Transition from Sagebrush Steppe to Annual Grass (Bromus tectorum): Influence on Belowground Carbon and Nitrogen

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ABSTRACT

Vegetation changes associated with climate shifts and anthropogenic disturbance have major impacts on biogeochemical cycling. Much of the interior, western, U.S., is currently dominated by sagebrush (*Artemisia tridentata* Nutt.) ecosystems. At low to intermediate elevations, sagebrush ecosystems are increasingly influenced by cheatgrass (*Bromus tectorum* L.) invasion. Little is currently known about the distribution of belowground organic carbon (OC) on these changing landscapes, how annual grass invasion affects OC pools, or the role that nitrogen (N) plays in carbon (C) retention. As part of a Joint Fire Sciences funded project called the Sagebrush Treatment Evaluation Project (SageSTEP), we quantified the depth distribution of soil OC and N at 7 sites experiencing cheatgrass invasion. We sampled plots which retained sagebrush, but represent a continuum of cheatgrass invasion into the understory. Eighty four soil cores were taken using a mechanically driven diamond tipped core drill to a depth of 90 cm, or until bedrock or a restrictive layer was encountered. Samples were taken in 15 cm increments and soil, rocks, and roots were analyzed for OC and total N. We determined that cheatgrass influences the vertical distribution of OC and N within the soil profile and may result in decreased SOC content below 60 cm. We also found that OC and total N associated with coarse fragments accounted for at least 10% of belowground pools. This emphasizes the need for researchers to quantify nutrients in deep soil horizons and coarse fragments.

Key words: carbon sequestration, cheatgrass, invasive annual grass, total nitrogen, sagebrush, soil organic carbon, climate change, biogeochemical cycles

INTRODUCTION

The sagebrush (*Artemisia tridentata* Nutt.) steppe is the most expansive shrubland ecotype in the U.S., and is considered to be one of the most threatened ecosystems in North America (Noss et al. 1995). In the interior western U.S., dramatic shifts in vegetation are occurring due to long term climate change, livestock grazing, rapid population growth, fire suppression, and introduction of exotic annual grasses (Miller and Tausch 2001). Sagebrush steppe ecosystems face declining herbaceous perennial understory components, and invasion of exotic annual grasses such as cheatgrass (*Bromus tectorum* L.) which can convert a site to near monoculture (Miller and Tausch 2001; Chambers et al. 2007).

Vegetation shifts can have large impacts on biogeochemical cycles in established ecosystems including changes in organic carbon (OC) and total nitrogen (N) accumulation (Schimel et al.1991, 1994). The sagebrush steppe is a fire adapted ecosystem with fire return intervals ranging from 20 – 90 years (Miller and Tausch 2001). Annual grass invasion may reduce aboveground C and N pools, and decrease fire return interval resulting in further C and N losses (D'Antonio and Vitousek 1992; Bradley et al. 2006). Similarly Sagebrush steppe conversion to annual grass dominance could reduce belowground C pools due to altered below ground interactions related to litter decomposition, root exudation, and soil biota (Schlesinger 1977; Norton et al. 2004). Changes in these processes alter the input vs. respiration balance which drives belowground C and N accumulation (Norton et al. 2008). Much of the current research and literature related to cheatgrass invasion and C has focused on aboveground biomass (Bradley et al. 2006). However, most carbon (C) and N in these arid ecosystems are stored in soils (Hooker et al. 2008). Research on soil OC and invassives often focuses on surface soil processes (Ogle et al. 2004; Wolkovich et al. 2010). There are several papers which describe deeper soil profile changes (Norton et al. 2004; Hooker et al. 2008; Blank et al. 2008); however, these studies were from individual sites (Hooker et al. 2008; Blank et al. 2008) or concentrated on one geographic area (Norton et al.2004). The current studies show conflicting results for the influence of cheatgrass invasion on soil organic carbon (SOC). Studies report increasing SOC in shallow horizons (Ogle et al. 2004). Others report increases in SOC through the entire soil profile (Hooker et al. 2008; Blank et al. 2008), and others report increases in SOC in near surface horizons, but decreases in SOC deeper in the soil profile (Norton et al. 2004). None of the current literature reports data on OC associated with > 2 mm coarse fragments (rocks). Several researchers have documented the importance of including coarse fragment estimates in C budgets (Fernandez et al. 1993; Ugolini 1996; Corti et al. 1998; Harrison et al. 2003). Given the current interest in CO_2 emissions and their interaction with climate we must attempt to quantify all OC pools when we discuss the effects of invasive species on OC sequestration. This study is an attempt to quantify total belowground OC changes associated with cheatgrass invasion over a broad geographic area. We sampled seven sagebrush steppe sites experiencing variable degrees of cheatgrass invasion within each site. This differs from previous studies which have primarily focused on comparisons between healthy sagebrush systems and cheatgrass monocultures. With these data we attempt to answer several questions: 1) Does cheatgrass invasion affect belowground storage of C and N? 2) Does cheatgrass invasion affect the partitioning of root and soil pools of C and N? and 3) What are the primary factors associated with belowground organic C retention in sagebrush steppe ecosystems?

METHODS

Experimental Area

This study is part of the Sagebrush Steppe Treatment Evaluation Project (SageSTEP) (www.sagestep.org). The seven sagebrush steppe sites for this study are spread across more than 1000 km from central Washington to west central Utah (Figure 1A). Although all seven sites are typical sagebrush steppe systems, they encompass a substantial range of conditions, in terms of soil types, plant communities, and the typical weather patterns observed (McIver et al. 2010). Soils within the network are typic aridisols, molisols, or entisols, most have sandy loam or silt loam surface textures, and vary in depth from 9 cm to > 1 m (Table 1).

Sample Collection and Processing

Each of the 7 sites contained 4 core treatment plots (50 - 200 ha) which had a fuels reduction and ecosystem maintenance treatment implemented after sampling (Figure 1B). For this study treatment is not considered and each core treatment plot is a replicate within site. Sub-plots (0.1 ha) within the core treatment plots were used to quantify vegetation cover and biomass at each location (McIver et al. 2010). All plots had intact sagebrush components ranging from 5 to 47% areal cover, and annual grass cover on sub-plots ranged from 0 to 50% areal cover. To assess how increasing cheatgrass cover influenced soil OC and total N we selected three sub-plots based on their relative cheatgrass cover. Each of the three sub-plots selected within a core plot had similar soil physical properties and sagebrush cover, but represented a different level of cheatgrass invasion. Extent of cheatgrass invasion was determined by dividing cheatgrass cover on each sub-plot by the total herbaceous understory cover (perennial grass + perennial forb + annual grass + annual forb) on each sub-plot. Sub-plots were than ranked as phase I, II, and III by relative annual grass cover within each core plot. By using relative cheatgrass cover rather than total cheatgrass cover we may be able to estimate how much of a sites potential herbaceous component has been converted to annual grass dominance. Total shrub, herbaceous, and cheatgrass cover was variable between sites and within sites. Sub-plots with the lowest cheatgrass relative cover were assigned phase I status and had a mean of 16 % relative cheatgrass cover. Plots with intermediate relative cheatgrass cover were assigned phase II status (mean 25 %). Sub-plots with the highest cheatgrass relative cover were assigned phase III status (mean 38 %). In order to minimize disturbance to individual sub-plots we sampled soils on the northeast corner of each plot (Figure 1C). At each sub-plot a soil core was taken from shrub interspaces using a two person power auger retro-fitted with a diamond tipped core bit (Rau et al. 2009). This device allows workers to core through large rock fragments and coarse roots to bedrock or a similar obstruction. The device also allows workers to estimate the bulk density of each soil increment if accurate depth measurements are taken. This methodology should provide similar estimates of below ground nutrient pools previously thought obtainable only from quantitative soil pits (Hamburg 1984; Harrison et al. 2003; Johnson et al. 2007). Soil cores were 7.62 cm in diameter and taken in 15 cm increments to a depth of 90 cm or until an impenetrable obstruction was encountered. Soil cores were placed in plastic lined paper bags, returned to the lab and dried at 50° C for 48 hours then weighed. Cores were sieved to 2 mm, and the coarse fragment was submerged and agitated in de-ionized water to separate roots from coarse mineral fragments by flotation, break up soil aggregates which did not pass though the sieve, and to remove adhered soil particles from roots and coarse fragments. Roots and water were decanted off coarse fragments, and passed through a 0.35 mm sieve into a drying tray to separate roots from water. Some < 2 mm sediment remained in with coarse fragment samples. The separate coarse fragment, root, and water fractions were re-dried at 50° C. After drying < 2 mm soil which had been adhered to coarse fragments and roots prior to flotation was again separated from coarse fragments using a 2 mm sieve. The sediment which was decanted along with roots, but which passed through the 0.035 mm sieve was removed from the drying tray and added back to the original < 2 mm fraction along with the second fraction separated from coarse fragments. The mass of all three fractions (> 2 mm roots, > 2 mm coarse fragments, and < 2 mm soil) was then determined (Figure 2). Although time consuming we believe this method maximizes separation of fractions and minimizes the cross contamination between fractions. Each fraction was then ground using an Udi cyclone™ or IKA impact head™ type mill. Soil and coarse fragment samples were subjected to a test for inorganic carbon using 0.1 M HCl. Samples which tested positive for inorganic C were completely digested with 0.1 M HCl to remove inorganic C (Sollins et al. 1999). Five samples (< 2 mm untreated soil, < 2 mm HCl treated soil, > 2 mm untreated coarse fragments, > 2 mm HCl treated coarse fragments, and > 2 mm organic) for each core sample were analyzed using a LECO Truspec® CN analyzer. For soil and coarse fragment material, the instrument was calibrated using a certified standard containing 1.30% C and 0.130% N; for roots, the instrument was calibrated using EDTA (41.02% C, 9.57% N). The HCl digest method may remove a small amount of organic C and total N from the samples which may result in an underestimate of organic C % and total N % in our samples (Sollins et al. 1999). Percent OC and total N were multiplied by each sample fraction's mass to obtain the mass of OC and total N per core sample. Dividing each fraction's OC and total N mass by the core volume and multiplying by the sample depth gives the mass of OC and total N per sample per unit area, and the sum of all samples from each core gives total OC and total N per unit area (Figure 2).

Statistical Analyses

Five variables for belowground OC were analyzed for the influence of annual grass invasion, soil depth, and their interactions: soil OC percent, soil OC content, mass of root C, coarse fraction OC content, and total belowground OC. Similarly, six variables for total belowground N were analyzed: soil N percent, soil N content, mass of root N, coarse fraction N content, total belowground N, and C:N.

All comparisons were evaluated using SAS™ generalized linear mixed models (Proc GLIMMIX). Differences in organic C and total N were evaluated by treating phase of annual grass invasion as main effect, soil depth was a split plot within annual grass invasion, and site was a considered a random affect (alpha = 0.05). Means comparisons were made using Tukey's test (alpha = 0.05).

Stepwise linear regression (SAS™ Proc REG) was used to determine the main factors related to total belowground organic carbon (root OC + soil OC + rock OC) accumulation in sagebrush steppe experiencing annual grass invasion. The main factors included in the analyses were sample depth, coarse fragment %, sand %, silt %, clay %, total belowground N, mean annual precipitation, mean annual temperature, shrub cover, perennial herbaceous cover, and annual grass cover. The regression analyses use an iterative process to find the best models for each number of variables utilized by the model. The criteria used to identify the best fit model values for the Delta Akaike Information Criterion (AIC) less than 2.0 (Burnham and Anderson 1992).

RESULTS and DISCUSSION

Carbon

Extent of annual grass invasion had a significant effect on soil OC (Table 2; Figure 3). Phase I and II plots had significantly higher soil OC% than phase III plots. This indicates that as cheatgrass invasion progresses soil OC% decreases. This same trend is apparent for soil OC content, and total belowground OC content (Figure 3).

The mixed model also indicates that depth was a statistically significant factor for all OC variables. Soil OC%, content, and root OC content all typically decreased with depth, which is typical of most soil profiles (Figure 4). However, coarse fragment bound OC content typically increased with soil depth (Figure 4). This is consistent with the distribution of coarse fragment mass within the soil profile. In our study we determined that OC content associated with coarse fragments contributed 10% of total belowground OC estimates. Researchers have previously documented that coarse fragment OC can account for as much as 20 to 50% of total belowground OC (Fernandez et al. 1993; Ugolini 1996; Corti et al. 1998; Harrison et al. 2003).

There were significant phase by depth interactions for both soil OC content and total belowground OC content (Table 2). Means comparisons confirm that soil OC content is significantly lower at the 60 - 75 cm depth increment in phase III plots compared to phase I and phase II plots (Figure 4). This is similar to data reported by Norton et al. (2004) who found that cheatgrass monocultures had significantly lower OC in the sub-surface compared to un-invaded sagebrush steppe plots. Our data set is also similar to the Norton et al. (2004) data set which shows there is a trend toward decreasing root biomass below 45 cm with annual grass invasion (Figure 4). We hypothesize that this is the mechanism responsible for decreasing soil OC with increasing annual grass cover. Annual grasses like cheatgrass tend to be shallow rooted species as opposed to perennial grasses and shrubs which are typically deep rooted in arid and semi-arid environments (Jackson et al. 2000). Fine root turnover has been proposed as one of the main factors which influence soil OC accumulation (Schlessinger 1977; Richter1999). Comparing total belowground OC content between phase I plots and Phase III plots we could estimate that the loss of root biomass and soil OC in the sub-surface could result in 6 to 9 Mg ha^{-1} of belowground OC lost by the replacement of perennial herbaceous vegetation with annual grass. This represents nearly twice the amount of OC lost from aboveground biomass due to cheatgrass conversion of sagebrush ecosystems (Bradley et al. 2006; Hooker et al. 2008). We further hypothesize the loss of belowground OC could be even larger if shrubs and their root systems are removed via disturbance or competition and decomposition.

Our data does not support the hypotheses proposed by Ogle et al. (2004) that annual grass invasion increased soil OC content after using the CENTURY model to verify data collected from the top 20 cm of soil. However, the Ogle et al. (2004) observations are consistent with observations made by Norton et al. (2004), Blank et al. (2008), and Hooker et al. (2008) who have documented that annual grass invasions may increase near surface soil OC. However, Norton et al. (2004) also documented the decrease in soil OC at depth that we describe. The decrease of soil OC at depth easily offset gains near the surface in their study. We therefore suggest that cheatgrass invasion could increase near surface OC in certain circumstances, but that these gains may often be offset by OC losses deeper in the soil profile. It is imperative that soils be sampled to the maximum depth feasible or reasonable so that plant soil interactions can be properly assessed when discussing ecosystem C and N budgets.

Nitrogen

There were no statistically significant changes in soil N when extent of annual grass invasion was considered alone; however, trends similar to OC are apparent (Table 2; Figure 5). All soil N variables had statistically significant relationships with soil profile depth, with results identical to those observed for soil OC variables (Figure 6). There were marginally significant phase by depth interaction terms for soil N content and total belowground N (Table 2).

Means comparisons confirm that phase III plots had a slightly lower N content in the 60 - 75 cm soil increment compared to phase I plots (Figure 6). Several authors have reported increased soil N content under cheatgrass monocultures (Norton et al. 2004; Blank 2008; Hooker et al. 2008). This data is somewhat surprising considering that cheatgrass is not an N-fixer. In addition to increased total N several authors have described increased inorganic–N including NO_3^- in lower soil horizons (Norton et al. 2004; Blank 2008; Hooker et al. 2008). This is logical if we accept that root biomass and therefore N-uptake has been reduced in lower soil horizons. The loss of root biomass and increasing NO_3^- concentrations in the sub-surface could result in the export of N from the system during episodic wet period or in more mesic environments. This may help to explain the loss of N in the sub-surface on our sites. N loss may certainly not be universal and may depend on climate and also atmospheric deposition rates.

Nitrogen content of the coarse fraction is not typically measured, but may account for 10 % of total belowground N estimated to 90 cm on our sites (Figure 5). It appears that this pool could be up to ten times larger than the amount of N found in root biomass (Figure 5). The N bound in coarse material could be of several forms: organic and inorganic N which has worked its way into pores or cracks within the rock surface, organic and inorganic N bound into sedimentary deposits, and inorganic N which has been bound into silicate minerals (Bohn et al. 2001; Holloway et al. 2001, Holloway and Dahlgren 1999; Ugolini et al. 1996). Most of our sites are derived from volcanic parent material, therefore, we hypothesize that most of the N associated with coarse fragments is in the form of organic matter which is adhered to the fragment’s surface. Even with careful washing of coarse fragments this pool remains quite large. We agree with other researchers that this results in a significant underestimate of belowground N (Fernandez et al. 1993; Ugolini 1996; Corti et al. 1998; Harrison et al. 2003).

Factors Related to Carbon Retention

The step wise regression analyses confirm that total belowground N is the factor most correlated with belowground organic C retention and explains nearly 60% of the variance (Table 3). Inclusion of variables which define climate explains another 2 - 3% of the variance, and further inclusions of variables which define soil texture and vegetation cover including annual grass explain another 1% of the variance (Table 3). The models suggest that total belowground organic C is consistently and positively correlated with total belowground N, mean annual precipitation, shrub cover, and perennial herbaceous cover. There are consistent negative correlations with increasing soil depth, coarse fragment content, sand%, silt%, mean annual temperature, and annual grass cover. This type of analysis is not meant as a predictive tool, but allows for the confirmation of hypotheses, and identification of relationships. Many of these relationships are not surprising. Soil N is the dominant factor controlling soil OC accumulation and retention (Lal 2008). Vegetation fixes atmospheric CO_2 and creates plant parts with C:N of 30:1 or greater. This biomass is subject to microbial decomposition and can eventually become soil OC with C:N close to 12:1. Microbial metabolism influences the C:N of soil OC, but the ratio tends not to range far from 12:1. Therefore, soil OC may not readily accumulate without a concurrent increase in soil N (Lal 2008). There was little evidence in our study that annual grass invasion influenced the C:N. Similarly it is commonly accepted that soil OC decreases with soil depth and that coarse grained soils typically store less OC than fine textured soils. Recent research has emphasized the importance of soil OC stabilization by formation of organo-mineral associations in fine textured soils (Lutzow et al. 2008; Torn et al. 1997). This data set re-iterates the influence that abiotic variables have on OC retention, especially N, but also highlights the interaction that shrubs, perennial herbaceous vegetation, and exotic grass invasion may have on soil OC.

IMPLICATIONS

Our research suggests that the exotic annual grass *Bromus tectorum* may reduce total belowground OC in sagebrush steppe ecosystems. Replacement of deep rooted perennial herbaceous vegetation by shallow rooted annual grass could be the mechanism by which the reduction in belowground OC occurs. We anticipate that further losses in belowground OC would occur if deep rooted native shrubs were removed by competition or disturbance such as fire. Conversion of sagebrush steppe ecosystems to annual grass communities results in a decrease in the fire return interval which could exacerbate the loss of C and N from these ecosystems (D'Antonio and Vitousek 1992). Given the importance of N to OC retention this could result in long term site degradation.

We determined that roughly 10% of belowground OC and N were associated with regolith coarse fragments, and recommend that researchers attempt to quantify these pools in biogeochemical studies. Furthermore we stress the importance of characterizing soil nutrient pools to bedrock, a restriction, or as deep as feasible so that redistribution of nutrients can be properly assessed with vegetation shifts.

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Table 1. Names, USDA Soil Classification, Parent Material, Location, Elevation, and Mean Annual Precipitation, Mean Annual Temperature, and soil depth to bedrock or a restriction for the 7 research sites within the Sage STEP network.

Site	Soil Classification	Geology	LAT	LONG	Elevation (m)	MAP (mm)	MAT (C)	Depth (cm)
Onaqui	Loamy-skeletal, mixed, active, mesic Xeric Haplocalcids	Limestone alluvium	40.19914166	-112.46043876	1660	300	9	70 to > 90
Owyhee	Loamy, mixed, superactive, mesic, shallow Vitrixerandic Argidurids	Ash and Loess over Basalt residuum	41.54761696	-116.88509809	1621	307	8	52 to > 90
Roberts	Loamy, mixed, superactive, frigid Lithic Xeric Haplocalcids	Loess over Basalt	43.76891468	-112.28263537	1483	263	6	9 to > 90
Grey Butte	Loamy, mixed, superactive, frigid, shallow Xeric Haplodurids	Basalt / Tuff	42.71219641	-119.43315265	1462	275	8	40 to > 90
Moses Coulee	Loamy-skeletal, mixed, superactive, mesic Calcidic Haploxerolls	Glacial Outwash / Loess	47.61747465	-119.68126830	632	258	9	15 to > 90
Rock Creek	Loamy, mixed, superactive, frigid, shallow Xeric Haplodurids	Basalt / Tuff	42.71718456	-119.49088703	1462	275	8	26 to > 90
Saddle Mountain	Coarse-silty, mixed, superactive, mesic Xeric Haplocambids	Loess over Lacustrine	46.74985749	-119.35260281	303	215	11	48 to > 90

Table 2. Results from the Generalized Linear Mixed Models comparing belowground organic carbon (OC) and total nitrogen.

		Soil OC%		Soil OC Content		Root OC Content		Coarse OC Content		Total Belowground OC Content	
Effect	**DF**	**F**	**Pr > F**	**F**	**Pr > F**	**F**	**Pr > F**	**F**	**Pr > F**	**F**	**Pr > F**
Phase	2	4.53	0.0114	1.43	0.2441	0.13	0.8777	0.14	0.8691	1.07	0.3459
Treatment(Site) error a	82										
Depth	5	11.91	<0.0001	4.20	0.0010	3.03	0.002	9.23	<0.0001	3.68	0.0029
Phase*Depth	10	0.74	0.6895	1.86	0.0486	0.21	0.9948	0.38	0.9543	1.88	0.0463
Treatment*Phase(Site) error b	391										

		Soil N%		Soil N Content		Root N Content		Coarse N Content		Total Belowground N Content		C:N	
Effect	**DF**			**F**	**Pr > F**	**F**	**Pr > F**	**F**	**Pr > F**	**F**	**Pr > F**	**F**	**Pr > F**
Phase	2	1.35	0.2612	0.28	0.7531	0.19	0.8271	0.13	0.8767	0.27	0.7677	0.35	0.7061
Phase(Site) error a	82												
Depth	5	15.97	<0.0001	6.32	<0.0001	4.6	0.0005	10.79	<0.0001	4.28	0.0008	1.73	0.1269
Phase*Depth	10	0.55	0.855	1.81	0.0570	0.22	0.9942	0.34	0.9685	1.81	0.0576	0.49	0.8961
Treatment*Phase(Site) error b	391												

Table 3. Results from the Stepwise Linear Regression for the best fit of belowground organic carbon. The best two models are presented for each addition of a new variable in the model. Where soil depth = Depth, soil coarse fragment percent = Coarse%, soil sand percent = Sand%, soil silt percent = Silt%, soil clay percent = Clay%, total nitrogen = TN, mean annual precipitation = MAP, mean annual temperature = MAT, percent shrub cover = Shrub, percent perennial herbaceous cover = Herb, and percent annual grass cover = Brome.

# of Variables in Model	Variable 1	Variable 2	Variable 3	Variable 4	Variable 5	Variable 6	Variable 7	Variable 8	Variable 9	Variable 10	Variable 11	r-Square
1	TN											0.587
1	MAT											0.099
2	TN	MAT										0.609
2	TN	MAP										0.603
3	Clay%	TN	MAT									0.614
3	TN	MAT	Brome									0.613
4	Clay%	TN	MAT	Shrub								0.617
4	TN	MAT	Shrub	Herb								0.617
5	Clay%	TN	MAT	Shrub	Herb							0.621
5	Depth	Clay%	TN	MAT	Shrub							0.621
6	Sand%	Silt%	TN	MAT	Shrub	Herb						0.624
6	Depth	Clay%	TN	MAT	Shrub	Herb						0.624
7	Depth	Sand%	Silt%	TN	MAT	Shrub	Herb					0.627
7	Coarse%	Sand%	Silt%	TN	MAT	Shrub	Herb					0.626
8	Depth	Coarse%	Sand%	Silt%	TN	MAT	Shrub	Herb				0.628
8	Depth	Sand%	Silt%	TN	MAP	MAT	Shrub	Herb				0.628
9	Depth	Coarse%	Sand%	Silt%	TN	MAP	MAT	Shrub	Herb			0.629
9	Depth	Coarse%	Sand%	Silt%	Clay%	TN	MAT	Shrub	Herb			0.629
10	Depth	Coarse%	Sand%	Silt%	TN	MAP	MAT	Shrub	Herb	Brome		0.630
10	Depth	Coarse%	Sand%	Silt%	Clay%	TN	MAP	MAT	Shrub	Herb		0.629
11	Depth	Coarse%	Sand%	Silt%	Clay%	TN	MAP	MAT	Shrub	Herb	Brome	0.630

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Figure 1. Location of the 7 sagebrush steppe sites in the intermountain western U.S. (Panel A). Generalized sub plot layout within core plots at each site (Panel B). Sample location at each sub-plot (Panel C).

Figure 2. Sample processing regime, and unit conversion for each core increment extracted.

Figure 3. Means and standard errors by phase of cheatgrass invasion for total belowground organic carbon content, soil organic carbon content, root organic carbon content, coarse fragment organic carbon content, and soil organic carbon percent. Lowercase letters represent statistical letter groups determined by the phase term in the generalized linear mixed model and Tukey's means comparisons ($P < 0.05$). Means not represented by a similar letter are different.

Figure 4. Means and standard errors by phase of cheatgrass invasion and soil depth increment for percent soil organic carbon, soil organic carbon content, root organic carbon content, and coarse fragment organic carbon content. Lowercase letters represent statistical letter groups for differences determined by the depth term in the generalized linear mixed model and Tukey's means comparisons ($P < 0.05$). Means not represented by a similar letter are different. Asterisks indicate differences determined by the phase by depth interaction term in the generalized linear mixed model and Tukey's means comparisons ($P < 0.05$).

Figure 5. Means and standard errors by phase of cheatgrass invasion for total belowground nitrogen content, soil nitrogen content, root nitrogen content, and coarse fragment nitrogen content.

Figure 6. Means and standard errors by phase of cheatgrass invasion and soil depth increment for percent soil nitrogen, soil nitrogen content, root nitrogen content, and coarse fragment nitrogen content. Lowercase letters represent statistical letter groups for differences determined by the depth term in the generalized linear mixed model and Tukey's means comparisons (P <

0.05). Means not represented by a similar letter are different. Asterisks indicate differences determined by the phase by depth interaction term in the generalized linear mixed model and Tukey’s means comparisons ($P < 0.05$).

Figure 1.

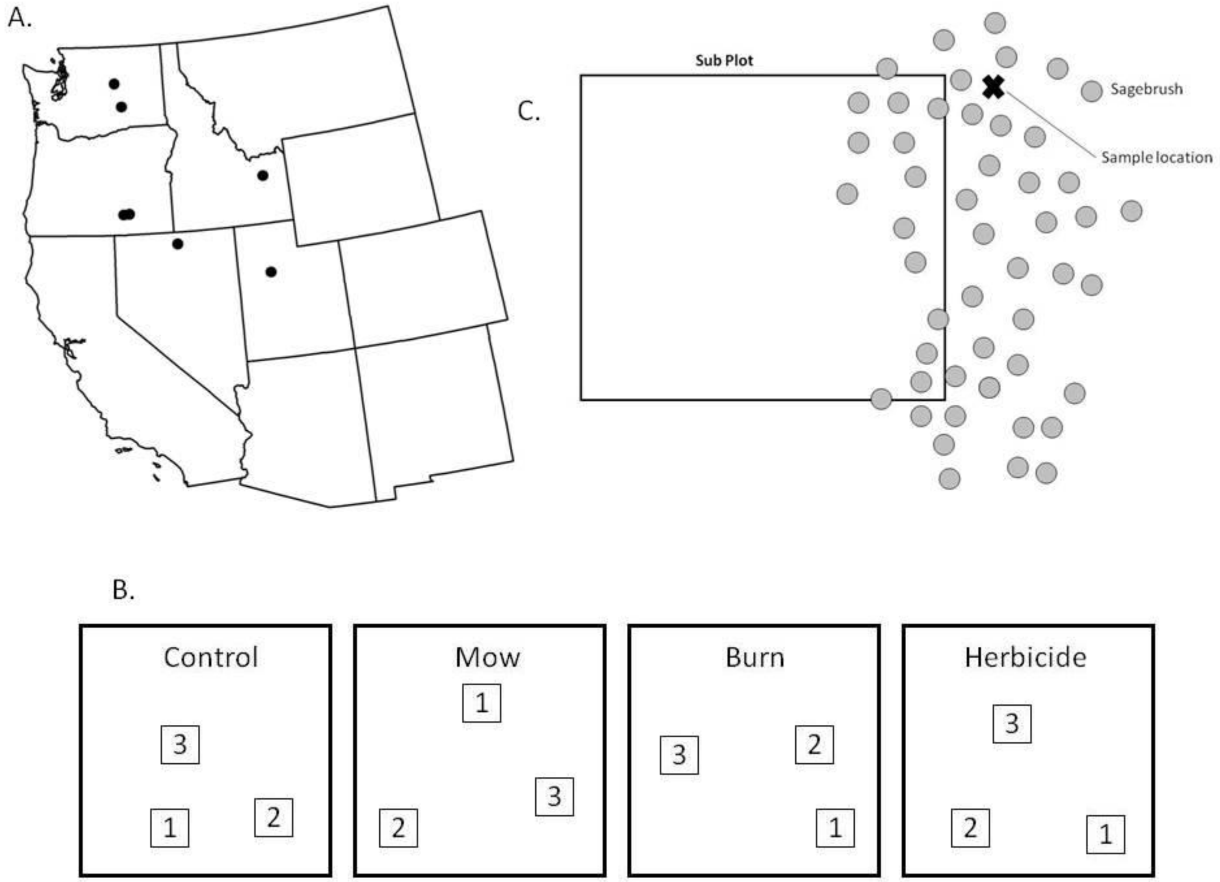
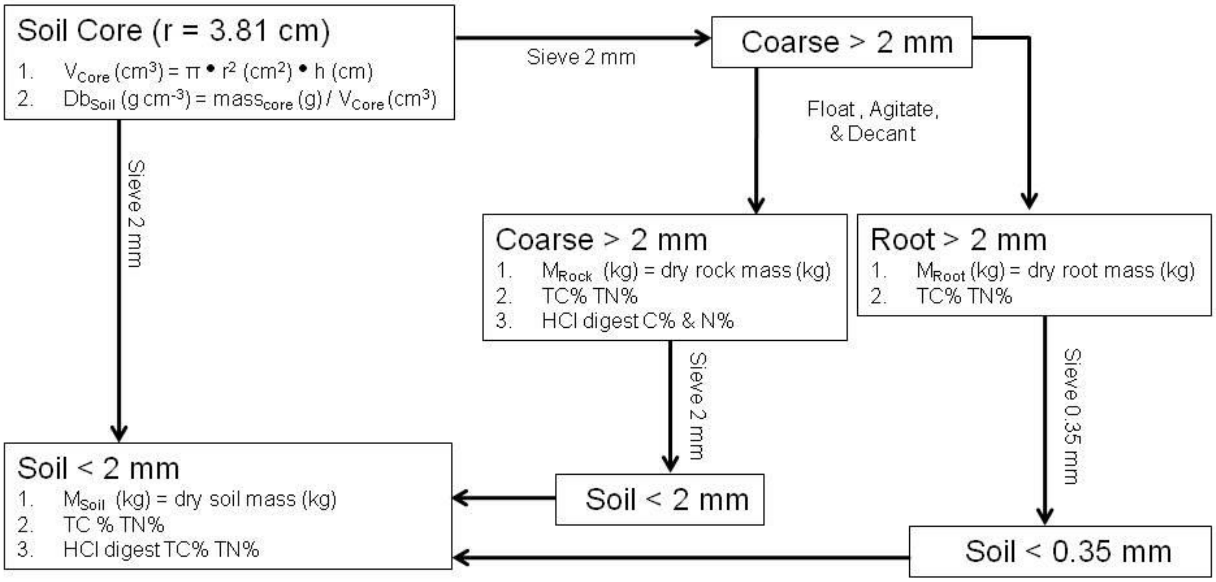

A.
C.
Sub Plot
Sagebrush
Sample location
B.
Control
3
1
2
Mow
1
3
2
Burn
3
2
1
Herbicide
3
2
1

Figure 2.



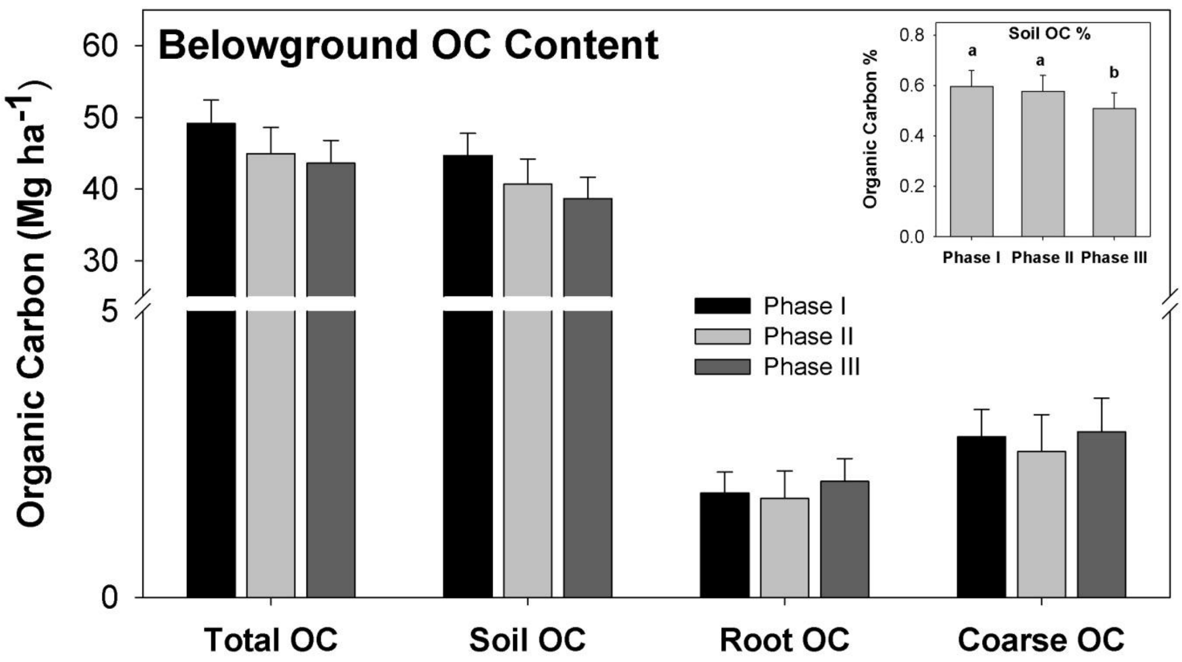
$$\text{Roots} > 2\text{ mm (Kg ha}^{-1}) = \{M_{Root}\text{ (kg)} / V_{core}\text{ (cm}^3)\} \bullet d\text{ (cm)} \bullet 100{,}000{,}000\text{ (cm}^2) \bullet C$$

$$\text{Coarse} > 2\text{ mm (Kg ha}^{-1}) = \{M_{Coarse}\text{ (kg)} / V_{core}\text{ (cm}^3)\} \bullet d\text{ (cm)} \bullet 100{,}000{,}000\text{ (cm}^2) \bullet C$$

$$\text{Soil} < 2\text{ mm (Kg ha}^{-1}) = \{M_{Soil}\text{ (kg)} / V_{core}\text{ (cm}^3)\} \bullet d\text{ (cm)} \bullet 100{,}000{,}000\text{ (cm}^2) \bullet C$$

Where (C) = nutrient concentration in fraction % and (d) = depth of the core increment

Figure 3.



Belowground OC Content
Organic Carbon (Mg ha^{-1})
60
50
40
30
5
0
Total OC
Soil OC
Root OC
Coarse OC
Phase I
Phase II
Phase III
Soil OC %
Organic Carbon %
0.8
0.6
0.4
0.2
0.0
a
a
b
Phase I
Phase II
Phase III

Figure 4.

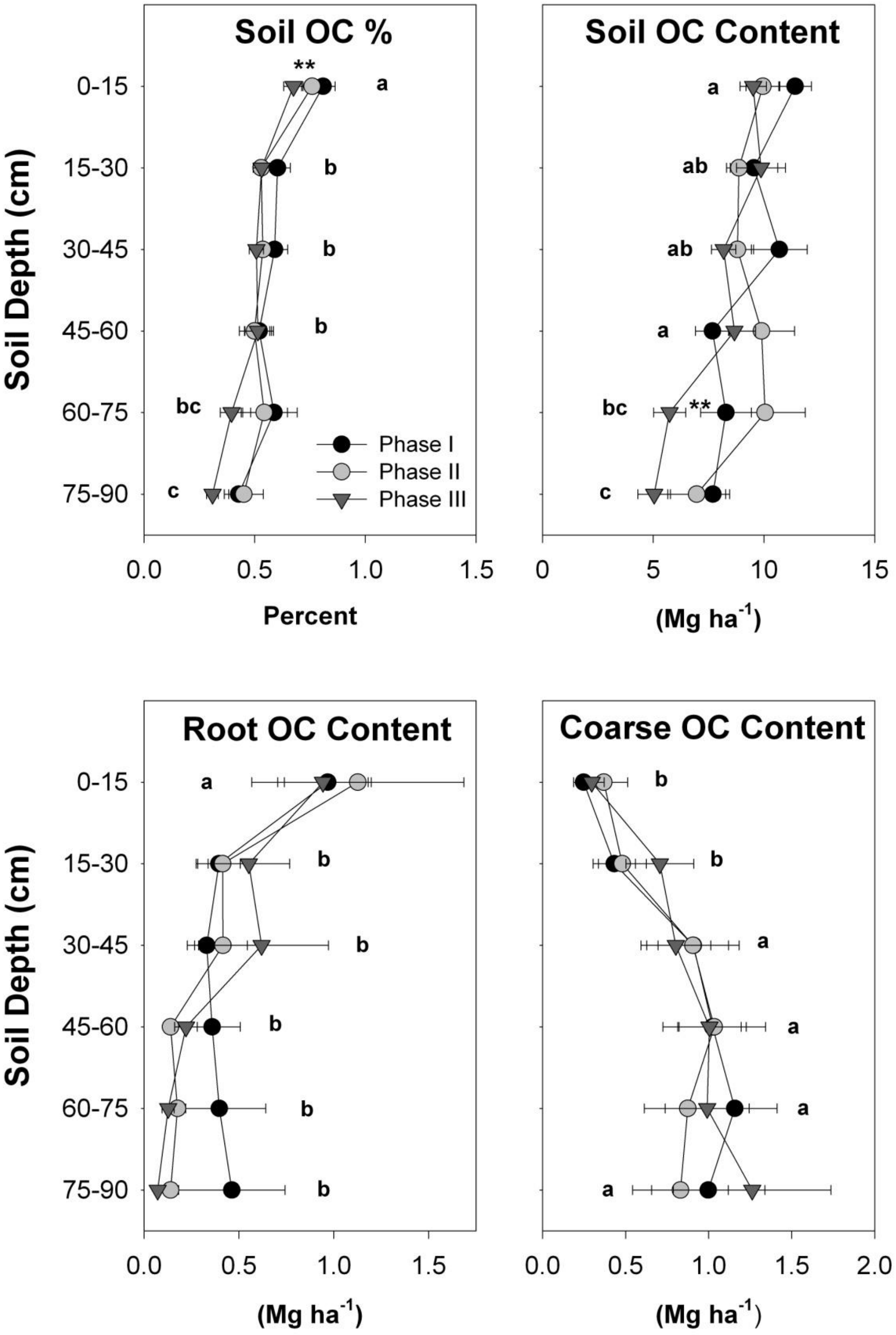

Soil OC %
Soil OC Content
Root OC Content
Coarse OC Content
Soil Depth (cm)
0-15
15-30
30-45
45-60
60-75
75-90
**
a
b
b
b
bc
c
Phase I
Phase II
Phase III
0.0
0.5
1.0
1.5
Percent
a
ab
ab
a
bc
**
c
0
5
10
15
(Mg ha^{-1})
a
b
b
b
b
b
0.0
0.5
1.0
1.5
(Mg ha^{-1})
b
b
a
a
a
a
0.0
0.5
1.0
1.5
2.0
(Mg ha^{-1})

Figure 5.

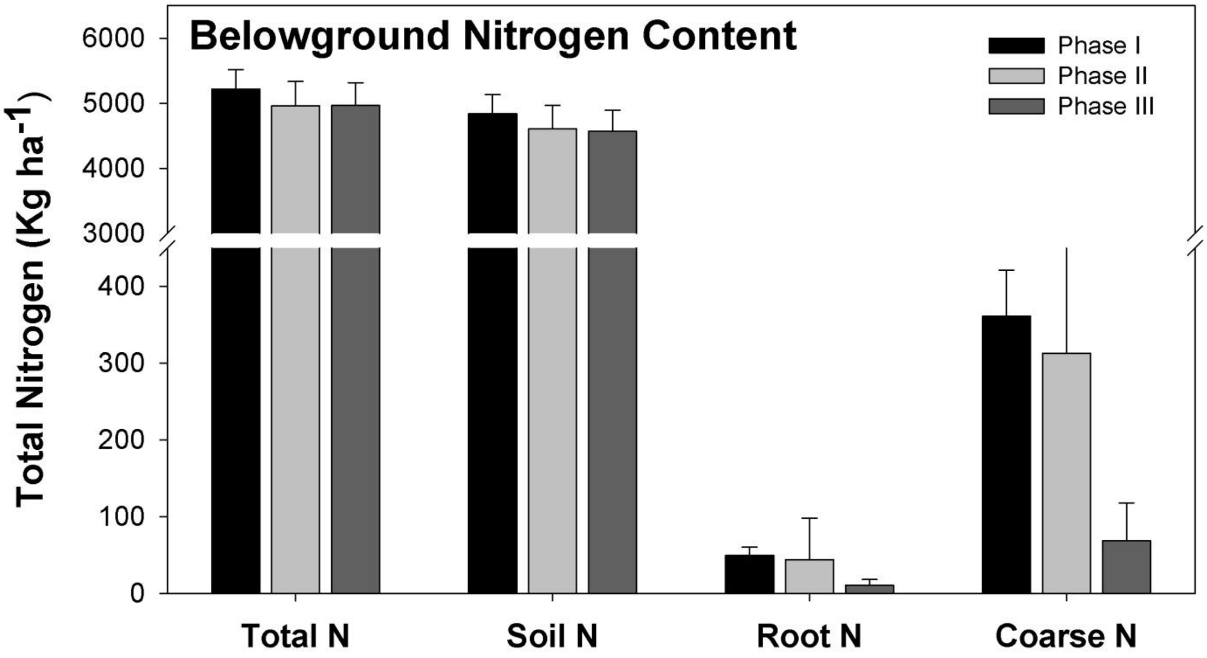
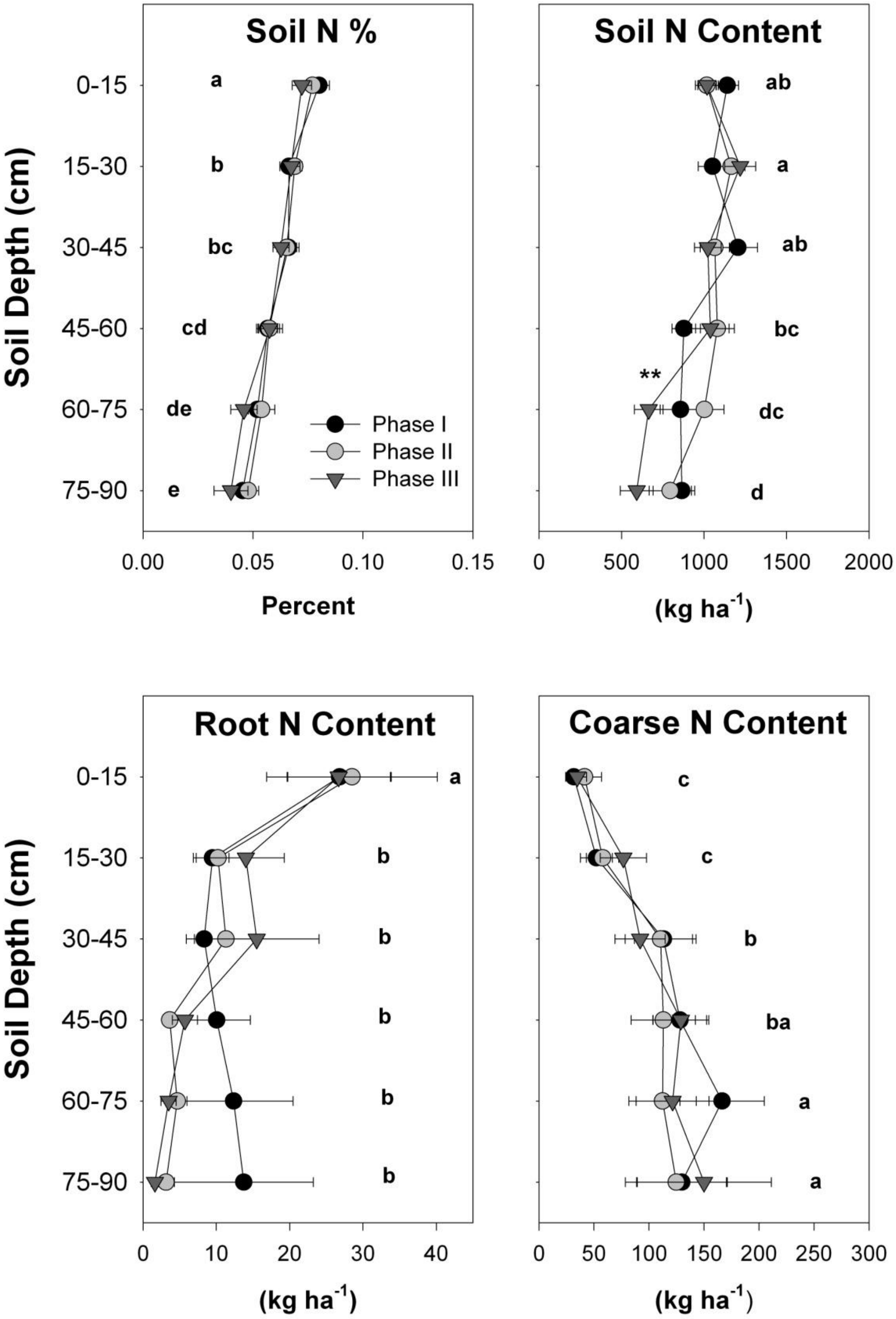

Belowground Nitrogen Content
Phase I
Phase II
Phase III
Total Nitrogen (Kg ha^{-1})
6000
5000
4000
3000
400
300
200
100
0
Total N
Soil N
Root N
Coarse N

Figure 6.


Soil N %
Soil N Content
Root N Content
Coarse N Content
Soil Depth (cm)
0-15
15-30
30-45
45-60
60-75
75-90
a
b
bc
cd
de
e
ab
a
ab
bc
**
dc
d
a
b
b
b
b
b
c
c
b
ba
a
a
Phase I
Phase II
Phase III
0.00
0.05
0.10
0.15
Percent
0
500
1000
1500
2000
(kg ha^{-1})
0
10
20
30
40
(kg ha^{-1})
0
50
100
150
200
250
300
(kg ha^{-1})