and aggregates together. They also excrete gums and glues upon lengthening deeper into the soil as particles abrade the root cap (Tisdall and Oades, 1982). Plant roots are the apex of microbial activity where microbial glues and gums are at maximum, products which are known to enhance soil aggregation (Tisdall and Oades, 1982; Amezkéta, 1999). Furthermore, plant canopies protect soil aggregates from the physical impact of precipitation, which has been observed to result in decreased aggregate stability of interspaces (Bird et al., 2002).

Subsurface aggregate stability was consistently higher than in the surface at all microsites and sites along the elevation gradient, significantly so for site GR5. Other researchers have found consistent decreases in aggregate stability with increasing depth in the soil profile in arid regions due to lower organic carbon contents in the soil subsurface (Bird et al., 2000). However, higher organic carbon and glomalin concentrations in the soil surface in this study do not correspond with higher aggregate stabilities. Two important surface features of the soils included in this study are the presence of vesicular horizons and coppice dunes. Vesicular horizons are widespread in the Great Basin, and occur at the soil surface within the interspace portions of arid landscapes (Wood et al., 1978). They have massive or otherwise weakly aggregated platy structure, and are composed primarily of silt (Wood et al., 1978). Coppice dunes are features common in arid regions, and are formed by the preferential trapping of fine eolian material around the crowns and trunk of shrubs transported by wind or water (Ravi et al., 2007). Higher organic carbon (Figure 20) and glomalin contents (Figure 21) in the surface of interspace and shrub soils don't necessarily translate into higher aggregate stabilities because of presence of loose, weakly aggregated eolian material skewing aggregate stability results.

Another possible explanation for the observed higher subsurface aggregate stabilities is the effect of surface transport processes common on mountain backslopes of the White Mountains (Marchand, 1978). Erosion from topographic highs cause debris accumulation on gentler slopes and in topographic lows, resulting in the accumulation of colluvium across the landscape surface, as well as superficially stratified soils (Marchand, 1978). It is possible that periodic or seasonal addition of colluvium to the soil surface could be confounding soil aggregate stability results.

Surface aggregate stability under shrubs was observed to be significantly higher than in the interspaces of the same depth at sites GR3 and GR5. This could be explained by a combination of physicochemical processes occurring underneath shrubs, and physical degradation processes occurring in the interspaces. At GR5, significantly higher shrub aggregate stability in the surface can be attributed to significant increases in glomalin (Figure 21) and SOC (Figure 20) under shrubs compared to interspaces, parameters which have been observed to substantially affect aggregate stability in other studies (Amezkéta, 1999; Tisdall and Oades, 1982; Wright and Upadhyaya, 1998; Bird et al., 2002), and which seem to be affecting microsite aggregate stability here. At GR3, no significant differences in either glomalin or SOC were observed between shrub and interspace microsites. However, SOC and glomalin values were higher under shrubs, and GR3 has the highest clay content of all sites on granite along the elevation transect (Table 8). Furthermore, the decline in surface interspace aggregate stability (Figure 19) as a function of elevation suggests that increased precipitation has a negative effect on aggregate stability in these open areas, and may be causing selective erosion in the surfaces of bare interspaces. In heterogeneous landscapes, soil moisture of the bare interspace microsites is lower than that of adjacent shrub sites due to lower infiltration (Pariente, 2002; Wood et al., 1978). Reduced infiltration causes runoff and erosion, often accompanied by mechanical breakdown and sealing of the soil surface (Le Bissonnais, 1990). Precipitation amount and duration significantly increases soil loss in arid regions (Snelder and Bryan, 1994), and the combined effect of increased glomalin and SOC under shrubs, and erosion in interspaces could explain the significant differences in microsite aggregate stability here.

Surface aggregate stability of the grassland site at the highest elevation was significantly lower at both depths than the other vegetated sites along the elevation gradient (Figure 16). Although glomalin and SOC are highest at BAR, the effect of cold and freezing temperatures has a negative effect on soil aggregate stability (Lavee et al., 1996; Amezkéta, 1999; Oztas and Fayetorbay, 2003). Freeze-thaw cycles have been observed to significantly decrease aggregate stability of soils of different parent materials, independent of organic carbon content and texture (Oztas and Fayetorbay, 2003). Freezing results in the expansion of ice crystals in the pores between aggregates which breaks particle bonds. Subsequent thawing of the soil decreases the pore volume, and causes aggregate collapse (Amezkéta, 1999; Kay et al., 1985).

Cold temperatures also constrain microbial activity, which reduces the production of microbial products that aid in aggregate formation and stabilization (Lavee et al., 1996). Relic evidence of cryoturbation in the soils of BAR suggests that, at high elevations where cryic soil temperatures may be preserving SOC, resulting in high organic carbon contents (Figure 19), they are simultaneously constraining microbial activity and causing freeze-thaw cycles that degrade soil aggregates by mechanical breakdown (Amezkéta, 1999; Lavee et al., 1996).

Conclusions

In this study, the effects of microsite and regional climatic differences on aggregate stability were investigated. The role of glomalin, clay and organic carbon on the stability of aggregates was also determined. Glomalin and clay were determined to be significant predictors of aggregate stability in the soils along this transect. Contrary to findings of other studies, aggregate stability was consistently greater in the subsurface than surface depths, and may be explained by surface features such as vesicular horizons and coppice dunes, as well as landscape- depositional processes that confound aggregate stability results of the soil surface. Differences in microsite characteristics arising from the presence or absence of shrubs significantly affected aggregate stability, showing higher aggregate stabilities under shrubs compared to shrub interspaces at all sites along the elevation gradient. Regional climate had variable effects on aggregate stability depending on depth and presence or absence of shrubs. In the surface, interspace aggregate stability decreased with increasing elevation, possibly due to more drying cycles at the lowest elevation which enhances aggregate stability, and more erosion due to increased precipitation at higher elevations. Under vegetation, no trend in aggregate stability was observed as a function of elevation. Although the highest elevation site BAR had highest SOC and glomalin concentrations, aggregate stability values at this site were the lowest, perhaps because of the cold soil temperatures which suppress microbial activity, and freeze-thaw cycles that mechanically breakdown soil aggregates. Under future warming scenarios, increases in aggregate stability might be observed at sites where freeze-thaw cycles currently induce mechanical breakdown of soil aggregates. However, losses in aggregate stability might also be observed if the heterogeneity of landscapes increases, as interspace regions of the landscape are associated with relatively low aggregate stabilities relative to that observed under shrubs.

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4. CONCLUSIONS

The distribution of SOC and water stable aggregates as affected by differences in landscape heterogeneity and regional climate was investigated by evaluating differences in these parameters between microsites at a given elevation, and between microsites as a function of elevation spanning 2221 and 3866 m. Landscape heterogeneity was found to strongly influence SOC distribution in these systems, as sites with the greatest spatial heterogeneity were also observed to have the greatest differences in microsite SOC storage. Climate is a strong control on SOC storage at the regional scale, but SOC did not exhibit a clear linear relationship observed between SOC and climate in other studies, a strong quadratic relationship was observed in this study due to shrub expansion induced by warmer temperatures at the lowest elevation site, and increased SOC storage and retention induced by cold temperatures at the highest elevation site. Interspace microsites were less influenced by climatic differences than shrub microsites along the climatological gradient, as decreased moisture in the interspace results in a decline of subsurface organic inputs by roots and soil fauna. The effects of parent material on SOC storage was also found to be significant, as soils on quartzite formed a well-developed desert pavement that captures eolian dust likely enriched in organic carbon. Under future warming scenarios, initial decreases in SOC caused by microbial-induced mineralization at higher elevations could be offset by gains as a result of shrub expansion and concomitant SOC storage at warmer elevations in these systems.

Landscape heterogeneity also had a substantial effect on aggregate stability, and resulted in higher aggregate stabilities under shrubs compared to interspaces at sites along the elevation gradient, mainly due to greater glomalin and SOC concentrations at these sites.

Regional climatic differences had variable effects on microsite aggregate stability. In the interspace, aggregate stability decreased as a function of elevation due to increased runoff and erosion induced by higher precipitation at higher elevations. Under shrubs, no trend in aggregate stability was observed as a function of elevation. At the highest elevation site, climate was found to be the most important factor influencing aggregate stability, as freeze-thaw cycles common in these soils degrade soil aggregates despite observed maxima in organic carbon and glomalin concentrations. Under future warming scenarios it is possible that landscape aggregate stability of high elevation arid systems may increase, but for different reasons depending on microsite. Under shrub microsites, warming soil temperatures would inhibit freeze-thaw cycles that degrade soil aggregates, resulting in increased soil aggregate stability. In the interspaces, decreased precipitation may reduce the amount of erosion common in these regions of the landscape, which would also lead to increased soil aggregate stability. Parent material had no significant effect on aggregate stability in this study.

5. APPENDIX

Appendix A. Raw data for calculation of SOC storage, where TC= total carbon, RF= rock fragments within soil horizon, IOC= inorganic carbon, and SOC=soil organic carbon. SOC for a given horizon is calculated by subtracting IOC from TC, and multiplying by the horizon bulk density, horizon thickness and rock fragment content. Columns D and E are conversion factors to obtain values on a mass per area basis. Pedon SOC (kg m^{-2}) is obtained by summing the SOC (kg m-2) of each horizon within a pedon. Interspace pedons selected for analysis by NSSL were sampled to a greater depth (2 m or until bedrock) than the other replicate pedons at a given elevation. SOC (kg m^{-2}), was determined for the horizons occurring at these greater depths, and was added to the shallower-sampled replicate pedons at the same elevation. The SOC added to the shallower-sampled replicate pedons was weighted, and include the depths occurring from the bottom of the last horizon of the shallower-sampled pedons, to the bottom of the last horizon in the deeper-sampled pedon.

Sample ID	% TC	Avg. ρb (g cm^{-3})	1,000,000 (cm^3 m^{-3})	1 kg 1000 g^{-1}	Thickness (m)	1-RF	TC (kg m^{-2})	IOC (kg m^{-2})	SOC (kg m^{-2})	Pedon SOC (kg m^{-2})
GR2-1I 0-6	0.32	1.34	1,000,000	1000	0.06	0.76	0.1955328	0	0.20	2.55
GR2-1I 6-11	0.41	1.24	1,000,000	1000	0.05	0.63	0.160146	0	0.16	
GR2-1I 11-21	0.33	1.19	1,000,000	1000	0.1	0.72	0.282744	0	0.28	
GR2-1I 21-27	0.3	1.13	1,000,000	1000	0.06	0.79	0.160686	0	0.16	
GR2-1I 27-50	0.11	1.13	1,000,000	1000	0.23	0.68	0.1944052	0	0.19	
GR2-1I 50-80								0	1.56	
GR2-1S 0-8	0.93	1.18	1,000,000	1000	0.08	0.73	0.6408816	0	0.64	3.78
GR2-1S 8-14	0.66	1.09	1,000,000	1000	0.06	0.63	0.2719332	0	0.27	
GR2-1S 14-32	0.36	1.17	1,000,000	1000	0.18	0.77	0.5837832	0.05	0.53	
GR2-1S 32-50	2.41	1.13	1,000,000	1000	0.18	0.65	3.186261	2.41	0.78	
GR2-1S 50-80								0	1.56	

GR2-2I 0-2	0.36	1.15	1,000,000	1000	0.02	0.73	0.060444	0	0.06	4.34
GR2-2I 2-8	0.38	1.43	1,000,000	1000	0.06	0.78	0.2543112	0	0.25	
GR2-2I 8-14	1.13	1.24	1,000,000	1000	0.06	0.63	0.5296536	0	0.53	
GR2-2I 14-27	1.37	1.13	1,000,000	1000	0.13	0.77	1.5496481	1.24	0.31	
GR2-2I 27-50	5.83	1.13	1,000,000	1000	0.23	0.68	10.3034756	8.68	1.62	
GR2-2I 50-80								0	1.56	
GR2-2S 0-4	1.31	1.18	1,000,000	1000	0.04	0.76	0.4699232	0	0.47	5.04
GR2-2S 4-10	0.47	1.18	1,000,000	1000	0.06	0.68	0.2262768	0	0.23	
GR2-2S 10-22	0.25	1.24	1,000,000	1000	0.12	0.71	0.26412	0	0.26	
GR2-2S 22-50	1.15	1.24	1,000,000	1000	0.28	0.63	2.515464	0	2.52	
GR2-2S 50-80								0	1.56	
GR2-3I 0-2	0.36	1.15	1,000,000	1000	0.02	0.73	0.060444	0.005	0.06	3.64
GR2-3I 2-6	0.29	1.53	1,000,000	1000	0.04	0.78	0.1384344	0	0.14	
GR2-3I 6-16	0.48	1.24	1,000,000	1000	0.1	0.63	0.374976	0	0.37	
GR2-3I 16-40	4.4	1.13	1,000,000	1000	0.24	0.79	9.426912	8.44	0.99	
GR2-3I 40-80	4.67	1.13	1,000,000	1000	0.4	0.69	14.564796	12.48	2.08	
GR2-3S 0-2	2.81	1.18	1,000,000	1000	0.02	0.73	0.4841068	0	0.48	6.97
GR2-3S 2-9	1.62	1.18	1,000,000	1000	0.07	0.72	0.9634464	0	0.96	
GR2-3S 9-22	1.25	1.24	1,000,000	1000	0.13	0.69	1.39035	0	1.39	
GR2-3S 22-50	1.29	1.13	1,000,000	1000	0.28	0.63	2.5713828	0	2.57	
GR2-3S 50-80								0	1.56	

GR2-4I 0-2	0.44	1.15	1,000,000	1000	0.02	0.73	0.073876	0	0.07	2.66
GR2-4I 2-7	0.36	1.53	1,000,000	1000	0.05	0.75	0.20655	0	0.21	
GR2-4I 7-15	0.63	1.24	1,000,000	1000	0.08	0.63	0.3937248	0	0.39	
GR2-4I 15-50	0.2	1.13	1,000,000	1000	0.35	0.72	0.56952	0.14	0.43	
GR2-4I 50-80								0	1.56	
GR2-4S 0-2	0.86	1.18	1,000,000	1000	0.02	0.73	0.1481608	0	0.15	4.34
GR2-4S 2-8	0.43	1.18	1,000,000	1000	0.06	0.59	0.1796196	0	0.18	
GR2-4S 8-15	0.83	1.09	1,000,000	1000	0.07	0.63	0.3989727	0	0.40	
GR2-4S 15-23	0.64	1.13	1,000,000	1000	0.08	0.76	0.4397056	0	0.44	
GR2-4S 23-36	0.5	1.13	1,000,000	1000	0.13	0.79	0.580255	0	0.58	
GR2-4S 36-43	3.12	1.13	1,000,000	1000	0.07	0.77	1.9002984	1.55	0.35	
GR2-4S 43-50	1.6	1.13	1,000,000	1000	0.07	0.54	0.683424	0	0.68	
GR2-4S 50-80								0	1.56	
GR3-1I 0-1	0.86	1.09	1,000,000	1000	0.01	0.69	0.0646806	0	0.06	3.48
GR3-1I 1-7	0.64	1.12	1,000,000	1000	0.06	0.78	0.3354624	0	0.34	
GR3-1I 7-16	0.46	1.23	1,000,000	1000	0.09	0.63	0.3208086	0	0.32	
GR3-1I 16-30	0.52	1.25	1,000,000	1000	0.14	0.73	0.6643	0	0.66	
GR3-1I 30-42	0.51	1.26	1,000,000	1000	0.12	0.69	0.5320728	0	0.53	
GR3-1I 42-50	5.08	1.26	1,000,000	1000	0.08	0.65	3.328416	2.44	0.89	
GR3-1I 50-60	4.41	1.26	1,000,000	1000	0.1	0.47	2.611602	1.94	0.67	
GR3-1S 0-4	2.73	1.1	1,000,000	1000	0.04	0.82	0.984984	0	0.98	2.99

GR3-1S 4-17	0.71	1.21	1,000,000	1000	0.13	0.79	0.8822957	0	0.88	
GR3-1S 17-32	0.49	1.25	1,000,000	1000	0.15	0.73	0.6706875	0	0.67	
GR3-1S 32-42	0.43	1.25	1,000,000	1000	0.1	0.68	0.3655	0	0.37	
GR3-1S 42-55									0.09	
GR3-1T 0-3	5.04	0.83	1,000,000	1000	0.03	0.84	1.0541664	0	1.05	2.75
GR3-1T 3-17	0.51	1.28	1,000,000	1000	0.14	0.81	0.7402752	0	0.74	
GR3-1T 17-29	0.47	1.25	1,000,000	1000	0.12	0.73	0.51465	0	0.51	
GR3-1T 29-41	0.26	1.25	1,000,000	1000	0.12	0.7	0.273	0	0.27	
GR3-1T 41-60	0.11	1.25	1,000,000	1000	0.19	0.65	0.1698125	0	0.17	
GR3-2I 0-6	0.43	1.12	1,000,000	1000	0.06	0.83	0.2398368	0	0.24	1.07
GR3-2I 6-10	0.61	1.23	1,000,000	1000	0.04	0.63	0.1890756	0	0.19	
GR3-2I 10-22	0.38	1.25	1,000,000	1000	0.12	0.74	0.4218	0	0.42	
GR3-2I 22-41	0.08	1.25	1,000,000	1000	0.19	0.71	0.1349	0	0.13	
GR3-2I 41-50	0.08	1.25	1,000,000	1000	0.09	0.65	0.0585	0	0.06	
GR3-2I 51-55									0.03	
GR3-2S 0-3	1.68	1.1	1,000,000	1000	0.03	0.75	0.4158	0	0.42	3.04
GR3-2S 3-10	0.7	1.21	1,000,000	1000	0.07	0.86	0.509894	0	0.51	
GR3-2S 10-19	0.63	1.25	1,000,000	1000	0.09	0.73	0.5173875	0	0.52	
GR3-2S 19-39	0.35	1.25	1,000,000	1000	0.2	0.72	0.63	0	0.63	
GR3-2S 39-51	3.55	1.25	1,000,000	1000	0.12	0.65	3.46125	2.52	0.94	
GR3-2S 51-55									0.03	

GR3-2T 0-2	1.98	0.83	1,000,000	1000	0.02	0.78	0.2563704	0	0.26	1.58
GR3-2T 2-9	0.38	1.28	1,000,000	1000	0.07	0.85	0.289408	0	0.29	
GR3-2T 9-14	0.27	1.25	1,000,000	1000	0.05	0.77	0.1299375	0	0.13	
GR3-2T 14-24	0.39	1.25	1,000,000	1000	0.1	0.73	0.355875	0	0.36	
GR3-2T 24-35	0.26	1.25	1,000,000	1000	0.11	0.73	0.260975	0	0.26	
GR3-2T 35-42	0.23	1.25	1,000,000	1000	0.07	0.65	0.1308125	0	0.13	
GR3-2T 42-50	0.20	1.25	1,000,000	1000	0.08	0.65	0.13	0	0.13	
GR3-2T 50-55									0.03	
GR3-3I 0-1	0.48	1.09	1,000,000	1000	0.01	0.69	0.0361008	0	0.04	1.10
GR3-3I 1-5	0.34	1.12	1,000,000	1000	0.04	0.86	0.1309952	0	0.13	
GR3-3I 5-18	0.27	1.23	1,000,000	1000	0.13	0.78	0.3367494	0	0.34	
GR3-3I 18-36	0.25	1.25	1,000,000	1000	0.18	0.73	0.410625	0	0.41	
GR3-3I 36-55									0.19	
GR3-3S 0-2	1.18	1.1	1,000,000	1000	0.02	0.76	0.197296	0	0.20	1.41
GR3-3S 2-9	0.35	1.21	1,000,000	1000	0.07	0.85	0.2519825	0	0.25	
GR3-3S 9-18	0.18	1.23	1,000,000	1000	0.09	0.75	0.149445	0	0.15	
GR3-3S 18-24	0.31	1.25	1,000,000	1000	0.06	0.73	0.169725	0	0.17	
GR3-3S 24-44	0.28	1.25	1,000,000	1000	0.2	0.7	0.49	0	0.49	
GR3-3S 44-50	0.25	1.25	1,000,000	1000	0.06	0.65	0.121875	0	0.12	
GR3-3S 50-55									0.03	

GR3-3T 0-3	5.35	1.10	1,000,000	1000	0.03	0.8	1.4124	0	1.41	2.94
GR3-3T 3-8	1.10	1.10	1,000,000	1000	0.05	0.86	0.5203	0	0.52	
GR3-3T 8-15	0.31	1.21	1,000,000	1000	0.07	0.78	0.2048046	0	0.20	
GR3-3T 15-25	0.37	1.25	1,000,000	1000	0.1	0.73	0.337625	0	0.34	
GR3-3T 25-35	0.32	1.25	1,000,000	1000	0.1	0.73	0.292	0	0.29	
GR3-3T 35-48	0.14	1.25	1,000,000	1000	0.13	0.65	0.147875	0	0.15	
GR3-3T 48-50	0.25	1.25	1,000,000	1000	0.02	0.65	0.040625	0.02	0.02	
GR3-3T 50-55										
GR3-4I 0-1	0.62	1.09	1,000,000	1000	0.01	0.69	0.0466302	0	0.05	1.73
GR3-4I 1-7	0.51	1.12	1,000,000	1000	0.06	0.86	0.2947392	0	0.29	
GR3-4I 7-11	0.6	1.23	1,000,000	1000	0.04	0.84	0.247968	0	0.25	
GR3-4I 11-36	0.46	1.25	1,000,000	1000	0.25	0.73	1.049375	0	1.05	
GR3-4I 36-55	0.08	1.26	1,000,000	1000	0.14	0.65	0.091728	0	0.09	
GR3-4S 0-4	1.95	1.1	1,000,000	1000	0.04	0.82	0.70356	0	0.70	1.71
GR3-4S 4-12	0.36	1.21	1,000,000	1000	0.08	0.83	0.2892384	0	0.29	
GR3-4S 12-19	0.24	1.25	1,000,000	1000	0.07	0.73	0.1533	0	0.15	
GR3-4S 19-29	0.21	1.25	1,000,000	1000	0.1	0.73	0.191625	0	0.19	
GR3-4S 29-44	0.25	1.25	1,000,000	1000	0.15	0.69	0.3234375	0	0.32	
GR3-4S 44-50	0.04	1.25	1,000,000	1000	0.06	0.65	0.0195	0	0.02	
GR3-4S 50-55									0.03	
GR3-4T 0-3	1.31	0.83	1,000,000	1000	0.03	0.8	0.260952	0	0.26	2.04
GR3-4T 3-11	0.56	1.28	1,000,000	1000	0.08	0.85	0.487424	0	0.49	

GR3-4T 11-23	0.45	1.25	1,000,000	1000	0.12	0.73	0.49275	0	0.49	
GR3-4T 23-58	0.28	1.25	1,000,000	1000	0.35	0.65	0.79625	0	0.80	
GR5-1I 0-3	0.65	1.17	1,000,000	1000	0.03	0.6	0.13689	0	0.14	1.41
GR5-1I 3-11	0.46	1.14	1,000,000	1000	0.08	0.64	0.2684928	0	0.27	
GR5-1I 11-29	0.5	1.1	1,000,000	1000	0.18	0.5	0.495	0	0.50	
GR5-1I 29-50	0.39	1.3	1,000,000	1000	0.21	0.48	0.511056	0	0.51	
GR5-1S 0-5	1.67	0.98	1,000,000	1000	0.05	0.66	0.540078	0	0.54	2.15
GR5-1S 5-22	0.84	1.05	1,000,000	1000	0.17	0.55	0.82467	0	0.82	
GR5-1S 22-50	0.53	1.1	1,000,000	1000	0.28	0.48	0.783552	0	0.78	
GR5-2I 0-1	0.9	1.17	1,000,000	1000	0.01	0.6	0.06318	0	0.06	1.66
GR5-2I 1-6	0.67	1.3	1,000,000	1000	0.05	0.68	0.29614	0	0.30	
GR5-2I 6-13	0.97	0.98	1,000,000	1000	0.07	0.59	0.3925978	0	0.39	
GR5-2I 13-45	0.54	1.1	1,000,000	1000	0.32	0.48	0.912384	0	0.91	
GR5-2S 0-3	1.53	0.98	1,000,000	1000	0.03	0.64	0.2878848	0	0.29	2.13
GR5-2S 3-9	0.73	1.1	1,000,000	1000	0.06	0.64	0.308352	0	0.31	
GR5-2S 9-17	0.84	1.05	1,000,000	1000	0.08	0.55	0.38808	0	0.39	
GR5-2S 17-37	0.87	1.1	1,000,000	1000	0.2	0.48	0.91872	0	0.92	
GR5-2S 37-45									0.23	
GR5-3I 0-1	1.05	1.17	1,000,000	1000	0.01	0.6	0.07371	0	0.07	1.29
GR5-3I 1-7	0.64	1.3	1,000,000	1000	0.02	0.68	0.113152	0	0.11	
GR5-3I 7-16	1.03	0.98	1,000,000	1000	0.09	0.59	0.5359914	0	0.54	
GR5-3I 16-30	0.49	1.1	1,000,000	1000	0.14	0.48	0.362208	0	0.36	
GR5-3I 30-47	0.23	1.1	1,000,000	1000	0.17	0.48	0.206448	0	0.21	

GR5-3S 0-6	1.03	0.98	1,000,000	1000	0.06	0.67	0.4057788	0	0.41	1.55
GR5-3S 6-14	1.19	1.05	1,000,000	1000	0.08	0.59	0.589764	0	0.59	
GR5-3S 14-23	0.49	1.1	1,000,000	1000	0.09	0.48	0.232848	0	0.23	
GR5-3S 23-41	0.27	1.1	1,000,000	1000	0.18	0.4	0.21384	0	0.21	
GR5-3S 41-45									0.11	
GR5-4I 0-1	0.64	1.17	1,000,000	1000	0.01	0.6	0.044928	0	0.04	1.85
GR5-4I 1-7	0.46	1.3	1,000,000	1000	0.06	0.68	0.243984	0	0.24	
GR5-4I 7-18	0.75	0.98	1,000,000	1000	0.11	0.55	0.444675	0	0.44	
GR5-4I 18-34	0.61	1.1	1,000,000	1000	0.16	0.48	0.515328	0	0.52	
GR5-4I 34-55									0.60	
GR5-4S 0-7	1.12	1.1	1,000,000	1000	0.07	0.65	0.56056	0	0.56	2.08
GR5-4S 7-19	0.96	1.05	1,000,000	1000	0.12	0.54	0.653184	0	0.65	
GR5-4S 19-25	0.56	1.1	1,000,000	1000	0.06	0.48	0.177408	0	0.18	
GR5-4S 25-50	0.52	1.1	1,000,000	1000	0.25	0.48	0.6864	0	0.69	
WP7 1I 0-7	0.73	1.18	1,000,000	1000	0.07	0.66	0.3979668	0	0.40	2.57
7-14	0.86	1.18	1,000,000	1000	0.07	0.66	0.4688376	0	0.47	
14-20	0.71	1.29	1,000,000	1000	0.06	0.63	0.3462102	0	0.35	
20-31	0.66	1.14	1,000,000	1000	0.11	0.59	0.4883076	0	0.49	
31-50	0.33	1.14	1,000,000	1000	0.19	0.43	0.3073554	0	0.31	
50-110									0.56	

WP7 1S 0-7	2.34	0.98	1,000,000	1000	0.07	0.66	1.0594584	0	1.06	3.55
7-15	0.78	1.12	1,000,000	1000	0.08	0.66	0.4612608	0	0.46	
15-23	0.77	1.29	1,000,000	1000	0.08	0.63	0.5006232	0	0.50	
23-34	0.82	1.14	1,000,000	1000	0.11	0.54	0.5552712	0	0.56	
34-50	0.53	1.14	1,000,000	1000	0.16	0.43	0.4156896	0	0.42	
50-110									0.56	
WP7 2I 0-4	1.46	1.18	1,000,000	1000	0.04	0.66	0.4548192	0	0.45	3.90
4-14	1.13	1.17	1,000,000	1000	0.1	0.66	0.872586	0	0.87	
14-29	0.86	1.29	1,000,000	1000	0.15	0.63	1.048383	0	1.05	
29-55	0.67	1.14	1,000,000	1000	0.26	0.43	0.8539284	0	0.85	
55-72	0.51	0.83	1,000,000	1000	0.2	0.37	0.313242	0	0.31	
72-110	0.18	0.83	1,000,000	1000	0.38	0.63	0.3576636	0	0.36	
WP7 2S 0-5	4.64	0.98	1,000,000	1000	0.05	0.66	1.500576	0	1.50	4.58
5-14	1.13	1.12	1,000,000	1000	0.09	0.66	0.7517664	0	0.75	
14-30	0.76	1.29	1,000,000	1000	0.16	0.63	0.9882432	0	0.99	
30-43	0.61	1.14	1,000,000	1000	0.13	0.43	0.3887286	0	0.39	
43-56	0.69	1.14	1,000,000	1000	0.13	0.43	0.4397094	0	0.44	
56-110									0.51	
WP7 3I 0-3	1.7	1.18	1,000,000	1000	0.03	0.66	0.397188	0	0.40	3.66
3-11	1.45	1.17	1,000,000	1000	0.08	0.66	0.895752	0	0.90	
11-29	0.78	1.29	1,000,000	1000	0.19	0.64	1.2235392	0	1.22	
29-45	0.67	1.14	1,000,000	1000	0.16	0.43	0.5254944	0	0.53	

45-50	0.23	1.14	1,000,000	1000	0.05	0.43	0.056373	0	0.06	
50-110									0.56	
WP7 3S 0-7	3.39	0.98	1,000,000	1000	0.07	0.66	1.5348564	0	1.53	5.46
7-19	1.72	1.12	1,000,000	1000	0.12	0.65	1.502592	0	1.50	
19-39	1.01	1.22	1,000,000	1000	0.2	0.63	1.552572	0	1.55	
39-52	0.66	1.14	1,000,000	1000	0.13	0.43	0.4205916	0	0.42	
52-62		0.83	1,000,000	1000	0.1	0.43	0	0	0.00	
62-110									0.45	
WP7 4I 0-7	1.03	1.18	1,000,000	1000	0.07	0.66	0.5615148	0	0.56	3.38
7-14	1.0	1.17	1,000,000	1000	0.07	0.66	0.54054	0	0.54	
14-23	1.04	1.29	1,000,000	1000	0.09	0.63	0.7606872	0	0.76	
23-39	0.8	1.14	1,000,000	1000	0.16	0.5	0.7296	0	0.73	
39-50	0.43	1.14	1,000,000	1000	0.11	0.43	0.2318646	0	0.23	
50-110									0.56	
WP7 4S 0-5	2.98	0.98	1,000,000	1000	0.05	0.66	0.963732	0	0.96	4.29
5-13	1.51	1.12	1,000,000	1000	0.08	0.66	0.8929536	0	0.89	
13-23	0.96	1.29	1,000,000	1000	0.1	0.63	0.780192	0	0.78	
23-42	0.79	1.14	1,000,000	1000	0.19	0.49	0.8384586	0	0.84	
42-56	0.45	1.14	1,000,000	1000	0.14	0.43	0.308826	0	0.31	
56-110									0.51	
BAR 1 0-3	3.69	1.18	1,000,000	1000	0.03	0.32	0.4180032	0	0.42	2.14
3-8	2.5	1.17	1,000,000	1000	0.05	0.41	0.599625	0	0.60	
8-21	0.37	1.29	1,000,000	1000	0.13	0.23	0.1427127	0	0.14	
21-40	0.48	1.34	1,000,000	1000	0.19	0.52	0.6354816	0	0.64	

40-63	0.13	1.34	1,000,000	1000	0.23	0.69	0.2764554	0	0.28	
63-152								0	0.07	
BAR 2 0-3	4.41	1.18	1,000,000	1000	0.03	0.32	0.4995648	0	0.50	2.25
3-20	1.93	1.17	1,000,000	1000	0.17	0.27	1.0364679	0	1.04	
20-33	0.42	1.29	1,000,000	1000	0.13	0.4	0.281736	0	0.28	
33-54	0.18	1.34	1,000,000	1000	0.21	0.69	0.3494988	0	0.35	
54-152								0	0.08	
BAR 3 0-4	3.69	1.18	1,000,000	1000	0.04	0.34	0.5921712	0	0.59	1.66
4-20	1.05	1.17	1,000,000	1000	0.16	0.26	0.511056	0	0.51	
20-33	0.32	1.29	1,000,000	1000	0.13	0.4	0.214656	0	0.21	
33-52	0.13	1.34	1,000,000	1000	0.17	0.69	0.2043366	0	0.20	
52-60	0.11	1.34	1,000,000	1000	0.08	0.54	0.0636768	0	0.06	
60-152									0.07	
BAR 4 0-2	4.02	1.18	1,000,000	1000	0.02	0.27	0.2561544	0	0.26	3.63
2-7	2.63	1.17	1,000,000	1000	0.05	0.41	0.6308055	0	0.63	
7-28	1.47	1.17	1,000,000	1000	0.21	0.23	0.8307117	0	0.83	
28-69	0.17	1.29	1,000,000	1000	0.41	0.69	0.6203997	0	0.62	
69-100	0.52	1.34	1,000,000	1000	0.31	0.58	1.2528464	0	1.25	
100-152	0.02	1.12	1,000,000	1000	0.52	0.36	0.0419328	0	0.04	

Appendix B. Example calculation of interspace, shrub and total SOC storage for site GR2. SOC from replicate microsite pedons (i.e.,GR2-1I, 2I, 31 and 41 calculated in Appendix A) are multiplied by the respective proportion of landscape they represent (Columns C for interspace and E for shrubs). This gives SOC storage for each replicate of each microsite type (Columns F and G). SOC storage of replicate pedons are then averaged to obtain microsite SOC storage for a given elevation.

A B C D E F G

	INTERSPACE SOC	**% INTERSPACE**	**SHRUB SOC**	**% SHRUB COVER**	**INTERSPACE SOC STORAGE**	**SHRUB SOC STORAGE**	**GR2-I Storage (kg m^{-2})**	**GR2-S Storage (kg m^{-2})**
GR2-1	2.55	0.28	3.78	0.72	0.714	2.7216	0.92	3.62
GR2-2	4.33	0.28	5.04	0.72	1.2124	3.6288		
GR2-3	3.64	0.28	6.96	0.72	1.0192	5.0112		
GR2-4	2.66	0.28	4.34	0.72	0.7448	3.1248		