

REVIEW

Grassland soil carbon sequestration: Current understanding, challenges, and solutions

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Grasslands store approximately one third of the global terrestrial carbon stocks and can act as an important soil carbon sink. Recent studies show that plant diversity increases soil organic carbon (SOC) storage by elevating carbon inputs to belowground biomass and promoting microbial necromass contribution to SOC storage. Climate change affects grassland SOC storage by modifying the processes of plant carbon inputs and microbial catabolism and anabolism. Improved grazing management and biodiversity restoration can provide low-cost and/or high-carbon-gain options for natural climate solutions in global grasslands. The achievable SOC sequestration potential in global grasslands is 2.3 to 7.3 billion tons of carbon dioxide equivalents per year ($\text{CO}_2\text{e year}^{-1}$) for biodiversity restoration, 148 to 699 megatons of $\text{CO}_2\text{e year}^{-1}$ for improved grazing management, and 147 megatons of $\text{CO}_2\text{e year}^{-1}$ for sown legumes in pasturelands.

Grassland ecosystems cover an area of 52.5 million km^2 , accounting for ~40.5% of the Earth's land surface excluding Greenland and Antarctica (1). Grasslands provide habitats for biodiversity, contribute to food production, and deliver many cultural services (1). They also store ~34% of the terrestrial carbon stock (1), with ~90% of their carbon stored belowground as root biomass and soil organic carbon (SOC), thus playing a vital role in soil carbon sequestration (1, 2). However, grasslands are highly vulnerable to human disturbance (e.g., overgrazing and land-use conversion to agriculture) and climate change (1–3). Worldwide, grasslands have undergone severe decreases in biodiversity and ecosystem functions, leading to reductions in SOC storage (2, 4, 5). Here, we review the recent advances in our understanding of SOC dynamics, current challenges, and possible solutions to enhance SOC sequestration in global grassland ecosystems. We address three questions: (i) How do key biotic and abiotic factors regulate grassland SOC formation, turnover, and stability?; (ii) how do climate warming, alterations in precipitation, and fire affect SOC storage?; and (iii) how does grazing management affect SOC and how can improved practices result in SOC sequestration?

Mechanisms and drivers of SOC sequestration

In grassland ecosystems, ~60% of net primary productivity is allocated belowground (6). Belowground carbon inputs are more often incorporated into SOC than aboveground inputs because of their chemical composition (e.g., aliphatic compounds and root exudates)

and their presence in the soil (Fig. 1) (6). On average, root carbon inputs have a SOC stabilization efficiency that is five times greater than aboveground carbon inputs (6).

Organic carbon in soil is distributed between particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions,

with only a minor portion (1 to 2%) present as dissolved organic matter. POM and MAOM differ in their formation, physical and chemical properties, and mean residence times in soil (7, 8). POM is formed from the fragmentation of plant and microbial residues, and therefore is composed of lightweight fragments made of large polymers (Fig. 1). MAOM, by contrast, is formed from single small molecules that are leached from plant residues or exuded from plant roots, which associate to minerals directly (ex vivo) or after microbial assimilation (in vivo) as microbial necromass (7, 8). MAOM on average has a lower carbon:nitrogen ratio because of its proportionally higher microbial origin, its longer mean residence time in soils (from decades to centuries) compared with POM (<10 years to decades), and its strong chemical bonding to minerals and physical protection in fine aggregates (7, 8). Therefore, MAOM contributes to longer-term carbon sequestration in soil. Root exudates such as dissolved sugars, amino acids, and organic acids are the key pathway to MAOM formation largely through microbial in vivo transformations (Fig. 1) (8, 9). Plant aboveground, root, and rhizodeposition inputs exhibit different

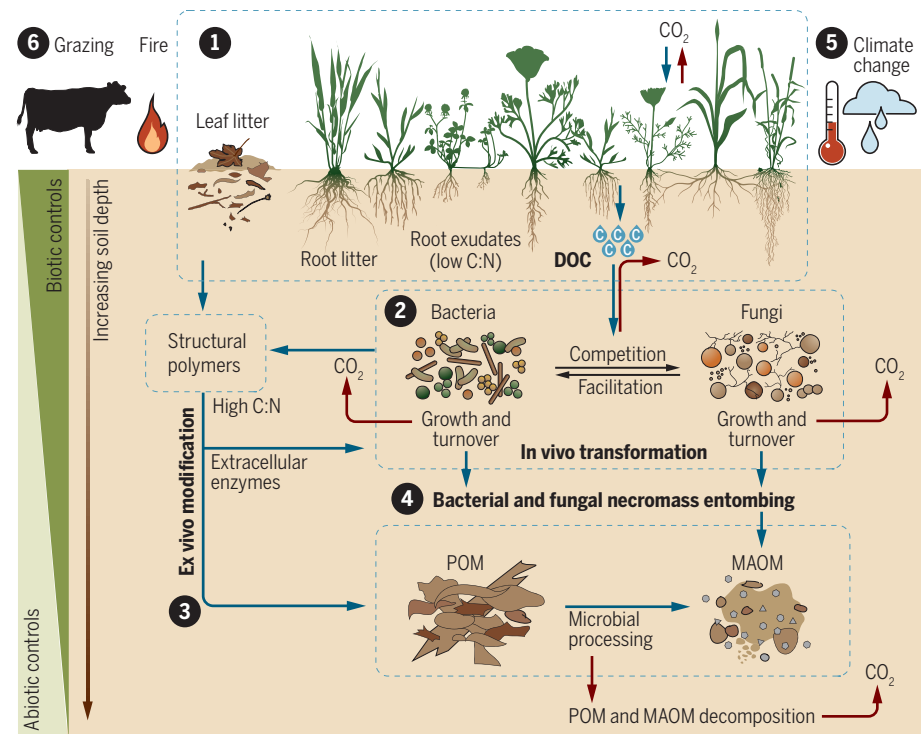


Fig. 1. Conceptual framework for key factors and mechanisms controlling SOC sequestration in grassland ecosystems. (1) Plant diversity controls on productivity, biomass allocation, and SOC inputs through litter and root exudates (6, 13, 14). (2) Key pathway of MAOM formation through microbial in vivo transformation (8, 17). (3) Pathway of POM formation through microbial ex vivo modification (8, 17). (4) Microbial necromass carbon (C) accumulation in MAOM (9, 11). (5) Climate change impacts on SOC sequestration through plant and microbial pathways (26, 28). (6) Grazing and fire impacts on SOC storage through pathways of plant and animal waste C inputs, compaction, and bioturbation (e.g., trampling and wallowing), microbial in vivo transformation, and microbial ex vivo modification (33, 36, 38, 46). C:N, carbon:nitrogen ratio; DOC, dissolved organic carbon.

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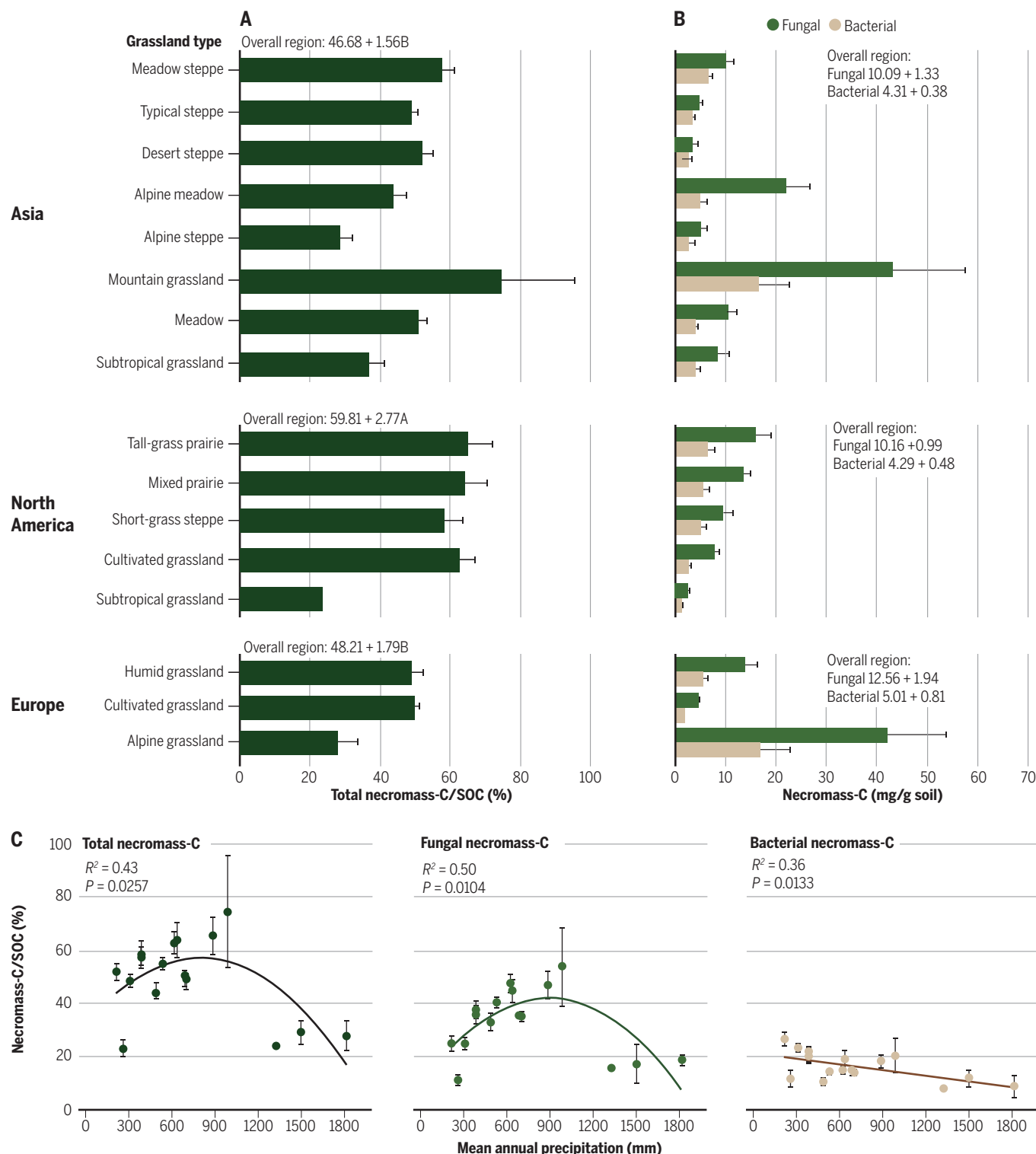


Fig. 2. Patterns and climatic drivers of microbial necromass contribution to SOC. (A) Microbial necromass C contribution to SOC. (B) Fungal and bacterial necromass C concentrations. (C) Relationships of total microbial, fungal, and bacterial necromass C contributions to SOC with mean annual precipitation in the topsoil of grassland systems in Asia, North America, and Europe. Data are from Liang *et al.* (17) and Wang *et al.* (18). Only the topsoil microbial necromass C and corresponding SOC data ($n = 223$) were used for global and regional synthesis. All data were classified into different grassland types within regions on the basis of sampling site information from the original study, Asia (eight grassland types,

$n = 122$), North America (five grassland types, $n = 47$), and Europe (three grassland types, $n = 54$). Within each grassland type, mean and standard error for each variable were calculated across different sampling sites. General linear model analyses were performed to explore whether the total microbial necromass C contribution to SOC and fungal and bacterial necromass C concentrations differ among different regions. Values with different letters are significantly different at the $P < 0.05$ level. Simple linear regression was used to analyze the relationship of mean annual precipitation with fungal, bacterial, and total microbial necromass C contributions to SOC across all grassland types on the global scale.

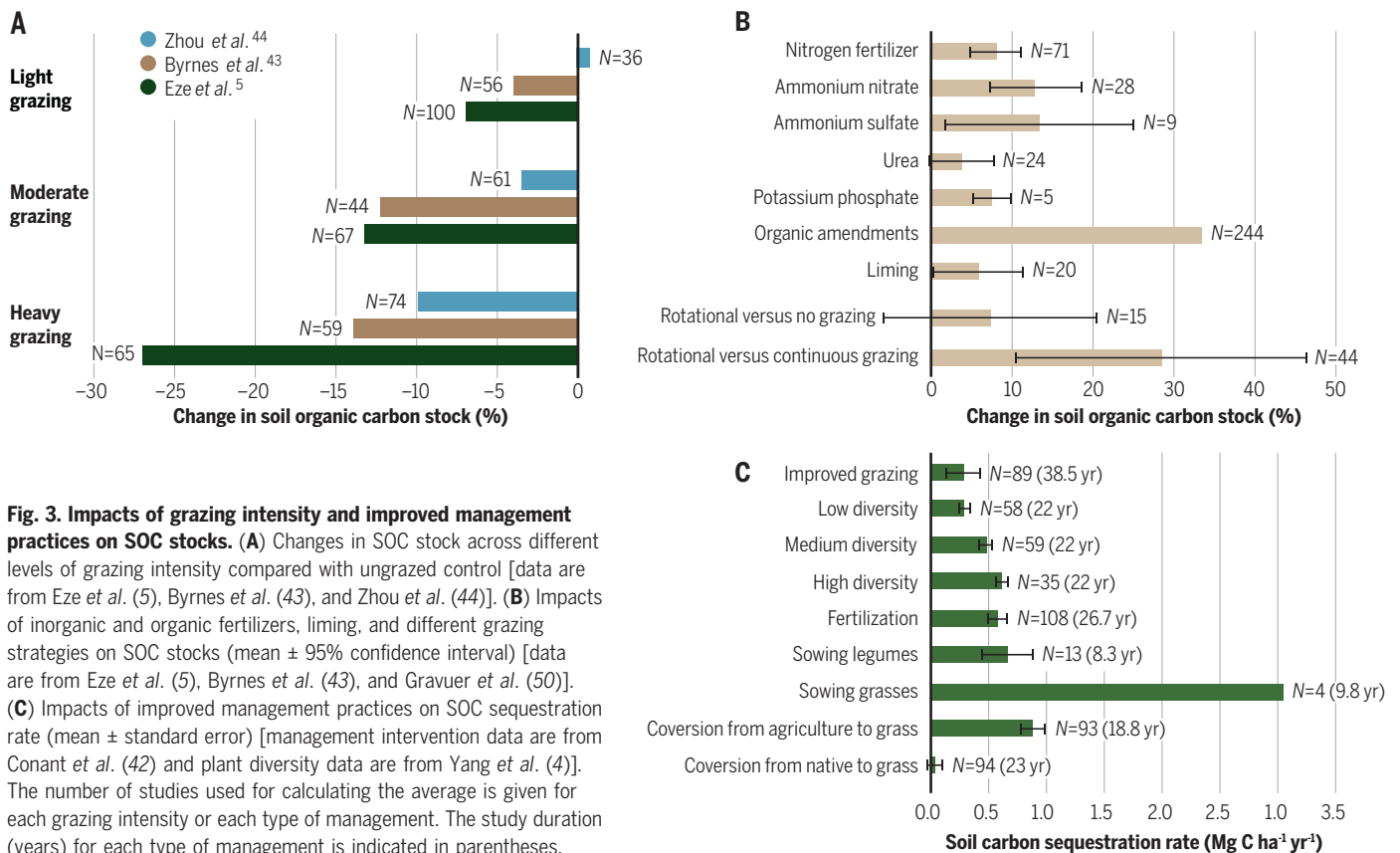


Fig. 3. Impacts of grazing intensity and improved management practices on SOC stocks.

(A) Changes in SOC stock across different levels of grazing intensity compared with ungrazed control [data are from Eze *et al.* (5), Byrnes *et al.* (43), and Zhou *et al.* (44)]. (B) Impacts of inorganic and organic fertilizers, liming, and different grazing strategies on SOC stocks (mean \pm 95% confidence interval) [data are from Eze *et al.* (5), Byrnes *et al.* (43), and Gravuer *et al.* (50)]. (C) Impacts of improved management practices on SOC sequestration rate (mean \pm standard error) [management intervention data are from Conant *et al.* (42) and plant diversity data are from Yang *et al.* (4)]. The number of studies used for calculating the average is given for each grazing intensity or each type of management. The study duration (years) for each type of management is indicated in parentheses.

POM and MAOM formation efficiencies. Approximately 46% of root exudates, 9% of root tissues, and 7% of aboveground carbon residues are transformed into MAOM, whereas 19% of root litter is transformed into POM across crops, grasses, and trees growing in the field and under controlled laboratory conditions (10). Thus, plants with greater carbon allocation to roots contribute more to soil carbon sequestration, particularly the formation of MAOM. However, it remains largely unclear how the contributions of roots (root exudates and root litter) and aboveground inputs to SOC accumulation (POM and MAOM) change with grassland types, soil properties, and climate conditions.

In grassland topsoils, 50 to 75% of SOC is found in MAOM. The average carbon:nitrogen varies from ~10 to ~12 for MAOM and from ~16 to ~18 for POM (3); therefore, the accrual of SOC in MAOM requires substantially greater nitrogen than the equivalent accrual in POM (11). The formation of POM is primarily driven by climate (temperature and precipitation). By contrast, the accumulation of MAOM is controlled by soil properties such as silt and clay content, cation-exchange capacity, and microbial nitrogen availability, which means that it may saturate (8, 12). In European grasslands, topsoil carbon storage in MAOM saturates at ~50 g C kg⁻¹ soil, beyond which the additional increase in SOC storage completely depends

upon accrual in POM (11). Currently, most European grasslands (80%) are below saturation, indicating a large capacity for SOC sequestration in their topsoils (11).

Plant diversity is a key driver of SOC formation and storage (4). High plant diversity enhances SOC storage by elevating belowground carbon (i.e., root biomass and root exudates) inputs (13, 14) and promoting microbial growth, turnover, and entombment of necromass (15). Maintaining consistently high levels of biodiversity and root carbon inputs is essential for enhancing SOC storage and persistence in grasslands (Fig. 1).

Fungi and bacteria have a strong influence on SOC accumulation, stabilization, and turnover in grasslands (Fig. 1), as in other terrestrial ecosystems (6, 16). Microbial necromass plays an important role in SOC accumulation and stabilization (9, 17). In the topsoil of global grasslands, the contribution of the microbial necromass to total SOC ranges from 23 to 74%, with an average of 50% (Fig. 2A), which is greater than its contribution in agricultural and temperate forest soils (17, 18). The contribution of necromass to SOC changes with soil depth (18) and is typically dominated by fungal necromass, with the fungi-to-bacteria necromass carbon ratio ranging from 1.2 to 4.1 across global grasslands (Fig. 2B). This is likely because fungi produce more chemically

recalcitrant structural compounds and have greater carbon use efficiency than bacteria (6, 16). Moreover, mycorrhizal fungi, which live in association with plant roots and derive their carbon directly from the plant, can regulate the carbon sequestration capacity in soil. Carbon sequestration capacity per unit nitrogen in soil is 1.7 times greater in ecosystems dominated by ectomycorrhizal fungi-associated plants (e.g., savannas, shrublands, and forests) than in systems dominated by arbuscular mycorrhizal fungi-associated plants (e.g., nonwoody grasslands) because ectomycorrhizal fungi can produce enzymes to degrade organic nitrogen from plant litter (19). However, MAOM is relatively higher in ecosystems that are dominated by arbuscular mycorrhizal fungi (13), such as grasslands.

Climate regulates the metabolic activity of microbes and thus controls large-scale patterns of microbial necromass and SOC storage (18, 20). At the global scale, cold, moist soils promote the accumulation of microbial necromass carbon. The maximum microbial necromass carbon occurs at a mean annual precipitation of 900 to 1000 mm with a mean annual temperature <0°C (Fig. 2C), indicating high priorities for preserving the current stocks in these systems. Few studies have measured the contribution of microbial necromass carbon to SOC in grassland soils, and data are lacking from

Africa, South America, and Australia (17, 18, 20). Microbial diversity may also affect SOC storage by regulating the efficiency of microbial assimilation of carbon and the production of organo-mineral associations in soils (21). Recently, microbial diversity was found to promote the stabilization efficiency of grass litter-derived POM but to reduce that of MAOM (22).

Climate change impacts on SOC sequestration

Sixty-seven percent of the world's grasslands are distributed in semiarid, arid, and cold climates, with only 23% occurring in humid climates (1). Thus, carbon sequestration in most grasslands is highly sensitive to climate change, which can exert strong and diverse impacts on SOC accrual and stability through plant- and microbial-mediated mechanisms (8). The impacts of climate change on soil carbon sequestration often vary with grassland type, climate, and soil conditions. In semiarid steppe, warming may enhance root-derived carbon input but inhibit the decomposition of MAOM by suppressing fungal growth and soil respiration, resulting in an increase in the MAOM pool (23). In humid tallgrass prairies, warming may increase C₄ grass cover and C₄-derived carbon input into soil organic matter, but it also increases the decay rate of these fractions, resulting in a negligible change in soil carbon sequestration (24). In alpine grasslands, warming-induced permafrost degradation reduces active-layer SOC storage by decreasing the stability of microbial networks and accelerating SOC (and specifically POM) decay (25). A recent meta-analysis demonstrated that long-term (≥5 years) warming increases the ratios of ligninase to cellulase activity and enhances microbial utilization of recalcitrant carbon, leading to a 14% reduction in the topsoil recalcitrant carbon pool (26). However, warming may increase the accumulation of root-derived carbon in the subsoil MAOM pool (27). POM is much more climate sensitive than MAOM (3, 11). The percent change in POM (-12.2%) with climate warming is on average three times greater than that in MAOM (-3.8%) in global grasslands (28). This suggests that grasslands with a high proportion of MAOM will contribute less to soil carbon-climate feedbacks.

Future projected precipitation anomalies and long-lasting droughts (29, 30) will likely influence soil carbon sequestration of grassland ecosystems by altering plant community composition, productivity and carbon allocation, and microbial processes. In the semiarid steppe, increased precipitation promotes soil aggregation by stimulating fungal growth and increasing soil-exchangeable magnesium (23). Precipitation anomalies (increases and decreases) can substantially alter root-to-shoot ratios and vertical root distribution in grasslands (31), thus regulating soil microbial growth and SOC storage. Reduced precipitation strong-

ly suppresses oxidase activity, whereas higher precipitation stimulates the activity of nitrogen-acquisition extracellular enzymes (32). However, on the global scale, only a negative tendency for POM and a positive tendency for MAOM and total SOC concentrations with increased precipitation were observed in grasslands because of the limited data availability (28).

Climate change-induced increases in fire frequency can substantially modify long-term SOC storage in grasslands, particularly in savanna grasslands, by intensifying nutrient limitation, which suppresses plant growth and carbon inputs. Elevated fire frequencies reduce soil carbon stocks on average by 0.21 megagrams of carbon per hectare per year (Mg C ha⁻¹ year⁻¹) in the upper soil layer (0 to 20 cm) in global savanna grasslands (33). However, a recent study showed that fire suppression (i.e., >60 years of fire exclusion) has little effect on total SOC storage (0 to 60 cm) in tropical savannas because C₄ grass-derived carbon dominates the SOC, particularly in deeper soil layers, where soil carbon is less affected by changes in fire frequencies (34). It remains unclear to what extent different fire regimes regulate plant diversity, above- and belowground biomass allocation, microbial-mediated processes, and SOC storage in shallower and deeper soil profiles.

Impacts of grazing pressure on grassland soil carbon

Natural grasslands are grazed by wild ungulates, which can enhance SOC storage because they graze for short periods of time and move across the landscape. This results in maintained plant cover, diversity and productivity, promotion of species with deep roots, microbial processing with the formation of both POM and MAOM, and soil-mixing processing by soil fauna (35, 36). Increases in ecosystem metabolism and plant labile carbon inputs (e.g., root exudates) are expected to increase both the ex vivo and in vivo formation of MAOM (9, 10, 37). Conversely, increased root inputs and allocation to depth result in higher POM in the subsoil (6, 38). In addition, large herbivores create habitats for many bioturbators (e.g., fossorial mammals and soil macrofauna) to loosen up soil and expose larger aggregates of soil organic matter to organo-mineral interaction by vertical soil mixing (36). However, both the direction and magnitude of effects of large wild herbivores on soil carbon storage can vary strongly with soil nutrient availability, across grasslands, and under different levels of herbivore density. For example, a recent short-term study suggested that nutrient availability strongly moderates the impact of herbivore grazing on soil carbon sequestration in herbaceous grasslands (39). Large herbivore grazing increases the upper-layer soil carbon storage under elevated nutrient (fertilization) conditions but has no effect

on soil carbon storage under ambient nutrient conditions (39). Sandhage-Hofmann *et al.* (40) report that elevated elephant densities enhance SOC stocks [4.7 tons (t) ha⁻¹] despite losses of woody biomass in moist, semiarid, wood-encroached savannas of south-central Africa. However, a synthesis of 174 experiments showed that large herbivore exclusion generally increases SOC storage across different biomes (grassland, forest, shrubland, tundra, woodland, etc.), suggesting an overall negative impact of large wild herbivores on soil carbon storage (41).

Livestock grazing is the most common use of grasslands worldwide. Some grasslands are managed to improve forage quantity and quality, thereby increasing livestock production and/or SOC storage (1, 2, 42). In livestock-dominated systems, these pathways are strongly controlled by grazing intensity and rest periods. Continuous livestock grazing reduces plant cover, diversity, and productivity, and thus root inputs and plant- and microbial-mediated SOC formation, while stimulating losses through microbial turnover and erosion caused by increased compaction and reduced cover (1, 2, 43). Eze *et al.* (5) demonstrated that livestock grazing on average decreases SOC stock by 15% across five continents, with the greatest reduction (-22.4%) in SOC stock in the tropics and the least reduction (-4.5%) in temperate grasslands. At the global scale, light grazing (e.g., seasonal and rotational grazing) shows the least negative effects or even promotes soil carbon storage, whereas moderate and heavy (continuous) grazing consistently reduces soil carbon stocks (Fig. 3A) (5, 43, 44). For a given category of grazing intensity, the discrepancy in magnitude of changes in SOC stocks between these studies may partly arise from the lack of quantitative measures of grazing intensity and the difference in data sources (5, 43, 44). Nevertheless, the magnitude and directions of grazing impacts on soil carbon sequestration are context dependent and vary with climate and soil conditions, vegetation properties, livestock type, herbivore diversity, grazing strategies (e.g., continuous versus rotational grazing), and grazing intensity and duration (5, 38, 43-45). The negative impact of increasing grazing intensity on SOC is lessened with greater water availability (5, 44) but is more severe with warmer temperatures and longer grazing duration in temperate grasslands (44). With moderate and heavy grazing, SOC increases in grasslands dominated by C₄ species and decreases in grasslands dominated by C₃ species (45). Sheep grazing generally has a greater negative impact on SOC than cattle grazing, and the reduction in SOC with grazing is substantially greater in topsoil than that in subsoil (44). A mixed cattle and megaherbivore system was shown to be a sustainable management strategy in African savanna ecosystems with high

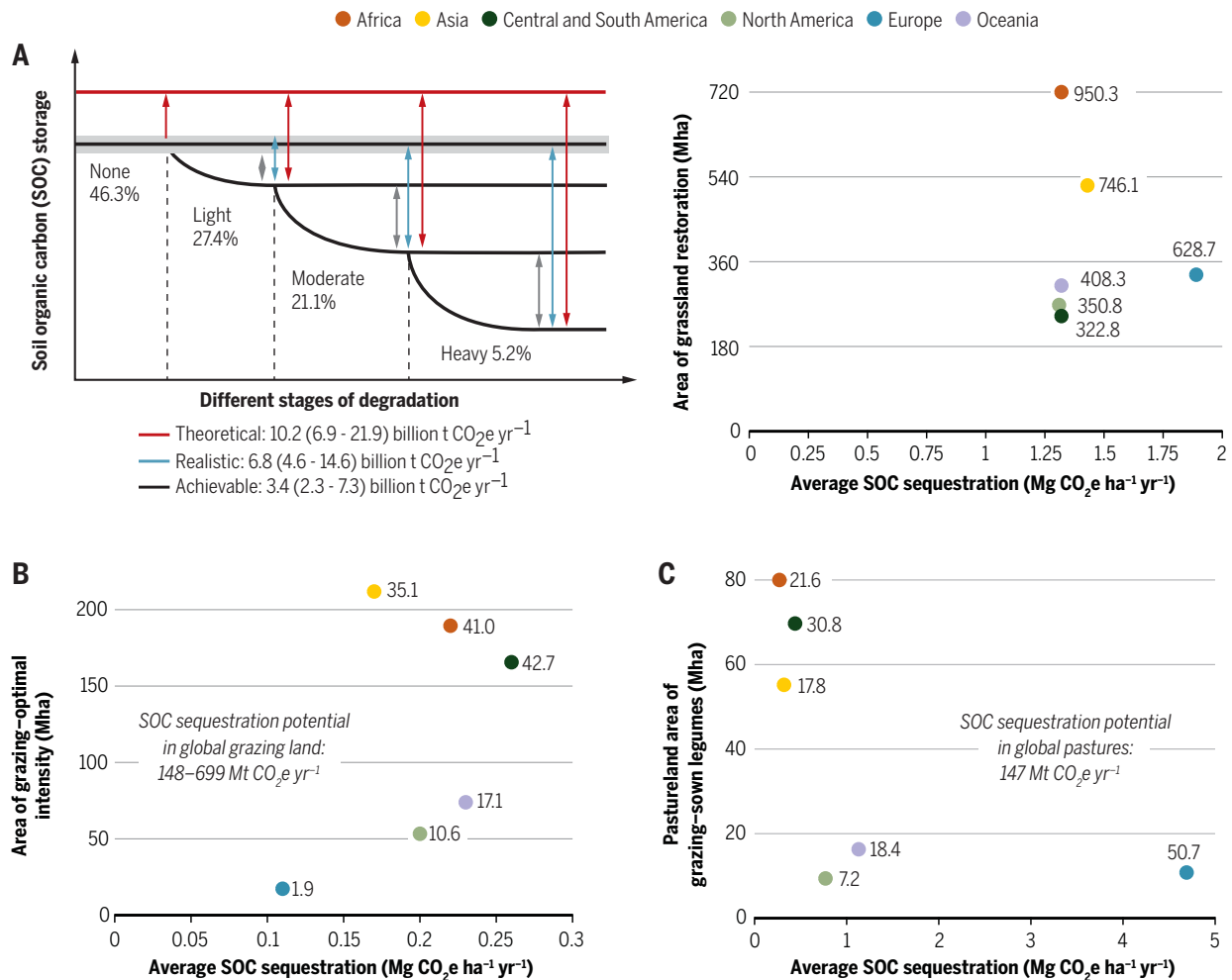


Fig. 4. Soil C sequestration potential of grassland ecosystems at the regional and global scales. SOC sequestration potentials are arranged according to average SOC sequestration rates and area of each management strategy for denoting their relative contributions. **(A)** Capacity and attainability of SOC sequestration by restoring degraded grasslands [data are from White *et al.* (1), De Deyn *et al.* (52), Deng *et al.* (54), and Fargione *et al.* (53)]. At the global scale, SOC sequestration potential is presented as theoretical, realistic, and achievable, respectively, based on Chapman (55). Means and the 95% confidence

herbivore diversity (46). Moreover, rotational grazing consistently shows higher SOC stocks compared with continuous grazing (or free grazing) (43), with gains observed specifically in the mineral associated fraction (47).

Managing for soil carbon storage in grasslands

Empirical and experimental studies have indicated that improving grassland management can increase SOC storage, thus mitigating carbon losses caused by climate change, long-term overgrazing, and grassland degradation (2, 42, 48). Management improvements may result in soil carbon accrual through several interrelated mechanisms (Fig. 1). Conversion from croplands to grasslands removes disturbance from tillage and increases root carbon inputs to soil (6, 42). Restoring the biodiversity of degraded grasslands may increase plant production and

promote microbial turnover and necromass entombment (4, 13, 15). Grazing improvement can increase higher-quality root carbon (lower carbon:nitrogen ratios) inputs (38) and/or nitrogen retention, thus promoting the formation and persistence of MAOM in soils (47). Sowing legumes increases soil carbon and nitrogen inputs by elevating root biomass, root exudates, and fine root turnover (42, 49). Applications of inorganic and organic fertilizers may stimulate primary productivity and high-quality plant carbon inputs to soil, resulting in more efficient microbial carbon use (5, 28, 50).

A number of management interventions have been adopted to restore grasslands (Fig. 3, B and C). On the global scale, the improved grassland managements increase SOC stocks on average by 0.47 Mg C ha⁻¹ year⁻¹ (42). This suggests that the world's grazing

intervals (parentheses) are given (left panel). At the regional scale, only achievable SOC sequestration potential are estimated because of the large uncertainties for estimating the theoretical and realistic SOC sequestration potentials in each region. For each region, the mean achievable SOC sequestration potential (Mt CO₂e year⁻¹) is given (right panel). **(B and C)** Global SOC sequestration potential (Mt CO₂e year⁻¹) through optimizing grazing intensity in grazing lands and sowing legumes in pasturelands [data are from Griscom *et al.* (51)]. Only maximum climate mitigation potential with safeguards for reference year 2030 is shown.

lands, which occupy an area of ~34 million km², have substantial potential to increase SOC storage (Fig. 4). Among all improved management practices, conversion from cultivation to grasslands, increasing plant diversity, sowing legumes and grasses, and fertilization are associated with the highest soil carbon sequestration rates (Fig. 3C) (4, 42). Under moderate grazing intensity, the average SOC stock increase (28.4%) is substantially greater with rotational grazing than that with continuous grazing (Fig. 3B). In the southeast United States, grassland soils managed with adaptive multi-paddock grazing that used a high-density-short-duration rotational grazing had more carbon (72.49 Mg C ha⁻¹) and nitrogen (9.26 Mg N ha⁻¹) stocks compared with continuous grazing (64.02 Mg C ha⁻¹ and 8.52 Mg N ha⁻¹) in the 0 to 100 cm soil layer (47). However, the

direction and magnitude of management effects on soil carbon stocks are context specific, depending on factors such as climate, plant community composition, and soil properties (5, 43, 50). Therefore, grazing practices need to be implemented with an understanding of context. Moreover, further studies are required to examine the synergy and trade-offs among grassland biodiversity, primary productivity, and soil carbon sequestration under management interventions.

Soil carbon sequestration potential varies in both quantity and attainability among grasslands with different degrees of degradation and across different regions (Fig. 4). Given that ~50% of the global grassland area has been degraded (1, 2), restoration of grassland cover and biodiversity is an effective strategy for promoting SOC storage and mitigating the negative impacts of global climate change (4, 15, 51–53). For example, the SOC accrual rate with grazing exclusion is on average 0.68 Mg C ha⁻¹ year⁻¹ in topsoil (0 to 30 cm) and 0.62 Mg C ha⁻¹ year⁻¹ in subsoil (30 to 100 cm) across 145 degraded grassland sites in China (54), indicating that it has not reached saturation over the 27-year period of grassland restoration.

Potential soil carbon sequestration capacities can be categorized as theoretical, realistic, or achievable (55). Theoretical soil carbon sequestration capacity refers to the estimate of restoring all soils to their natural capacity or even enhancing it through management interventions, realistic soil carbon sequestration capacity refers to the optimistic value accounting for social and economic constraints, and achievable capacity is the value of a pragmatic scenario based on the current trends (55). At the global scale, the mean theoretical, realistic, and achievable capacities of SOC sequestration with grassland restoration are estimated to be 10.2, 6.8, and 3.4 billion t CO₂ equivalents per year (CO₂e year⁻¹), respectively (Fig. 4A). At the regional scale, Africa, Asia, and Europe are projected to have the largest achievable capacity of soil carbon sequestration with grassland restoration, with Oceania and North and South America exhibiting the least SOC sequestration potential (Fig. 4A). These global patterns of SOC sequestration potential are primarily caused by the differences in average soil carbon sequestration rate and the area of degraded grassland in different regions. The greater SOC sequestration potential with grassland restoration in Africa and Asia is due to the larger areas of degraded grasslands in these continents, whereas European grasslands have a higher average soil carbon sequestration rate (Fig. 4A). In addition, optimizing grazing intensity (e.g., rotational grazing) is projected to increase soil carbon sequestration potential by 148 to 699 megatons (Mt) CO₂e year⁻¹ in global grazing lands (Fig. 4B), with the greatest

SOC sequestration potential occurring in Central and South America, Africa, and Asia (51). Moreover, sowing legumes is projected to enhance SOC storage by 147 Mt CO₂e year⁻¹ in global pasturelands (51), with Europe exhibiting the greatest soil carbon sequestration potential caused by both the largest pastureland areas and the highest average soil carbon sequestration rate (Fig. 4C). At both the regional and global scales, large uncertainties exist regarding the projected soil carbon sequestration potential and rate of accrual. These uncertainties are caused by the complex interactions among climate change, human activities, and spatial and temporal variations in ecosystem and soil responses (51, 53, 56). Scientific research and management innovations are required in the future to maximize the attainable SOC storage in global grasslands.

Conclusion

Recent studies have made considerable progress toward addressing major challenges associated with identifying the capacity and key mechanisms of various grasslands to sequester and preserve carbon in soils and developing knowledge-based strategies to restore biodiversity, preserve current SOC stocks, and promote additional sequestration for climate change mitigation and sustainable management in grasslands. These advances highlight the important roles of plant and soil biodiversity in regulating the formation of microbial necromass carbon, MAOM, and POM, mediating the impacts of climate change, and promoting SOC storage through management improvements and restoration in global grasslands. They also demonstrate that the impacts of climate change, grazing, fire, grassland restoration, and mitigation solutions on soil carbon sequestration are moderated by multiple context-dependent factors. Future research is needed to address the uncertainty and context dependency of the proposed mitigation solutions and their carbon sequestration potentials and to consider their possible synergies and trade-offs for biodiversity conservation, climate mitigation, and food production.

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ACKNOWLEDGMENTS

We thank S. P. Chen, J. Q. Tian, Y. J. Zhao, S. X. Zheng, Y. Wang, X. M. Lu, B. Tang, J. Man, and J. S. Su for discussion on the topic of grassland carbon sequestration. **Funding:** This work was supported by the National Natural Science Foundation of China (grant no. 32192464) and the Strategic Priority Research Program of the Chinese Academy of Sciences (grant no. XDA23080000). **Author contributions:** Y.F.B. conceived the concept, structure, and writing of the manuscript. M.F.C. contributed to the development of ideas and writing of the manuscript. **Competing interests:** M.F.C. provides consulting services for C quester Analytics. Services are provided to a number of companies invested in soil carbon sequestration, including by the adoption of regenerative grazing management. The remaining authors declare no competing interests. **License information:** Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

Submitted 13 April 2022; accepted 15 June 2022
10.1126/science.abo2380



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Science, **377** (6606), .

DOI: 10.1126/science.abo2380

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