ELSEVIER

Environmental Pollution 116 (2002) 457–463

ENVIRONMENTAL POLLUTION

www.elsevier.com/locate/envpol

Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands

J.D. Reeder[a,*], G.E. Schuman[b]

[a]USDA-ARS, Crops Research Laboratory, 1701 Centre Avenue, Fort Collins, CO 80526, USA
[b]USDA-ARS, High Plains Grasslands Research Station, 88408 Hildreth Road, Cheyenne, WY 82009, USA

Received 1 July 2001; accepted 24 July 2001

"Capsule": *Grazing resulted in higher soil carbon due to more rapid annual shoot turnover and changes in species composition.*

Abstract

We evaluated the effects of livestock grazing on C content of the plant–soil system (to 60 cm) of two semi-arid grasslands: a mixed-grass prairie (grazed 12 years), and a short-grass steppe (grazed 56 years). Grazing treatments included season-long grazing at heavy and light stocking rates, and non-grazed exclosures. Significantly higher soil C (0–30cm) was measured in grazed pastures compared to non-grazed exclosures, although for the short-grass steppe higher soil C was observed with the heavy grazing treatment only. Excluding grazing caused an immobilization of C in excessive aboveground plant litter, and an increase in annual forbs and grasses which lack dense fibrous rooting systems conducive to soil organic matter formation and accumulation. Our data indicate that higher soil C with grazing was in part the result of more rapid annual shoot turnover, and redistribution of C within the plant–soil system as a result of changes in plant species composition. Published by Elsevier Science Ltd.

Keywords: Carbon; C storage; Grasslands; Grazing; Great Plains

1. Introduction

Grazing lands comprise the largest and most diverse single land resource in the USA and in the world, and as such represent an important component of terrestrial C cycling and sequestration. Over 160 Mha (million hectares) of native grazing lands are located in the western US (Sobecki et al., 2001), but few data exist quantifying the magnitude and distribution of C stored in these semi-arid lands. Moreover, the effects of grazing management on the biogeochemial processes that control the exchange of C between the soil and atmosphere are not well understood.

Few studies have actually measured the complete C budgets of native grasslands, but the data available suggest that C content varies widely among different grassland types. A comparison of 14 native grassland sites across nine states in the historic grasslands of the USA reported an average of 123±48 MT/ha C to a depth of 2 m (Follett, 2001). Variation in C content across grassland types is largely a function of climatic and edaphic factors. Organic C tends to increase with soil clay content (Bauer et al., 1987) and annual precipitation (Burke et al., 1989), and decrease with increases in mean annual temperature (Thorp, 1948; Burke et al., 1989).

Although the total amount of C varies significantly across different grassland types, the relative distribution of organic C is fairly consistent in perennial grassland ecosystems (Burke et al., 1997). Unlike forest ecosystems which store a large amount of organic C aboveground, generally less than 1% of grassland organic C is in aboveground plant biomass (Burke et al., 1997). The portion of grassland C residing in plant biomass is relatively small (~10%) with the majority of plant C belowground in plant roots. The largest reservoir of organic C in grassland ecosystems is the soil organic matter (SOM), which contains about 90% of the total system organic C. Typically, grassland

* Corresponding author. Tel.: +1-970-498-4236; fax: +1-970-482-2909.
E-mail address: jdreeder@lamar.colostate.edu (J.D. Reeder).

0269-7491/01/$ - see front matter Published by Elsevier Science Ltd.
PII: S0269-7491(01)00223-8

SOM concentrations are highest in the surface soil and decrease with depth (Thorp, 1948; Paul and Clark, 1996). However, the subsoil usually contains a significant portion of total ecosystem C and is therefore an important component of the C sequestered in grasslands. About 40% of tall-grass soil organic C and about 50% of short-grass soil C can be stored below 30 cm in the soil profile, but sampling to 60 cm usually captures about 90% of the root biomass and soil organic C of grassland ecosystems (Weaver, 1935; Gill, 1998; Reeder et al., 2001). Inorganic soil C is also an important component of sequestered C in the semi-arid grasslands of western USA, but the role of soil carbonate C in the global C cycle is uncertain (Monger and Martinez-Rios, 2001).

The effects of grazing management on the ecosystem processes that control C cycling and distribution have not been sufficiently evaluated in native grassland ecosystems. Current literature suggests no clear general relationships between grazing management and C sequestration. Some studies have reported no effect of grazing on soil organic C (e.g. Johnston et al., 1971; Dormaar et al., 1977; and Milchunas and Laurenroth, 1993), while several others reported increases (e.g. Smoliak et al., 1972; Derner et al., 1997; Schuman et al., 1999; Weinhold et al., 2001), and a few reported decreases (e.g. Bauer et al., 1987; Frank et al., 1995; Derner et al., 1997) in soil C as a result of grazing. Differences in the response of ecosystem C to grazing are the result of differences in climate, inherent soil properties, landscape position, plant community composition, and grazing management practices among reported studies. Schuman et al. (1999) suggested that variance in the measured response of grassland ecosystem organic C to grazing also results from soil variations within individual studies, differences in the depth of soil profile being evaluated, and lack of a thorough evaluation of organic C distribution within the system.

Although inconsistencies in grassland organic C response to grazing have been reported, several generalizations concerning the impact of grazing on grassland ecosystem C can be made. Grazing management techniques that have been developed to increase forage production for livestock also have the potential to increase SOM and C sequestration (Conant et al., 2001). However, increases in C sequestered as SOM have been reported even when grazing management results in decreased production. This can occur where grazing-induced changes in species composition result in lower forage production but greater root-to-shoot ratios and thus increased allocation of C belowground (Schuman et al., 1999). Soil organic C content also could potentially increase if decreased aboveground plant inputs to the soil are offset by manure inputs or if grazing results in lower standing stocks of biomass but increased production and turnover (Conant et al., 2001). Finally, because grazing affects photosynthetic rate and C allocation patterns differently among grass species (Dyer and Bokhari, 1976; Detling et al., 1979; Painter and Detling, 1981), grazing management has a varying effect on the magnitude, distribution and cycling of C in different grassland ecosystems.

We conducted studies to characterize the impact of livestock grazing intensity on the C and N balance of two grassland types predominant in the Great Plains, northern mixed-grass prairie (Schuman et al., 1999) and the short-grass steppe (Reeder and Schuman, in preparation). This paper compares response differences between these two grassland types to grazing intensity and consequent differences in organic C cycling, distribution, and C sequestration potential.

2. Materials and methods

2.1. Study sites

We evaluated the effects of livestock grazing on the organic C balance of two semi-arid grasslands that dominate the northern and central Great Plains: northern mixed-grass prairie in southeastern Wyoming, and the short-grass steppe in northeastern Colorado. The mixed-grass prairie is located at the High Plains Grasslands Research Station (HPGRS) near Cheyenne, Wyoming, with elevations ranging from 1910 to 1950 m, annual frost-free period of 127 days, and average annual precipitation of 366 mm, of which 70% occurs during the growing season (National Oceanic and Atmospheric Administration, 1994). Vegetation biomass is 80% grasses (55% cool-season C_3 species and 25% warm-season C_4 species), and 20% forbs, sedges and half-shrubs. Dominant cool-season species are western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love) and needleandthread (*Stipa comata* Trin & Rupr.), and the dominant warm-season species is blue grama (*Bouteloua gracilis* (H.B.K) Lab. Ex Steud.). Annual production averages 1100 kg ha^{-1}, and ranges from 550 to 1900 kg ha^{-1} on grazed pastures. Dominant soil series are Ascalon and Altvan sandy loams (mixed, mesic Aridic Argiustolls; Stevenson et al., 1984).

The short-grass steppe is located at the Central Plains Experimental Range (CPER) 40 km northeast of Fort Collins, Colorado, and 29 km southeast of the HPGRS, with elevations ranging from 1600 to 1690 m, average frost-free period of 133 days, and average annual precipitation of 325 mm, of which 50–80% occurs during the growing season (Hart, 2000). Vegetation biomass is 80% grasses (70% warm-season species and 10% cool-season species), 10% forbs, sedges and prickly pear, and 10% shrubs. Warm-season grasses include the shortgrasses blue grama (the dominant species) and

SOM concentrations are highest in the surface soil and decrease with depth (Thorp, 1948; Paul and Clark, 1996). However, the subsoil usually contains a significant portion of total ecosystem C and is therefore an important component of the C sequestered in grasslands. About 40% of tall-grass soil organic C and about 50% of short-grass soil C can be stored below 30 cm in the soil profile, but sampling to 60 cm usually captures about 90% of the root biomass and soil organic C of grassland ecosystems (Weaver, 1935; Gill, 1998; Reeder et al., 2001). Inorganic soil C is also an important component of sequestered C in the semi-arid grasslands of western USA, but the role of soil carbonate C in the global C cycle is uncertain (Monger and Martinez-Rios, 2001).

The effects of grazing management on the ecosystem processes that control C cycling and distribution have not been sufficiently evaluated in native grassland ecosystems. Current literature suggests no clear general relationships between grazing management and C sequestration. Some studies have reported no effect of grazing on soil organic C (e.g. Johnston et al., 1971; Dormaar et al., 1977; and Milchunas and Laurenroth, 1993), while several others reported increases (e.g. Smoliak et al., 1972; Derner et al., 1997; Schuman et al., 1999; Weinhold et al., 2001), and a few reported decreases (e.g. Bauer et al., 1987; Frank et al., 1995; Derner et al., 1997) in soil C as a result of grazing. Differences in the response of ecosystem C to grazing are the result of differences in climate, inherent soil properties, landscape position, plant community composition, and grazing management practices among reported studies. Schuman et al. (1999) suggested that variance in the measured response of grassland ecosystem organic C to grazing also results from soil variations within individual studies, differences in the depth of soil profile being evaluated, and lack of a thorough evaluation of organic C distribution within the system.

Although inconsistencies in grassland organic C response to grazing have been reported, several generalizations concerning the impact of grazing on grassland ecosystem C can be made. Grazing management techniques that have been developed to increase forage production for livestock also have the potential to increase SOM and C sequestration (Conant et al., 2001). However, increases in C sequestered as SOM have been reported even when grazing management results in decreased production. This can occur where grazing-induced changes in species composition result in lower forage production but greater root-to-shoot ratios and thus increased allocation of C belowground (Schuman et al., 1999). Soil organic C content also could potentially increase if decreased aboveground plant inputs to the soil are offset by manure inputs or if grazing results in lower standing stocks of biomass but increased production and turnover (Conant et al., 2001). Finally, because grazing affects photosynthetic rate and C allocation patterns differently among grass species (Dyer and Bokhari, 1976; Detling et al., 1979; Painter and Detling, 1981), grazing management has a varying effect on the magnitude, distribution and cycling of C in different grassland ecosystems.

We conducted studies to characterize the impact of livestock grazing intensity on the C and N balance of two grassland types predominant in the Great Plains, northern mixed-grass prairie (Schuman et al., 1999) and the short-grass steppe (Reeder and Schuman, in preparation). This paper compares response differences between these two grassland types to grazing intensity and consequent differences in organic C cycling, distribution, and C sequestration potential.

2. Materials and methods

2.1. Study sites

We evaluated the effects of livestock grazing on the organic C balance of two semi-arid grasslands that dominate the northern and central Great Plains: northern mixed-grass prairie in southeastern Wyoming, and the short-grass steppe in northeastern Colorado. The mixed-grass prairie is located at the High Plains Grasslands Research Station (HPGRS) near Cheyenne, Wyoming, with elevations ranging from 1910 to 1950 m, annual frost-free period of 127 days, and average annual precipitation of 366 mm, of which 70% occurs during the growing season (National Oceanic and Atmospheric Administration, 1994). Vegetation biomass is 80% grasses (55% cool-season C_3 species and 25% warm-season C_4 species), and 20% forbs, sedges and half-shrubs. Dominant cool-season species are western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love) and needleandthread (*Stipa comata* Trin & Rupr.), and the dominant warm-season species is blue grama (*Bouteloua gracilis* (H.B.K) Lab. Ex Steud.). Annual production averages 1100 kg ha^{-1}, and ranges from 550 to 1900 kg ha^{-1} on grazed pastures. Dominant soil series are Ascalon and Altvan sandy loams (mixed, mesic Aridic Argiustolls; Stevenson et al., 1984).

The short-grass steppe is located at the Central Plains Experimental Range (CPER) 40 km northeast of Fort Collins, Colorado, and 29 km southeast of the HPGRS, with elevations ranging from 1600 to 1690 m, average frost-free period of 133 days, and average annual precipitation of 325 mm, of which 50–80% occurs during the growing season (Hart, 2000). Vegetation biomass is 80% grasses (70% warm-season species and 10% cool-season species), 10% forbs, sedges and prickly pear, and 10% shrubs. Warm-season grasses include the shortgrasses blue grama (the dominant species) and

buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.), and the midgrass red threeawn (*Aristida longiseta* (Steud.) Vasey). Cool-season midgrasses include western wheatgrass and needleandthread. Other gramminoids include *Carex eleocharis* (Bailey), *Elymus elymoides* [Raf. Swezey], and *Sporobolus cryptandrus* [Torr. Gray]. The cactus *Opuntia polyacantha* (Haw.) is extremely abundant, *Artemesia frigida* (Willd.) is the most common semi-shrub, and *Sphaeralcea coccinea* [Pursh Rydb.] is the most common perennial forb (Hart, 2000). Annual production averages 600 kg ha^{-1}, and ranges from 200 to 1100 kg ha^{-1} on grazed pastures. Dominant soil types are fine sandy loams, Olney (fine-loamy, mixed, mesic, Ustollic Haplargid) and Remmit (coarse-loamy, mixed mesic, Ustollic Camborthids; Peterson and Kelly, 1994).

2.2. Grazing treatments

Grazing treatments were established on the mixed-grass prairie at the HPGRS in 1982 in an area that had not been grazed by domestic livestock for over 40 years. Treatment pastures were established in a randomized block design with two replicate blocks (pastures) for each of seven grazing strategy-stocking rate treatment combinations (Hart et al., 1988). After 12 years of imposed grazing treatments, five of the seven treatments were evaluated for soil organic C mass. However, for the purposes of this paper, we will only be discussing: (1) EX, nongrazed exclosures, (2) CL, pastures with continuous season-long grazing at a light stocking rate (average 20 steer-days ha^{-1}, 5–15% utilization), and (3) CH, pastures with continuous season-long grazing at a heavy stocking rate (average 59 steer-days ha^{-1}, 35–45% utilization). The light stocking rate is ~35% below, and the heavy stocking rate ~33% above the stocking rate recommended by the Natural Resources Conservation Service for the conditions of the site.

Grazing intensity studies were established on the short-grass steppe of the CPER in 1939. A 4-replication study of continuous season-long grazing (May through October) at light, moderate and heavy stocking rates was initiated, but replications were dropped over the years until a single pasture of each stocking rate remained. After 55 years of imposed grazing treatments, two of these grazing treatments, and their adjacent exclosures, were evaluated for soil organic C mass: (1) CL, pasture with continuous season-long grazing at a light stocking rate (average 18 heifer-days ha^{-1}, 20–40% utilization), (2) EX-Lt, a fenced area next to the CL treatment that was excluded from livestock grazing, (3) CH, pasture with continuous season-long grazing at a heavy stocking rate (average 37 heifer-days ha^{-1}, 60–75% utilization), and (4) EX-Hv, a fenced area next to the CH treatment that was excluded from livestock grazing. Although the lack of true replication of grazing treatments at the CPER restricts inference regarding the impact of grazing intensity across the short-grass steppe landscape, it does not preclude the general comparison of C distribution on the dominant upland landscape positions and soil types of the two grassland ecosystems.

2.3. Field sampling

At both locations, 50-m transects were established in each grazing treatment pasture and exclosure on near-level sites of the dominant soil series for each location. (Ascalon sandy loam on the mixed-grass prairie at HPGRS, and Olney fine sandy loam on the short-grass steppe at CPER). Soil and plant samples were collected at peak standing crop at 10-m intervals along each 50-m sampling transect. The aboveground plant component was sampled by clipping 0.18 m^2 quadrats at each sampling site along each transect, and partitioning plant phytomass into surface litter, standing dead, and live biomass by plant species. All plant litter was removed from the soil surface before soil samples (4.6 cm diameter) were collected to 90-cm depth in bare areas between grass crowns with a hydraulic soil sampling machine. Soil samples were segregated into 0–3.8, 3.8–7.6, 7.6–15, 15–30, 30–45, 45–60, and 60–90 cm increments, placed in sealed plastic bags and transported to the laboratory in coolers. At both locations, the first three segments, 0–15cm, represent the soil A horizon, while the 15–90 cm segments represent the various components of the soil B horizon. Because the soil profiles were extremely dry below 60 cm, we were unable to collect a complete set of soil samples for the 60–90 cm depth; therefore, comparisons of the organic C balances of the two soil–plant systems were assessed to the 60 cm depth. We judged this depth to be sufficient for interpreting organic C dynamics because we estimate it captures approximately 90% of the root biomass and SOM of these two ecosystems (Weaver et al., 1935; Gill, 1998; Reeder et al., 2001; Reeder and Schuman unpublished data). Separate cores (10-cm diameter) were collected at each sampling location and partitioned into 0–15, 15–30 and 30–60 cm increments to assess root biomass and root C content. Bulk density also was assessed on separate soil cores (Blake and Hartge, 1986).

2.4. Laboratory and statistical analyses

Soil samples intended for C analyses were passed through a 2-mm screen to remove plant crowns and visible roots and root fragments. Samples were air-dried and analyzed for total C by the Walkley-Black dichromate oxidation procedure (Nelson and Sommers, 1982). Root separation from root cores was accomplished by hand with the washing method described by Laurenroth and Whitman (1971). Plant components were dried at 60 °C, weighed, ground, and analyzed

for organic C content with a Carlo-Erba automated dry combustion analyzer.[1]

Because grazing treatments on the short-grass steppe lacked true replication, statistical analyses were performed separately for the two communities. For the mixed-grass prairie, analysis of variance was used to test stocking rate effects on soil organic C mass using a randomized complete block design with replicate pastures treated as blocks. One-way analysis of variance was used to test stocking rate effects on soil organic C for the short-grass steppe. Least-significant-differences (LSD) procedures were used for treatment mean separation ($P \leqslant 0.10$; Steel and Torrie, 1980).

3. Results and discussion

The two grassland ecosystems differ in total organic C content of the plant–soil (0–60 cm) system. The more mesic mixed-grass prairie is dominated by cool-season mid-grasses, and has approximately 80% higher organic C content ($\sim$100 Mg/ha^{-1} C), than the short-grass steppe ($\sim$55 Mg/ha^{-1} C) dominated by warm-season short-grasses (Table 1). Both ecosystems display a typical distribution of C in grassland ecosystems (Burke et al., 1997); over 90% of plant–soil C is in soil organic matter, and less than 10% of system C is in plant components, with 80–90% of plant C belowground in root biomass (Figs. 1 and 2).

In both grassland systems, aboveground plant C (live + litter) decreased as grazing intensity increased, but the impact of grazing on root C was largely obscured by high variability in measured root biomass (Figs. 1 and 2). Significantly higher soil organic C (0–30 cm) was measured in both grasslands in grazed pastures compared to non-grazed exclosures. However, the effect of grazing on soil organic C content was more pronounced on the mixed-grass, where the surface 30 cm of the soil profile was about 10 Mg/ha^{-1} higher in C in both lightly grazed and heavily grazed pastures compared to non-grazed exclosures (Fig. 1). On the short-grass steppe, significantly higher soil organic C content with grazing was apparent only in the 15–30 cm depth increment of the heavily grazed treatment (16.9 Mg ha^{-1} C) compared to the lightly grazed (14.3 Mg ha^{-1} C) or non-grazed (13.0 Mg ha^{-1} C) treatments (Fig. 2).

The observed differences in organic C distribution within the plant and soil components of both ecosystems occurred in large part as a result of grazing-induced redistribution of existing system C. A number of ecosystem processes contribute to this redistribution, including changes in the rate of recycling of aboveground plant C into the soil, and changes in plant community composition. Recycling of aboveground plant C to the soil is restricted when grazing is excluded and C is immobilized in plant litter accumulating on the soil surface (Schuman et al., 1999). A build-up of litter on the soil surface also affects soil temperature and soil water content, which will in turn affect plant residue and SOM decomposition rates and thus C and nutrient cycling (Reeder et al., 2001). Grazing reduces litter mass accumulation because animal traffic enhances physical breakdown and incorporation of litter into the soil (Naeth et al., 1991), which can increase the rate of decomposition of litter and transfer of C and nutrients into the soil (Sharif et al., 1994). Reduction in litter accumulation with grazing can also facilitate earlier spring green-up and higher photosynthetic rates because of better canopy light penetration and a warmer soil surface (LeCain et al., 2000). In both of the grassland ecosystems we evaluated, as grazing intensity increased, the proportion of aboveground plant C in litter decreased, and apparent annual shoot turnover increased (Table 1). However, the impact of grazing on litter decomposition, stimulation of recycling of aboveground plant C to the soil, and the consequent increase in soil organic C, was more apparent on the mixed-grass prairie, where over half of aboveground plant C was immobilized in litter when grazing was excluded. In comparison, recycling of aboveground plant C appeared to affect belowground C content less on the short-grass steppe, where litter C represented less than 25% of aboveground plant C when livestock grazing was excluded (Table 1).

Perhaps the biggest impact of grazing on system C dynamics arose from the influence of grazing intensity on plant community composition. On both the mixed-grass and short-grass, light-to-moderate levels of grazing generally have resulted in a richer diversity of plant species than when livestock grazing is excluded (Hart et al., 1988; Manley et al., 1997; Hart, 2001). Excluding grazing by livestock has encouraged invasion by weedy annual forbs and grasses (Milchunas et al., 1992; and Schuman et al., 1999), and these species do not have dense fibrous rooting systems conducive to soil organic matter formation and soil C sequestration (Reeder et al., 2001). We think that the significantly lower soil C content of non-grazed exclosures compared to lightly grazed pastures on the mixed-grass was largely the result of significantly higher production of weedy annuals at the expense of perennial grasses in the exclosures (Schuman et al., 1999), as well as immobilization of C in excessive aboveground plant litter (Table 1). In comparison to the mixed-grass, the blue grama-dominated plant community of the short-grass steppe is highly resistant to grazing by cattle (Milchunas et al., 1989, 1990, 1998), and the relatively smaller response of the plant community to light grazing is reflected in the lack of significant difference in soil C pools between the lightly grazed and non-grazed treatments (Table 1).

[1] Mention of a commercial product does not imply USDA-ARS endorsement of that product over similar products.

for organic C content with a Carlo-Erba automated dry combustion analyzer.[1]

Because grazing treatments on the short-grass steppe lacked true replication, statistical analyses were performed separately for the two communities. For the mixed-grass prairie, analysis of variance was used to test stocking rate effects on soil organic C mass using a randomized complete block design with replicate pastures treated as blocks. One-way analysis of variance was used to test stocking rate effects on soil organic C for the short-grass steppe. Least-significant-differences (LSD) procedures were used for treatment mean separation ($P \leqslant 0.10$; Steel and Torrie, 1980).

3. Results and discussion

The two grassland ecosystems differ in total organic C content of the plant–soil (0–60 cm) system. The more mesic mixed-grass prairie is dominated by cool-season mid-grasses, and has approximately 80% higher organic C content ($\sim$100 Mg/ha^{-1} C), than the short-grass steppe ($\sim$55 Mg/ha^{-1} C) dominated by warm-season short-grasses (Table 1). Both ecosystems display a typical distribution of C in grassland ecosystems (Burke et al., 1997); over 90% of plant–soil C is in soil organic matter, and less than 10% of system C is in plant components, with 80–90% of plant C belowground in root biomass (Figs. 1 and 2).

In both grassland systems, aboveground plant C (live + litter) decreased as grazing intensity increased, but the impact of grazing on root C was largely obscured by high variability in measured root biomass (Figs. 1 and 2). Significantly higher soil organic C (0–30 cm) was measured in both grasslands in grazed pastures compared to non-grazed exclosures. However, the effect of grazing on soil organic C content was more pronounced on the mixed-grass, where the surface 30 cm of the soil profile was about 10 Mg/ha^{-1} higher in C in both lightly grazed and heavily grazed pastures compared to non-grazed exclosures (Fig. 1). On the short-grass steppe, significantly higher soil organic C content with grazing was apparent only in the 15–30 cm depth increment of the heavily grazed treatment (16.9 Mg ha^{-1} C) compared to the lightly grazed (14.3 Mg ha^{-1} C) or non-grazed (13.0 Mg ha^{-1} C) treatments (Fig. 2).

The observed differences in organic C distribution within the plant and soil components of both ecosystems occurred in large part as a result of grazing-induced redistribution of existing system C. A number of ecosystem processes contribute to this redistribution, including changes in the rate of recycling of aboveground plant C into the soil, and changes in plant community composition. Recycling of aboveground plant C to the soil is restricted when grazing is excluded and C is immobilized in plant litter accumulating on the soil surface (Schuman et al., 1999). A build-up of litter on the soil surface also affects soil temperature and soil water content, which will in turn affect plant residue and SOM decomposition rates and thus C and nutrient cycling (Reeder et al., 2001). Grazing reduces litter mass accumulation because animal traffic enhances physical breakdown and incorporation of litter into the soil (Naeth et al., 1991), which can increase the rate of decomposition of litter and transfer of C and nutrients into the soil (Sharif et al., 1994). Reduction in litter accumulation with grazing can also facilitate earlier spring green-up and higher photosynthetic rates because of better canopy light penetration and a warmer soil surface (LeCain et al., 2000). In both of the grassland ecosystems we evaluated, as grazing intensity increased, the proportion of aboveground plant C in litter decreased, and apparent annual shoot turnover increased (Table 1). However, the impact of grazing on litter decomposition, stimulation of recycling of aboveground plant C to the soil, and the consequent increase in soil organic C, was more apparent on the mixed-grass prairie, where over half of aboveground plant C was immobilized in litter when grazing was excluded. In comparison, recycling of aboveground plant C appeared to affect belowground C content less on the short-grass steppe, where litter C represented less than 25% of aboveground plant C when livestock grazing was excluded (Table 1).

Perhaps the biggest impact of grazing on system C dynamics arose from the influence of grazing intensity on plant community composition. On both the mixed-grass and short-grass, light-to-moderate levels of grazing generally have resulted in a richer diversity of plant species than when livestock grazing is excluded (Hart et al., 1988; Manley et al., 1997; Hart, 2001). Excluding grazing by livestock has encouraged invasion by weedy annual forbs and grasses (Milchunas et al., 1992; and Schuman et al., 1999), and these species do not have dense fibrous rooting systems conducive to soil organic matter formation and soil C sequestration (Reeder et al., 2001). We think that the significantly lower soil C content of non-grazed exclosures compared to lightly grazed pastures on the mixed-grass was largely the result of significantly higher production of weedy annuals at the expense of perennial grasses in the exclosures (Schuman et al., 1999), as well as immobilization of C in excessive aboveground plant litter (Table 1). In comparison to the mixed-grass, the blue grama-dominated plant community of the short-grass steppe is highly resistant to grazing by cattle (Milchunas et al., 1989, 1990, 1998), and the relatively smaller response of the plant community to light grazing is reflected in the lack of significant difference in soil C pools between the lightly grazed and non-grazed treatments (Table 1).

[1] Mention of a commercial product does not imply USDA-ARS endorsement of that product over similar products.

Table 1
Comparison of the effects of stocking rate on the C balance of two grassland ecosystems

	Mixed-grass prairie (HPGRS)				Short-grass steppe (CPER)				
	Exclosure (EX)	Light grazing (Lt)	Heavy grazing (Hv)	LSD $_{0.10}$	Exclosure—light (Ex—Lt)	Light grazing (Lt)	Exclosure—heavy (Ex—Hv)	Heavy grazing (Hv)	LSD $_{0.10}$
% of Botanical biomass as warm season grasses	16.5	17.0	27.1	9.2	31.9	45.0	33.8	73.8	14.1
Ratio of aboveground litter C to total aboveground plant C	0.63	0.55	0.48	0.12	0.24	0.20	0.12	0.08	0.10
Ratio of root C to aboveground plant C	6.0	6.8	11.2	2.6	4.0	4.6	4.8	12.9	4.6
Apparent annual Shoot turnover (live/(live + litter) ×100)	31%	40%	46%	12	73%	77%	87%	90%	9
Total ecosystem C, Mg/ha^{-1}[a]									
To 30 cm	58.3	67.4	66.5	4.3	37.4	38.2	37.3	42.3	3.6
To 60 cm	98.5	101.4	109.4	ns	52.6	55.3	57.8	65.0	5.5

[a] Total ecosystem C data for mixed-grass prairie from Schuman et al. (1999).

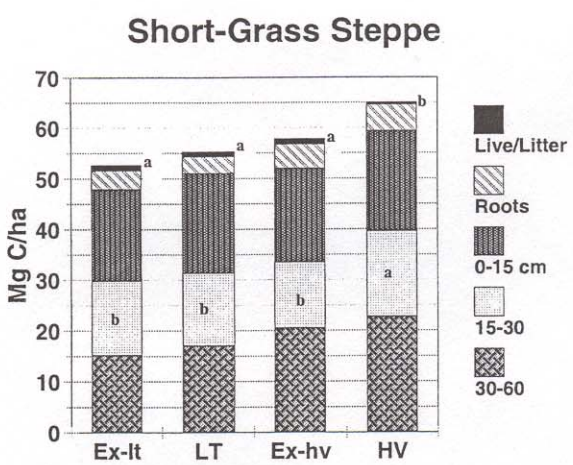

Fig. 1. Distribution of C mass in the aboveground and belowground vegetation components and soil (0–60 cm) of a short-grass steppe, as affected by stocking rate. EX, non-grazed exclosures; LT, grazing at a light stocking rate; HV, grazing at a heavy stocking rate. (* mass of soil C in the 15–30 cm depth increment is significantly higher in heavily grazed compared to lightly grazed or non-grazed pastures, $P \leqslant 0.10$).

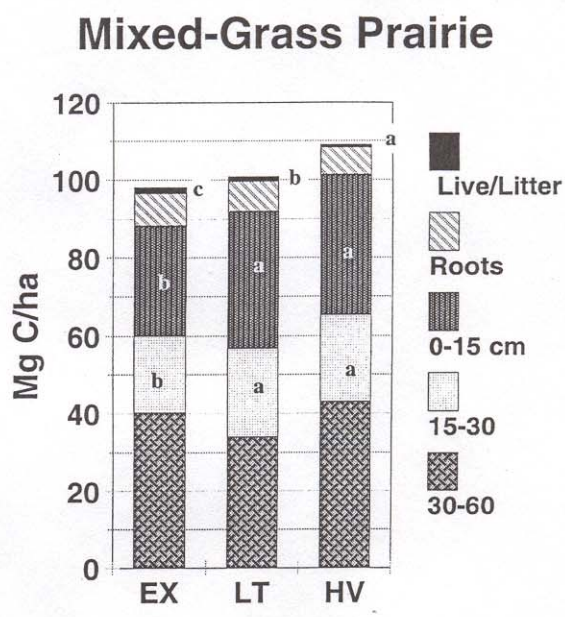

Fig. 2. Distribution of C mass in the aboveground and belowground vegetation components and soil (0–60 cm) of a mixed-grass prairie, as affected by stocking rate. EX, non-grazed exclosures; LT, grazing at a light stocking rate; HV, grazing at a heavy stocking rate. (* mass of soil C in the 0–15 and 15–30 cm depth increments are significantly lower in non-grazed compared to grazed pastures, $P \leqslant 0.05$).

In contrast to grazing at a light or moderate stocking rate, long-term grazing at heavy stocking rates has tended to decrease plant species diversity in both the mixed-grass prairie (Manley et al., 1997; Schuman et al., 1999) and the short-grass steppe (Hart, 2000; Reeder and Schuman, unpublished data). Selective grazing of cool-season mid-grasses by the livestock appears to be the major cause of the decrease in species diversity (Hart, 2001), and has resulted in an increase in the warm-season short-grass blue grama relative to the preferred cool-season mid-grasses western wheatgrass and needleandthread (Table 1). We think that a major contributor to significantly higher soil organic C with heavy grazing in both the short-grass and mixed-grass was the grazing-induced increase in blue grama, which has a higher root-to-shoot ratio and transfers more C belowground than do the cool-season mid-grass species (Coupland and Van Dyne, 1979). Some

evidence suggests that blue grama may be a more efficient producer of soil organic C than other species because it may respond to grazing by rapidly translocating C to crowns and roots, and by increasing root exudation rates (Dyer and Bokhari, 1976; Detling et al., 1979). Most studies on the Great Plains that have reported increased soil organic C with grazing have been conducted on sites where grazing has resulted in a significant increase in blue grama at the expense of cool-season mid-grasses (Smoliak et al., 1972; Frank et al., 1995; Schuman et al., 1999).

Besides redistributing existing system C, did grazing also result in an actual increase in system C and thus an increase in C sequestration? In the mixed-grass, total ecosystem C (plant + soil) to 30 cm was significantly higher with grazing, but total system C to 60 cm was not significantly different (Table 1). This suggests that the higher level of soil C in the 0–30 cm depth increment of grazed pastures compared to exclosures primarily was the result of redistribution of existing system C. In the short-grass, however, total ecosystem C to 60 cm was significantly higher with heavy grazing compared to either light grazing or the exclosures, and this suggests that the large increase in warm-season short-grasses, primarily blue grama, associated with heavy grazing may have resulted in an actual increase in the amount of C in the plant–soil system as well as redistribution of system C. Studies are currently underway using ^{13}C to evaluate the influence of grazing on the rates of plant metabolism and the pathways of C allocation as they relate to SOM accumulation.

Although grazing increased the amount of C sequestered in the surface 30 cm of the soil, the decrease in cool-season mid-grasses with prolonged heavy grazing is undesirable for livestock production and community ecology, and the decrease in browse shrubs is undesirable for wildlife and community ecology (Hart, 1999). Grazing at light to moderate stocking rates resulted in stable, diverse plant communities dominated by forage grasses with dense, fibrous rooting systems conducive to soil organic matter formation and thus C sequestration in the soil. The native grassland ecosystems of the semi-arid Great Plains evolved under grazing by large herbivores; therefore, without an appropriate level grazing, deterioration of the plant–soil system, and possible declines in C sequestered in the soil, are indicated.

Acknowledgements

This paper was presented at the USDA Forest Service Southern Global Change Program sponsored Advances in Terrestrial Ecosystem: Carbon Inventory, Measurements, and Monitoring Conference held 3–5 October 2000 in Raleigh, North Carolina.

References

Bauer, Armand, Cole, C.V., Black, A.L., 1987. Soil property comparisons in virgin grasslands between grazed and nongrazed management systems. Soil Science Society of America Journal 51, 176–182.

Blake, G.R., Hartge, K.H., 1986. Bulk density–core method. In: Klute, A. (Ed.), Methods of Soil Analysis, Part 1, 2nd Edition. Agronomy Monograph 9. American Society of Agronomy, Madison, Wisconsin, USA, pp. 363–375.

Burke, I.C., Laurenroth, W.K., Milchunas, D.G., 1997. Biogeochemistry of managed grasslands in central North America. In: Paul, E.A., Paustian, K., Elliott, E.T., Cole, C.V. (Eds.), Soil Organic Matter in Temperate Agroecosystems: Long-term Experiments in North America. CRC Press, Boca Raton,FL, pp. 85–102.

Burke, I.C., Yonker, C.M., Parton, W.J., Cole, C.V., Flach, K., Schimel, D.S., 1989. Texture, climate, cultivation efects on soil organic matter content in US grassland soils. Soil Science Society of America Journal 53, 800–805.

Conant, R.T., Paustian, K., Elliott, E.T., 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecological Applications 11 (2), 343–355.

Coupland, R.T., VanDyne, G.M., 1979. Systems synthesis. In: Coupland, R.T. (Ed.), Grassland Ecosystems Of The World: Analysis of Grasslands and Their Uses. International Biological Programme 18. Cambridge University Press, Cambridge UK, pp. 97–106.

Derner, J.D., Beriske, D.D., Boutton, T.W., 1997. Does grazing mediate soil carbon and nitrogen accumulation beneath C4, perennial grasses along an environmental gradient? Plant and Soil 191, 147–156.

Detling, J.K., Dyer, M.I., Winn, D.T., 1979. Net photosynthesis, root respiration and regrowth of *Bouteloua gracilis* following simulated grazing. Oecologia 41, 127–134.

Dormaar, J.F., Johnston, A., Smoliak, S., 1977. Seasonal variations in chemical characteristics of soil organic matter of grazed and ungrazed mixed prairie and fescue grassland. Journal of Range Management 30, 195–198.

Dyer, M.I., Bokhari, U.G., 1976. Plant–animal interactions: studies of the effects of grasshopper grazing on blue grama grass. Ecology 57, 762–772.

Follett, R.F., 2001. Organic carbon pools in grazing land soils. In: Follett, R.F., Kimble, J.M., Lal, R. (Eds.), The Potential of US Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect. Lewis Publishers, Boca Raton FL, pp. 65–86.

Frank, A.B., Tanaka, D.L., Hofmann, L., Follett, R.F., 1995. Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. Journal of Range Mangement 48 (5), 470–474.

Gill, R.A., 1998. Biotic controls over the depth destribution of soil organic matter. Doctoral dissertation in Ecology, Colorado State University, Fort Collins, CO.

Hart, R.H., 1999. Cattle grazing intensity and plant biodiversity on shortgrass steppe after 55 years. In: Eldridge, D., Freudenberger, D. (Eds.), Proceedings of the VI International Rangeland Congress. Townsville, Australia, pp. 646–647.

Hart, R.H., 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. Plant Ecology 00, 1–7.

Hart, R.H., Samuel, M.J., Test, P.S., Smith, M.A., 1988. Cattle, vegetation and economics responses to grazing systems and grazing pressure. Journal of Range Management 41, 282–286.

Johnston, A., Dormaar, J.F., Smoliak, S., 1971. Long-term grazing effects on fescue grassland soils. Journal of Range Mangement 24, 185–188.

Laurenroth, W.K., Whitman, W.C., 1971. A rapid method for washing roots. Journal of Range Management 24, 308–309.

evidence suggests that blue grama may be a more efficient producer of soil organic C than other species because it may respond to grazing by rapidly translocating C to crowns and roots, and by increasing root exudation rates (Dyer and Bokhari, 1976; Detling et al., 1979). Most studies on the Great Plains that have reported increased soil organic C with grazing have been conducted on sites where grazing has resulted in a significant increase in blue grama at the expense of cool-season mid-grasses (Smoliak et al., 1972; Frank et al., 1995; Schuman et al., 1999).

Besides redistributing existing system C, did grazing also result in an actual increase in system C and thus an increase in C sequestration? In the mixed-grass, total ecosystem C (plant + soil) to 30 cm was significantly higher with grazing, but total system C to 60 cm was not significantly different (Table 1). This suggests that the higher level of soil C in the 0–30 cm depth increment of grazed pastures compared to exclosures primarily was the result of redistribution of existing system C. In the short-grass, however, total ecosystem C to 60 cm was significantly higher with heavy grazing compared to either light grazing or the exclosures, and this suggests that the large increase in warm-season short-grasses, primarily blue grama, associated with heavy grazing may have resulted in an actual increase in the amount of C in the plant–soil system as well as redistribution of system C. Studies are currently underway using ^{13}C to evaluate the influence of grazing on the rates of plant metabolism and the pathways of C allocation as they relate to SOM accumulation.

Although grazing increased the amount of C sequestered in the surface 30 cm of the soil, the decrease in cool-season mid-grasses with prolonged heavy grazing is undesirable for livestock production and community ecology, and the decrease in browse shrubs is undesirable for wildlife and community ecology (Hart, 1999). Grazing at light to moderate stocking rates resulted in stable, diverse plant communities dominated by forage grasses with dense, fibrous rooting systems conducive to soil organic matter formation and thus C sequestration in the soil. The native grassland ecosystems of the semi-arid Great Plains evolved under grazing by large herbivores; therefore, without an appropriate level grazing, deterioration of the plant–soil system, and possible declines in C sequestered in the soil, are indicated.

Acknowledgements

This paper was presented at the USDA Forest Service Southern Global Change Program sponsored Advances in Terrestrial Ecosystem: Carbon Inventory, Measurements, and Monitoring Conference held 3–5 October 2000 in Raleigh, North Carolina.

References

Bauer, Armand, Cole, C.V., Black, A.L., 1987. Soil property comparisons in virgin grasslands between grazed and nongrazed management systems. Soil Science Society of America Journal 51, 176–182.

Blake, G.R., Hartge, K.H., 1986. Bulk density–core method. In: Klute, A. (Ed.), Methods of Soil Analysis, Part 1, 2nd Edition. Agronomy Monograph 9. American Society of Agronomy, Madison, Wisconsin, USA, pp. 363–375.

Burke, I.C., Laurenroth, W.K., Milchunas, D.G., 1997. Biogeochemistry of managed grasslands in central North America. In: Paul, E.A., Paustian, K., Elliott, E.T., Cole, C.V. (Eds.), Soil Organic Matter in Temperate Agroecosystems: Long-term Experiments in North America. CRC Press, Boca Raton,FL, pp. 85–102.

Burke, I.C., Yonker, C.M., Parton, W.J., Cole, C.V., Flach, K., Schimel, D.S., 1989. Texture, climate, cultivation efects on soil organic matter content in US grassland soils. Soil Science Society of America Journal 53, 800–805.

Conant, R.T., Paustian, K., Elliott, E.T., 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecological Applications 11 (2), 343–355.

Coupland, R.T., VanDyne, G.M., 1979. Systems synthesis. In: Coupland, R.T. (Ed.), Grassland Ecosystems Of The World: Analysis of Grasslands and Their Uses. International Biological Programme 18. Cambridge University Press, Cambridge UK, pp. 97–106.

Derner, J.D., Beriske, D.D., Boutton, T.W., 1997. Does grazing mediate soil carbon and nitrogen accumulation beneath C4, perennial grasses along an environmental gradient? Plant and Soil 191, 147–156.

Detling, J.K., Dyer, M.I., Winn, D.T., 1979. Net photosynthesis, root respiration and regrowth of *Bouteloua gracilis* following simulated grazing. Oecologia 41, 127–134.

Dormaar, J.F., Johnston, A., Smoliak, S., 1977. Seasonal variations in chemical characteristics of soil organic matter of grazed and ungrazed mixed prairie and fescue grassland. Journal of Range Management 30, 195–198.

Dyer, M.I., Bokhari, U.G., 1976. Plant–animal interactions: studies of the effects of grasshopper grazing on blue grama grass. Ecology 57, 762–772.

Follett, R.F., 2001. Organic carbon pools in grazing land soils. In: Follett, R.F., Kimble, J.M., Lal, R. (Eds.), The Potential of US Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect. Lewis Publishers, Boca Raton FL, pp. 65–86.

Frank, A.B., Tanaka, D.L., Hofmann, L., Follett, R.F., 1995. Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. Journal of Range Mangement 48 (5), 470–474.

Gill, R.A., 1998. Biotic controls over the depth destribution of soil organic matter. Doctoral dissertation in Ecology, Colorado State University, Fort Collins, CO.

Hart, R.H., 1999. Cattle grazing intensity and plant biodiversity on shortgrass steppe after 55 years. In: Eldridge, D., Freudenberger, D. (Eds.), Proceedings of the VI International Rangeland Congress. Townsville, Australia, pp. 646–647.

Hart, R.H., 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. Plant Ecology 00, 1–7.

Hart, R.H., Samuel, M.J., Test, P.S., Smith, M.A., 1988. Cattle, vegetation and economics responses to grazing systems and grazing pressure. Journal of Range Management 41, 282–286.

Johnston, A., Dormaar, J.F., Smoliak, S., 1971. Long-term grazing effects on fescue grassland soils. Journal of Range Mangement 24, 185–188.

Laurenroth, W.K., Whitman, W.C., 1971. A rapid method for washing roots. Journal of Range Management 24, 308–309.

LeCain, D.L., Morgan, J.A., Schuman, G.E., Reeder, J.D., Hart, R.H., 2000. Carbon exchange rates in grazed and ungrazed pastures of Wyoming. Journal of Range Management 53, 199–206.

Manley, W.A., Hart, R.H., Samuel, M.J., Smith, M.A., Waggoner Jr., J.W., Manley, J.T., 1997. Vegetation, cattle and economic responses to grazing strategies and pressures. Journal of Range Management 50, 638–646.

Milchunas, D.G., Laurenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63 (4), 327–366.

Milchunas, D.G., Laurenroth, W.K., Burke, I.C., 1998. Livestock grazing, animal and plant biodiversity of shortgrass steppe and relationship to ecosystem function. Oikos 83, 64–74.

Milchunas, D.G., Laurenroth, W.K., Chapman, P.L., 1992. Plant competition, abiotic, long- and short-term effects of large herbivores on demography of opportunistic species in semiarid grassland. Oecologia 92, 520–531.

Milchunas, D.G., Laurenroth, W.K., Chapman, P.L., Kazempour, M.K., 1989. Effects of grazing, topography and precipitation on the structure of a semiarid grassland. Vegetatio 80, 11–23.

Milchunas, D.G., Laurenroth, W.K., Chapman, P.L., Kazempour, M.K., 1990. Community attributes along a perturbation gradient in a shortgrass steppe. Journal of Vegetation Science 1, 375–384.

Monger, H.D., Martinez-Rios, J.J., 2001. Inorganic carbon sequestration in grazing lands. In: Follett, R.F., Kimble, J.M., Lal, R. (Eds.), The Potential of US Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect. Lewis Publishers, Boca Raton FL, pp. 87–118.

Naeth, M.A., Bailey, A.W., Pluth, D.J., Chanasyk, D.S., Hardin, R.T., 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. Journal of Range Management 44 (1), 7–12.

National Oceanic and Atmospheric Administration, 1994. Local Climatological Data—Cheyenne, Wyoming. National Climate Data Center, Ashville, North Carolina, USA.

Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon, organic matter. In: Page, A.L., Miller, R.H., Kenney, D.R. (Eds.), Methods of Soil Analysis, Part 1, 2nd Edition. Agronomy Monograph 9. American Society of Agronomy, Madison, Wisconsin, USA, pp. 539–580.

Painter, E.L., Detling, J.K., 1981. Effects of defoliation on net photosynthesis and regrowth of western wheatgrass. Journal of Range Management 34, 68–70.

Paul, E.A., Clark, F.E., 1996. Soil Microbiology and Biochemistry, 2nd Edition. Academic Press, San Diego CA.

Peterson, M., Kelly, G., 1994. Central Plains Experimental Range, Detailed Soil Survey. Colorado State University Extension Service, US Department of Agriculture Natural Resource Conservation Service.

Reeder, J.D., Franks, C.D., Milchunas, D.G., 2001. Root biomass and microbial processes. In: Follett, R.F., Kimble, J.M., Lal, R. (Eds.), The Potential of US Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect. Lewis Publishers, Boca Raton FL, pp. 139–166.

Schuman, G.E., Reeder, J.D., Manley, J.T., Hart, R.H., Manley, W.A., 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9 (1), 65–71.

Shariff, A.R., Biondini, M.E., Grygiel, C.E., 1994. Grazing intensity effects on litter decompostiion and soil nitrogen mineralization. Journal of Range Management 47, 444–449.

Sobecki, T.M., Moffitt, D.L., Stone, J., Franks, C.D., Mendenhall, A.G., 2001. A broad-scale perspective on the extent, distribution and characteristics of US grazing lands. In: Follett, R.F., Kimble, J.M., Lal, R. (Eds.), The Potential of US Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect. Lewis Publishers, Boca Raton FL, pp. 21–64.

Smoliak, S., Dormaar, J.F., Johnston, A., 1972. Long-term grazing effects on *Stipa-Bouteloua* prairie soils. Journal of Range Management 25, 246–250.

Steel, R.G.D., Torrie, J.H., 1980. Principles and Procedures of Statistics: A Biometrical Approach, 2nd Edition. McGraw-Hill, New York NY.

Stevenson, A., Baumgartner, R.E., Schuman, G.E., 1984. High Plains Grasslands Research Station, Detailed Soil Survey (1-84/1C/3.62). United States Department of Agriculture, Agricultural Research Service, Cheyenne, Wyoming, USA.

Thorp, J., 1948. How soils develop under grass. In: Anderson, C.P. (Ed.), Grass: The Yearbook of Agriculture. United States Department of Agriculture, US Government Printing Office, Washington, DC.

Weaver, J.E., Hougen, V.H., Weldon, M.D., 1935. Relation of root distribution to organic matter in prairie soil. The Botanical Gazette 96 (3), 389–420.

Wienhold, B.J., Hendrickson, J.R., Karn, J.F., 2001. Pasture management influences on soil properties in the Northern Great Plains. Journal of Soil and Water Conservation 56 (1), 27–31.