



OPEN Short-duration, managed grazing system increases net ecosystem carbon uptake and water use efficiency on a working ranch

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Grasslands are globally significant carbon (C) sinks, but data quantifying how multi-paddock, managed grazing systems alter ecosystem fluxes and the annual C budget are limited. We hypothesized a high-intensity (150 cow-calf pair), short-duration (2 days), rotational grazing system targeting 50% utilization, followed by extended rest and recovery, could improve net C uptake (net ecosystem production; NEP), water use efficiency (WUE), and the net amount of C sequestered (C budget) by the ecosystem annually. We quantified water and C fluxes over two full years using eddy covariance and field-based measurements of C removed by grazers on a U.S. northern prairie working cattle ranch. Managed grazing nearly doubled annual NEP for both yearly cycles, as compared to ungrazed control. The net amount of C sequestered under managed grazing reached 1.01 and 0.37 Mg C ha⁻¹ yr⁻¹ in the first and second cycle, respectively—53% and 23% greater than ungrazed control. Grazing initially decreased leaf area index and daily C uptake, but the ecosystem gradually recovered through autumn, with elevated C uptake and resource-use efficiencies. Our findings demonstrate that improvements in grassland C uptake, C sequestration, and allocation of water to production can be achieved through inclusion of grazers and adaptive grassland management.

Keywords Net ecosystem exchange, Carbon sequestration, WUE, LAI, Grassland

Grazing is the most widespread land use in grassland ecosystems with the potential to greatly influence ecosystem carbon (C) dynamics and processes leading to C sequestration^{1–3}. Grazing management has been proposed as both a conservation tool^{4–6} and a nature-based climate mitigation strategy^{7,8} because management can increase soil C stocks and lower the C footprint of beef production⁹. Although grazing can enhance soil organic carbon (SOC) under certain environmental conditions and stocking intensities^{9–12}, few studies explicitly quantify how multi-paddock, managed grazing systems affect ecosystem-scale carbon dioxide (CO₂) exchange relative to an ungrazed control. Data reflecting temporal dynamics of CO₂ exchange are needed, so managers can better understand how grazing decisions influence pasture production on a daily basis¹³. For example, grasslands store most photosynthate below ground, particularly in autumn, when additional stores are needed to survive the winter^{14–16}, so tracking how rest and recovery influences C exchange weeks after grazing would advance understanding of processes influencing grassland production and the overall health of the ecosystem.

Cattle grazing experiments commonly report the influence of management applied over a growing season, often referred to as season-long grazing, with grazing intensity classified as light, moderate, or heavy on small plots or paddocks. Grazing intensity often remains constant year-to-year¹⁷, rather than adapting to changing conditions⁶. Nonetheless, season-long grazing can lead to enhancements in production^{11,18}, resource use efficiencies^{18,19}, SOC^{9,17}, and allocation of photosynthate below ground^{15,20,21} using plots and soil cores. For high-intensity, short-duration grazing systems, it is useful to define an ecosystem boundary, where grazers are considered external to the system and serve as agents that remove and deposit C^{22,23}. The net annual C budget, where an amount of C imported through plant production is reduced by a lesser amount of C exported through grazer removal, was reported as positive for an improved (seeded, fertilized, and irrigated) paddock under dairy production²³. This system-boundary approach focuses on factors influencing the grassland C sink rather than the C footprint of grazing animals. Knowledge of how a multi-paddock, rotational system can be used to

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enhance plant production and rates of C sequestration in an agricultural production setting is needed to advance understanding and adoption of regenerative practices^{5,24}.

Adaptive, multi-paddock (AMP) grazing systems have gained in popularity among ranchers in recent decades, with conservation benefits widely reported^{4,6,25}. These systems employ a high stocking density for a short duration within an individual paddock until a targeted level of leaf area removal is achieved, after which livestock are moved to a new paddock with fresh forage. The previously grazed paddock is then allowed to rest and recover, often for the remainder of the growing season in northern climates. Grazing timing and intensity are adaptively adjusted by managers in response to environmental conditions and available forage. The AMP management approach reduces compaction caused by trampling²⁶ and improves H₂O infiltration²⁷, aboveground primary production²⁸, and other benefits²⁹. By coupling defoliation intensity with recovery periods, AMP grazing has the potential to alter canopy structure, phenology, and resource use efficiencies in ways that may influence ecosystem C and water (H₂O) exchange^{25,30}.

Grassland vegetation of central and western North Dakota is northern mixed-grass prairie, but floristic diversity has declined in recent decades due to invasions by introduced species *Poa pratensis* L. and *Bromus inermis* Leyss.^{31–33}. Plant production is regulated primarily by precipitation³⁴, and season-long grazing of native prairie is a standard practice. Some ranchers have adopted the AMP grazing approach, often with cost-share assistance by governmental and non-governmental conservation organizations that recognize ranching as essential to the maintenance of grassland habitat³⁵. Prairie grasslands are one of the most converted and least protected biomes³⁶, so management that enhances the health and sustainability of rangelands is highly encouraged. To better understand how AMP management influences ecosystem C uptake, a partnership among scientists, ranchers, industry, and conservation organizations was formed with the goal of quantifying C and H₂O fluxes on a privately owned, native prairie section (250 ha). Within this study area, comparable neighboring pastures (20-ha each) were delineated on the basis of similar soil series, management history, and vegetation cover to evaluate C and H₂O fluxes for a 4-paddock, managed grazing (MG) system and an ungrazed control (UC)^{6,37}.

Here, we examine how a short-duration (24–48 h.), high-intensity (150 cow-calf pair), leaf-area-driven AMP management system influences C and H₂O fluxes by quantifying gross primary production (GPP), ecosystem respiration (Re), net ecosystem exchange of CO₂ (NEE), evapotranspiration (ET), and associated resource use efficiencies, such as light use efficiency (LUE), C use efficiency (CUE), and water use efficiency (WUE), relative to a neighboring, ungrazed control. Field and imagery-based data were collected to assess biomass-C and leaf area index (LAI) removed by grazers. The goal of this project was to compare a managed grazing system with an ungrazed control for two annual cycles with respect to: (1) cumulative NEE (net C uptake), (2) cumulative amount of C sequestered by the ecosystem (the C budget), and (3) resource use efficiencies. To our knowledge, this study provides one of the first ecosystem-scale assessments detailing how an AMP grazing system influences resource-use efficiency dynamics and the C sink strength on a working cattle ranch.

Results

Grazing, LAI, and biomass removal

Figure 1 depicts pastures under managed grazing (MG) and ungrazed control (UC). Table 1 provides details of grazing events for each of the four paddocks, and Table 2 provides a summary for each annual cycle. The sum of all dry matter (DM) biomass removed by grazers was 0.84 Mg DM ha⁻¹ and 1.29 Mg DM ha⁻¹, respectively, for the first and second annual cycle (Table 1). Biomass was 42% C, so the sum of all C removed by grazers was 0.35 Mg C ha⁻¹ and 0.54 Mg C ha⁻¹, respectively, for the first and second annual cycle (Table 1). Based on herd number, grazing duration, and DM removed at each event (Table 1), each cow-calf pair removed an average 14.5 kg DM pair⁻¹ day⁻¹ and 14.8 kg DM pair⁻¹ day⁻¹, respectively, for the first and second cycle. The average fraction of LAI removed across all grazing events was 0.43 and 0.50, respectively, in 2023 and 2024. While the difference in the fraction of LAI removal between cycles was only 0.07, the difference in DM biomass removal was disproportionately higher. An additional 0.45 Mg DM ha⁻¹ was removed in the second cycle, which was 54% greater than the first cycle. Supplementary Figure S1 depicts the steeper relationship in 2024 between DM biomass and LAI (slope = 1.33, R² = 0.97), as compared to 2023 (slope = 1.13, R² = 0.95). Animal impacts associated with greater vegetation utilization in the second cycle include increased deposition of excreta (Table 1) and greater penetration of light through the plant canopy.

Figures 2 and 3 summarize daily precipitation and temperature, respectively. For the first cycle (2023–2024), annual precipitation was 558 mm, and for the second cycle (2024–2025), annual precipitation was 390 mm. Specific leaf area (SLA) also trended lower during the second cycle (Supplementary Fig. S2). Average SLA by date the first annual cycle ranged from 6.02 to 16.72 m² kg⁻¹ and from 5.85 to 11.94 m² kg⁻¹ the second annual cycle. Winter snowfall was light (Fig. 2), and snow depth ranged from 0 to 20 cm. Average annual soil temperature near the surface (2 mm depth) for the first and second cycle was 9.1 °C and 8.5 °C, respectively, and average air temperature was 6.3 °C and 5.8 °C (Fig. 3).

Field-based estimates of LAI are shown in Fig. 4, along with the paddock number at the time each paddock was grazed (Table 1). Initially, average LAI was similar for both pastures. After the first grazing event, LAI for the MG pasture dipped below the UC pasture, with values of 2.08 and 2.47, respectively, for the first annual cycle and values of 1.49 and 1.83 for the second annual cycle. This trend over time in LAI alternated at the end of July for the first cycle and at the end of August for the second cycle, when MG pasture average LAI rose above UC pasture average LAI. Grazing system positively affected LAI, with significant differences between pastures for both annual cycles ($F_{1,158}$ or $F_{1,237} \geq 4.27$; $p < 0.05$). Even after pasture biomass was harvested by grazers, LAI for the MG pasture rose above LAI for the UC pasture in autumn. Cumulative NEE and GPP trajectories also varied with LAI, as detailed in the following section.

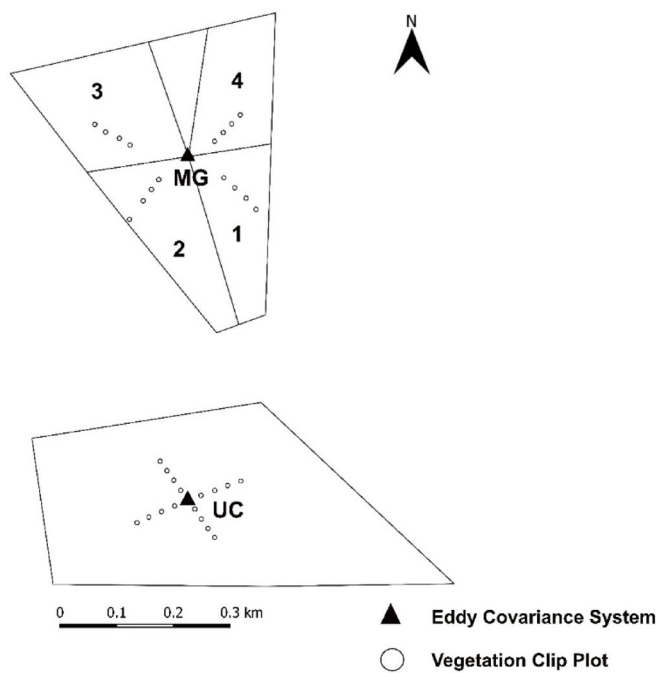


Fig. 1. Pasture layout for managed grazing (MG) and ungrazed control (UC). Identical IRGASON (i.e., Integrated CO₂/H₂O open-path analyzer and 3D sonic anemometer) eddy covariance systems (Campbell Scientific, UT, USA) were deployed in each pasture. Vegetation clip plot coordinates are denoted in Table S11. Eddy covariance data collected while wind flows from area directly behind the IRGASON (0 ~ 15° or 345 ~ 360° in the sonic coordinate system) were excluded.

Paddock	Paddock	Grazing Dates	Herd	Amount Removed		C Deposited		C Export	*C Import
ID	Area		Number	LAI	Green DM	Urine C	Dung C	FC _{grazing}	FC _{excreta}
	(ha)		(pair)	(fraction)	(Mg)	(Mg C)	(Mg C)	(Mg C)	(Mg C)
1st Annual Cycle, 2023									
SE	4.10	May 31, 2023	95	0.48	1.14	0.02	0.18	0.48	0.20
SW	4.40	June 27, 28, 2023	146	0.51	4.96	0.07	0.76	2.08	0.83
NW	5.05	July 27, 28, 2023	155	0.42	5.06	0.07	0.78	2.13	0.85
NE	4.45	Sep 1, 2, 2023	155	0.29	3.99	0.08	0.61	1.67	0.69
Mg C yr ⁻¹					15.15			6.36	2.58
Mg C ha ⁻¹ yr ⁻¹					0.84			0.35	0.14
2nd Annual Cycle, 2024									
SE	5.05	Jun 5, 6, 12, 2024	110	0.44	4.80	0.08	0.74	2.02	0.82
SW	4.45	Jul 26, 27, 28, 2024	110	0.52	6.98	0.08	1.07	2.93	1.15
NW	4.10	Aug 5, 6, 7, 2024	165	0.55	6.97	0.12	1.07	2.93	1.19
NE	4.45	Aug 31, Sep 1, 2, 2024	165	0.48	4.57	0.12	0.70	1.92	0.82
Mg C yr ⁻¹					23.32			9.79	3.98
Mg C ha ⁻¹ yr ⁻¹					1.29			0.54	0.22

Table 1. Paddock and herd size and dates grazed, along with amount of dry matter (DM) biomass removed, fraction of LAI removed, and amounts of excreta deposited each annual cycle. The sum of DM C, dung C, and urine C was divided by sum of paddock areas to determine Mg C ha⁻¹ imported as excreta and exported as DM. *Based on 10 urinations day⁻¹pair⁻¹ and 2 L per urination and 12 g C L⁻¹ and dung as 41.5% carbon.

Seasonal variations in LAI data collected at the sensor onboard the Sentinel 2 satellite and modeled using Sentinel Application Platform (SNAP)³⁸ are shown in Supplementary Figure S3. Average modeled SNAP LAI during the first cycle was 0.80 ± 0.32 and 0.91 ± 0.32, respectively, for UC and MG pastures and 0.71 ± 0.53 and 0.68 ± 0.44 during the second cycle. The repeated measures analysis of variance for these modeled data indicated that the effect of the grazing system on SNAP LAI varied with time for the first cycle ($F_{1,286} = 9.15; p < 0.005$) and the second cycle ($F_{1,382} = 2.76; p < 0.1$). The magnitude in SNAP LAI values was consistently lower than field LAI

Carbon flux components ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$)						
Pasture	GPP	R_e	FC	FC_{grazing}	FC_{excreta}	Net C sequestered
1st Annual Cycle, 2023						
Ungrazed Control (UC)	9.73	9.07	0.66			0.66
Managed (MG)	11.17	9.95	1.22	0.35	-0.14	1.01
2nd Annual Cycle, 2024						
Ungrazed Control (UC)	7.58	7.28	0.30			0.30
Managed (MG)	9.10	8.41	0.69	0.54	-0.22	0.37

Table 2. Net amount of C sequestered annually from Eq. 1, in terms of cumulative gross primary production (GPP), cumulative ecosystem respiration (R_e), cumulative net C flux (FC), total C exported by grazers (FC_{grazing}), and total C imported as excreta (FC_{excreta}).

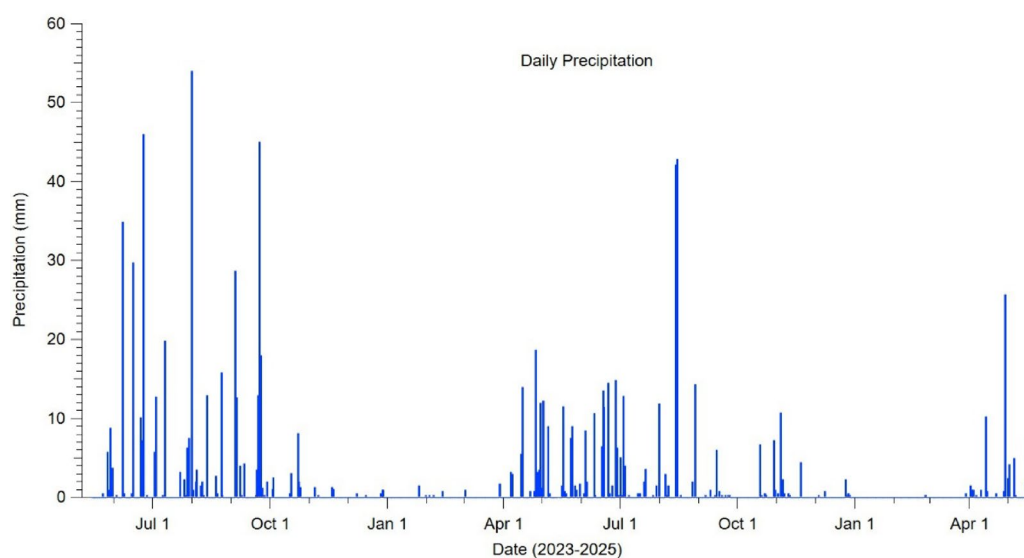


Fig. 2. Daily precipitation from May 15, 2023, to May 14, 2025.

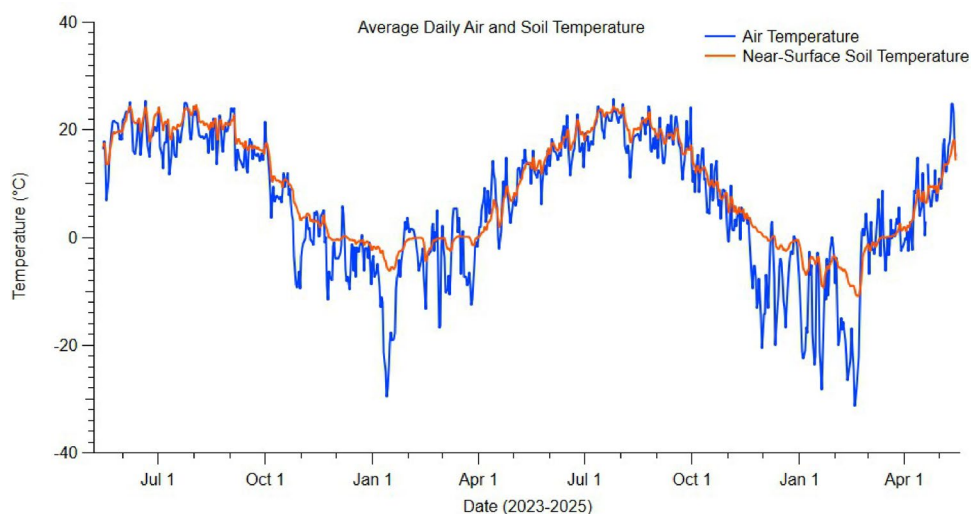


Fig. 3. Daily average near-surface soil temperature (2 cm depth) and air temperature from May 15, 2023, to May 14, 2025.

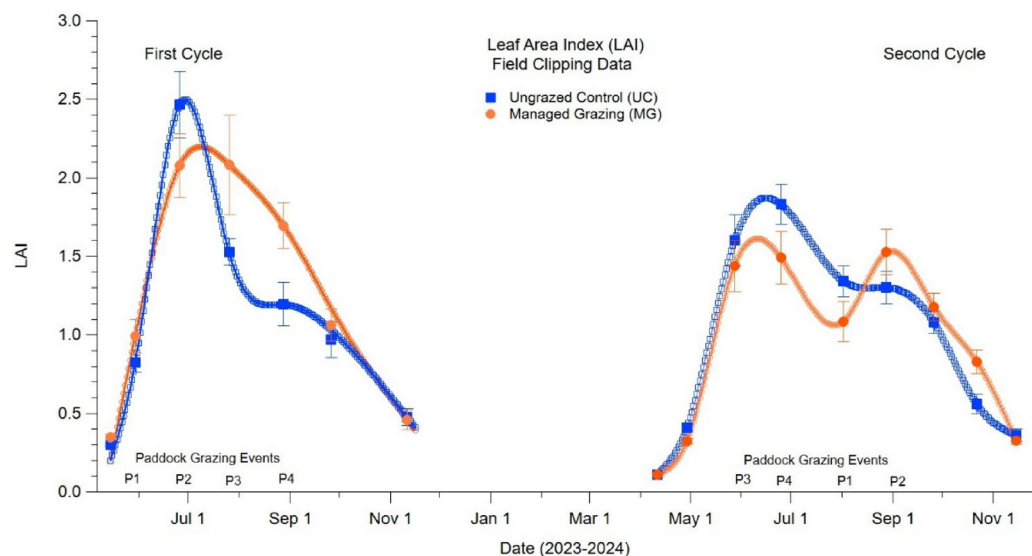


Fig. 4. Leaf area index (LAI) for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle). Markers are average LAI collected in the field from 16 plots in each pasture ($\pm$ standard error) prior to grazing events. Data between markers were interpolated using the cubic spline⁸⁴. Paddock numbers (P1–P4) designate when each quadrant of the field was grazed.

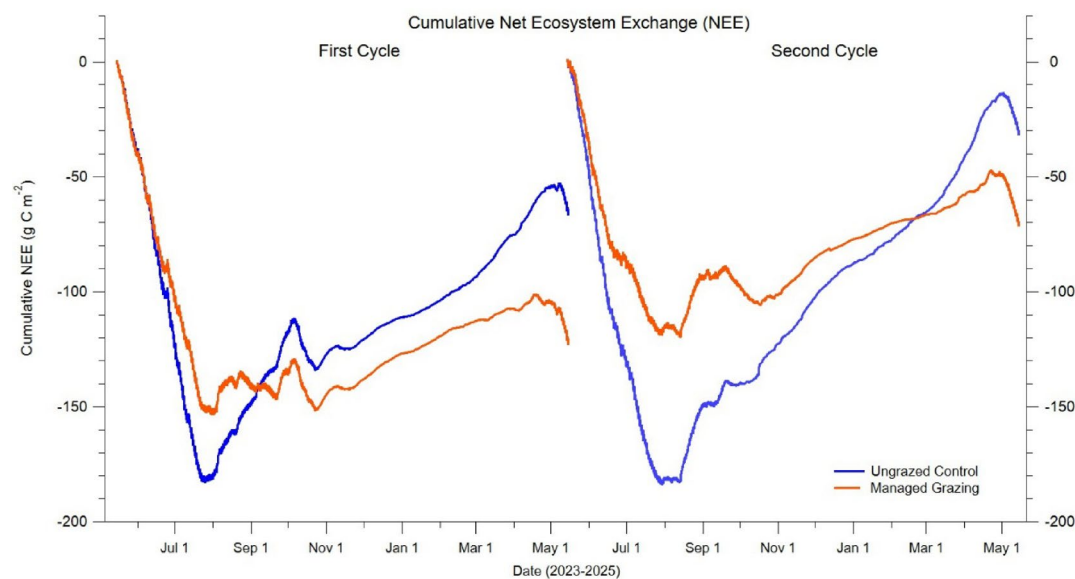


Fig. 5. Cumulative net ecosystem exchange (NEE) of carbon for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle).

values (Fig. 4). However, the SNAP LAI data did reflect seasonal shifts in the treatment effect trend for the MG pasture—from similar or lower LAI in summer to higher LAI in autumn.

Net annual C budget

Figure 5 depicts cumulative net ecosystem exchange (NEE) over time for both annual cycles, where more negative values for NEE represent greater C uptake. At the beginning of the experiment in May 2023, cumulative NEE was similar for the MG and UC pastures. Following intensive, short-duration grazing and reduction in LAI (Fig. 4), cumulative NEE at the UC pasture declined below that of MG. In early September 2023, this pattern reversed, and cumulative NEE at the MG pasture declined below UC for the remainder of the measurement year. The following spring, cumulative NEE for both pastures began to decline again on May 1, 2024. By the end

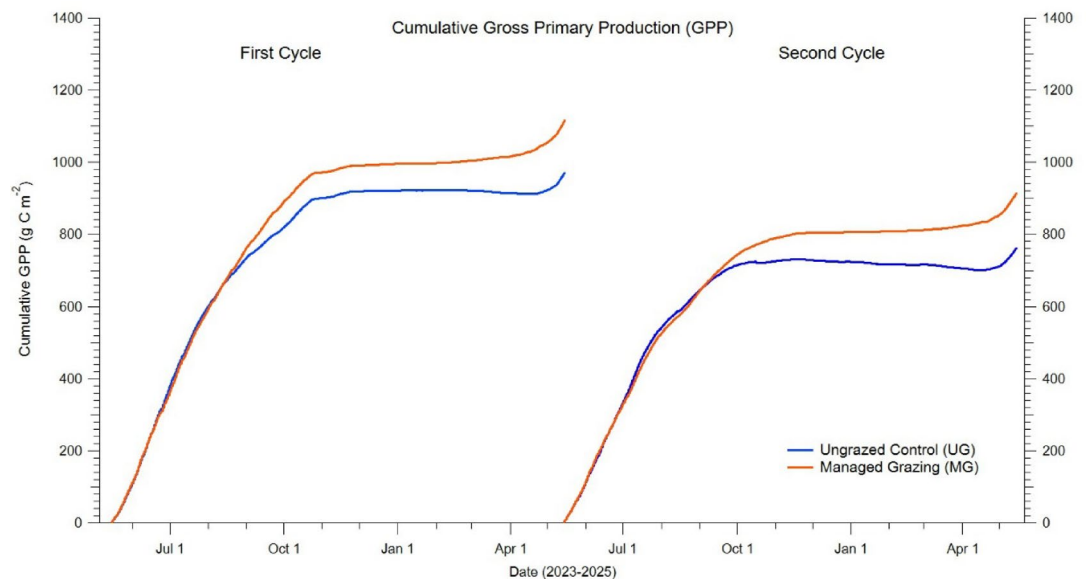


Fig. 6. Cumulative gross primary production (GPP) of carbon for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle).

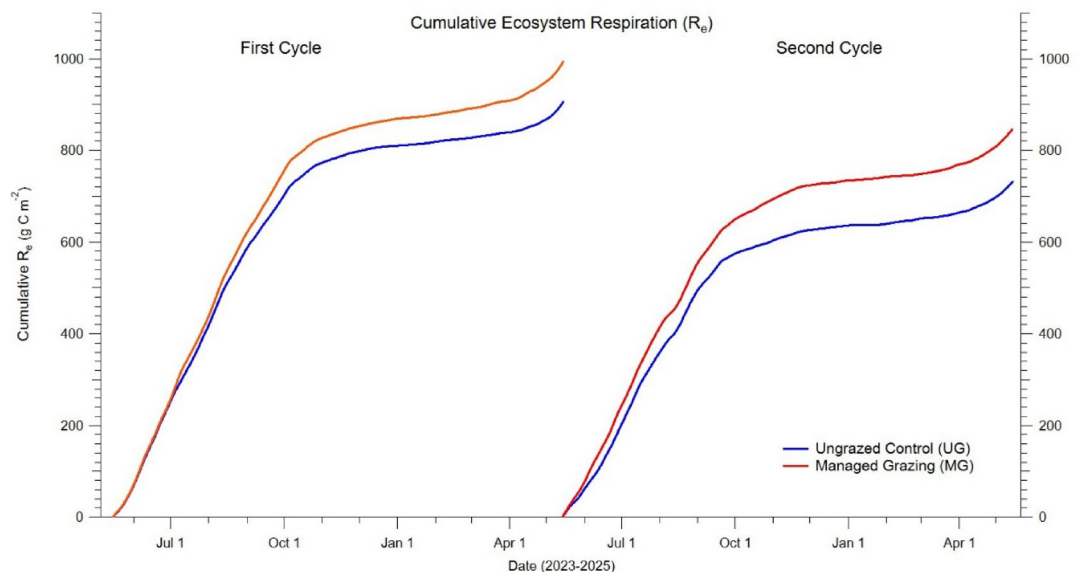


Fig. 7. Cumulative ecosystem respiration (R_e) of carbon for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle).

of the first 365-day measurement cycle, cumulative NEE was $-66 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the UC pasture and $-122 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the MG pasture, where the negative sign indicates C uptake (Fig. 5). Like the first measurement cycle, cumulative NEE during the second cycle was similarly affected by grazing management (see Fig. 5), with differences between cycles in precipitation affecting the magnitude and timing of treatment effects. By the end of the second 365-day measurement cycle, cumulative NEE was $-30 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the UC pasture and $-69 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the MG pasture.

Cumulative GPP and R_e (Figs. 6 and 7) depict cumulative values for the MG pasture rising above the UC pasture, particularly in autumn, which coincided with greater LAI (Fig. 4). The fraction of GPP carbon respired by the ecosystem (R_e), however, was lower at the MG pasture. At the end of the first 365-day measurement cycle, cumulative GPP for the UC and MG pasture was 973 and $1,118 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively, and R_e was 907 and $995 \text{ g C m}^{-2} \text{ yr}^{-1}$. At the end of the second 365-day measurement cycle, cumulative GPP for the UC and MG

pasture was 750 and 909 g C m⁻² yr⁻¹, respectively, and R_e was 728 and 841 g C m⁻² yr⁻¹, respectively. The ratio of R_e to GPP for the UC and MG pasture was 0.93 and 0.89, respectively, for the first cycle and 0.97 and 0.93, respectively, for the second cycle. The MG pasture ratio of R_e to GPP was 4% lower than the UC pasture for both annual cycles.

Table 2 summarizes C component fluxes contributing to the calculation of the net amount of C sequestered (GPP, R_e, FC, FC_{grazing}, and FC_{excreta}), where net cumulative C flux (FC) is cumulative NEE multiplied by -1. For the first cycle, FC was 0.66 and 1.22 Mg C ha⁻¹ yr⁻¹, respectively, for UC and MG pastures and 0.30 and 0.69 Mg C ha⁻¹ yr⁻¹, respectively, for the second cycle. Annual amount exported by grazers (FC_{grazing}) was 0.35 and 0.54 Mg ha⁻¹ yr⁻¹, respectively, for the first and second cycle. Annual amount returned to the pasture as dung and urine (FC_{excreta}) was 0.14 and 0.22 Mg C ha⁻¹, respectively, for the first and second cycle. The net amount of C sequestered for the first cycle was 0.66 and 1.01 Mg C ha⁻¹ yr⁻¹, respectively, for UC and MG pastures and 0.30 and 0.37 Mg C ha⁻¹ yr⁻¹, respectively, for the second cycle (Table 2).

Seasonal variations in growing-season daytime fluxes and resource use efficiencies

Figures 8, 9, 10, 11 and 12 depict daytime sums for GPP, NEE, and resource use efficiencies, which provide deeper insight into how managed grazing interacted with time to improve ecosystem C and H₂O dynamics. The effects of managed grazing on daytime GPP (Fig. 8) and NEE (Fig. 9) varied with time during the growing season. The time x treatment interaction was most evident in autumn, with the greatest differences between pastures occurring from mid-August to early-October for the first annual cycle (GPP: F_{1,368} = 2.90; p < 0.1 and NEE: F_{1,368} = 5.19; p < 0.05) and from late-August to late-October for the second annual cycle (GPP: F_{1,368} = 8.21; p < 0.005 and NEE: F_{1,368} = 121.75; p < 0.0001). Daytime NEE tended to be lower and GPP slightly higher for the UC pasture during mid-summer, while daytime NEE was significantly lower and GPP significantly higher for the MG pasture in autumn. Average daytime GPP for the UC and MG pasture was 4.57 ± 2.74 and 4.87 ± 2.49 g C m⁻² day⁻¹, respectively, in 2023 and 3.68 ± 2.67 and 4.07 ± 2.26 g C m⁻² day⁻¹ in 2024. Average daytime NEE for the UC and MG pasture was -2.56 ± 1.98 and -2.74 ± 1.63 g C m⁻² day⁻¹, respectively, in 2023 and -2.07 ± 1.92 and -2.23 ± 1.46 g C m⁻² day⁻¹ in 2024. Average daytime NEE for the pasture under managed grazing was 7% lower than the ungrazed pasture for both cycles.

Annual WUE, the ratio of cumulative GPP to cumulative ET, was 1.79 and 2.04 g C kg H₂O⁻¹, for the UC and MG pastures, respectively, during the first cycle and 1.52 and 1.77 g C kg H₂O⁻¹ for the second cycle. Figure 10 shows how managed grazing significantly improved daytime WUE in the first cycle (F_{1,368} = 3.96; p < 0.05) and interacted with time in the second cycle (F_{1,368} = 40.89; p < 0.0001), with greater WUE from September to November 2024. Average daytime WUE for the first annual cycle was 2.28 ± 0.80 and 2.45 ± 0.80 g C kg H₂O⁻¹ for the UC and MG pastures, respectively, and was 1.71 ± 0.71 and 2.15 ± 0.63 g C kg H₂O⁻¹, respectively, for the second cycle. Supplementary Figure S4 shows average daytime ET, which was 2.23 mm H₂O day⁻¹ in 2023 and 2.01 mm H₂O day⁻¹ in 2024 for both pastures. Annual carbon use efficiency (CUE), the ratio of cumulative FC to cumulative GPP, was 0.068 and 0.109, for the UC and MG pastures, respectively, during the first cycle and 0.039 and 0.076 for the second cycle.

Values for LUE were calculated based on manual collection of LAI in the field (Fig. 4) and on the SNAP LAI product (Supplementary Fig. S3). Average LUE based on LAI in the field, was 1.72 ± 0.69 and 1.76 ± 0.69 g C MJ APAR⁻¹ for the UC and MG pastures, respectively, between May and November in the first cycle and was 1.16 ± 0.65 and 1.47 ± 0.57 g C MJ⁻¹ in the second cycle (Fig. 11). Average LUE, using SNAP LAI, was 1.94 ± 0.80

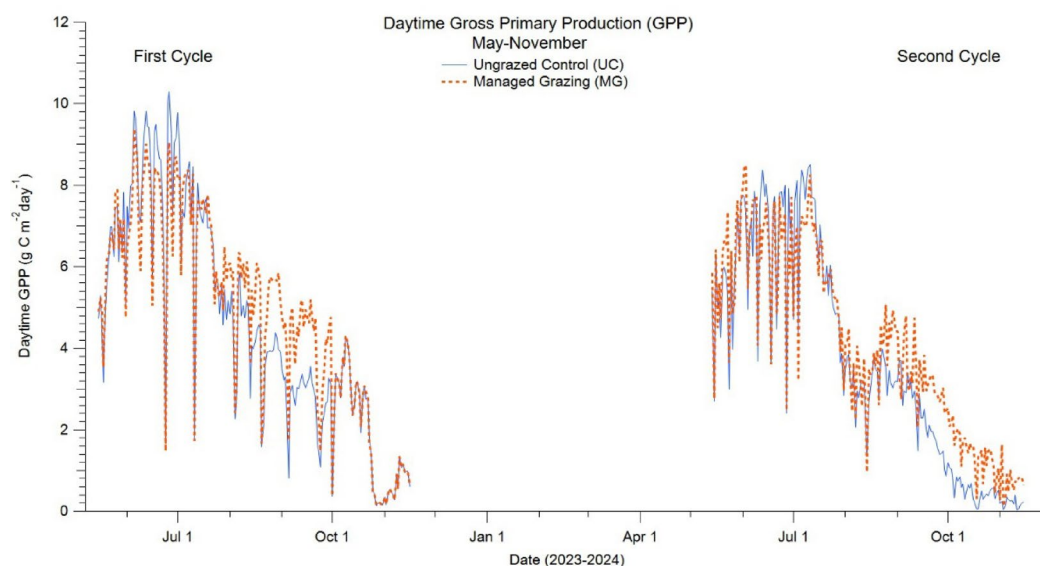


Fig. 8. Daytime gross primary production (GPP) for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle). Half-hour data collected during daytime were summed by day between May and Nov.

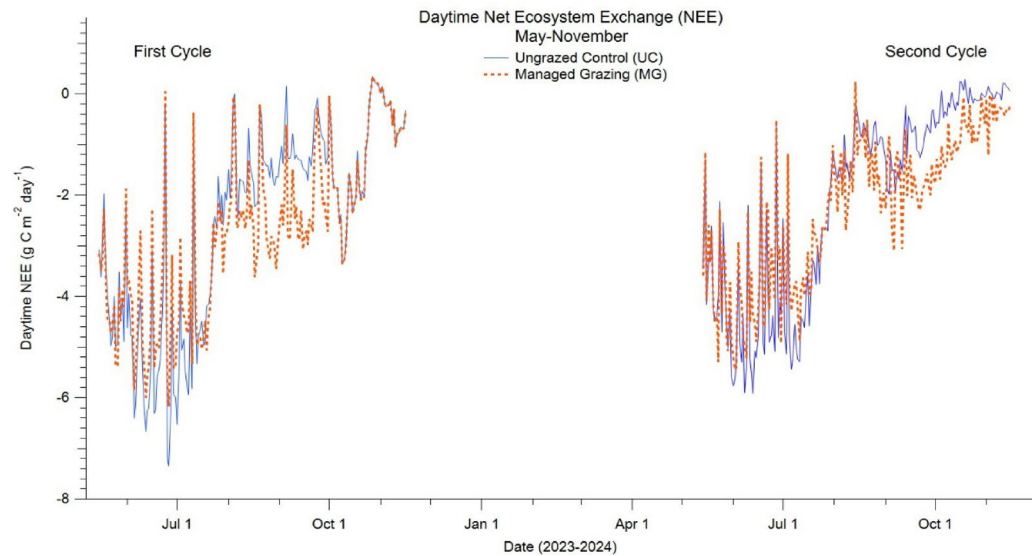


Fig. 9. Daytime net ecosystem exchange (NEE) for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle). Half-hour data collected during daytime were summed by day between May and Nov.

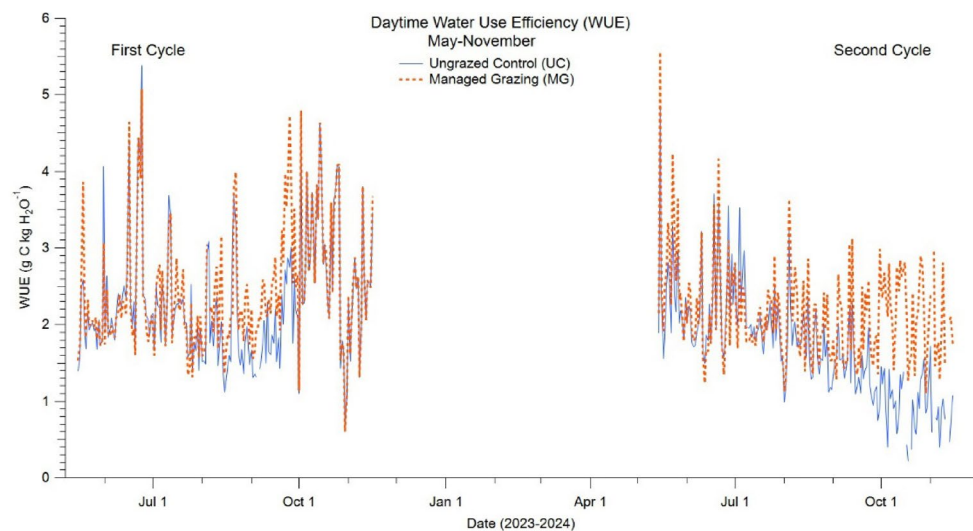


Fig. 10. Daytime water use efficiency (WUE) for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle). Half-hour data collected during daytime were summed by day between May and Nov.

and 2.10 ± 0.78 g C MJ⁻¹ for the UC and MG pastures, respectively, between May and November in the first cycle and was 1.40 ± 0.73 and 1.94 ± 0.70 g C MJ⁻¹ in the second cycle (Fig. S5). The MG pasture LUE was greater than the UC pasture in autumn during the second cycle, with a significant time $\times$ treatment interaction for field-based LUE ($F_{1,368} = 15.64$; $p < 0.0001$) and SNAP-based LUE ($F_{1,368} = 89.27$; $p < 0.0001$). There was no effect of treatment for the first cycle. The increase in LUE under managed grazing during autumn for the second cycle coincided with heavier animal feed (DM removal; Table 1). LUE calculated using SNAP LAI product overestimated LUE, as compared to LUE calculated using LAI collected in the field, but both sources of data reflect a trend toward relatively higher LUE for the MG pasture in autumn (Fig. 11, Supplementary Fig. S5).

Supplemental Figure S6 shows prediction of daytime GPP using absorbed photosynthetically active radiation (APAR) calculated using LAI collected in the field between May and November. Supplementary Figure S7 shows differences between cycles using APAR calculated using SNAP LAI. Slopes using APAR based on LAI collected in the field (2023: slope = 1.56, $R^2 = 0.94$; 2024: slope = 1.39, $R^2 = 0.92$) and from SNAP LAI data (2023: slope = 1.97, $R^2 = 0.95$; 2024: slope = 1.61, $R^2 = 0.94$) were greater in 2023 than in 2024.

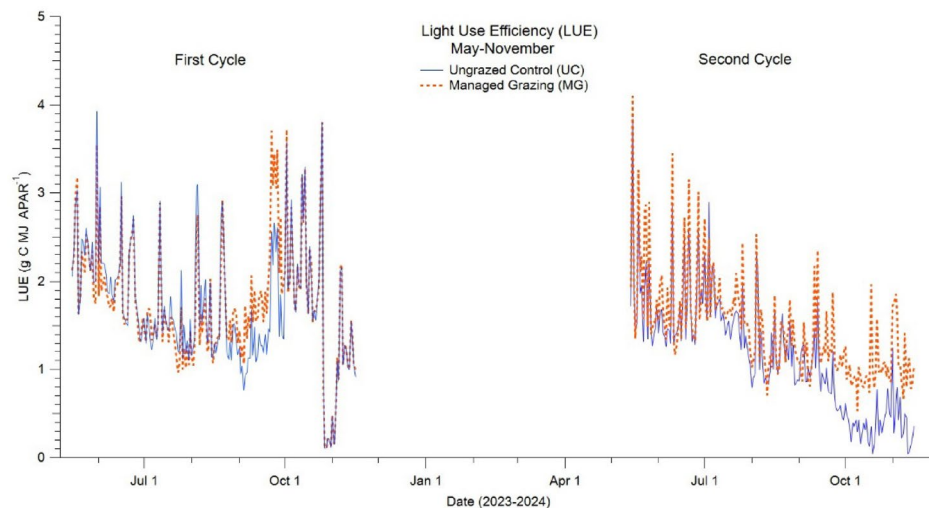


Fig. 11. Light use efficiency (LUE), using field-based estimates of LAI, for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle). Half-hour data collected during daytime were summed by day between May and Nov.

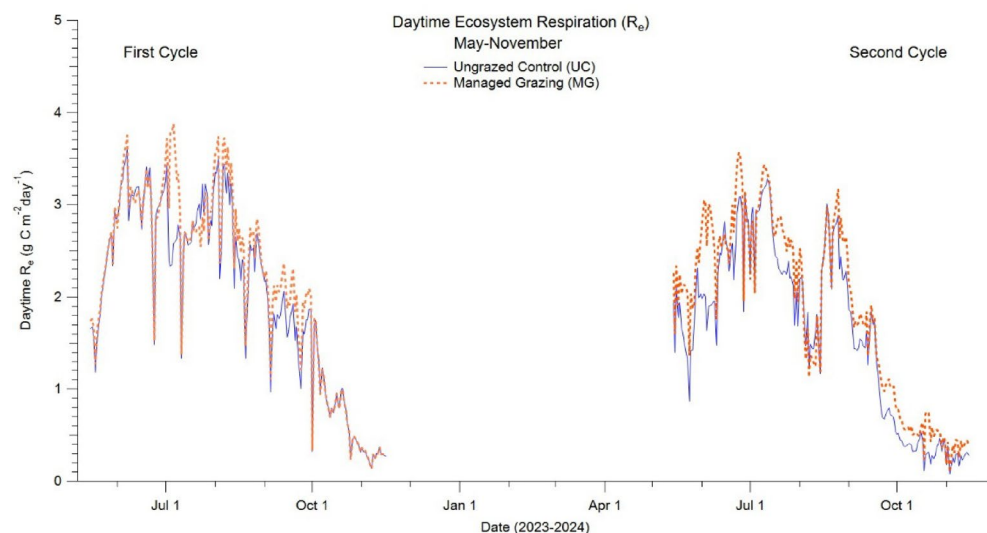


Fig. 12. Daytime ecosystem respiration (R_e) for managed grazing and ungrazed control pasture from May 15, 2023, to May 14, 2024 (first annual cycle) and from May 15, 2024, to May 14, 2025 (second annual cycle). Half-hour data collected during daytime were summed by day between May and Nov.

Figure 12 shows how ecosystem respiration (R_e) during the daytime only was not significantly affected by the grazing system treatment during the first cycle ($F_{1,368} = 3.11$; $p > 0.05$) but was affected by the grazing system treatment during the second cycle ($F_{1,368} = 12.77$; $p < 0.0005$). The response in the second cycle coincided with heavier animal feed (FC_{grazing}) and greater animal excreta (FC_{excreta}). Average daytime R_e was 2.02 ± 0.99 and 2.14 ± 1.05 $\text{g C m}^{-2} \text{ day}^{-1}$ at the UC and MG pastures, respectively, for the first cycle and was 1.61 ± 0.94 and 1.84 ± 0.97 $\text{g C m}^{-2} \text{ day}^{-1}$ for the second cycle.

Discussion

This report of net annual gains in ecosystem C adds to the body of evidence that well-managed, rotational grazing systems can lead to improvements in grassland health, including water quality³⁹, soil C stocks^{9,40} biodiversity^{41,42}, and flood reduction⁴³. Here, LAI was used as a metric to inform rotational grazing decisions instead of stocking rate⁴⁴ to better control biomass-C removal. Reported effects of grazing on soil C stocks vary widely in the literature^{24,45,46} which could, in part, arise from year-to-year variation in biomass-C removal by grazers. When stocking rate remains constant and plant production decreases, greater biomass-C is removed (FC_{grazing})—potentially resulting in a negative net annual C budget. In the two annual cycles reported here,

greater biomass-C removal during the second cycle negatively impacted the net annual C budget (Table 2). If the FC_{grazing} and FC_{excreta} terms had been similar both years, which were 0.35 and 0.14 Mg C ha⁻¹ yr⁻¹, respectively, in the first cycle, relative differences in C sequestration between UC and MG pastures would have likely been over 50% for both cycles. Monitoring FC_{grazing} or LAI is essential to C management for this type of AMP grazing system.

The net annual ecosystem C budget is strongly influenced by harvest methods and duration of grazing. Season-long grazing, for example, does not allow for plant recovery because cattle will preferentially graze the same plant species as new, green and tender leaves regrow. Season-long grazing and mowing often result in a negative net ecosystem C budget, with an average C loss of -29.9 g C m⁻² yr⁻¹ for grasslands, as compared to -110 g C m⁻² yr⁻¹ for croplands⁴⁷. A comparable, northern prairie, semi-arid grassland that was annually mowed for 4 years⁴⁸ lost an average of -137 g C m⁻² yr⁻¹, even though average annual precipitation during this study was 20% above the long-term average. Another, rotationally grazed paddock under irrigation²³, reported a net C gain of 103 g C m⁻² yr⁻¹. Our results corroborate reports that well-managed, rotationally grazing is a more effective C sequestration tool than mowing⁴⁹ and point to the cumulative weight of multiple management decisions (grazing duration and intensity^{19,21}, recovery⁵⁰, amount harvested¹¹) that influence the delicate balance between annual C gains and losses⁵¹.

Comparable grazing lands flux experiments, where the net annual ecosystem C budget is evaluated and animals are considered external to the system, are limited. This approach was applied by researchers in Switzerland using dairy cows on improved and fertilized grasslands⁵². In this instance, where average annual rainfall is 1075 mm, cumulative NEE during this one-year study was -248 g C m⁻² yr⁻¹. Other researchers in New Zealand used a similar approach to study an improved, fertilized, and irrigated dairy pasture for one year²³. Here, annual rainfall of 1014 mm was supplemented by 425 mm of irrigation, and cumulative NEE was -408 g C m⁻² yr⁻¹. At our unimproved, dryland site in North Dakota, where annual precipitation ranged from 390 to 558 mm, NEE during the first year under managed grazing was -122 g C m⁻² yr⁻¹. Flux tower and remote sensing-based data were modeled for grasslands of the U.S. Great Plains⁵³, and estimates for NEE were in the range reported here. The model did not include management, but NEE data collected between 2000 and 2008 ranged from -0.3 g C m⁻² yr⁻¹ to -47.7 g C m⁻² yr⁻¹, with an average of -24 g C m⁻² yr⁻¹. While management can significantly influence grassland NEE, NEE is more strongly controlled by precipitation than management.

Precipitation is the primary regulator of NEE in U.S. rangelands³⁴ and grazing lands globally⁵⁴. We found NEE was less negative (less C uptake) during the second, drier cycle for both pastures. Evidence of stress on plant growth for the second cycle was also evident in (a) the reduction in the response of daytime GPP and to an increase in absorbed photosynthetically active radiation (APAR)⁵⁵, (b) reductions in SLA, and (c) greater DM biomass removal for a given LAI. While both pastures received the same amount of precipitation each annual cycle, the relative magnitude in NEE between the first, wetter cycle and the second, drier cycle was more pronounced at the UC pasture. This is another indication that the managed grazing system more effectively used the limited amount of available water towards production than the ungrazed control. Others have found increases in WUE following defoliation at species⁵⁶ and plot¹⁹ scales, with the magnitude of this effect varying over time^{19,56}. This 14 and 16% increase in annual WUE indicated water was more efficiently conserved, and more water was allocated to plant production under this AMP system. Further, greater CUE for the MG pasture both cycles indicated the AMP managed grazing system more effectively converted CO₂ into biomass and storage than the ungrazed control.

This study focuses on short-duration grazing impacts on grasslands and does not evaluate the C footprint of grazers, including emissions of enteric CH₄, which vary with individual production system⁵⁷. Results pertain to impacts on grassland C, and any CH₄-C emissions would have originated from C harvested by grazers. The importance of organic C on soil health is well-known, and these results suggest managed grazing could enhance soil health by increasing ecosystem C. Funding restraints limited the system of interest such that cattle were external to the system and present only a few days each cycle, so any enteric CH₄-C emissions in this experiment originated from FC_{grazing} and may be negligible at an annual scale. If these emissions are considered using C accounted for in FC_{grazing} , published values can be applied to approximate enteric CH₄ emissions during grazing events. Based on enteric emissions of 200 g CH₄ head⁻¹ dy⁻¹⁵⁸, approximately 3% of biomass-C removed by grazers was likely transformed to CH₄ while these cattle were on this pasture.

Typically, extrapolation of field-study results from a single site depends on representativeness of the study area. Our study area is comprised of soil series that are extensive in North Dakota, with floristic composition of the two primary invasive species comparable to other grasslands in the region³¹ (see Supplemental Table S1, Table S2). Floristic composition recorded at 419 prairie sites in North Dakota indicate relative frequency of occurrence for invasives *P. pratensis* and *B. inermis* combined was 54%³¹, which is in the range reported here (51% and 58%). For species richness, we report a maximum of 37 unique species (Supplementary Results), which is lower than the 45 and 52 unique species reported for 26 paired sites in North and South Dakota⁵⁹. Timing and intensity of defoliation are factors known to alter C pools^{11,19,21,60}, and this unreplicated study links a single defoliation strategy to annual production and rates of C sequestration. The experiment was conducted on an actively managed working ranch to better reflect the operational realities faced by grassland managers and to incorporate producer-driven decision-making²⁴, which is uncommon in plot-scale or research station studies^{5,29}. We suggest site-specific limitations may partially be addressed by the observed compensatory response to grazing⁶¹, as previously reported at plant, plant community, and plot scales^{11,21,62,28}.

Temporal changes in NEE, LAI and resource-use efficiencies indicate plants recovering from grazing were more productive and more able to utilize water and light effectively to extend the growing season. Additional factors likely contributed to enhanced NEE, GPP, and WUE during the recovery phase in autumn, such as increased demand for photosynthate and translocation to roots following defoliation^{14,15,21}. Continued research into grazing-grassland feedback mechanisms at an ecosystem scale under variable weather conditions are needed

to better constrain impacts of management on the C budget. If relationships observed here between managed grazing, LAI, light, water, and production are consistent among other semi-arid regions for several cycles, then potential implications include improved C models, particularly those that evaluate grazing optimization as a climate mitigation opportunity^{7,63}. More accurate predictive models could inform policymakers, C marketers, and land managers interested in grassland health and nature-based C solutions⁸.

Grassland ecosystems worldwide rival forests in their capacity to sequester excess CO₂ below ground⁶⁴, and we show how a managed grazing system in North Dakota can enhance this function by stimulating plant production and WUE in autumn, a time when regrowth from previously defoliated plants allocate more carbohydrate reserves below ground^{14,16}. Differences between pastures in LAI, GPP, and NEE converged again near the beginning of October for the first cycle and near the beginning of November for the second cycle—data points representing cessation of compensatory growth in response to grazing and completion of the recovery phase. Continued work is needed to confirm if changes in LAI over time are reliable indicators of pasture recovery. If so, remote sensing-based tools, such as SNAP LAI, could be applied to assist with development of alternative, low-cost, C management and monitoring tools.

Seasonal dynamics observed here for both annual cycles show greater photosynthetic capacity, compensatory growth, and allocation of water to production—factors that contribute to grassland health and resiliency⁵⁶—occur near the end of the growing season. If LAI associated with compensatory growth were removed in autumn, prior to completion of recovery, the C sequestration benefit would have been negatively impacted. This multi-paddock approach to grazing native prairie, as described here, enhanced productivity and ecosystem C, but its effectiveness as a natural climate solution is highly dependent on the manager's ability to adapt to changing conditions. Rewarding managers that apply AMP to regenerate grasslands while supporting animal husbandry would lead to greater adoption of management that sequesters C and improves grassland health on working lands^{29,65}.

Materials and methods

Study site and herd management

Field research was performed on a historically native rangeland at the Heaton Home Ranch near McKenzie, North Dakota (46°56'34.49" N, 100°26'24.40" W). Two 20-ha pastures were instrumented within a 250-ha rangeland. The climate is semi-arid, with annual mean temperature and precipitation (1903–2023) of 5.6 °C and 420 mm, respectively. The pastures are historically native prairie, with no known history of tillage or seeding. Plant species cover is dominated by introduced species which is common among native prairie grasslands in the region^{31,33}. Cattle have moderately grazed this rangeland for over 50 years. The soils at the site are dominated by Williams-Bowbells loams, which consist of very deep well and moderately well drained soils formed in calcareous glacial till and alluvium from glacial till. Both Williams and Bowbells soil series are geographically extensive in the state⁶⁶. Prior to grazing, soil cores and vegetation cover data were collected to confirm pastures were comparable with respect to initial conditions for soil organic matter and vegetative cover (see Supplementary Materials Fig. S8, Fig. S9, Table S1).

One pasture was fenced for managed grazing (MG) and the other for ungrazed control (UC). The MG pasture, located 800 m north of the UC pasture, was fenced into five paddocks, and the UC paddock was fenced around its perimeter to form a single paddock (Fig. 1) using t-posts and 14-gauge wire. Near the center of each pasture, identical eddy covariance-energy balance (EC-EB) systems (*Campbell Scientific, Logan, UT*) were deployed in May 2023. The current study includes two annual cycles of data, from May 15, 2023, to May 14, 2025. Four of the MG paddocks were scheduled for short-term (24–48 h., Table 1), high-intensity (approximately 150 cow-calf pairs, Table 1) grazing, with each paddock grazed once at different times during the growing season to achieve 50% LAI removal. The southeast (SE) paddock was scheduled for grazing in spring, the southwest (SW) paddock in early summer, the northwest (NW) paddock in late summer, and the northeast (NE) paddock in autumn. The fifth paddock behind the EC-EB system was an area where data were excluded due to flux interference by instruments. The rancher moved cattle off the research paddock at night, between approximately 2100 and 0700, to ensure instruments were not disturbed by cattle.

The livestock used for this project are not part of a research herd but instead are privately owned. Livestock were handled exclusively by the rancher in accordance with animal husbandry practices refined through decades of range management experience. Herd size varied according to calving and breeding activities, from 95 to 165 cow-calf pairs (Table 1). Grazing dates and duration were planned but needed to be adjusted with weather conditions and the amount of forage available. Since paddocks were grazed at different times, we needed to account for differences among paddocks in vegetation height and incorporate these data into the flux calculation. These four paddocks are smaller (4–5 ha) than typically used by ranchers in production with a herd of 150 cow-calf pairs. Paddock configurations were constrained by existing fence lines, herd size, duration of grazing, and the flux footprint^{67,68}. Our goal was to simulate the Heaton Ranch managed grazing system while evaluating fluxes and the annual C budget for the entire MG pasture, as compared to the entire UC pasture.

Within each pasture, four transects were delineated that radiated from the EC-EB system in southeasterly, southwesterly, northwesterly, and northeasterly directions. Along each transect, permanent reference plots (3 m x 3 m) were marked every 20 m for a total of four plots per transect. These 16 reference plots per pasture were established for the purpose of collecting preliminary soil and vegetation cover data (see Supplementary Materials) to ensure pastures were comparable. Reference plots were also used for monitoring vegetation height, species, biomass, and LAI (Fig. 1). Plot location coordinates are provided in Supplementary Table S3. Field measurements occurred between snowmelt and snowfall, which were between May 1 and November 20, 2023, for the first annual cycle and between April 11 and November 16, 2024, for the second one.

For the purposes of this study, managed grazing consisted of (1) cattle graze the paddock for the duration necessary to remove approximately 50% of the available green LAI and (2) each paddock is grazed at a different

time during the growing season once per year. Grazing based on LAI removal is considered a regenerative practice because enough LAI remains to support plant recovery and increased production¹¹. After grazing, the herd is moved off the experimental pasture, so grazers are within the flux footprint < 3% of the year. As such, the amount of forage removed by grazers is considered C exported from the ecosystem, and neither fluxes during grazing nor cattle respiration are included in the net annual C budget (defined below).

In this experiment, grazers are treated as external to the system, where they serve as harvesters of C export through rapid removal of aboveground biomass and agents of C import through the deposition of dung and urine. Net ecosystem exchange (NEE) values are recorded by the eddy-covariance energy-balance (EC-EB) system. These NEE values are negative when plants remove CO₂ from the atmosphere during the daytime. When calculating the net annual C budget, net cumulative C flux (FC)²³, which is sometimes referred to as net ecosystem production⁵¹, is commonly defined as the opposite sign of NEE⁶⁹. In this instance, annual C gains through plant production are positive while annual C losses are negative. We account for C sequestered in vegetation from net ecosystem production (FC), in addition to C removed by grazers (FC_{grazing}), and C returned (FC_{excreta}) by livestock. The net annual C budget, or the amount of C retained by the ecosystem, from these fluxes are defined here as follows:

$$\text{Net Annual C Budget} = FC - FC_{\text{grazing}} + FC_{\text{excreta}} \quad (1)$$

$$FC = \text{Gross Primary Production (GPP)} - \text{Ecosystem Respiration (Re)} \quad (2)$$

where FC is the opposite sign of cumulative NEE, FC_{grazing} is dry biomass C removed by grazing, and FC_{excreta} is C imported by excreta on the pasture. Net ecosystem exchange is measured at high frequency (20 Hz) for daily and yearly flux calculations over the study pastures and does not include animal respiration^{23,60,61}.

All three variables are expressed in a unit of g C m⁻² yr⁻¹. In a grassland ecosystem, NEE is quantified by the EC-EB system^{23,70,71}. Carbon removed by grazing is estimated from biomass clippings collected before and after grazing events, which are then used, together with livestock intake assumptions, to estimate C returned to the pasture as excreta²³. Since grazers are external to the pasture ecosystem, C emitted by cattle as methane (CH₄) originates from the ingested biomass and is thus already counted in the C budget as an export term. Other fluxes, such as dissolved organic C losses, soil CH₄-C fluxes, and CH₄-C losses from decomposition of excreta are expected to be minor in this dryland system and are not included here^{22,23,72}.

Instruments and setup

A duplicate set of instruments were procured at the same time for this study, so that both UC and MG pastures were set up with the same package of two open-path eddy-covariance flux systems along with micrometeorological and energy balance sensors comprising the EC-EB system (Supplementary Table S4) and the software of EasyFlux_{CR1000X} (Campbell Scientific Inc, 2020) was customized specifically for footprint analysis of different MG paddocks. The EC-EB systems measure the fluxes of CO₂, water vapor, sensible heat, and momentum along with energy balance terms. Each system consists of a three-dimensional sonic anemometer equipped with an open-path CO₂-H₂O infrared gas analyzer as a single system (IRGASON, Campbell Scientific, USA). This was mounted 2.5 m above the ground in both pastures. This height was determined based on footprint analysis, given average grassland canopy heights varying from 0.1 to 0.4 m. The anemometer and the analyzer digitally output high-frequency fluctuations in 3-D wind velocities, sonic temperature, water vapor and CO₂ densities. The data were collected at 20 Hz, and averaged every 30 min, which were stored in a MicroSD card of CR1000X Datalogger (Campbell Scientific Inc., UT, USA). The gas analyzers were factory calibrated at the beginning of the experiment, and CO₂ and H₂O zero values were checked monthly in the field. Both values were zeroed and spanned whenever the values significantly drifted⁴⁴. Along with the flux measurements, we continuously measured standard meteorological and soil parameters with an array of sensors. Air temperature and relative humidity were measured with a temperature and relative humidity probe mounted on the tower at the height of 2.5 m for dew point and vapor pressure deficit calculations. Soil temperature and moisture for computation of soil heat fluxes at the surface were measured at 8 cm soil depth, and soil heat flux plates were placed 16 cm beneath the surface (Campbell Scientific, HFP01 Manual, Fig. 7–1). Net radiation, along with its four components, is measured by the NR01 net radiometer. Precipitation was measured by a tipping bucket rain gauge at a height of 1.5 m. Photon flux density was measured 2.0 m above the ground using a quantum sensor. The instruments and measurement parameters used in this study are listed in Supplementary Table S4.

Vegetation sampling

Plant biomass and LAI data were collected monthly, from May to November, at the 32 reference plots designated in Fig. 1 using a frame (0.3 m × 0.2 m) thrown blindly within each plot. Attached vegetation was clipped to within 2 cm near the soil surface and kept cool before separating into green and senescent vegetation groups. Unattached vegetation (litter) was removed by hand and placed in a separate bag. Immediately after separating green from senescent vegetation, LAI was determined by using a leaf area meter LI-3200 (LICOR Biosciences, NE, US). All samples were weighed for green mass and dried at 60 °C until constant weight to determine dry matter (DM) biomass prior to grinding in preparation for laboratory analyses of C, nitrogen, and digestibility. The ratio of LAI to DM was used to determine specific leaf area (SLA), an indicator of water stress⁷³.

Models using imagery data collected at the sensor onboard satellite platforms provide tools for grassland productivity assessment of large landscapes⁷⁴. So, we modeled LAI collected from Sentinel-2 at the 16 plots per pasture using Sentinel Application Platform (SNAP)³⁸ at 10-m spatial resolution to determine if seasonal changes in LAI occurred using both field and image-based data. Images were collected May 30, June 14, July 2, 9, Aug 28, Oct 7, and Nov 11 in 2023, and April 9, 12, 24, May 29, June 23, July 3, 11, 18, Aug 10, 30, Sept 26,

Oct 21, and Nov 13 in 2024. The LAI product was calculated using SNAP^{38,75}. Plant biomass and LAI were also collected in the field before and after each grazing event to determine the amount of biomass harvested by cattle and the fraction of LAI removed, which required additional data points for the grazed paddock. Two additional transects were identified along either side of the original transect for a total of 12 plots. Data were collected for these before and after each grazing event. The difference in green biomass and LAI before and after each grazing event was used to calculate C exported by cattle and C deposited in dung and urine²³.

Canopy height (h_c) was measured every 10–21 days at the 32 reference plots, with greater frequency during the growing season. Average in h_c values by paddock were entered into the EasyFlux datalogger program (Campbell Scientific Inc., 2020) program. EasyFlux considers the influence of h_c on zero-plane displacement height (d), according to Eq. 4.5 in Rosenberg, et al. (1983)⁷⁶:

$$d = 10^{0.979 \log 10 h_c - 0.154} \quad (3)$$

Typically, the average h_c at a specific time point is similar throughout a flux footprint. The multi-paddock approach required accounting for variations in h_c among paddocks, so we modified the EasyFlux program by allowing assignment of unique values of h_c for each paddock. In flux computations, d from h_c is used to compute aerodynamic height (i.e., measurement height minus d). The aerodynamic height is a parameter in cospectrum of vertical wind with CO₂, H₂O, or air temperature⁷⁷. The cospectra is used for flux frequency correction⁷⁸. The zero-plane displacement height d also is a parameter in flux footprint Eqs. ^{67,68}. The flux footprint equations are used for footprint analysis in flux measurements⁷⁹. The upwind distribution of interest for each paddock was configured in the program according to Fig. 1. Values for d were calculated according to these assigned values of h_c by paddock. Both UC and MG dataloggers used the modified EasyFlux program. The multi-paddock approach required accounting for variations in h_c among paddocks, so the EasyFlux program could ensure the quality of the data in each paddock.

Calculations

Treating the grazers as external to the pasture ecosystem results in exclusion of data collected when grazers are present. Therefore, excluded CO₂ exchange data during grazing events were replaced with modeled estimates of NEE using an established gap-filling method. Respired CO₂ by grazers and CH₄ emitted by grazers originate from the grazed biomass and so are not specified in Eq. 1.

Annual FC was calculated from gap-filled flux data. The uncertainties of NEEs were determined from combined random and systematic uncertainties. Random uncertainty was estimated from varying the input data before gap filling (adding random noise or additional gaps) and systematic uncertainty was estimated from varying the applied selection threshold for stable turbulence conditions (frictional velocity u^* filtering). In these budget calculations, we neglect C loss due to leaching and erosion because they could not be measured in this experiment and are assumed to be very small for dryland pastures, as compared to the major fluxes.

Ecosystem GPP is correlated with the amount of photosynthetically active radiation (PAR) that is absorbed by the plant canopy (APAR; MJ m⁻² day⁻¹)⁵⁵, calculated as the daily sum, where

$$GPP = APAR \times LUE = PAR \times fAPAR \times LUE \quad (4)$$

and LUE is light use efficiency (g C MJ APAR⁻¹).

A daily sum of APAR was calculated by summing incident PAR for each 30-min interval over the daylight period by an estimate for the fraction of PAR absorbed by the plant canopy ($fAPAR$). The $fAPAR$ was calculated from seasonal trajectories in LAI using the Beer–Lambert Law:

$$fAPAR = 0.95 (1 - e^{-kLAI}) \quad (5)$$

where k is the radiation extinction coefficient and 0.95 is the proportion of intercepted PAR that is

absorbed by plants⁸⁰. We used the Polley et al. (2011)⁵⁵ model developed using data for multiple rangeland sites in the Great Plains and multiple site-years to estimate the extinction coefficient k , which allows k to vary rather than remain static according to the following:

$$k = 0.30 + 1.28 e^{(-2.70LAI)} \quad (6)$$

Allowing k to vary more closely approximated extinction coefficient calculated using PAR measurements collected at a single point near the instrument array both above and below the plant canopy.

The value for LUE each day between May 15 and Nov 16 each annual cycle was determined by dividing the sum of daily GPP during the daylight period by the sum of daily APAR.

Water use efficiency (g C kg H₂O⁻¹) was defined as follows:

$$WUE = GPP/ET \quad (7)$$

Carbon use efficiency (CUE) was determined on an annual basis using cumulative NEE (Mg C ha⁻¹ yr⁻¹), cumulative FC (Mg C ha⁻¹ yr⁻¹), and cumulative GPP (Mg C ha⁻¹ yr⁻¹) as follows:

$$CUE = \frac{FC}{GPP} = \frac{NEE}{GPP} \quad (8)$$

Data processing and quality control

Flux data were discarded for wind direction between 15° and 345° in the sonic anemometer coordinate system (where equipment obstructed wind turbulent flows), insufficiently developed turbulence⁷¹, CO₂ flux stationarity criterion⁸¹, and low friction velocity. The ReddyProc online tool was applied for processing flux data because it provides standardized methods⁸² for quality checks, gap-filling, and partitioning flux data into GPP and R_e (www.bgc-jena.mpg.de/bgi/index.php/Services/REddyProcWeb)⁸². The gap filling and flux partitioning tool in ReddyProc uses gap size dependent, adaptive look-up tables of meteorological conditions (radiation, water vapor pressure deficit, and latent heat flux), and temporal autocorrelations to fill gaps in the CO₂ flux dataset⁸³. For the partitioning of NEE into R_e and GPP the Reichstein et al. (2005)⁶⁹ procedure models R_e as a function of soil temperature based on nighttime fluxes using the Lloyd and Taylor equation followed by extrapolation to daytime. GPP was determined by subtracting the parameterized daytime ecosystem respiration (R_e) from the gap filled NEE datasets.

Dung and urine carbon imports

Excreta C inputs were estimated from published values and established methods. Total dung and urine deposited by grazing animals was calculated²³ using known values, based on herd size, the amount of dry matter removed at each grazing event, and the number of hours cattle grazed on each paddock. Digestibility and crude protein were determined on dry matter collected prior to each grazing event, and digestibility was based on percent digested over a 48-hour incubation (Dairyland Laboratories, Wisconsin, US). We used published values for carbon in urine (12 g C l⁻¹) and dung (41.5% C), with 2 L per urination and 10 urinations per day per pair²³.

Ethics declaration

Appropriate permissions were obtained from the landowner to enter the study area and for the collection of any plant and soil material. Vegetation surveys were recorded in the field by a team led by Sara Simmers of Meadowlark Environmental (North Dakota, U.S.), but no recorded species were on the list of Species at Risk of Extinction. We fully complied also with the IUCN Policy Statement on Research Involving Species at Risk of Extinction and the Convention on the Trade in Endangered Species of Wild Fauna and Flora. A voucher specimen was not collected and was not deposited in a publicly available herbarium. All experimental protocols were approved by the Attending Veterinarian in charge of Institutional Animal Care and Use Committee (IACUC) protocol development at North Dakota State University, where it was determined that IACUC was not required. All methods were carried out in accordance with relevant guidelines and regulations.

Statistics

Statistical tests for differences between pastures in SOC, Field-LAI, SNAP-LAI, and DM biomass were performed in SAS using a repeated measure, mixed analysis of variance, with plot is nested within paddock and pasture. Daytime sums between May 15 and November 16 each annual cycle were also evaluated for effects of treatment and time using a repeated measure, mixed analysis of variance (SAS Institute, Cary, ND). Each model included tests for effects of grazing treatment, time, and treatment x time interaction. The interaction was retained in each model where $p < 0.1$.

Data availability

The data that support the findings of this study and the program used for data collection are available from the corresponding author, R.L. Phillips, following a 6-month embargo from the date of publication.

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Declarations

Competing interest

The authors submit that there are no competing interests.

Additional information

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