THE CARBON BUDGET IMPACT OF SAGEBRUSH DEGRADATION

by

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ABSTRACT

More than 20,000 km^2 of sagebrush (*Artemesia* spp.) ecosystems within the Great Basin have been replaced, often following wildfire, by the nonnative winter annual cheatgrass (*Bromus tectorum*). At a field site in the central Snake River Plain of southern Idaho, the impact of this invasion on the soil carbon (C) reservoir has been evaluated and the potential soil C benefits of bunchgrass (*Agropyron cristatum*) seeding was assessed. Using a large soil C dataset (n = 850), differences in total organic carbon and root biomass were quantified in immediately-adjacent sagebrush, cheatgrass, and bunchgrass communities. Statistical significance was determined by employment of nonparametric analysis using bootstrap resampling and the two-population Kolmogrov-Smirnov test for statistical significance. Replacement of sagebrush by cheatgrass following fire has resulted in a 50% loss in below-ground carbon (56 to 29 Mg C ha^{-1}, over a 27 yr period), with decreased root-C accounting for 20% of the total below-ground carbon loss. Bunchgrass seeding immediately following the fire reduced the amount of C lost to sagebrush degradation by 30% (31 vs. 40 Mg C ha^{-1}). There is a positive relationship between above-ground biomass and below-ground soil carbon, however C loss is an order of magnitude greater in below-ground compared to above-ground C pools (27 vs. 3 Mg ha^{-1}). Observed changes in soil structure, in particular the loss of large soil aggregates, and altered soil moisture conditions may contribute to the observed soil carbon loss. Extension of these results to the entire Great Basin, suggest the total below-

ground carbon loss with cheatgrass invasion is on the order of 60 Mt C and projected losses may exceed 2 Gt C. Conversely, treatment with bunchgrass or recovery of the original sagebrush may achieve similarly large carbon storage benefits.

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LIST OF ABBREVIATIONS

C	Carbon
TC	Total Below-ground Carbon
TOC	Total Below-ground Organic Carbon
TIC	Total Below-ground Inorganic Carbon
SOC	Soil Organic Carbon
R_b	Below-ground Root Biomass
TN	Total Nitrogen
K-S test	Two-population Kolmogrov-Smirnov Test for Significant Difference
BREB	Bowen Ratio Energy Balance
POM	Particulate Organic Matter
SOM	Soil Organic Matter
AM Fungi	Vesicular Arbuscular Mycorrhizal Fungi
O-	Occluded in Macroaggregates

CHAPTER ONE: INTRODUCTION

1.1 Degradation and Reclamation of the Sagebrush-steppe Ecosystem

The sagebrush-steppe ecosystem (*Artemisia* spp.) is one of the most expansive in the U.S., covering approximately 480,000 km^2 and distributed across 13 states (Connelly, Knick, Schroeder, & Stiver, 2004). Healthy sagebrush-steppe ecosystems (sagebrush) are important social and economic resources that support a diversity of wildlife and livestock grazing (Mack et al. 2000). However, during the last century sagebrush-steppe communities of the Great Basin and elsewhere have been dramatically affected by climate change and anthropogenic activities where, often following wildfire or other disturbance, invasion by the nonnative winter annual, cheatgrass (*Bromus tectorum*), is widely observed (Bradley 2009). Cheatgrass invasion reduces ecosystem function by diminishing resources such as livestock grazing and wildlife diversity. This ecological shift is challenging to remediate because, once established, cheatgrass is more fire prone, limiting the ability of more slow growing sagebrush to compete (DiTomaso 2000). Accordingly, cheatgrass infestation has been a cause of ecosystem degradation throughout the Intermountain West, specifically within the Great Basin (Bradley 2009; Connelly et al. 2004). A qualitative survey conducted by the U. S. Bureau of Land Management (BLM) in 1991 that spanned 400,000 km^2 (Idaho, Oregon, Nevada, Utah, Washington), estimated that cheatgrass has displaced over 11,000 $km^2$of sagebrush habitat and become a major understory component in a further 57,000 km^2 of BLM-managed public lands (Pellant 1994). More recently, Bradley & Mustard (2005) analyzed

satellite imagery and mapped over 20,000 km^2 of cheatgrass monocultures within the Great basin, whereas Bradley (2009) mapped 760,000 km^2 of land in the western U.S. at risk of cheatgrass invasion under current climatic conditions.

One promising solution to cheatgrass degradation of sagebrush ecosystems involves introducing species other than sagebrush that are more effective competitors (M. Pellant, 2010, personal communication). One such strategy that has shown success is seeding certain bunchgrass species such as Crested Wheatgrass (*Agropyron cristatum*) either immediately following fire or after active removal of cheatgrass. Once bunchgrass is established, it may then be possible to reintroduce sagebrush (M. Pellant, 2010, personal communication).

The goal of this research was to quantify changes in below-ground carbon storage associated with: (1) cheatgrass degradation of sagebrush ecosystems and (2) cheatgrass remediation via bunchgrass seeding. This was done in an effort to provide the framework for a long-term approach to mitigate CO_2 emissions while simultaneously improving the health of cheatgrass-degraded sagebrush ecosystems.

1.2 Previous Research

1.2.1 The Soil Carbon Reservoir: Functional Pools and the Influence of Vegetation

There are large differences in the physiology of plant species, implying that a change in species dominance can greatly affect the degree to which carbon (C) is introduced and retained in soils. Consequently, a shift in the dominant plant life form can alter the size and nature of the underlying soil C reservoir. Such physiological shifts are apparent in plant communities that represent degradation and improvement of disturbed

sagebrush (cheatgrass and bunchgrass, respectively), where senescence of cheatgrass, bunchgrass, and sagebrush occurs in late spring, early summer, and late summer, respectively. Cheatgrass allocates much of its resources to seed and shoot production while generating a dense and shallow root system (Upadhaya, Turkington, & McIlride 1986), whereas sagebrush and bunchgrass dedicate more resources to producing deeply penetrating perennial root systems (Caldwell, White, Moore, & Camp 1977; Dahlman & Kucera 1965; Hooker et al. 2008). These differences reflect the timing and duration of CO_2 fixation, as well as the allocation of that carbon, and thus the size of the soil C reservoir.

Carbon derived from living and dead roots is extremely important to below-ground C fluxes (Jackson, Mooney, & Schulze 1997). Living roots contribute carbon in the form of sugars and organic acids through rhizodeposition, whereas dead roots are incorporated into the soil matrix by bacterial decomposition (Stevensen 1994). Roots tend to be more resistant to decomposition than above-ground litter because of high lignin content (Lorenz & Lal 2005) and, consequently, increased root input promotes C storage. In addition, some researchers have documented variability in root turnover rates with depth (Gill, Burke, Milchunas, & Lauenroth 1999; Ares 1976; Dahlman & Kucera 1965); this is an important distinction because the residence time of root-derived C may vary with depth due to changing soil temperature and moisture regimes (Gill, Burke, Milchunas, & Lauenroth 2002).

Carbon respiration is equally critical in determining the size of the soil C reservoir and can be largely influenced by vegetation (Lorenz & Lal 2005). Both the composition and timing of inputs for above- and below-ground material are important to carbon

mineralization rates. Similarly, higher soil moisture and temperature can enhance respiration rates while being influenced by vegetation (Wedin & Tilman 1990, Gill et al. 1999).

There are specific functional pools within the soil C reservoir, each having unique dynamics and residence times (Lorenz & Lal 2005; Christensen 1992; Stevensen 1994; Gill & Burke 1999). An accurate description of the C budget impact of vegetative shifts therefore requires quantification of specific C pools. Total carbon (TC) within soils includes total inorganic carbon (TIC) and total organic carbon (TOC). TIC consists of carbonates that are deposited by processes of soil formation, whereas TOC represents all organic carbon that is the product of biological activity in any stage of decay (Christensen 1992). TOC can be classified as either root-C or soil organic carbon (SOC). In this study, root-C represents various types of plant residue within soil that is greater than 250 µm, including roots and other partially decomposed material, whereas SOC is a metabolic product of root-C. SOC typically has longer soil residence times in soils (Brady & Weil 2008; Stevenson 1994).

The development of soil structure can strongly influence the nature and degree of soil carbon sequestration (Six, Bossuyt, Degryze, & Denef 2004). Soil macroaggregates (>250 µm) can form within soils, physically preserving root-C and SOC. Within macroaggregates, metabolized organic C becomes encrusted with clay particles and microbial products, forming very stable microaggregates (250 -53µm). Eventually, these microaggregates break down into less stable silt- and clay-sized organo-mineral complexes (Six et al. 2004). Stable isotope and radiocarbon studies have corroborated the theory that soil C residence times are negatively correlated to SOC aggregate sizes

(Christensen 1992; Gill & Burke 1999; Del Galdo, Six, Peressottis, & Cotrufo 2003; Marzioli et al. 2010; and others), although whether or not this trend is due to organic recalcitrance or physical exclusion is still debated (McCarthy, Ilvasky, Jastrow, Mayer, & Perfect 2008). Therefore, in order to accurately describe changes in SOC storage and dynamics, it is important to investigate changes in the distribution of SOC within soil aggregates.

1.2.2 Soil Carbon Investigation within Sagebrush-steppe Ecosystems

Several researchers have attempted to quantify C budget changes associated with shifts in species dominance of semi-arid ecosystems (Gill & Burke 1999; Potter, Torbert, Johnson, & Tischler 1999; Chen & Stark 2000; Norton, Monaco, Norton, Johnson, & Jones 2004; Hooker et al. 2008; Rau, Johnson, & Blank 2011) (Table 1). In comparing the SOC content of near surface soils (0-10 cm), Hooker et al. (2008) reported cheatgrass to have significantly higher SOC content compared to sagebrush soils, whereas Gill et al. (1999) found higher soil carbon content within shrubs (*Atriplex confertifolia*) compared to cheatgrass. Norton et al. (2004) found no significant differences in near surface C between sagebrush-steppe and cheatgrass soils. Norton et al. (2004) also observed the most variability in OC content of cheatgrass soils compared to the shrub-grass-interspace soils in sagebrush, as proposed by Chen and Stark (2000). This lack of scientific consensus on the impact of cheatgrass invasion on the soil C reservoir may be attributable to: (1) variability in stand age, (2) level of cheatgrass encroachment, (3) contrasting concentrations of antecedent soil carbon, and (4) differences in experimental design. Potter et al. (1999) found SOC to be linearly correlated with stand age in reclaimed grasslands, and Rau et al. (2011) showed the level of cheatgrass invasion to be inversely

correlated with OC content. Importantly, Rau et al. (2011) concluded that replacement of perennial grasses with cheatgrass could result in a net loss of 6-9 Mg C ha^{-1} for sagebrush ecosystems, while also predicting loss of sagebrush to cause a further decline in SOC content.

Potter et al. (1999) documented a significant decrease in SOC when grasslands were degraded by cultivation (inversion tillage) and that subsequent restoration of these grasslands produced a linear increase in SOC storage (447 kg C ha^{-1} yr^{-1}). Similarly, Del Galdoet al. (2003) used ^{13}C stable isotope signatures to show that forestation of cultivated lands significantly increased SOC within distinct aggregate sizes. The results of these studies are potentially relevant as several researchers have likened the effects of cheatgrass invasion to cultivation for agriculture (Norton et al. 2004; Schimel 1986). In this study, we quantify differences in below ground carbon with cheatgrass invasion, demonstrating, for the first time, dramatic declines in soil carbon content.

CHAPTER TWO: MATERIALS AND METHODS

2.1 Introduction

Key components of our research approach included (1) locating a site with homogeneous properties of climate, soil, and stand age, (2) designing efficient field and lab methods that facilitate the processing of large quantities of samples, (3) accurately quantifying distinct C pools, and (4) using statistical analyses to quantify uncertainty of observed trends.

2.2 Study Site

2.1.1 Site Location

Kuna Butte, located in the western Snake River Plain of Southern Idaho (43°27'55"N, 116°28'55" W, elevation 915 m; Figure 1), is public land administered by the Bureau of Land Management (mean temp and precipitation is 11 °C and 280 mm yr^{-1}, respectively). The soil (70 to 90 cm total depth) is a loamy, mesic shallow Xerollic Duragid, with parent material of loess over basalt bedrock (Barker, McDole, & Logan 1983), providing relatively flat topography. Approximately 20 cm of duripan lies above bedrock, providing an ideal boundary condition for quantifying C pools.

Covariates between vegetative stands are minimal at Kuna Butte, owing to a juxtaposition of the three plant communities representing each stage of sagebrush alteration (initial condition, cheatgrass-degraded, and partially reclaimed). Importantly,

the vegetative stands representing stages of sagebrush alteration (cheatgrass and bunchgrass) have been established for equal and extended periods of time, potentially long enough to affect soil C stores; this conjecture is based on the work of Potter et al. (1999) who documented differences in soil C of reclaimed agricultural soils after six years of growth.

2.1.2 Site History

Kuna Butte experienced a wildfire in the spring of 1983, which consumed a large portion of sagebrush, except for an area that was excluded from fire due to the presence of a small dirt road (Figure 2). In late fall of 1983, a 25 m wide strip of Fairway Crested Wheatgrass (*Agropyron cristatum)* was drill seeded (4.5 lbs·seed·acre^{-1}) beginning near the road. The spring of 1984 revealed that the seeded area had high germination and growth rates, and cheatgrass (*Bromus tectorum*) dominated the adjacent unseeded area (Johansen 1984). The path of crested wheatgrass (bunchgrass) seeding was well pronounced at the time of this study, forming a sharp transition between bunchgrass and cheatgrass communities, indicating that neither grass species has invaded the other since establishment. Conversely, cheatgrass has remained present in sagebrush interspaces, occupying approximately 80% of sagebrush interspace during the time of this study.

2.2 Field Methods

2.2.1 Soil Sampling for Total Carbon (TC), Total Organic Carbon (TOC), Soil Organic Carbon (SOC), and Below-ground Biomass (Rb)

Along four 30 m long transects (15 m in each vegetation type) orientated perpendicular to species community boundaries, soil cores were extracted at a 1 m

spacing. The four sampling transects crossed the species boundaries in the following manner: cheatgrass/bunchgrass (C/B), cheatgrass/sagebrush (C/S), sagebrush/bunchgrass (S/B), and cheatgrass/bunchgrass (C/B 2). Due to the presence of the road, the two transects including sagebrush were discontinuous. Accordingly, each half of the C/S and S/B transects began more than 10 m from the road to avoid potential disturbances. This sampling scheme was designed to compare the effects of species dominance and natural variation of plant biomass and soil carbon, but also to investigate changes in soil carbon with respect to distance from species boundary.

All samples were collected from July to early September of 2010 using a 7 cm sand auger (AMS, 300.41). This auger provided the ability to remove and retain roots, allowing estimation of below-ground biomass in each plant community. The upper 3 cm of soil was sampled using a bulb planter to isolate elevated C content from litter incorporation. Following removal of the upper 3 cm of the soil profile, samples were collected at 5 cm increments to a depth of 18 cm and every other 5 cm increment was retained for analysis thereafter. Sampling depth did not exceed 58 cm because this was approximately the depth at which duripan was encountered. Samples were stored in plastic bags and frozen at -10 °C until analysis.

2.2.2 Soil Sampling for Aggregates Containing of Soil Organic Carbon

Soil aggregate samples were collected within the same transects established for soil carbon samples. A 7 cm sand auger (AMS, 300.41) was used to remove the upper 0-5 cm of soil and a 5 cm diameter slide hammer (AMS, 404.61) was used to collect a continuous 10 cm sample from 5-15 cm. This depth increment was chosen for aggregate sampling because it was deemed to be actively influenced by root exudation and assumed

to be deep enough so that influence of above-ground processes are insignificant. All samples were stored at 10 °C until analysis could be carried out.

2.2.3 Soil Sampling for Bulk Density and Grain Size

Four soil pits, each located throughout the study site and within contrasting plant communities (Figure 2), were excavated by hand to allow field classification of soil properties following USDA protocols (SSDS 1993). Samples were collected from pit walls with a 5 x 10 cm diameter slide hammer (AMS, 404.61) for laboratory analysis of grain size and bulk density. All samples were centered at the same depth increments as those for soil carbon analysis, excluding the 0-3 cm increment. If compaction of samples was evident, the sample was discarded and another was collected.

2.2.4 Quantification of Canopy Cover

Canopy cover was estimated in an effort to quantify potential differences between sample locations but within plant communities. However, cheatgrass communities were not included in estimation of canopy cover because little to no bare ground was present within transects and all populations were assumed to be monocultures representing 100% canopy cover. Canopy cover was estimated by linearly classifying ground cover as either bare ground, beneath canopy, or invaded by cheatgrass, at a resolution of 5 cm along each transect. Additionally, the number of soil cores taken beneath canopy for each transect was documented.

2.2.5 Sample Collection of Above-ground Biomass

Above-ground biomass was estimated for each plant community following U.S. Department of the Interior protocols (Habich 2001). For cheatgrass and bunchgrass, three

9 m^2 plots representing the range in biomass for each species was selected for destructive harvest. For sagebrush communities, six 6.25 m^2 plots were selected as being representative and cut to the soil surface. A wood chipping device was used to homogenize biomass and to ease transport and weighing for sagebrush populations. All samples were subsequently dried until no further decrease in mass was observed and weighed to determine moisture content. Biomass was estimated on a mass per unit area basis for entire stands. Dried biomass samples were frozen (-10 °C) until analyzed for carbon content.

2.3 Laboratory Methods

2.3.1 Homogenization and Subsampling

Samples collected via sand auger were used for quantification of multiple below-ground C pools (TC, TOC, TIC, root-C, or SOC). Samples were first removed from frozen storage, weighed, dried at 90 °C for 24 h, and reweighed for determination of gravimetric moisture content. Samples were then placed in a standard blender used in food preparation to aid in the breakdown of cemented soil clods and to improve homogenization of roots and organic matter. Samples were then passed through a 2 mm (10 mesh) sieve to remove and quantify rock fragments, and to ensure that roots were small enough to allow adequate homogenization. The entire sample passing the 2 mm sieve (including root-C) was then further homogenized by overturning and pouring the sample into “cones” five times (after Schumacher, Shines, Burton, & Papp 1990). The sample was then split in half using a standardized 17 mm riffle splitter (W.S. Tyler, SS-

50). Half of the original sample (average 200 g) was used in analysis of TC, TOC, TIC, and SOC, whereas the remaining half was used in quantification of root-C.

Allowing root-C to be incorporated into soil samples, as in this study, is atypical for many soil C studies. However, since the main goal of this study was to quantify the total below-ground organic carbon, it was appropriate and efficient to include all below-ground organic C pools in a single analysis. Incorporation of root-C within a soil sample allows processing of many more samples, providing the ability to generate a more robust dataset.

2.3.2 Processing of Laboratory Duplicates

Laboratory duplicates were generated for every 10^{th} sample processed. Duplicates were generated by homogenizing and splitting the initial sample into four subsamples via riffle splitter (average mass 100 g). Two of the four subsamples would be used as root-C duplicates and the remaining two were used for TC, TOC, and TIC duplicates. Since duplicates were generated during the first step of sample preparation, they represent the combined error of all lab processing.

2.3.3 Analysis of Total Carbon (TC), Total Organic Carbon (TOC), Total Inorganic Carbon (TIC), and Total Nitrogen (TN)

Half of the original soil sample (splitting described previously) was further homogenized by overturning the sample three times and randomly removing a 10 g subsample after each repetition. The final subsample, which was a combination of three 10 g subsamples (~ 30 g total mass), was again homogenized by overturning, and a final 10 g sample was removed for grinding. The 10 g sample was then ground via mortar and pestle to pass a 125 µm (120 mesh) sieve. This sieve size was chosen based on replicate

analysis and by visual confirmation that all roots and organic matter was indistinguishable. The sample was then dried at 105°C for 24h and concentrations of TC and nitrogen were determined for a 60 mg sample using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ).

Because significant concentrations of carbonates are present throughout soil profiles in this area (Barker et al. 1983), all samples required pretreatment for removal of carbonates in order to quantify TOC. Approximately 300 mg of ground sample (120 mesh) was treated with 3 mL of 0.73 M H_2SO_3 and dried at 105 °C as described by Nelson & Sommers (1996). According to Heron, Barcelona, Andersen, & Christensen (1997), this ratio of solids to acid is sufficient to remove approximately 7% TIC by weight. Approximately 60 mg of pretreated sample was then analyzed for carbon and nitrogen concentrations using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ) and results were reported as wt. % TOC. Because TC and TOC were both quantified using the same pulverized sample, TIC could be calculated as TIC = TC – TOC.

2.3.4 Quantification of Below-ground Biomass (Rb) and Root-Carbon

Quantification of root biomass (R_b) and, accordingly, organic carbon present as root biomass (root-C) was achieved through modification of a root flotation method outlined by Al-Khafaf (1977). This method consisted of the following steps: (1) half of the original soil sample (splitting described previously) was further homogenized, split, and mass (*m*) was determined, Accordingly, 25% of the original sample was used in quantification of R_b (average mass 100 g). This subsample size was chosen based on efficiency requirements and on the work of Schroth & Kolbe (1994), in their

investigation of subsample sizes needed to accurately represent root mass within soil cores. In short, they concluded that 5-10% of a total sample was needed to adequately estimate plot scale (70 m^2) root mass in a groundnut field using combined soil cores. (2) Approximately 100 g of soil was weighed and added to a 500 mL graduated cylinder containing a solution of 4% (wt/wt) $(NaPO_3)_6$ for deffloculation of clays. (3) The cylinder containing the soil solution was placed on a 250 µm (60 mesh) sieve that was partially submerged in DI water within a plastic tub. (4) 50 mL of 50% $CaCl_2$ solution was then added to the soil solution to flocculate clays and increase the solution density to approximately 1.1 $g \cdot cm^{-3}$, causing the flotation of roots. (5) DI water was then added to completely fill the cylinder so that roots could be flushed onto the 250 µm sieve. Because flocculation was extremely rapid, some roots were quickly buried in soil and further agitation of the soil solution was repeated until no roots floated to the surface. (6) The material remaining on the sieve was rinsed, dried at 70 °C for 24-hr, and R_b mass (z) was determined at a precision of 0.1 mg. R_b was then calculated as $R_b = 100 \cdot z \div m$. R_b samples were then ground to pass a 120 mesh sieve and analyzed for carbon concentrations using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ). Root-C was then calculated as root-C= R_b x weight % Root-Carbon ÷ 100.

Quantification of R_b and root-C via root flotation was performed on samples ranging from 0 to 38 cm depth. Samples taken from deeper in the profile were not able to be processed by this method because they contained extremely low concentrations of roots, possibly due to the presence of carbonates. A subset of samples taken from the 43-48 and 53-58 cm depth intervals were handpicked for roots to verify that an insignificant

amount of R_b and, accordingly, root-C was present at these depths. Additionally, the root flotation method was validated using 12 samples that were homogenized and split (as previously described), creating replicate samples. R_b content of replicate samples was then quantified in one of two ways: either root flotation, or handpicking of roots.

2.3.5 Physical Fractionation of Soil Aggregates

Soil samples collected via slide hammer were fractionated by aggregate size according to the wet sieving procedure outlined by Elliott (1986), consisting of the following steps: (1) field moist samples were removed from cold storage (4 °C) and passed through a 4.75 mm (4 mesh) sieve and subsampled. (2) Gravimetric moisture content was determined (dried 105 °C, 24 h) and the dry weight of each subsample (*i*) was calculated (~50 g). (3) The sample was slacked for 5 min. on a 250 µm (60 mesh) sieve and (4) floating roots were removed by vacuum. (5) The sieve was then moved with a slight angle at a 3 cm amplitude for 50 repetitions during a 2 min period; the remaining material was backwashed into an aluminum pan and classified as small macroaggregates. (6) Material passing the 60 mesh sieve was poured onto a 53 µm (270 mesh) sieve and the wet sieving procedure repeated; the material remaining on the sieve (microaggrgates) was backwashed into an aluminum pan, whereas all passing material was classified as silt + clay. (7) Aluminum pans containing DI water and aggregates were dried at 105 °C. (8) Dry mass of each size fraction (*d*) was determined and the mass percentage of aggregate fractions (*Z*) were calculated as $Z=100 \times d \div i$. (10) SOC content (*f*) was determined on each fraction after acidification (0.73 M H_2SO_3) using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ). (9) Percent of total SOC (*w*) within each aggregate size was then calculated as $w = f \times Z \div 100$.

The composition of macroaggregates was determined using the microaggregate isolation methodology described in Six, Elliott, & Paustian (2000). Physical fractions occluded in macroaggregates were classified as occluded particulate organic matter (*O*-POM), occluded microaggregates (*O*-microaggregates), or occluded silt and clay (*O*-silt+clay).

2.3.6 Quantification of Bulk Density and Grain Size

Samples collected via slide hammer from soil pits excavated throughout the field site (Figure 2) were used for quantification of bulk density and grain size distribution. Dry bulk density and gravimetric soil moisture was calculated by combining oven-dried soil mass (105°C, 24 hr) determined after removal of gravel and the known volume of the soil corer. Grain size distributions were calculated using a combination of dry sieving and hydrometer analysis, as outlined in ASTM D422-63.

2.3.7 Analysis of Carbon Content of Above-ground Biomass

Carbon content of above-ground biomass was determined for the three plant communities (cheatgrass, bunchgrass, and sagebrush) for a 20 g subsample. Samples of dry biomass were removed from frozen storage and finely ground using a standard coffee grinder. Pulverization was continued by hand until samples passed a 125 µm (120 mesh) sieve. Approximately 10-20 mg of pulverized sample was analyzed for carbon content using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ) calibrated using aspartic acid and peach leaves.

2.4 Statistical Analyses

2.4.1 Non-Parametric Analysis

The Lilliefors goodness-of-fit test for composite normality was used to determine if the data respected normally. The Lilliefors test calculates the empirical cumulative distribution function (ECDF) for a sample population and applies a 2-sided goodness-of-fit test using a normally distributed CDF with mean and standard deviation calculated from the sample population (Lilliefors 1967). The largest difference between the two distributions is quantified and compared to a table of critical values to determine a *p*-value for the comparison. If the *p*-value is sufficiently low (≤ 0.05), the null hypothesis of normality is disproved and the sample population can be viewed as non-normal. The Lilliefors test is included in the MATLAB statistics package and was applied to the data. Approximately 40% of the sample populations tested (depth x vegetation type) did not appear to respect normally (Table 2), and therefore nonparametric statistical analyses were used to examine all data.

2.4.2 Bootstrap Sampling to Quantify Uncertainty in Mean Values

A bootstrap sampling routine was coded in MATLAB and used to determine the uncertainty in estimating the true mean carbon values (reported as 95% range) at each depth increment and within each vegetation type. Bootstrap sampling operates on the postulation that a set of samples can be viewed as one realization out of an infinite number of possible sample sets taken from a study site (Martínez & Martínez 2008). By resampling a dataset with replacement (bootstrapping), it is possible to choose the same

sample more than once or not at all during subsequent realizations. This permits quantification of the variability of a statistic of interest for a given dataset. For each bootstrap simulation, a mean is calculated and stored and the true mean is estimated by calculating the mean of all bootstrap simulations and the uncertainty in this estimate is reported as the 95% range of the means calculated from all 100 simulations. A similar strategy has been demonstrated by Poussartet al. (2004) to be applicable for quantification of differences in soil carbon between two populations, specifically when data non-normality is observed.

2.4.3 Two-Population Kolmogrov-Smirnov Test (K-S test) for Significant Difference

The two population Kolmogrov-Smirnov test (K-S test) is used to determine if, given the variability of soil carbon values, one population can be deemed to have significantly greater below-ground carbon. Similar to the Lilliefors test, the K-S test compares two ECDFs generated from each of the sample populations while making no assumptions about the underlying distribution of the data. The null hypothesis of the K-S test is that the two populations being tested are from the same distribution. If the largest distance between the two ECDFs is larger than a critical value, the null hypothesis is disproved and the test concludes that the samples are from two distinct populations ($p \leq 0.05$). The K-S test is included in the MATLAB statistics package and was applied to each of the datasets of below-ground carbon (vegetation type x depth) in a two-by-two fashion.

In addition to applying the K-S test to the entire sample population, the results of the K-S test were investigated for varying population sizes. A bootstrap routine that applied the K-S test to increasing sample sizes was coded into MATLAB and 1000

simulations were preformed for each comparison and for a given sample size. For each sample size, the bootstrap routine simulated 1000 alternative datasets (realizations) for cumulative TOC to a depth of 38 cm using data from two vegetation types. A K-S test was applied to each of the 1000 realizations and an average *p*-value was calculated for a given sample size (modified from Poussart, Ardo, & Olsson 2004). Lower depth increments (43-48 and 53-58 cm) were not included in this analysis because fewer samples were collected at these depths due to obstructions. Due to the low variability in TOC at these depths (Figure 11, Table 7), it was assumed that their exclusion would not affect the results.

CHAPTER THREE: RESULTS

3.1 Laboratory Duplicate Analysis of Total Carbon (TC), Total Organic Carbon, and Below-ground Biomass (R_b)

A total of 67, 68, and 52 laboratory duplicates were analyzed for TC, TOC, and R_b, respectively (Table 3). The mean difference in laboratory duplicates was 8.2 (5.4% median) and 11% (8% median) for TC and TOC, respectively, where the largest differences generally occurred at low concentrations. R_b duplicates produced mean and median differences of approximately 19 and 16%, respectively. In addition to laboratory duplicates, the accuracy of the root flotation method was investigated using 12 replicate samples that were handpicked to determine R_b content. Linear regression of the two methods produced an R^2 value of 0.95 (Figure 3).

3.2 Bulk Density, Grain Size, and Gravimetric Moisture Content

Bulk density averaged approximately 1200 $kg \cdot m^{-3}$ throughout the site and no trends with depth or vegetation were observed (Figure 4). Depth-averaged grain size was approximately 18, 56, and 26 % for sand, silt, and clay, respectively, corresponding to a silt loam textural class. Clay content increased to a profile maximum of 37 % within the 13-18 cm depth increment (Figure 5; Table 4) and decreased with depth thereafter. Depth-averaged gravimetric moisture content indicated higher summertime moisture contents under cheatgrass and lower values under sagebrush for two consecutive years (Figures 6 and 7).

3.3 Above-ground Biomass

Above-ground biomass increased in the order where: cheatgrass<bunchgrass <sagebrush, corresponding to 1.7, 2.9, and 8.4 $Mg \cdot ha^{-1}$, respectively. Carbon content was 46, 43, and 50 wt. %, corresponding to above-ground C storage of 0.8, 1.3, and 4.2 $Mg \cdot ha^{-1}$ for cheatgrass, bunchgrass, and sagebrush, respectively (Figure 8; Table 2).

3.4 Canopy Cover of Sampling Transects

Canopy cover in areas sampled within cheatgrass communities was approximately 100% for replicate sample populations throughout the study site, with the exception of CB2, which contained significant cover (~20 %) of Rush Skeleton weed (*Chondrilla juncea*). Similarly, canopy cover within replicate bunchgrass communities was similar, estimated as ranging from 42 to 50% within transects (Figure 9), likely due in part to the drill seeding method used in bunchgrass establishment. In contrast, replicate canopy cover in sagebrush populations varied from 28 to 40% for S and CS transects, respectively.

3.5 Below-groundTotal Inorganic Carbon (TIC)

Total inorganic carbon (TIC) averaged 32, 46, and 57 $Mg \cdot ha^{-1}$ for cheatgrass, bunchgrass, and sagebrush, respectively, but was not significantly different between plant communities (Table 5). There was a significant difference in TIC within the 53-58 cm depth interval for all three vegetation types, with TIC increasing where: cheatgrass < bunchgrass < sagebrush (Figure 12). The uncertainties in estimating TIC were relatively large due to the additive error produced when combining measurements of TC and TOC.

3.6 Below-ground Total Organic Carbon (TOC)

Below-ground total organic carbon (TOC) was significantly reduced in cheatgrass. Cumulative TOC averaged 29, 41, and 56 Mg C·ha^{-1} for cheatgrass, bunchgrass, and sagebrush, respectively. The results of the K-S test and the bootstrap routine indicated that greater TOC within sagebrush relative to cheatgrass was significant for all depths, with the exception of the 18-28 cm interval (Figure 10, Table 6). The cumulative TOC decrease in cheatgrass relative to sagebrush represented approximately 27 Mg·ha^{-1}, corresponding to a 50% decrease. The largest differences in TOC were between sagebrush and cheatgrass and occurred in the upper 18 cm of soil, where this decrease accounted for 63% of the total loss in TOC. Mean values of TOC for bunchgrass were significantly greater than cheatgrass at all depths below 8 cm (Figure 10, Table 6); excluding the upper 8 cm of the soil profile, this corresponds to a cumulative increase of 9 Mg·ha^{-1} (53%) TOC. Increased TOC in bunchgrass relative to cheatgrass was approximately equal at all depths below 8 cm as the two populations had similar depth distributions of TOC.

The trends reported for TOC were reproducible for both grass communities at locations separated by approximately 200 m (Figure 11, Figure 2). In contrast, replicate sagebrush populations, “S” and “CS”, separated by approximately 35 m displayed similar depth distributions of TOC, but exhibited significant differences in TOC content (49 vs. 64 Mg·ha^{-1}, respectively).

3.7 Below-ground Biomass (R_b) and Root-Carbon (C)

Root biomass (R_b) averaged 11, 22, and 31 Mg·ha^{-1} for cheatgrass, bunchgrass, and sagebrush, respectively (Table 8). R_b content within sagebrush and bunchgrass

communities was significantly greater than cheatgrass at all depths below 3 cm, whereas bunchgrass and sagebrush were statistically indistinguishable at all depths (Figure 13, Table 6). R_b content in the upper 0 to 3 cm of the soil profile accounted for approximately 65, 51, and 61 % of total profile R_b in cheatgrass, bunchgrass, and sagebrush communities, respectively, while accounting for 70% of the error in estimating total profile R_b. R_b content was below detection level for all depths below 38 cm.

Trends with depth were reproducible for replicate populations where, specifically, sagebrush replicates display a decrease in TOC and a parallel decrease in R_b within the "S" population relative to the "CS" population (Figures 12 and 15). C content of R_b samples (n = 47) averaged approximately 27 wt. % and was not significantly different between communities. Accordingly, root-C and R_b depth distributions are similar, but differ in magnitude by a factor of 0.27.

3.8 Soil Organic Carbon (SOC)

Total profile SOC averaged 23, 33, and 44 $Mg \cdot ha^{-1}$ for cheatgrass, bunchgrass, and sagebrush, respectively (Figure 15; Table 9). Importantly, because R_b content was found to be insignificant at depths exceeding 38 cm, SOC was assumed to equal TOC for depths ranging from 38 to 58 cm. This model appears reasonable as the distribution of SOC with depth remains uniform for depths exceeding 38 cm.

3.9 SOC Content of Aggregate Fractions

Soil macroaggregates (> 250 µm) were present at significant levels (22% soil mass) in sagebrush communities only; cheatgrass and bunchgrass had no detectable quantity of macroaggregates (Figure 16, Table 10). Conversely, microaggregate

concentrations (53 – 250 µm) were similar in all three plant communities and accounted for approximately 50% soil mass. Silt+clay sized particles (< 53 µm) represented 45% of soil mass in both grass communities, and accounted for 27% soil mass in sagebrush. The remaining proportions of soil mass were characterized by sand fractions.

Cumulative SOC of all size fractions after acidification and root removal corresponded to 0.25, 0.32, and 0.81 wt. % for bunchgrass, cheatgrass, and sagebrush, respectively; these values of SOC were roughly equivalent to those previously determined by subtracting root-C from TOC (Figure 16). SOC content of macroaggregates within sagebrush populations was approximately 3 g kg^{-1}, which corresponded to approximately 36% of total SOC for sagebrush. For sagebrush, microaggregates occluded within macroaggregates contained 18% (1.5 g kg^{-1}) of the total SOC, whereas occluded silt+clay and POM accounted for the remaining 7 (0.6 g kg^{-1}) and 11% (0.9 g kg^{-1}), respectively.

Average SOC concentrations of free microaggregates corresponded to 1.2, 1.6, and 3.6g kg^{-1} for cheatgrass, bunchgrass, and sagebrush, respectively. SOC concentration of the silt+clay fraction was equivalent for bunchgrass and sagebrush (1.6 g kg^{-1}) but was less for cheatgrass populations (1.3 g kg^{-1}).

Carbon/Nitrogen (C:N) ratios were calculated for non-occluded size fractions within vegetation type. C:N ratios were positively correlated with aggregate size for all vegetation types (Table 11). Additionally, C:N ratios increased in the order where: cheatgrass< bunchgrass< sagebrush for all aggregate sizes, although this trend was not statistically significant.

3.10 Total Nitrogen (TN)

Total nitrogen (TN) was determined to be 6, 6, and 8 $Mg \cdot ha^{-1}$ within cheatgrass, bunchgrass, and sagebrush populations, respectively (Figure 17). The depth distribution of TN was similar to TOC for all three vegetation types. Both cheatgrass and bunchgrass had low variability in TN but were indistinguishable at all depths, whereas sagebrush had significantly greater TN at all depths with higher variability.

3.11 Sample Sizes Required to Demonstrate Significant Differences in TOC

Cumulative TOC values (0-38 cm) obtained from each community indicated that, to reach a *p*-value less than 0.05, 24 soil cores would be needed from each population to distinguish differences in cheatgrass compared to sagebrush (Figure 18). The results also indicate that at least 36 soil cores would be needed from each population for statistical distinction of bunchgrass from either sagebrush or cheatgrass at a *p*-value less than 0.05, which was more than obtained in this study. Application of the K-S test to discrete depth increments using the current data set (Table 6) indicates that the additional samples required may be confined to the upper 8 cm of soil when comparing cheatgrass to sagebrush, whereas intermediate depths would require additional samples when comparing bunchgrass to sagebrush.

CHAPTER FOUR: DISCUSSION

4.1 Rates of Change in the Carbon Budget

Part of an established sagebrush community was lost to wildfire in the spring of 1983, 27 years prior to this study; the burned area was immediately converted to either a cheatgrass or crested wheatgrass monoculture. Rates of C loss may be on the order of 1 Mg C ha^{-1} yr^{-1}, twice the rate of C gain in restored grasslands (447 kg C ha^{-1} yr^{-1}) reported by Potter et al. (1999). The initial rate of C loss may be enhanced in bunchgrass communities at Kuna Butte due to the soil aeration caused by drill seeding. However, the loss rates may decrease non-linearly in grass communities as labile C becomes limited during establishment and, subsequently, plant-derived inputs begin to offset losses.

4.2 Loss of Total Inorganic Carbon (TIC) Following Sagebrush Degradation

The significant decrease in TIC concentration at depth (53-58 cm) in cheatgrass (Figure 12) is in contrast to the results of Chen & Stark (2000), where they documented a trend in TIC where: sagebrush < bunchgrass < interspace soils. They attributed this trend to increasing respiration and organic acid production in bunchgrass and sagebrush, which could dissolve and prevent carbonate precipitation. However, increased photosynthesis would also correspond to an increase in evapotranspiration and, consequently, carbonate precipitaiton, producing the trends in soil moisture and TIC at Kuna Butte (Figures 6 and 7). Alternatively, differences in TIC at depth could also be due to decreased profile thickness or an underestimation of coring depth in sagebrush. The former was

investigated via soil pits and determined to be unlikely while the latter is improbable as underestimation of coring depth would likely be random in all plant communities.

Greater TIC in shallow sagebrush soils, although not statistically significant, may be due to increased capture of aeolian carbonates caused by denser ground cover in sagebrush communities (see Norton et al. 2004). Alternatively, Emmerich (2003) documented 15% annual variation in TIC of shallow grass- and brushland soils, indicating that significant cycling of TIC does occur and may be dependent on vegetation. Our estimated C losses from sagebrush degradation do not include TIC pools due to lack of any specific mechanism.

4.3 Changes in TOC Distribution: Pool and Depth Allocation

Our results indicate that both sagebrush and bunchgrass had higher concentrations of root-C in the subsoil; this was also documented by Hooker et al. (2008). This implies higher C input at lower depths within sagebrush and bunchgrass communities where rates of decomposition can be reduced due to lower soil temperatures, anaerobic conditions, and pH changes (Lorenz & Lal 2005). This claim was supported by Gill et al. (1999) who used ^{14}C labeling to identify decreasing SOC decomposition rates with depth.

The second peak in SOC at the 13-28 cm depth observed in grass communities (Figure 16) corresponds to increased clay content (Figure 5). A similar distribution of SOC was documented by Gill et al. (1999) within a shortgrass-steppe ecosystem and also corresponded to increased clay content. This correlation suggests that higher clay content contributes to SOC stabilization, likely due to greater occlusion (Lorenz & Lal 2005; Six et al. 2004).

The relative contribution of root-C and SOC to TOC was not markedly different between communities for specific depths, or throughout the entire profile (Table 12); both root-C and SOC decreased across the entire profile. This indicates that C loss following sagebrush degradation was not limited to near surface soils or a specific C pool. The observation of declining carbon across the entire profile is in contrast to previous studies that documented significant differences to exist only within shallow soils (Hooker et al. 2008; Norton et al. 2004; Gill et al. 1999). The observation of proportional declines in SOC and root-C also suggests changes in both root-C input and SOC stabilization.

4.4 Potential Mechanisms for TOC Loss Following Sagebrush Degradation

4.4.1 Decreased Input Quantity

Using annual root turnover rates of 1 and 0.5 yr^{-1} for cheatgrass and bunchgrass, respectively (Gill & Jackson 2000), our observed values indicate annual root-C inputs of approximately 3 Mg $C \cdot ha^{-1}$ for both grass communities, whereas a root turnover rate of 0.3 yr^{-1} for sagebrush (Caldwell et al. 1977) corresponds to an input of 2.4 Mg root-$C \cdot ha^{-1} \cdot yr^{-1}$. Accounting for the cheatgrass presence in sagebrush at Kuna Butte (~60% areal cover) increases our estimate of root-C input to 5.6 Mg $ha^{-1} \cdot yr^{-1}$ for sagebrush; these results are higher than those reported by Gilmanov, Svejcar, Johnson, Angell, & Nicanor, (2006), who used Bowen ratio-energy balance (BREB) instrumentation to calculate annual respiration and primary production in a sagebrush-steppe of southeastern Idaho (annual precipitation 283 mm, 40% canopy cover); average primary productivity and respiration was reported as 4.4 and 3.7 Mg $C \cdot ha^{-1} \cdot yr^{-1}$,

respectively; using a root/shoot ratio of 4, as calculated in this study, their results correspond to a root-C input of 3.3 Mg $ha^{-1} \cdot yr^{-1}$.

We did not distinguish between living and dead roots or plant residue in determining root-C. Estimates of annual root-C input may therefore be overestimated due to inclusion of dead plant material in root-C estimates. Greater than 50% of all root-C is located within the upper 3 cm of soil for all three plant types (Table 8); this may be an artifact of litter incorporation into the shallow subsurface, however studies have reported between 50 and 80% of total root biomass within the upper 10 cm of soil (Rau et al. 2011; Hooker et al 2008; Gill et al. 1999; Dahlman 1965, and others). Other studies in similar environments have quantified root-C by removing roots using sieves ranging from 2 to 4 mm (Gill & Burke 1999; Gill et al. 1999; Hooker et al. 2008; Norton 2004; Svejcar & Sheley 2001, and others) while average root diameters are documented to range from 0.1 to 0.3 mm (Hooker et al. 2008; Gill et al. 2002). This discrepancy may indicate an underestimation of root-C in past studies; Rau et al. (2011) reported root-C to be 25% of those reported for sagebrush. In addition, the shallow subsurface boundary condition at Kuna Butte may produce higher concentrations of root-C in near surface soils.

4.4.2 Decreased Quality of Inputs

Higher TOC content may be produced by greater recalcitrance of sagebrush roots; however our observed C:Nfor R_b (mean of 25) are similar to those of Svejcar and Sheley (2001), who reported no significant differences in C:N of R_b for sagebrush and cheatgrass. In contrast, Hooker et al. (2008) documented significantly higher C:N in bunchgrass roots while also reporting higher lignin, a chemically recalcitrant compound (Lorenz & Lal 2005), in sagebrush roots compared to bunchgrass. Their results may

provide the mechanism for documenting a higher accumulation of root-C in the subsurface of sagebrush and bunchgrass compared to cheatgrass soils. Alternatively, researchers have shown root turnover to be positively correlated with diameter (Gill et al. 2002) and, although not quantified in this study, we observed larger root diameters within bunchgrass and sagebrush communities. Additionally, Norton et al. (2004) reported cheatgrass to have no roots larger than 1 mm in diameter, whereas sagebrush-steppe ecosystems had significant quantities of roots in the 1-2 mm class size, suggesting that sagebrush communities have lower root turnover and potentially longer residence times of root-C.

4.4.3 Differences in C Mineralization

Lower soil C content may be produced by higher rates of carbon mineralization. Increased mineralization of SOC could be caused by cheatgrass invasion and may be the result of: (1) production of less recalcitrant root-C, corresponding to shorter residence time in soils, (2) modifying edaphic factors such as temperature and moisture which can influence kinetics of decomposition, or (3) decreased occlusion of organic matter by loss of soil aggregate stabilization.

Soil moisture can often limit bacterial respiration of soil organic matter (Lorenz & Lal 2005; Gill et al. 1999). We observed an inverse correlation between soil moisture and SOC, with the highest summer soil moisture observed in cheatgrass, followed by bunchgrass, with sagebrush exhibiting the lowest summer soil moisture contents (Figures 6 and 7). Increased soil moisture in grass communities (bunchgrass <cheatgrass) is likely due to cessation of evapotranspiration upon plant senescence, which is earliest in cheatgrass followed by bunchgrass and sagebrush. Lower surface temperatures from

canopy cover may explain greater near surface soil moisture in bunchgrass and sagebrush communities (Figure 9). These results are similar to those of Prater, Obrist, Armone, & DeLucia (2006) who reported higher soil temperature and moisture in cheatgrass compared to sagebrush and bunchgrass. Gill et al. (1999) were also able to positively correlate decomposition rates to the amount soil moisture available for respiration. At Kuna Butte, we documented similar but unequal distributions of SOC within both grasses, but the same distribution was not documented for root-C; this disconnect may indicate greater decomposition rates in cheatgrass, possibly due to higher soil moisture availability. The inverse correlation between root-C and soil moisture also explains the loss of both root-C and SOC following sagebrush degradation.

Our third hypothesis, loss of aggregate stabilization, was documented within cheatgrass by the loss of macroaggregates. Although not definitive, these findings indicate the likelihood that hypotheses 2 and 3 are correct in that decreased SOC stabilization is likely due to both increased soil moisture and decreased aggregation in degraded sagebrush ecosystems.

4.5 The Role of Soil Structure in Carbon Preservation

4.5.1 Macroaggregates

Sagebrush degradation caused a loss of physically occluded POM with a corresponding decrease in SOC and root-C. This is in agreement with mechanistic models of aggregate dynamics where aggregate formation can be largely dictated by root dynamics (Brady & Weil 2008; Gregory 2006; Six et al. 2004; Angers & Caron 1998), and higher SOC content can enhance macroaggregate stability (Brady & Weil 2008; Six

et al. 2004; Christensen 1992, and others). The trends in R_b at Kuna Butte are similar to Tisdall & Oades (1982), who showed that conversion of grassland to arable cropping caused a decrease in SOC and macroaggregates, where they attributed this loss to decomposition of roots and fungal hyphae. Additionally, the larger diameters of sagebrush roots may correspond to slower decomposition rates (Gill et al. 2002) as well as decreased disruption of aggregate structure (Gregory 2006; Angers & Caron 1998).

Concentrations of fungal hyphae may not be ubiquitous between plant communities. Both sagebrush and bunchgrass are obligate symbionts with vesicular arbuscular mycorrhizal (AM) fungi, whereas cheatgrass is merely a facultive symbiont and, accordingly cheatgrass often has low AM fungal populations compared to bunchgrass and sagebrush communities (Ypsilantis 2003). This is an important distinction because, in addition to the work of Tisdall and Oades (1982), several researchers have demonstrated that AM fungi can dramatically affect soil aggregation by excreting glomalin and producing hyphae that act as a support structure for aggregates (Brady & Weil 2008; Gregory 2006; Angers & Caron 1998).

Wetting-drying dynamics have been shown to influence the formation of soil aggregates by promoting fragmentation (Six et al. 2004, Angers & Caron 1998), whereas the stability of aggregates has been shown to increase with decreasing soil moisture due to greater cohesion (Horn, Taubner, Wuttke, & Baumartl 1994). This is also consistent with the results from Kuna Butte, where macroaggregates were found only within sagebrush communities that had the lowest soil moisture. We propose that the presence of macroaggregates within sagebrush could be due to (1) decreased soil moisture, (2) higher concentrations of roots, (3) concentrations of AM fungi, or (4) root exudates.

The greater degree of soil aggregation (macroaggregates) beneath sagebrush communities likely contributes to the overall health and productivity of soil by increasing aeration, infiltration, and reducing compaction (Brady & Weil 2008), but may also be promoting increased SOC storage. Treseder, Egerton-Wardurton, Allen, Cheng, & Oechel, (2003) found that SOC content quickly increased within macroaggregates following CO_2 fertilization of a shrubland; they credited this to AM fungi acting as conduits for SOC deposition within macroaggregates. This process could result in increased deposition of labile C within physically protected macroaggregates, promoting lower C turnover and, potentially, long term C storage. The loss of large-scale soil aggregation following sagebrush replacement by cheatgrass is likely an important driver of observed declines in soil carbon content.

4.5.2 The Composition of Macroaggregates in Sagebrush

The SOC associated with *O*-microaggregates represents a very stable fraction of SOC (Six et al. 2004) that is lost following sagebrush degradation; nearly 20% of sagebrush SOC is contained within this fraction (Figure 16). The decrease in the silt+clay soil fraction (Table 10) and the existence of *O*-microaggregates may suggest less destabilization of microaggregates in sagebrush. Additionally, the existence of *O*-POM demonstrates increased physical protection of labile C in sagebrush.

4.5.3 Free Microaggregates

The decreased SOC content within free microaggregates of grasses accounted for approximately 40% of the total SOC lost following sagebrush degradation (Figures 17 and 18). Current models for microaggregate formation specify the formation of microaggregates within macroaggregates (Six et al. 2004). If these models describe microaggregate formation at Kuna Butte, microaggregates within grass communities may be remnants of sagebrush; suggesting that greater SOC content within bunchgrasses relative to cheatgrass may be due to slower decomposition of microaggregate SOC, possibly due to lower soil temperature and moisture relative to cheatgrass. Alternatively, if microaggregates are formed independently of macroaggregates, as proposed by Tisdall and Oades (1982), the intermediate SOC content of microaggregates within bunchgrass (Figure 16) may be due to greater preservation of SOC within microaggregates. Importantly, the fraction of soil characterized by microaggregates was not different between communities (Table 10), but rather, the SOC content of microaggregates decreased where sagebrush >bunchgrass >cheatgrass. Changes in vegetation may therefore alter the input of SOC associated with microaggregates without affecting their formation or stability in soil.

The results of recent studies are generally in agreement that microaggregate fractions have some of the longest turnover times of SOC (McCarthy et al. 2008; Six et al. 2004; Del Galdo et al 2003; Christenson 1992, and others). SOC preservation within this fraction may therefore facilitate long term C storage and should be considered an important metric when determining the relative ability of vegetation to promote long term storage of atmospheric CO_2. The decreased SOC concentration of microaggregates within

cheatgrass communities should then be regarded as a reduction in long term C storage capacity due to sagebrush degradation.

4.6 Upscaling Results

Our results indicate that the 20,000 km^2 of Great Basin vegetation displaced by cheatgrass monocultures (Bradley & Mustard 2005) represent significant C emissions. If the C losses documented in this study are to the entire Great Basin, approximately 60 Mt C has been lost to cheatgrass invasion. In addition, Bradley (2009) estimated that an additional 760,000 km^2 within the Great Basin is at risk of cheatgrass invasion under current climatic conditions; with a predicted future emission of more than 2 Gt C. Conversely under the same scenario, bunchgrass seeding following fire may prevent the loss of nearly 700 Mt C.

Importantly, the current study used a sagebrush-cheatgrass community to quantify baseline C content, but the initial loss of perennial herbaceous vegetation in sagebrush interspace may represent an additional loss of C (see Rau et al. 2011) and, consequently, we may have underestimated total C emission associated with cheatgrass degradation of natural sagebrush-steppe ecosystems. At Kuna Butte, bunchgrass seeding prevented the loss of 9 Mg $C \cdot ha^{-1}$ in the subsurface following the abatement of sagebrush. These results corroborate the projection of Rau et al. (2011), where their results suggest replacement of bunchgrasses with cheatgrass in sagebrush interspaces would cause a loss of 6-9 Mg $C \cdot ha^{-1}$.

CHAPTER FIVE: CONCLUSIONS

We quantified below-ground C loss associated with conversion of a sagebrush ecosystem to contrasting grass monocultures. Our study led to four main results: (1) In contrast to previous studies, we demonstrated that conversion of sagebrush ecosystems to cheatgrass monocultures caused a 50% loss in below-ground TOC (30 Mg C·ha^{-1}). (2) Bunchgrass seeding immediately following fire reduced the amount of TOC lost to sagebrush degradation by 30%. The significantly greater TOC in subsurface soils of bunchgrass corresponded to a 9 Mg C·ha^{-1} reduction in the amount of C lost after sagebrush degradation for depths between 8 and 58 cm. (3) Significant differences were observed within specific C pools beneath different plant communities. Because we documented significant losses within multiple pools of C, namely root-C and SOC, we cannot solely attribute the C lost following sagebrush degradation to either decreased C input, or greater decomposition of more labile C compounds. (4) Loss of macroaggregate stability following sagebrush degradation inhibits physical protection of labile C inputs, which would increase the proportion of SOC metabolized by soil biota. SOC content within microaggregates decreased following loss of sagebrush, where cheatgrass communities had the lowest concentrations of SOC within microaggregates. The inverse correlation between soil moisture and microaggregate SOC suggests that sagebrush degradation may stimulate greater decomposition stable C fractions.

Future work should focus on accurately characterizing the decomposability of specific C pools for each stage of sagebrush alteration. This could be accomplished via fractionation and laboratory incubations and would serve to address uncertainties regarding the stability of various C pools; this may provide an indication of the state of equilibrium of these ecosystems. The use of radiogenic C isotopes to estimate C pool turnover times may also prove useful in identifying either decreased stabilization or input as being the dominant mechanism for C loss following sagebrush degradation. In addition, the C budget consequences of decreased fire return intervals characteristic of cheatgrass communities should be investigated; such results may further indicate the need to prevent cheatgrass degradation of sagebrush ecosystems.

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APPENDIX A

Figures

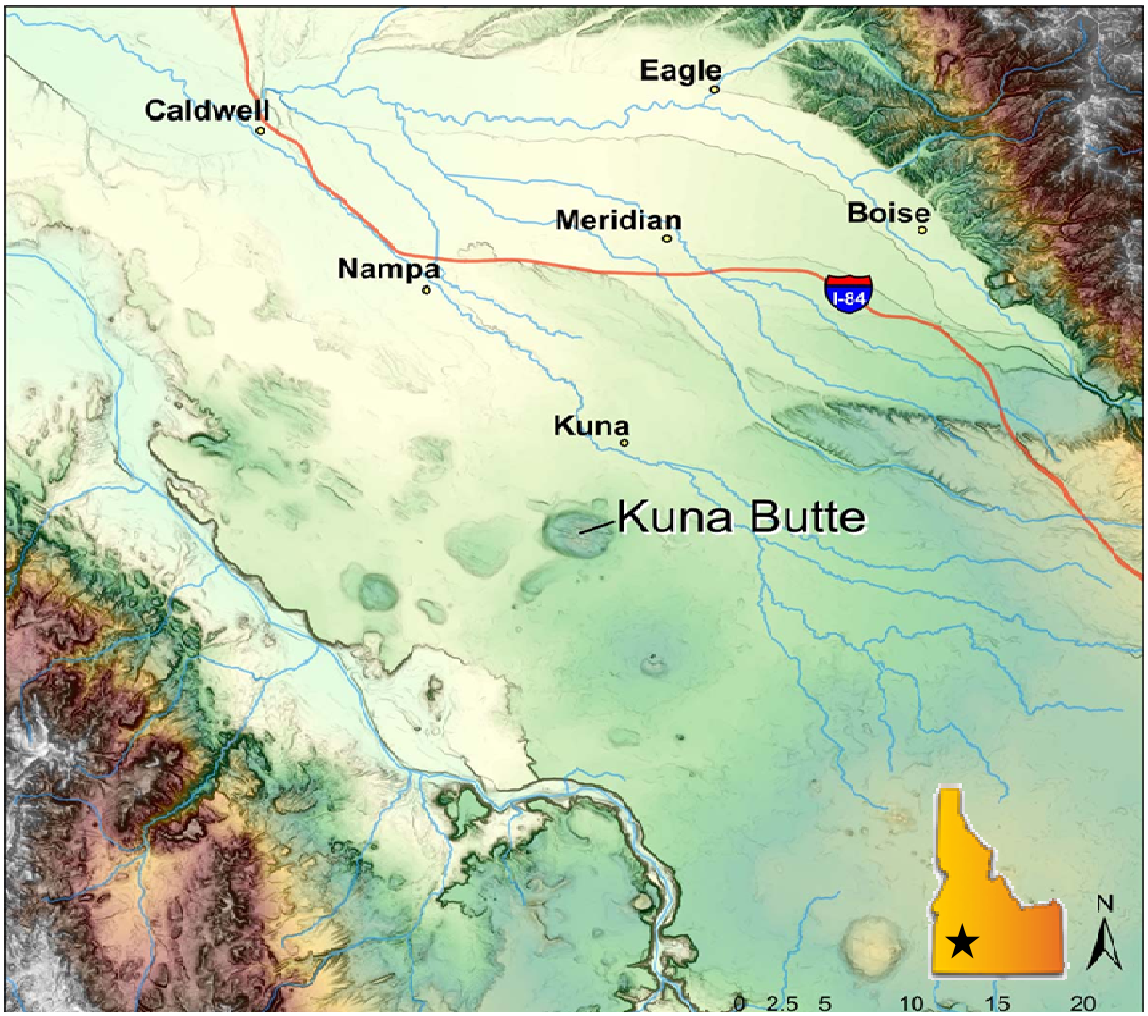

Figure A.1: Map showing the location of Kuna Butte

Figure A.2: Location of transects and soil pits at Kuna Butte. Letters indicate vegetation type and transect label where C, B, and S corresponds to cheatgrass, bunchgrass, and sagebrush, respectively. Lines and circles designate transects and soil pits, respectively.

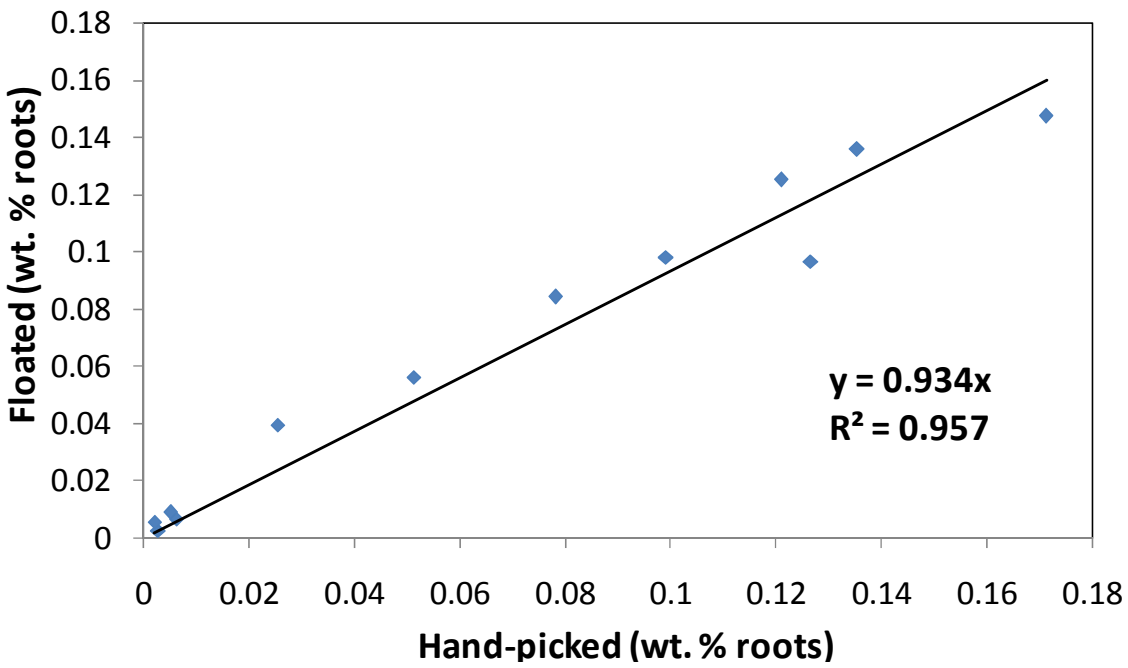

Figure A.3: Qualification of root flotation method used for quantifying R_b and root-C. R_b content was quantified by both handpicking and root flotation of replicate samples to compare values.

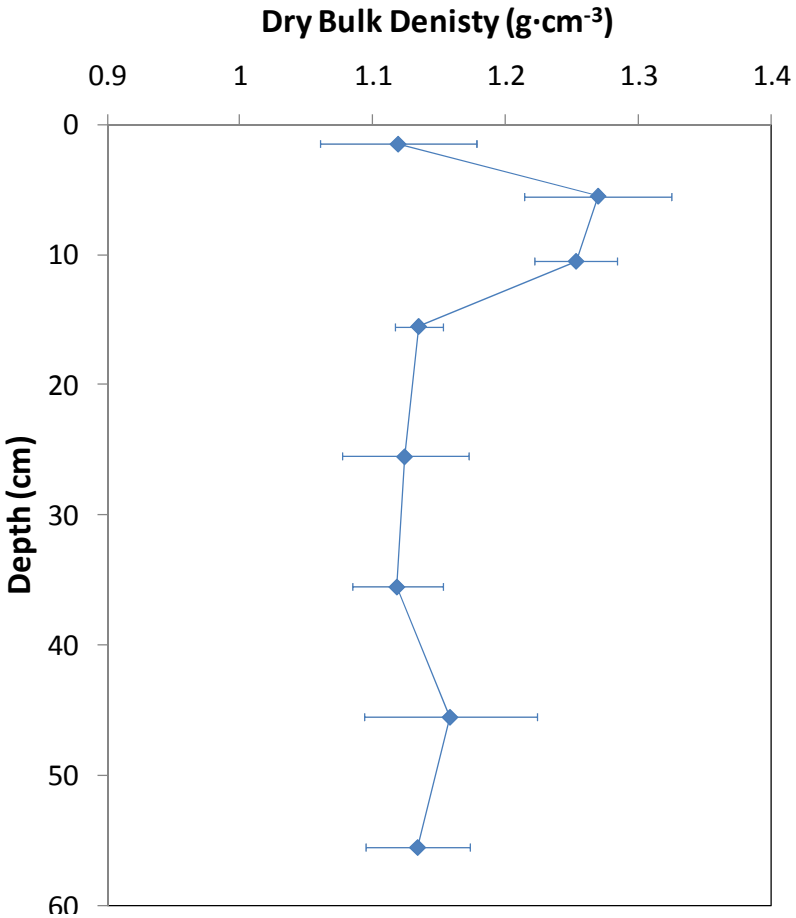

Figure A.4: Depth distribution of dry soil bulk density. Error bars are +/- one standard error (*n* = 4). See Figure 2 for sampling locations.

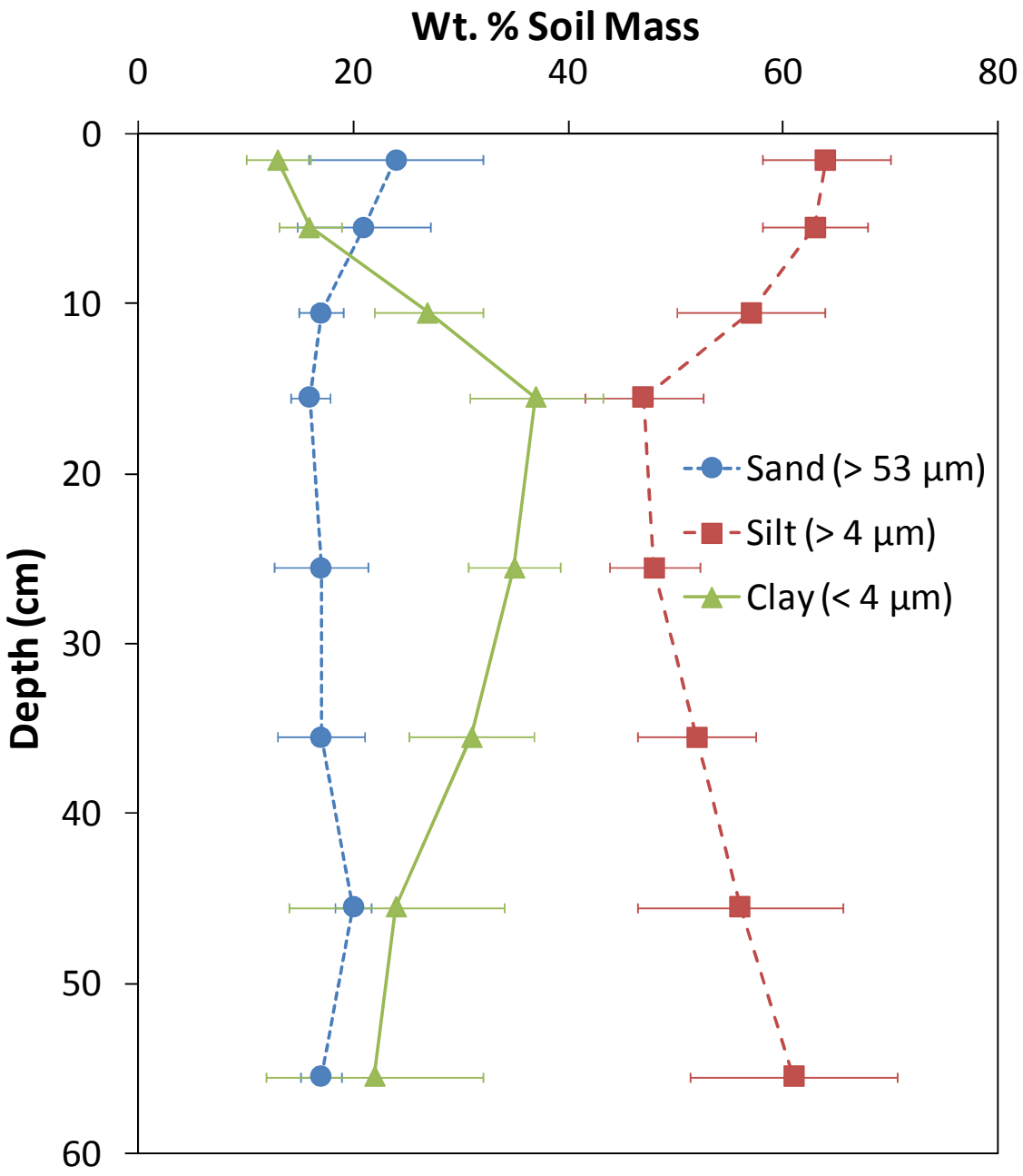

Figure A.5: **Depth distribution of grain size classes. Error bars are +/- 1 standard error (*n* = 4). See Figure 2 for sampling locations.**

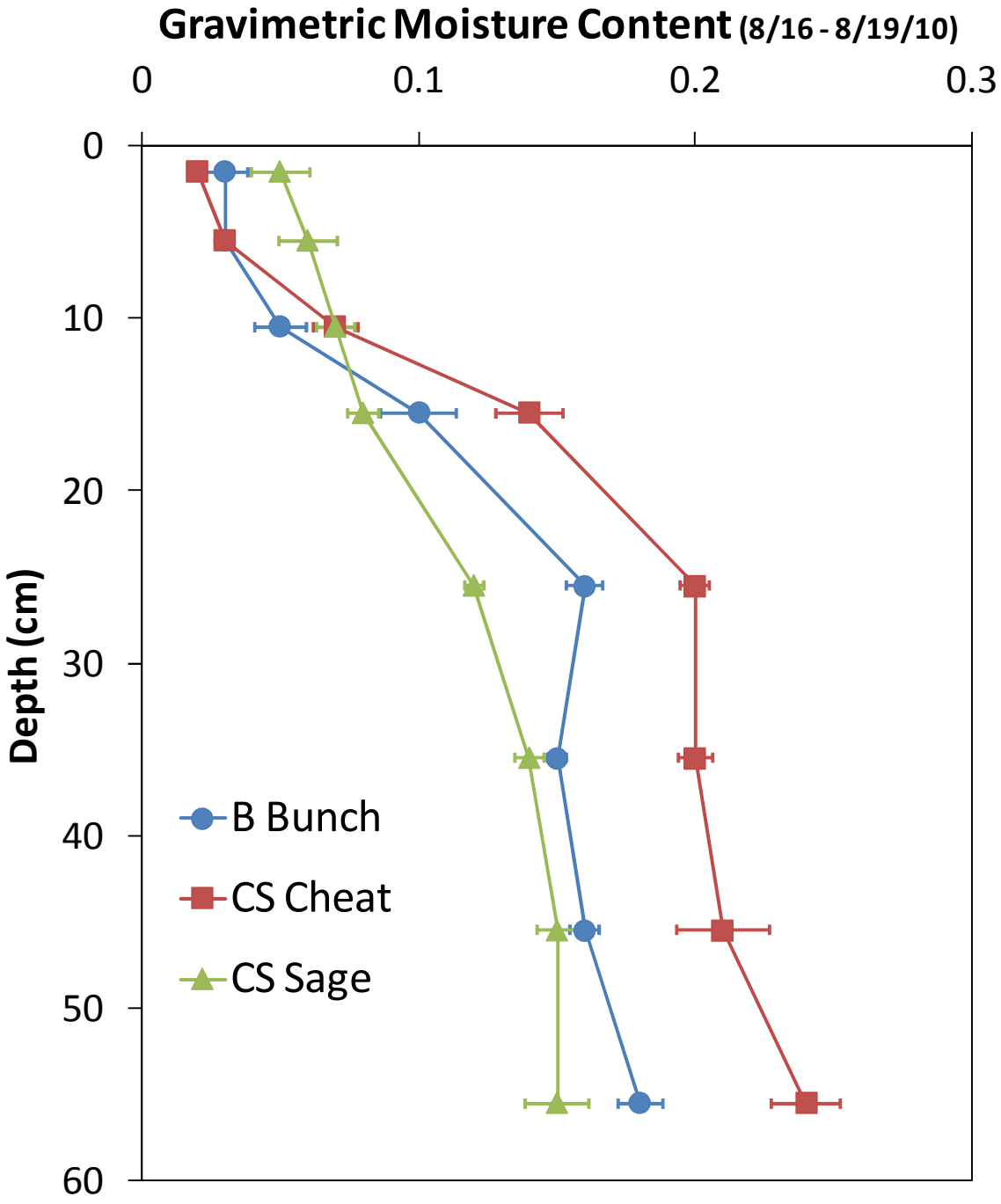

Figure A.6: Depth Distribution of gravimetric moisture content in August 2010. Error bars represent +/- 1 standard error (*n* = 10). See Figure 2 for sampling locations.

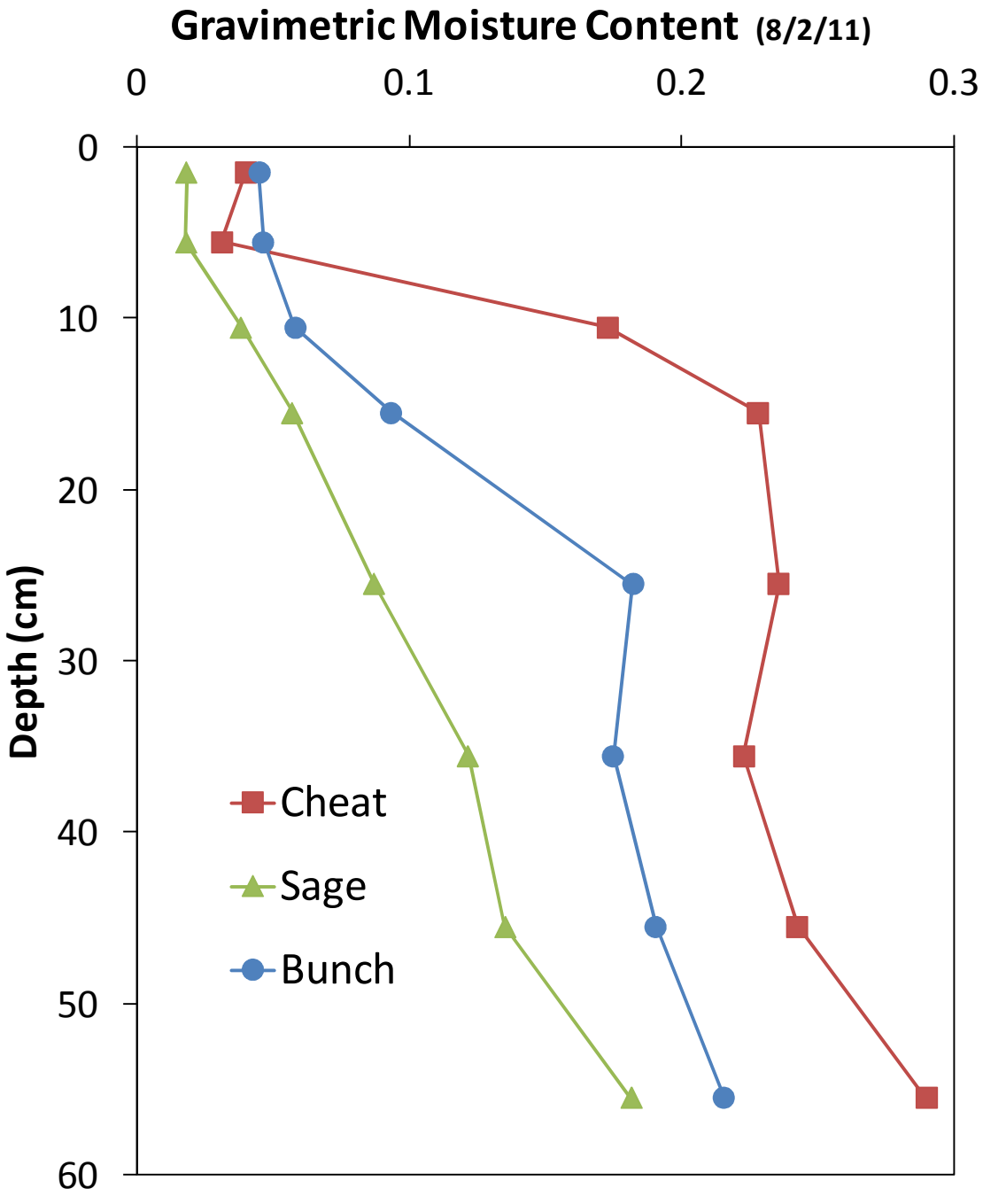

Figure A.7: Depth Distribution of gravimetric moisture content in August 2011. Lack of error bars is due to small sample sizes. See Figure 2 for sampling locations.

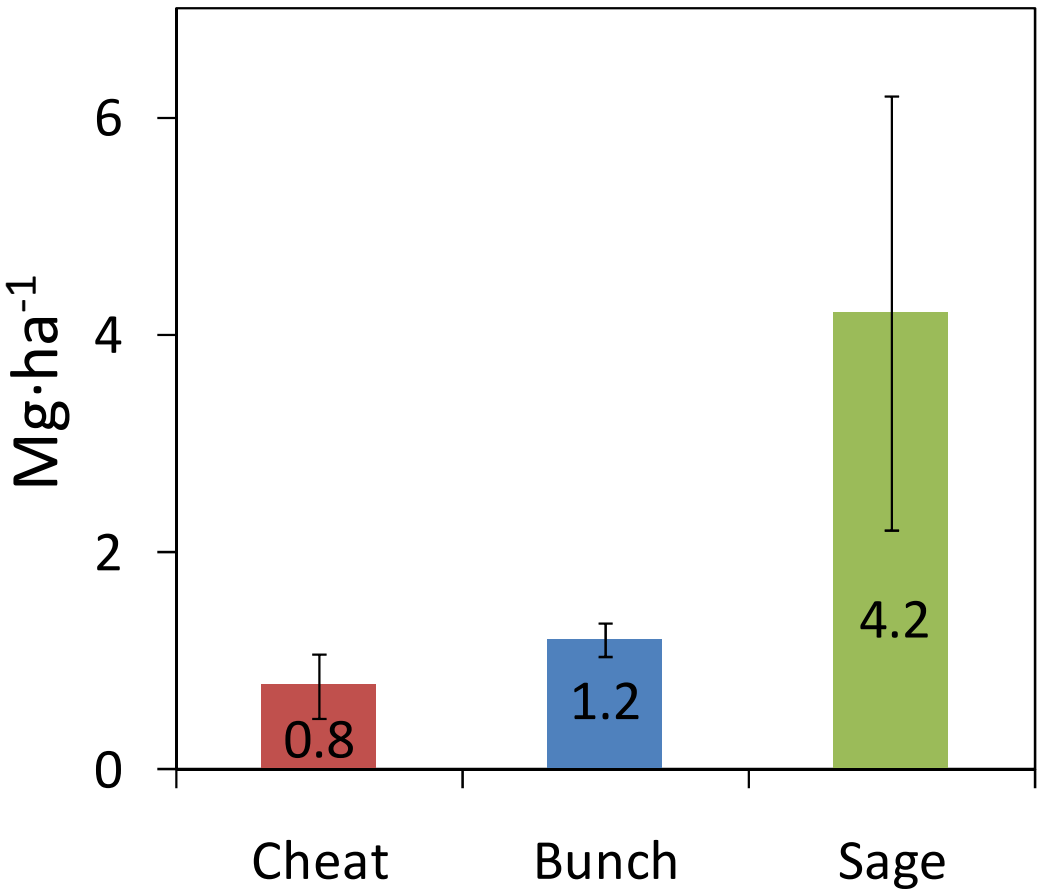

Figure A.8: Results for above-ground biomass. Error bars represent +/- 1 standard deviation (*n* = 3, 3, and 6 for cheat, bunch, and sage, respectively).

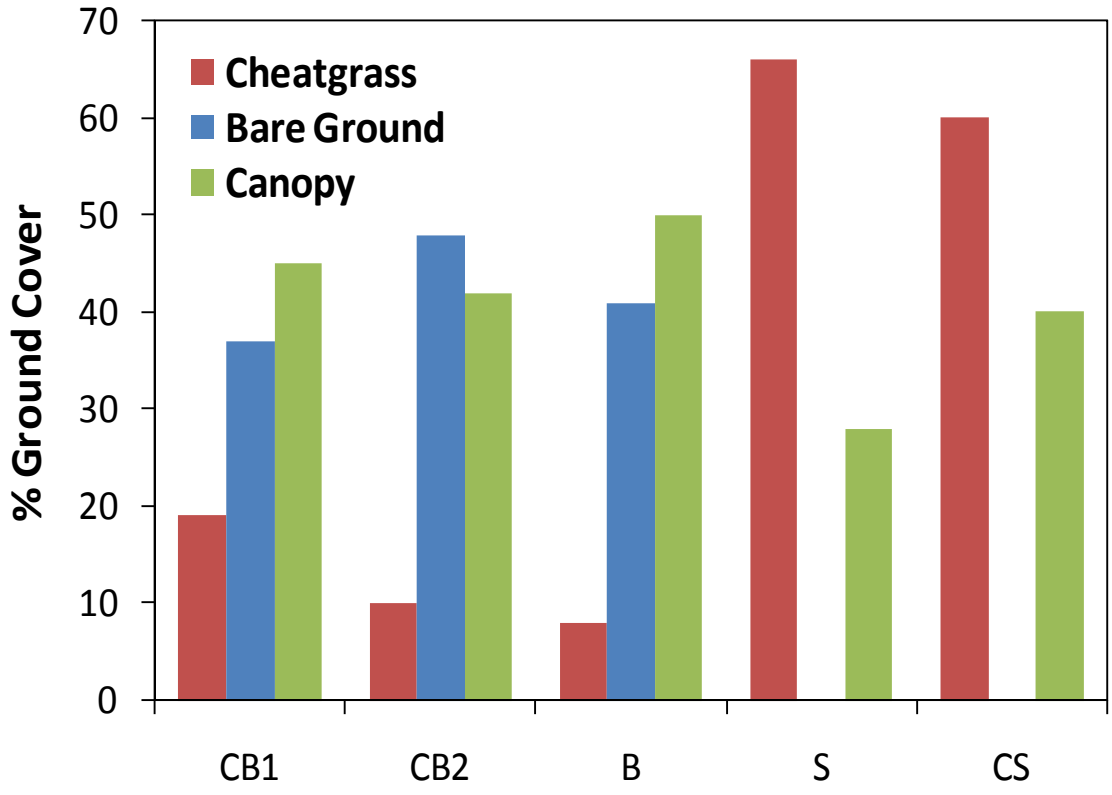

Figure A.9: Percent of ground cover for sampling transects. Ground cover calculated at 5 cm resolution. See Figure 2 for transect locations.

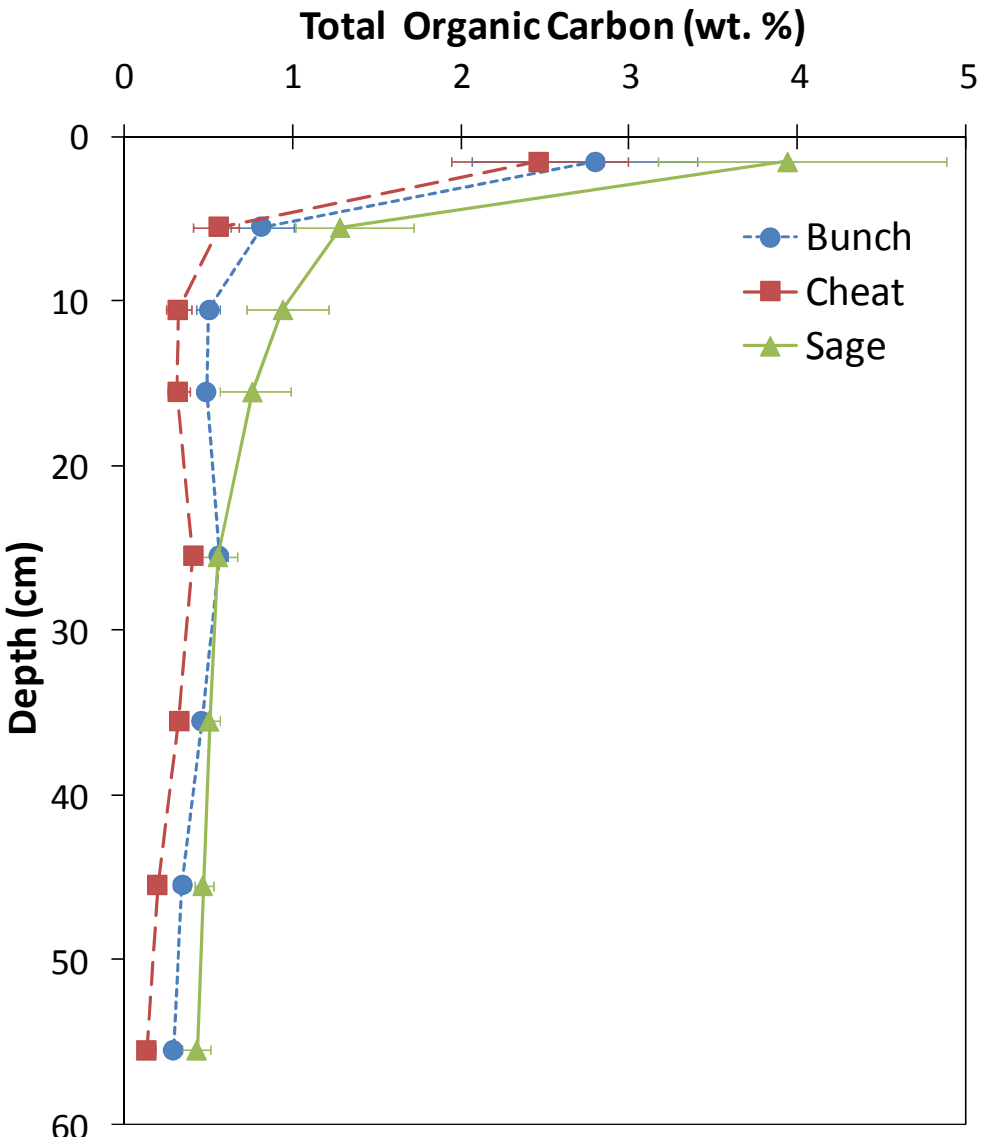

Figure A.10: Total Organic Carbon (TOC) wt. % for each plant community. Population sizes for cheatgrass, bunchgrass, and sagebrush were 38, 31, and 30, respectively, for each depth increment. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations.

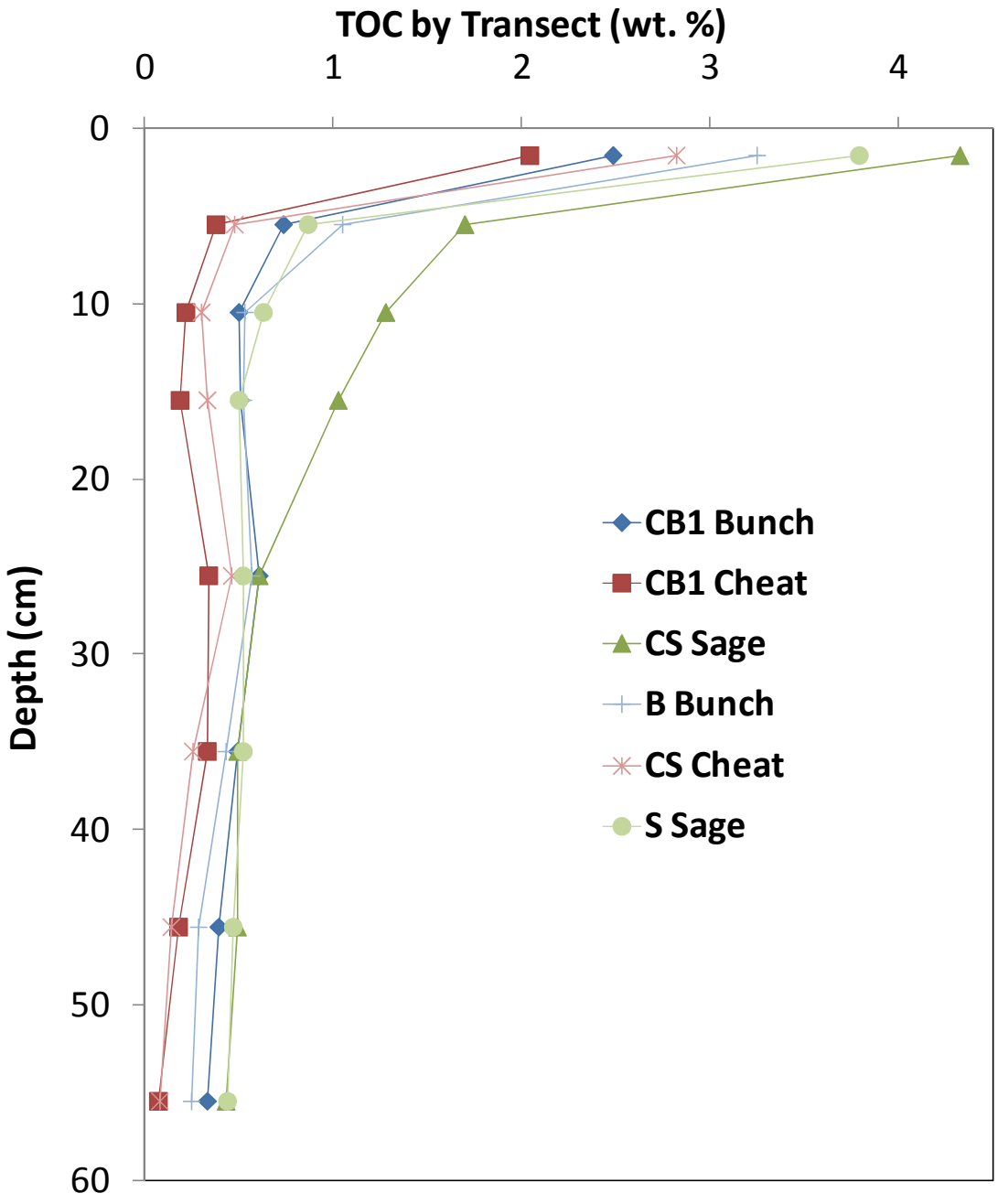

Figure A.11: Total Organic Carbon (TOC) wt. % for each plant community and for individual transects. See Figure 2 for transect locations.

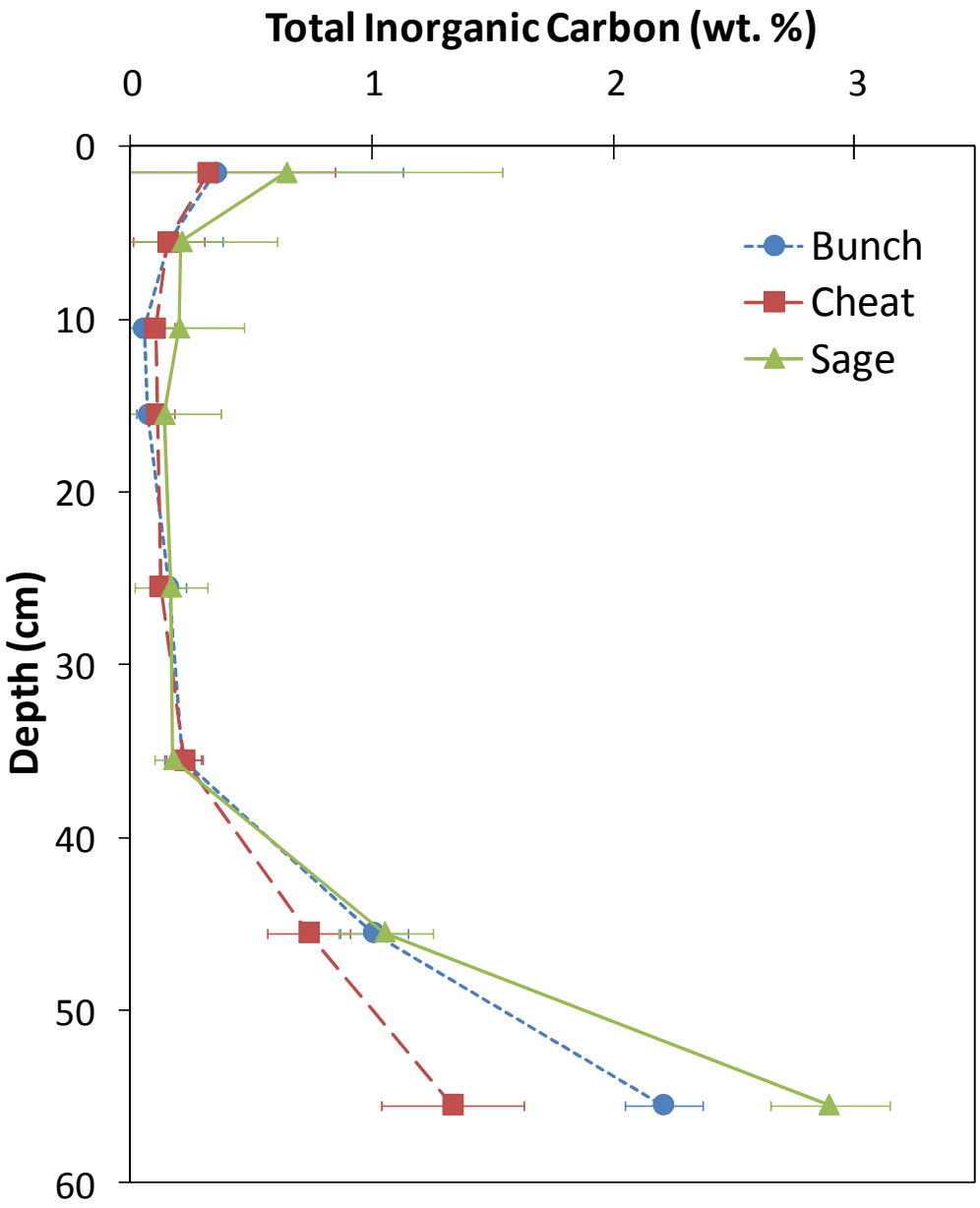

Figure A.12: Total Inorganic Carbon (TIC) wt. % for each plant community. Population sizes for cheatgrass, bunchgrass, and sagebrush were 38, 31, and 30, respectively, for each depth increment. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations.

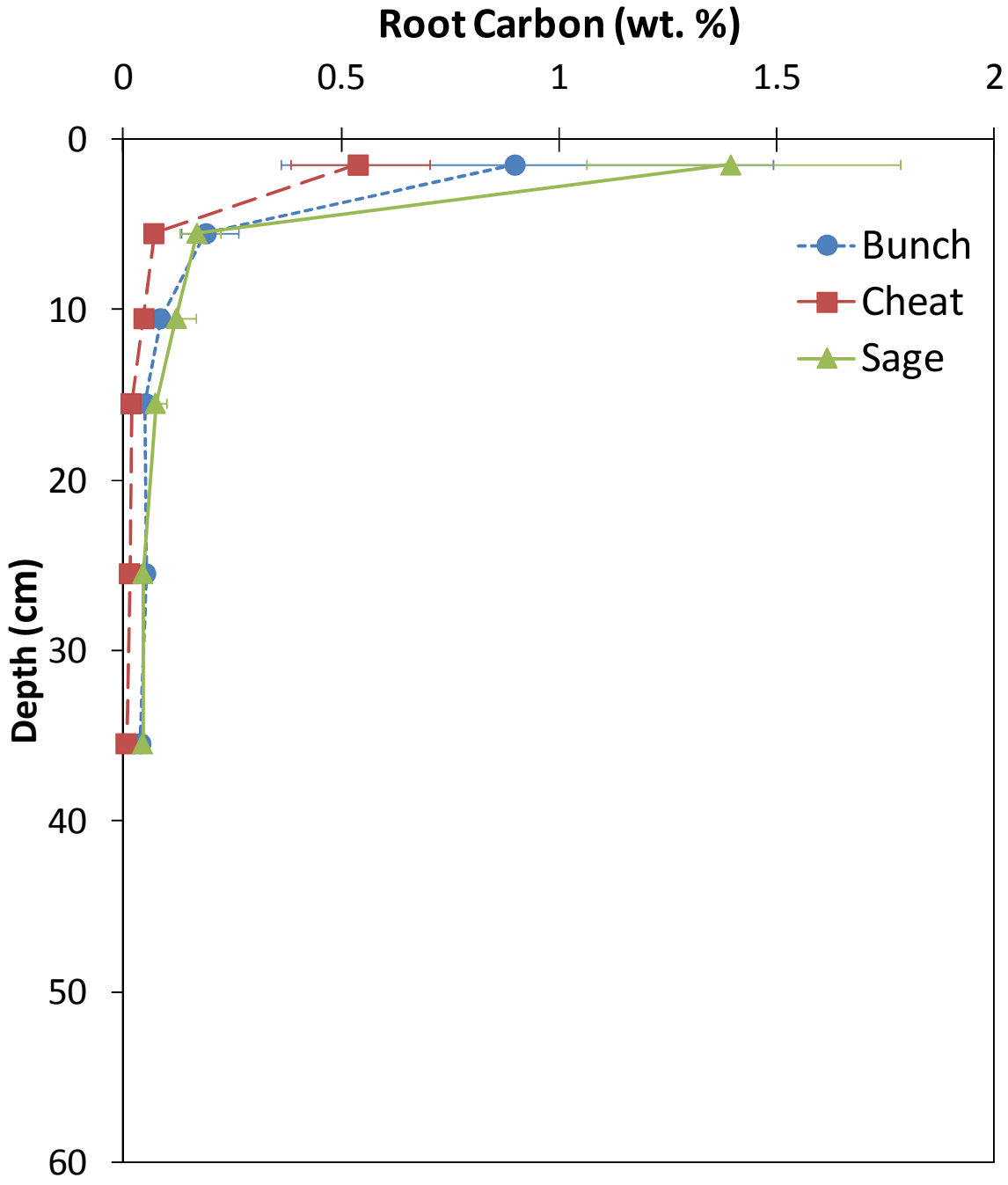

Figure A.13: Root carbon (wt. %) for each plant community. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations. Where error bars are not visible, symbol sizes encompass the error range. R_b values can be calculated by multiplying the above concentrations of root C by a factor of 3.7.

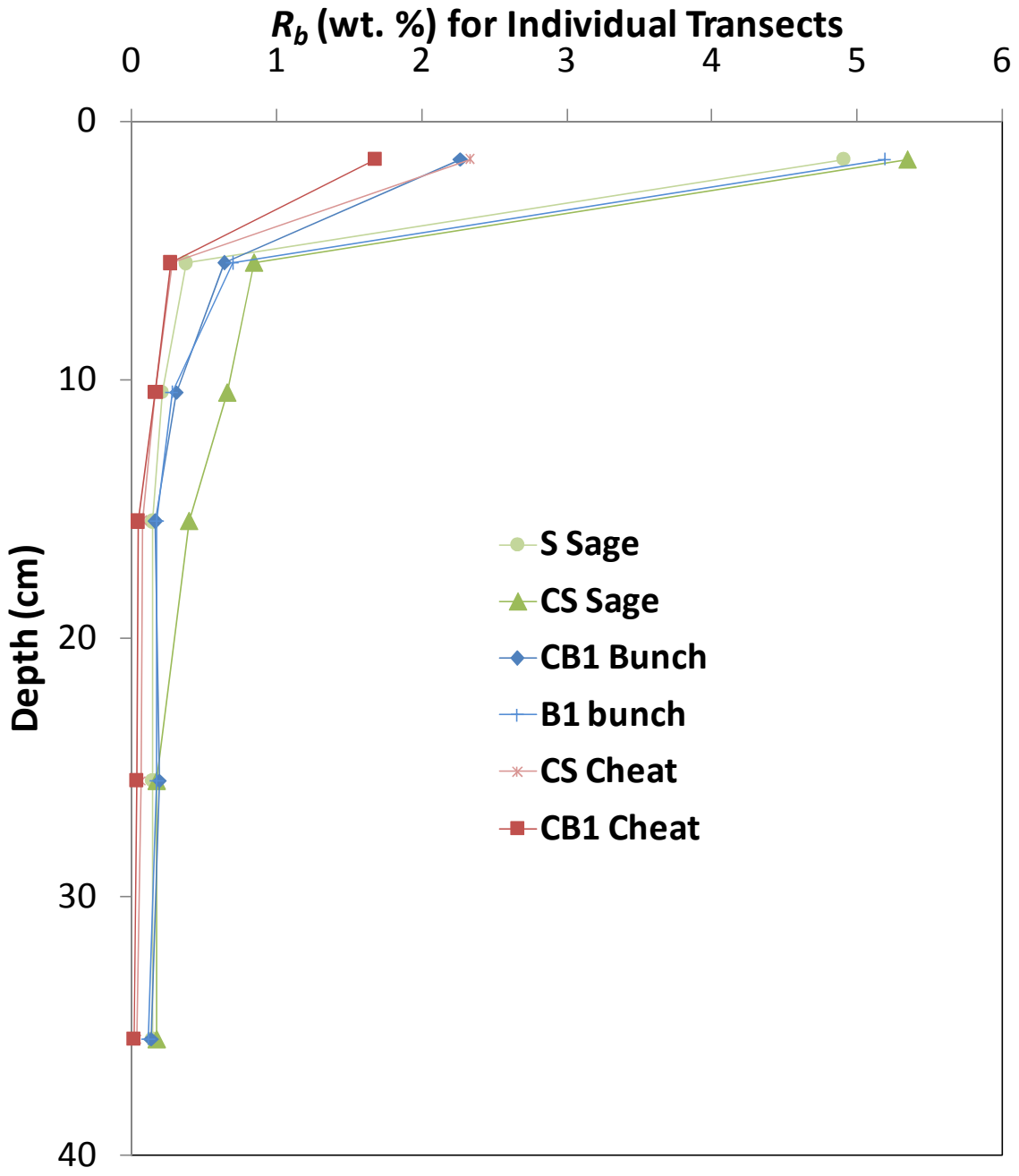

Figure A.14: Root Biomass wt. % (R_b) for each plant community and for individual transects. Root C values can be calculated by multiplying the above concentrations of R_b by a factor of 0.27. See Figure 2 for transect locations.

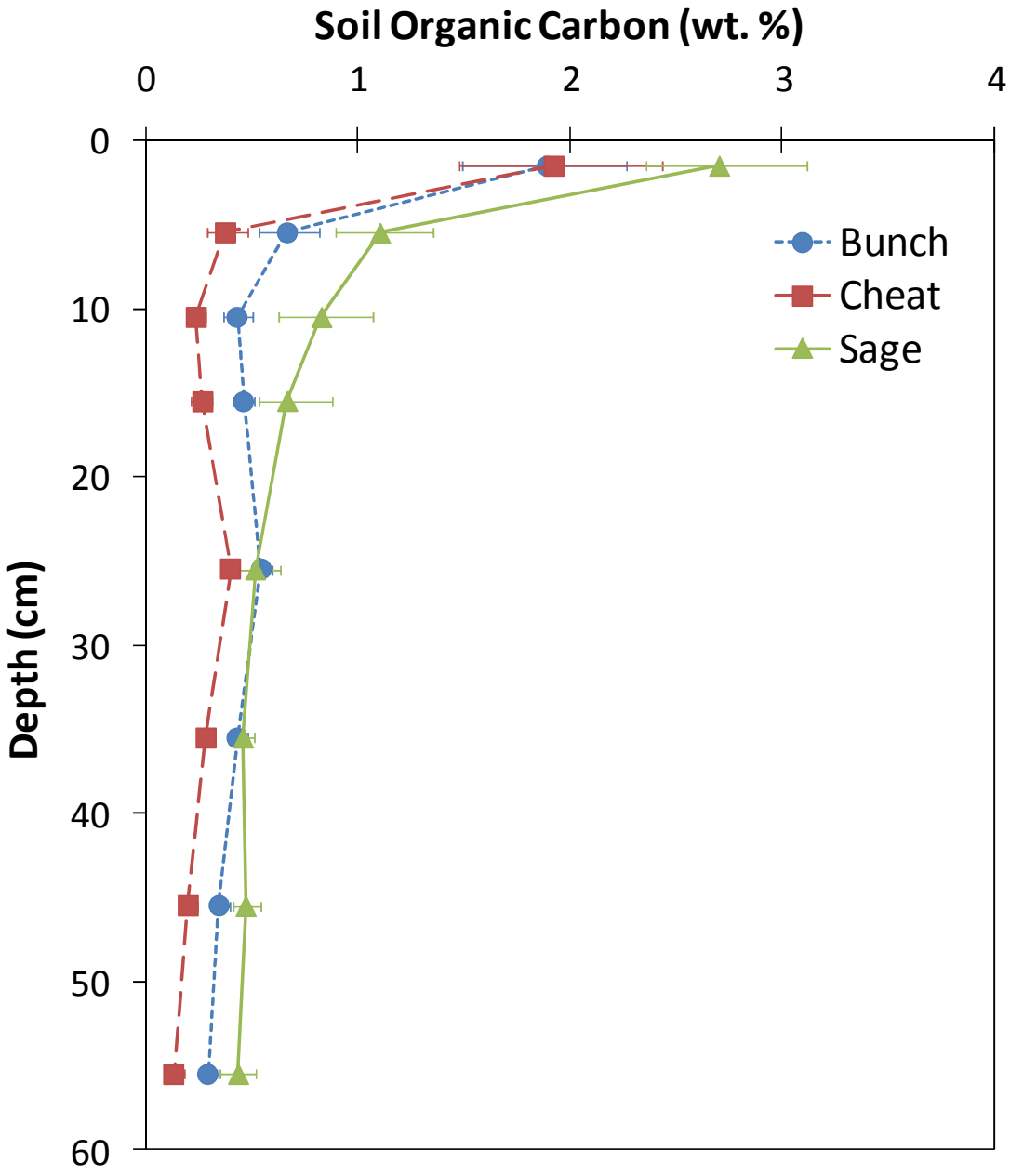

Figure A.15: Soil Organic Carbon wt. % (SOC) for each plant community. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations. Where error bars are not visible, symbol sizes encompass the error range.

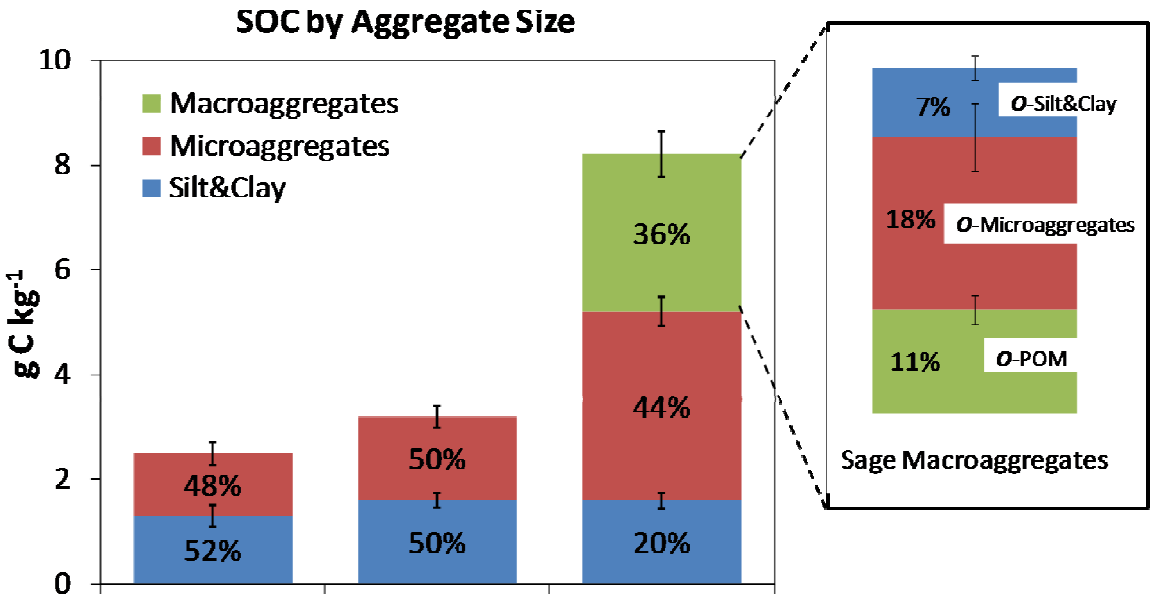

Figure A.16: Grams of SOC per kg soil. Data labels are weighted percent of total Soil Organic Carbon (SOC) by aggregate size for each community. Error bars represent +/- 1 standard error for *n* = 10 (5 from each transect, see Figure 2).

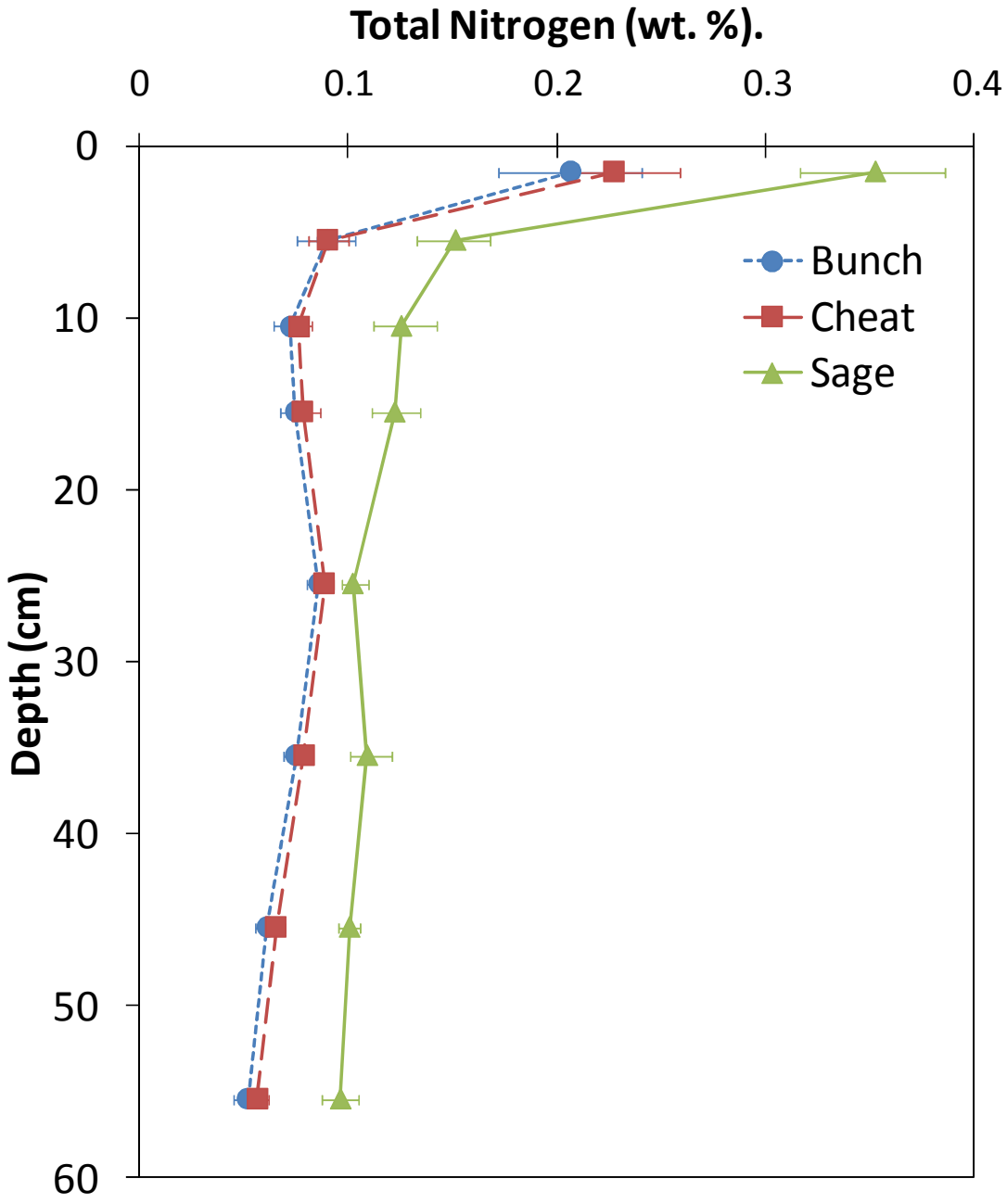

Figure A.17: Total Nitrogen (wt. %) for each plant community. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations. Where error bars are not visible, symbol sizes encompass the error range.

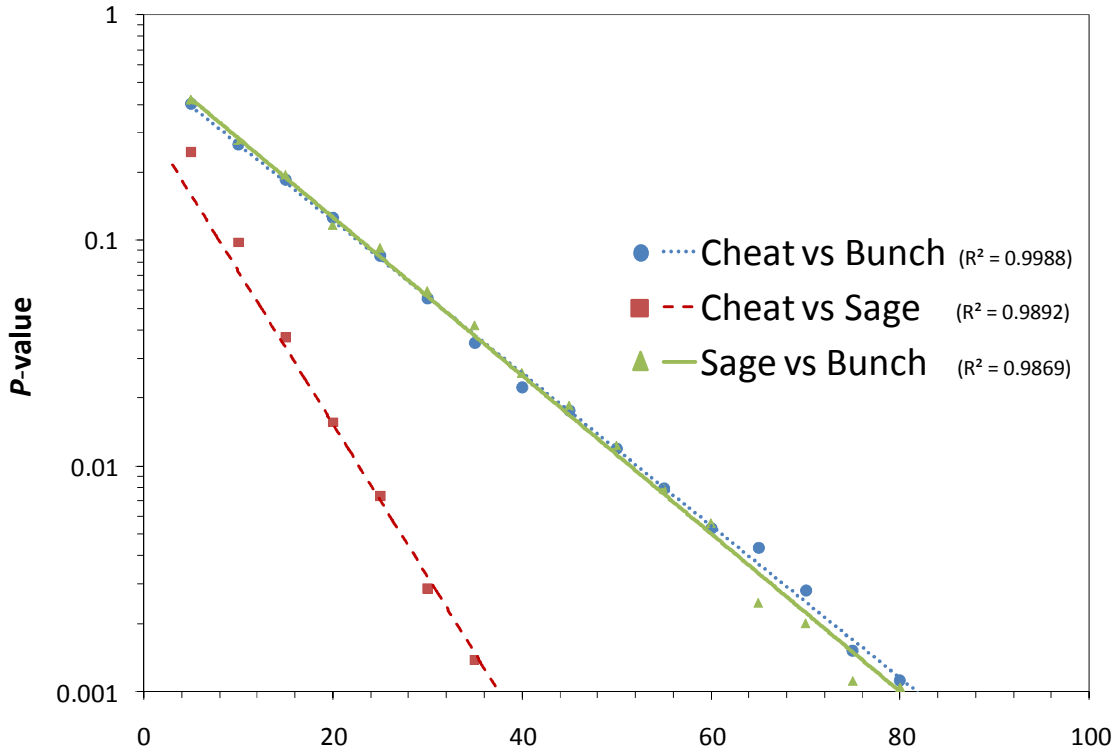

Figure A.18: Estimated number of soil cores needed to determine if two communities are significantly different using the K-S test ($p \leq 0.05$). Average *p*-value is reported for 1000 bootstrap simulations run for each sample size using the current data set.

* Number of Cores indicates the estimated number of soil cores from *each population* to reach a given *p*-value.

APPENDIX B

Tables

Table B.1: Previous Results for Studies Estimating Organic Carbon Pools

C pool	Study	# cores /community	*p* -value	*Sample depth*	Cheat		Bunch		Sage	
Aboveground					% Cover	MgC·ha^{-1}	% Cover	MgC·ha^{-1}	% Cover	MgC·ha^{-1}
	Hooker et al (2008)				80%	1.2 (0.1)	37%	1.3 (0.1)	38%	3.8 (0.7)
	Bradley et al (2006)[1] ‡				2(1) - 37(4)	0.22(0.02)-0.94 (0.26)	---	---	35(5) - 36(7)	3.4 (1.5) - 6.7 (2.9)
	Svejcar and Sheley (2001)[2] ‡				~100	0.12-.14	--	--	1-3	0.1-0.29 *
	This Study				~100	0.8 (0.3)	40-50	1.3 (0.15)	28-40	4.2 (2)
TOC										
	Hooker at al (2008)	20	0.21	0-100 cm		74.1 (4.2)		72.2 (3.5)		64.4 (4.5)
	Norton et al (2004) ‡	21		0-50 cm		18(12)-140(22)		--		36(15)-130 (13)
	Rau et al (2011)[3]	21		0-90 cm		--		--		43-49
	Chen and Stark (2000) ‡	5[†]	0.12	0-10 cm		--		42**		43**
	Gill et al (1999)	4	0.19	0-100 cm		80		89		102***
	Svejcar and Sheley (2001)[2] ‡	3		0-30 cm		12-17		--		10-16
	Bradley et al (2006)[1] ‡	40		0-10 cm		5.8 (0.3)-16.4 (0.5)		--		10.2(0.4)-12.4 (0.4)
	This Study	30		0-60 cm		26 (7)		35 (10)		48 (14)

* Data for sagebrush collected from sagebrush-steppe communities (bunchgrasses present within interspaces)

** Data collected within sage-steppe communities. Carbon content determined for soils beneath canopies of respective species.

*** Data for shadscale (*Atriplex confertifolia*) reported in place of sagebrush

[†] Core samples were composited from 9 separate cores collected within a plot (45 total)

‡ A value of 1.2 g·cm^{-3} was used to convert carbon concentrations to units of mass·area^{-1}

[1] Ranges correspond to increaseing levels of cheatgrass invasion and variable bunchgrass compositions

[2] Root mass & root C content averaged for 0 -10 and 10-30 cm depth increments as determined in May 1994. Root C was dded to SOC values determined in July 1994

[3] Data collected within sagebrush communities representing a continuum of cheatgrass invasion.

Table B.2: Results of the Lilliefors Test for Normally Distributed Data

	Cheatgrass						Bunchgrass						Sagebrush					
	TC		**TOC**		**R_b**		**TC**		**TOC**		**R_b**		**TC**		**TOC**		**R_b**	
Depth	*D* [1]	*Pr > D* [2]	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*
0-3	0.139	0.06	0.001	0.2	0.001	0.22	0.321	0.001	0.001	0.339	0.001	0.321	0.118	0.346	0.5	0.098	0.001	0.215
3-8	0.15	0.03	0.072	0.136	0.001	0.211	0.16	0.04	0.027	0.167	0.001	0.271	0.206	0.002	0.022	0.173	0.011	0.184
8-13	0.125	0.135	0.07	0.137	0.002	0.203	0.094	0.5	0.5	0.099	0.002	0.238	0.218	0.001	0.002	0.211	0.001	0.247
13-18	0.166	0.01	0.146	0.123	0.001	0.22	0.084	0.5	0.456	0.108	0.364	0.132	0.256	0.001	0.001	0.235	0.001	0.254
23-28	0.088	0.5	0.5	0.074	0.001	0.214	0.233	0.001	0.315	0.118	0.303	0.137	0.321	0.001	0.001	0.276	0.128	0.141
33-38	0.275	0.001	0.409	0.102	0.001	0.231	0.187	0.007	0.398	0.112	0.301	0.138	0.186	0.011	0.111	0.146	0.112	0.146
43-48	0.322	0.001	0.095	0.137	--	--	0.109	0.448	0.5	0.084	--	--	0.131	0.5	0.5	0.102	--	--
53-58	0.262	0.001	0.005	0.206	--	--	0.106	0.5	0.171	0.135	--	--	0.145	0.477	0.043	0.216	--	--

[1] *D* is the maximum vertical deviation of the empirical cumulative distribution function from a normally distributed cumulative distribution function.

[2] *Pr > D* indicates the probability the two populations are from normal distributions. If less than 0.05, the null hypothesis (of normality) is typically rejected.

Table B.3: Percent Difference in Lab Duplicates for Specific C Pools

	Min	Max	Mean	Median
TC (*n* = 67)	0.33%	54%	8.2%	5.4%
TOC (*n* = 68)	0%	110%	11%	8%
$\mathbf{R_b}$ (*n* = 52)	0%	82%	19%	16%

Table B.4: Mass Percentage by Particle Size Class

Depth	% Sand	% Silt	% Clay	Textural Class
0-3	24 (8)	64 (6)	13 (3)	silt loam
3-8	21 (6)	63 (5)	16 (3)	silt loam
8-13	17 (2)	57 (7)	27 (5)	silt loam
13-18	16 (2)	47 (6)	37 (6)	silty clay loam
18-28	17 (4)	48 (4)	35 (4)	silty clay loam
28-38	17 (4)	52 (6)	31 (6)	silty clay loam
38-38	20 (2)	56 (10)	24 (10)	silt loam
48-58	17 (2)	61 (10)	22 (10)	silt loam

Values in parantheses indicate standard deviation (*n* = 4).

Table B.5: C Pool Sizes by Plant Community

	$Mg\ C \cdot ha^{-1}$		
C Pool	**Cheat**	**Bunch**	**Sage**
Aboveground	0.8 (0.3)a	1.2 (0.2)ab	4.2 (2)b
TC	61 (16)a	87 (14)ab	113 (22)b
TOC	29 (6)a	41 (7)ab	56 (12)b
TIC	32 (22)	46 (21)	57 (34)
Root C	3 (.8)a	6 (3)ab	8 (2.2)b
SOC	26 (5)a	35 (5)ab	48 (9)b

* Within the same row, values with different letters are significantly different ($p \leq 0.05$)

Table B.6: Results of the K-S Test for Significant Difference

	Cheat vs Sage				Cheat vs Bunch				Bunch vs Sage			
	TOC		**R_b**		**TOC**		**R_b**		**TOC**		**R_b**	
Depth	*D* [1]	*Pr > D* [2]	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*
0-3	0.432	0.0025	0.468	0.0017	0.14	0.8705	0.183	0.7359	0.533	0.0002	0.509	0.002
3-8	0.477	0.0006	0.414	0.0072	0.292	0.0881	0.397	0.022	0.349	0.0362	0.165	0.835
8-13	0.599	< 0.0001	0.54	0.0001	0.441	0.0016	0.537	0.0005	0.434	0.0046	0.249	0.344
13-18	0.472	0.0007	0.61	< 0.0001	0.52	0.0001	0.579	0.0001	0.401	0.0101	0.239	0.394
23-28	0.263	0.1655	0.67	< 0.0001	0.517	0.0001	0.663	< 0.0001	0.306	0.0914	0.252	0.33
33-38	0.526	0.0001	0.83	< 0.0001	0.5	0.0002	0.794	< 0.0001	0.175	0.708	0.186	0.721
43-48	0.714	< 0.0001			0.521	0.0001			0.503	0.0025		
53-58	0.713	< 0.0001			0.637	< 0.0001			0.621	0.0003		

[1] *D* is the maximum vertical deviation of the empirical cumulative distribution functions for the two populations being compared.

[2] *Pr > D* indicates the probability the two populations are from different distributions. If less than 0.05, the null hypothesis (populations from the same distribution) is typically rejected.

Table B.7: Depth Distribution of TOC

	TOC ($Mg \cdot ha^{-1}$)		
Depth	**Cheat**	**Bunch**	**Sage**
0-3	8.9 (1.9)a	10.1 (2.4)ab	14.2 (3.5)b
3-8	3.4 (0.8)a	4.9 (1.1) ab	7.7 (1.9)b
8-13	1.9 (0.4)a	3 (0.4)b	5.7 (1.3)c
13-18	1.9 (0.4)a	2.9 (0.3)b	4.6 (1.3)c
18-28	4.9 (0.5)a	6.8 (0.6)b	6.7 (1.4)ab
28-38	3.9 (0.5)a	5.5 (0.5)b	6.1 (0.8)b
38-48	2.4 (0.5)a	4.2 (0.5)b	5.7 (0.8)c
48-58	1.6 (0.5)a	3.5 (0.6)b	5.2 (1)c
Total	29 (5.5)a	40.9 (6.4)ab	55.9 (12)b

* Within the same row, values with different letters are significantly different ($p \leq 0.05$)

Table B.8: Depth Distribution of Root C

	Root C ($Mg \cdot ha^{-1}$)		
Depth	**Cheat**	**Bunch**	**Sage**
0-3	1.9 (0.6)a	3.2 (2)ab	5 (1.3)b
3-8	0.4 (0.08)a	1.1 (0.4)b	1 (0.3)b
8-13	0.3 (0.06)a	0.51 (0.14)b	0.7 (0.2)b
13-18	0.1 (0.03)a	0.29 (0.06)b	0.4 (0.13)b
18-28	0.2 (0.04)a	0.63 (0.13)b	0.5 (0.12)b
28-38	0.1 (0.03)a	0.46 (0.11)b	0.5 (0.11)b
Total	2.8 (0.8)a	6.3 (2.9)ab	8.3 (2.2)a

* Within the same row, values with different letters are significantly different ($p \leq 0.05$). R_b values can be calculated by multiplying the above values by a factor of 3.7.

Table B.9: Depth Distribution of SOC

	SOC ($Mg \cdot ha^{-1}$)		
Depth	**Cheat**	**Bunch**	**Sage**
0-3	6.9 (1.8)	6.8 (1.8)	9.7 (1.6)
3-8	2.3 (0.5)a	4 (1.1)b	6.6 (1.6)b
8-13	1.4 (0.4)a	2.6 (0.4)b	5 (1.2)c
13-18	1.6 (0.3)a	2.8 (0.3)b	4 (1)b
18-28	4.8 (0.5)a	6.5 (0.6)b	6.2 (1.1)b
28-38	3.4 (0.5)a	5.2 (0.4)b	5.5 (0.5)b
38-48 *	2.4 (0.5)a	4.2 (0.5)b	5.7 (0.8)c
48-58 *	1.6 (0.5)a	3.5 (0.6)b	5.2 (0.1)c
Total	25.5 (5)a	34.7(5.7)ab	47.9 (8.8)b

* Root C was below level of detection. and SOC was assumed to equal TOC

** Within the same row, values with different letters are significantly different ($p \leq 0.05$). R_b values can be calculated by multiplying the above values by a factor o 3.7.

Table B.10: Mass Percentage of Soil and SOC Content of Aggregates

	Agggregate Size					
	> 250 µm		**53-250 µm**		**< 53 µm**	
Community	wt. % Soil	wt. % SOC	wt. % Soil	wt. % SOC	wt. % Soil	wt. % SOC
Bunch	6	0*	50	0.33	44	0.36
Cheat	7	0*	47	0.24	45	0.27
Sage	22	1.49	49	0.73	27	0.62

* Particles greater than 250 µm consisted entirely of rock and root fragments

Table B.11: C/N Ratio of Aggregate Sizes

	Aggregate Size		
	> 250 µm	**53-250 µm**	**< 53 µm**
Bunch		3.8 (0.5)	3.4 (0.3)
Cheat		3.1 (0.6)	2.6 (0.4)
Sage	8.7 (0.7)	6.4 (0.5)	5.2 (0.4)

Values in parantheses are one standard error (n= 10).

Table B.12: Percentage of TOC by Mass (Root C and SOC)

	Cheat		Bunch		Sage	
	Root C	SOC	Root C	SOC	Root C	SOC
0-3	22	78	32	68	35	65
3-8	13	87	23	77	13	87
8-13	15	85	17	83	13	87
13-18	6	94	10	90	10	90
18-28	3	97	9	91	8	92
28-38	2	98	8	92	9	91
38-48 *	0	100	0	100	0	100
48-58 *	0	100	0	100	0	100
Total	**10**	**90**	**15**	**85**	**14**	**86**

Values are percent mass of total organic carbon (TOC) for distinct C pools and for each plant community.