Title

Evaluation of plant-grazer-soil interactions and agroecosystem carbon cycling properties in California perennial crop-livestock systems

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Publication Date

2022

Evaluation of plant-grazer-soil interactions and agroecosystem carbon cycling properties in California perennial crop-livestock systems

BY

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DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Soils and Biogeochemistry

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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ACKNOWLEDGEMENTS

This process and the outcomes of my work are first and foremost dedicated to my late mother, Debra Kathleen Lawrence. Your memory guides me and my aim is always to make you proud. I wish you were here to see me pass this finish line.

It is also with deep gratitude that I thank the fiercely intelligent and passionate members of the Gaudin Agroecology Lab, led by my advisor Dr. Amélie Gaudin. Thank you all for your invaluable wisdom, thoughtfulness, creativity, and support throughout the years. Amélie, you took a chance on me. I was not a sure bet and anyone who knows anything about anything knows that I required unique support, understanding, and mentorship. I would not be here without you believing in me and I hope to have shown it was worth it. Thank you.

Throughout my time here, I have not always felt that I belonged nor that I could thrive. This institution is not intended to be accessible for everyone and, like many others, this has at times caused struggle and a sense of exclusion and otherness. However, not all, but some of those challenges facilitated my development as a student, scientist, educator, and active participant in my community. For this, I am humbled and remain steadfast to these lessons learned and the need to continue learning and growing. My time here has taught me many lessons on pedagogy, mentorship, knowledge creation, community-building, and the art and practice of science. I leave here a better person than when I arrived. As such, additional gratitude is owed to some wonderful scientists and educators here who inspired me along the way: Dr. Randy Southard and Dr. Kate Scow (who, in part, inspired my deep curiosity of soils), Dr. Toby O'Geen (the OG, who provided more support and education than he's likely to take credit for), and Dr. Cristina

Lazcano (for providing a model approach to this work that I could relate to when I needed it most). Thank you, all.

I can go no further lest to express the endless value and appreciation I hold for Krista Marshall – my partner; anchor of support; inspiration; brilliant and distinguished mind; and the most deeply thoughtful, caring, and considerate person I have ever met. We have learned together, created together, reinforced our values and frameworks together, and profoundly grown along the way. I love you. I am also grateful to your family, especially Sue Marshall, for accepting me and taking me in. I give additional thanks to my community in Sacramento that (fortunately) includes far people than I can name here. This community has been a source of inspiration in my development for so many years. In particular, I must thank my longest friend (and brother), Joseph Costa. You've helped me learn how to be a friend. Special recognition must go to Ram Khatiwoda, who's life story, generosity, kindness, and knowledge overflows – it has been sobering, grounding, and revelatory to work alongside you on the farm. I'm also thankful to NorCal Resist, especially Autumn Gonzalez and Ruth Ibarra, who are some of the most dedicated people I have met and do the most effective and genuinely beneficial work I have seen. Thank you for welcoming and supporting me and for co-creating the vision of our mutual aid urban farm, Seeds of Solidarity. This act of community creation and solidarity has given me purpose.

Finally, thank you to all of my peers, colleagues, and collaborators throughout my Ph.D. process. In particular, thank you to Rebecca Burgess (I also would not be here without you), Jaime and Robert Irwin (Kaos Sheep Outfit is an inspirational model), and all of my lab mates and cohort in the UC Davis Soils and Biogeochemistry program. This includes Alex Gulachenski, Mariana Muñoz-Araya, Frieda Schwebel, Ivan Martinez, Peter Geoghan, Sequoia Williams, Daniel Ortiz Gonzalo, Vivian Wauters, Katie Simpson-Johnson, Leah Renwick, Caitlin Peterson, Kalyn Diederich, and Hannah Waterhouse from whom I have drawn inspiration and learned so much.

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RESEARCH NOTES

Agricultural soils are a vital resource, and maintaining their long-term viability is essential for global food security, environmental stewardship, and the fostering of dignified livelihoods for both rural and urban people (Amundson et al., 2015). Agricultural soils have recently garnered considerable attention for their potential capacity to sequester atmospheric carbon, which plays an important role in combatting the increasingly drastic impacts of global climate change (Lal, 2016). Despite this nearly ubiquitous understanding, pervasive and escalating trends of industrialization continue to spread across our agricultural landscapes, with increasingly high usage of non-renewable external inputs and greenhouse gas (GHG) intensive farming methods. The widespread industrial intensification of agriculture is well understood to contribute substantially, both historically and presently, to anthropogenic climate change and the collapse of biodiversity and ecosystem functionality globally (Campbell et al., 2017; Cardinale et al., 2012; Harris et al., 2022; Lal, 2015; Lark et al., 2020; Matson et al., 1997; Tilman, 1999; Vermeulen et al., 2012; Zabel et al., 2019). These industrial agricultural models are also increasingly threatening our soil's capacity to function, as widespread soil degradation across the world's agricultural landscapes accelerates as a result of the continued intensification of global farmland (Kopittke et al., 2019; Pozza and Field, 2020; Song et al., 2018; Wiesmeier et al., 2016; Winkler et al., 2021).

Justifications for the hegemony of this agricultural paradigm relate almost exclusively to its capacity for the provisioning of material or energy outputs such as food, fiber, and fuel (Altieri, 2018; Lal, 2015). However, while diversified agroecosystems continue to close the yield gap with industrial farming (Lark et al., 2020; Ponisio et al., 2015; Ricciardi et al., 2021), the yields of industrialized farmland appear to have plateaued (Grassini et al., 2013) and their stability projects to decline (Challinor et al., 2014; Zhao et al., 2017). Low applications of strategic biodiversity and extraordinarily simplified ecological functioning have left these landscapes highly vulnerable to a variety of economic and climatic impacts (Altieri, 1999; Altieri et al., 2015; Tscharntke et al., 2012). These factors combine to not only weaken the capacity of our agricultural landscapes to provide essential services that are necessary for the regulation of critical planetary functions, but also the longevity, sustainability, and sufficiency of food production (Janzen et al., 2021; Lal, 2016).

As such, there is a growing consensus across scientific, policy, and land stewardship communities alike that our agricultural management must transition toward paradigms which not only reduce environmental degradation, but move beyond to revitalize and enhance soil functioning (Bezner Kerr et al., 2022). This is considered necessary to support food production and the well-being of communities while improving our adaptive capacity to the increasingly adverse growing conditions brought about by natural resource limitations and intense and erratic weather events (Keesstra et al., 2018; Kopittke et al., 2022, 2019; Lin, 2011; P. Smith et al., 2015; Wright et al., 2020). It is also essential toward the endeavor of mitigating global climate change, to whatever degree that sequestering atmosphere GHGs may be achieved through increasing soil carbon storage across our agricultural landscapes. Given the vulnerability of our current agricultural paradigm, as well as its overwhelming contributions to GHG emissions and global ecosystem collapse, there is now sobering urgency to transition our working lands toward models that improve land stewardship and soil conservation.

Recently, growing demand to reorient agricultural research platforms and invest toward resource conservation practices in the U.S. has been met with willingness on the part of farmers, yet difficulty envisioning accessible transition opportunities (Houser et al., 2020). While much of the advances in industrial farming methods can be credited to high rates of investment in research and infrastructure, the same degree of effort and attention has not been paid to the advancement of ecological management paradigms (DeLonge et al., 2016; Horlings and Marsden, 2011). The implementation of agroecological design and management principles show excellent promise to support agricultural transitions toward models that ameliorate much of the human-social and environmental costs associated with food production (Altieri, 2018; Rachel Bezner Kerr et al., 2022; Houser et al., 2020; Marshall and Brewer, 2020; Petersen-Rockney et al., 2021). This remains one of humanity's most daunting 21st century challenges, and all efforts toward this goal are worthwhile of pursuit.

ABSTRACT

One historically foundational, yet scientifically understudied, agroecological diversification strategy is the integration of animals and crops within the same production system (Russelle et al., 2007). Integrated crop-livestock (ICL) systems, where animals provide various grazing-based services for crop production (Brewer and Gaudin, 2020; Niles et al., 2018; Sanderson et al., 2013) and the diversification of on-farm income (Garrett et al., 2020, 2017; Niles et al., 2018), are common across much of the world's subsistence farming communities (Entz et al., 2005; Garrett et al., 2020). Global practitioners of ICL management rely on extensively developed local and indigenous knowledge systems, with regional specificity and complexity in the

coordination of components (Altieri, 1992; Altieri et al., 2012; Garrett et al., 2020; Sekaran et al., 2021b).

However, the industrial intensification of agriculture, especially throughout the last century, has increasingly resulted in highly specialized, mechanized, and de-coupled crop and animal production throughout much the world's market-based agricultural systems (Baur and Iles, 2022; Garrett et al., 2020, 2017). This is currently understood to contribute to poor nutrient (re)cycling within and between agricultural operations, higher rates of external input, reduced adaptive capacity, and an increased environmental footprint (GHG emissions, land-use conversion, etc.) of both crop and animal productions (Brewer and Gaudin, 2020; Garrett et al., 2017; Lemaire et al., 2014; Petersen-Rockney et al., 2021). Current and developing models of ICL systems employ diverse, adaptable, and feasible management practices that can be strategically implemented across various scales and crop production systems, and may further facilitate transitions from petrochemical-intensive and externally-regulated management practices toward more soil-centric and internally-regulated management paradigms (Bell et al., 2014; Garrett et al., 2020, 2017; Lemaire et al., 2014).

Grazing-based practices have shown potential to improve landscape multi-functionality and impact multiple ecosystem processes related to resource utilization and efficiency, biogeochemical cycling, and soil organic carbon (SOC) storage and turnover (Rumpel et al., 2015; P. Smith et al., 2015; Zhou et al., 2017). While cropland-specific impacts are less understood, research throughout diverse grazed ecosystems show feedbacks between grazing intensity (density and duration) and periodicity (seasonality and frequency) that exert unique selective pressure over understory plant community composition, primary productivity, and the allocation of energy and nutrients above- and belowground (Bardgett and Wardle, 2003; Cong et al., 2014; Dawson et al., 2009; Rumpel et al., 2015; Tian et al., 2016). Recent research has found that these plant-grazer-soil interactions have significant, yet understudied implications for the quantity, quality, and spatial distribution of carbon and nutrient inputs – as well as a suite of soil microbial community processes that regulate nutrient cycling and SOC transformations (Cotrufo et al., 2013; Kibblewhite et al., 2008). However, these grazing dynamics have rarely been explored under the context of cropland integration and the potential for SOC storage remains largely unknown.

The goal of the research presented here was to narrow critical knowledge gaps specific to perennial ICL management outcomes, especially as they relate to soil nutrient cycling and carbon flux and storage dynamics within semi-arid climates. Collectively, the experiments in this study aim to observe perennial ICL outcomes across both spatial (i.e. bulk vs. rhizosphere soils) and temporal (i.e. long-term vs. short-term adoption; intra-seasonal vs. inter-seasonal monitoring) scales. The value of this information is in validating the potential usefulness of ICL for the purposes of energy and nutrient cycling, soil carbon sequestration, and the provisioning of other key soil ecosystem services. More specifically to the cycling of carbon, this research explored if and how these more complex and diversified ICL systems impact: (1) functional traits of the forage plant community; (2) soil physicochemical characteristics; (3) recycling and retention of carbon and nutrients; (4) soil biological activity and carbon substrate utilization; and (5) SOC biochemical and physical partitioning into storage pools. This information is critical for informing future integrated-systems research platforms and management applications; toward the goal of developing ICL production models with well-coordinated and strategically applied grazing practices.

To carry forth this work, a comprehensive review of ICL literature was first conducted (Chapter 1). The broad aim of this review was to identify the status of ICL research, especially as it pertained to biogeochemical dynamics of carbon and nutrients within agroecosystems. Whereas the state of ICL literature is currently scarce, the aim of this review shifted toward providing a perspective and the development of working hypotheses and potential mechanistic frameworks. The goal was to appraise whole-system ICL interactions and their potential to support a suite of essential soil ecosystem functions (Brewer and Gaudin, 2020). Next, *in-situ* and laboratory experimental approaches were utilized in a series of California-based integrated sheep-vineyard (ISV) research projects. This included a survey of paired vineyards with long-term management legacies (Chapter 2) and a short-term (2 year) field monitoring trial (Chapter 3), to assess agroecosystem dynamics within vineyards utilizing both sheep-integration (ISV) and conventional understory management techniques (CONV). This contributes novel ISV management data by quantifying field-scale shifts in a suite of soil physical, chemical, and biological properties over both short- and long-term temporal scales, as well as some first insights into the impact of perennial ICL management on above- and belowground understory plant community dynamics. This research contributes more mechanistic understanding of how perennial ICL management impacts specific plant-grazer-soil interactions and biogeochemical properties regulating SOC deposition, storage, and turnover.

Collectively, the experiments and framework development in this study provide some of the first insights into the potential SOC storage benefits associated with perennial cropland grazing, particularly within subsoils. Our observations provide early evidence that *high-density, short-duration rotational grazing* management in perennial croplands holds significant potential to increase SOC storage, with proposed mechanisms related to the rate and efficiency of microbial carbon accrual. The paired survey experiment showed significant SOC storage increases within long-term ISV sites, including in the persistent mineral-associated organic carbon (MAOC) pool. Similar benefits were observed over the course of the two-year monitoring trial, which saw significant increases in SOC under ISV management relative to the vineyard utilizing mowing (CONV). Across both experiments, there was an extremely strong trend of larger labile SOC flux pools and increasing soil C flux rates in vineyards utilizing ISV grazing. In particular, vineyards using grazing had substantially larger soil microbial communities. Laboratory incubations showed higher rates of soil C mineralization under ISV management across spatial (i.e. bulk vs. rhizosphere soil) and temporal (i.e. long-term ICL legacy effects vs. short-term intra-seasonal monitoring) scales. However, the carbon use-efficiency of microbial communities varied across experimental scales. Microbial energy investment strategies and metabolic utilization patterns showed notable differences between grazed and ungrazed vineyards, but will require substantially more experimental investigation to accurately identify the underlying mechanisms and interpret their meaningful consequences.

Importantly, results from multiple scales indicate that perennial ICL adoption is unlikely to provide substantial negative consequences for no-till perennial cropping systems. In the comparison of long-term managed ISV sites, soil structural indicators remained similar if not slightly improved. Both nutrient retention and plant-available nutrients also appeared to increase under ISV management. While intra-seasonal monitoring showed increased rates of soil CO_2

efflux in grazed vineyards, it is unclear the extent to which this translates to long-term GHG emissions; especially when considering observed benefits for SOC storage. However, these outcomes are likely influenced by the intensity and periodicity (seasonality and frequency) of grazing events, as well as site-specific edaphic and climatic limitations. Soil biogeochemical outcomes may therefore be highly variable under different agroecosystem and grazing management regimes, and how these components are synchronized across time and space.

Considerations of cropland co-management strategies, such as understory species composition and tillage regime, will interact to determine some soil habitat and resource conditions. The strategic application of grazing in coordination with knowledgeable shepherding practitioners is therefore necessary to optimize potential soil benefits. Where perennial cropland agroecosystem design and management may be easily altered to facilitate both spatial and temporal livestock re-integration, better understanding of the mechanistic pathways between grazing disturbances and cropland SOC cycling will be useful toward strategically improving the internal regulation of soil functions and increasing longer-term SOC storage. As such, my work highlights certain benefits of using updated soil carbon conceptual frameworks for linking SOC flux and storage indicators within applied agricultural research contexts. Future ICL research, design, and management should continue to develop across multiple spatial scales – the farm, landscape, and region – and explore the potential benefits for multifunctional landscape productivity, the efficient (re)cycling of energy and nutrients, and the support of various ecologically-based benefits that are critical for planetary regulation and societal prosperity. Meanwhile, this early research suggests that the adoption of perennial ICL practices should continue to expand, with strong potential of beneficial outcomes and preliminary assurance of minimal trade-offs.

Chapter 1: Potential of crop-livestock integration to enhance carbon sequestration and agroecosystem functioning in semi-arid croplands

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ABSTRACT

While characteristics of semi-arid climates place limitations on soil organic carbon (SOC) storage, there is opportunity and urgency for increasing the quality and long-term persistence of cropland SOC content within these agroecosystems. Livestock re-integration into cropland shows potential to improve semi-arid agroecosystem functioning through shifts in biogeochemical processes and the facilitation of multiple ecosystem services involved in carbon and nutrient cycling and use-efficiency. Here we review the characteristics of grazing-based Integrated Crop-Livestock (ICL) systems and how various associated management practices may interplay with semi-arid agroecological and biogeochemical dynamics to influence soil microbial ecology and SOC accumulation and stabilization. We argue that livestock re-integration holds notable potential to increase cropland SOC through controls on landscape net primary productivity, allocation of biomass belowground, efficient recycling of residual crop nutrients, and soil biological activity related to a suite of soil ecosystem services. Achieving the full SOC

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* A version of this chapter was published as "Brewer, K.M., Gaudin, A.C.M., 2020. Potential of crop-livestock integration to enhance carbon sequestration and agroecosystem functioning in semi-arid croplands" in the journal Soil Biology and Biochemistry.

accumulation potential of ICL management will require site-specific consideration of feedbacks between herbivory, soil microbial ecology, soil disturbance, and forage species interactions. Future research should focus on optimizing plant-soil-grazer feedbacks and understanding of mechanistic drivers of ICL system outcomes to optimize the design and management of semi-arid regional ICL systems for enhanced SOC quality and persistence.

1.1 INTRODUCTION

Livestock reintegration into cropland has been proposed as a strategy to sustainably intensify food, fiber, and fuel production systems and reduce the greenhouse gas footprint of agriculture (Garrett et al., 2017; Rota and Sperandini, 2009). Integrated crop-livestock (ICL) systems are characterized by the utilization of on-site animal services as a resource for crop production and/or the use of cropland to support livestock production. These ICL systems are in fact foundational components to agriculture for over two-thirds of global farmers, contributing to about half of the world's food production (Herrero et al., 2010). However, market forces have led to the decoupling of crop and livestock production systems in industrialized agroecosystems, resulting in poor nutrient cycling within and between agricultural operations and an underutilization of ecosystem services provided by such integrated systems (Entz et al., 2005; Lemaire et al., 2014).

ICL practices employ diverse management tools and can be implemented across various scales of cropping systems (Table 1). These grazing- based practices provide economic and biological diversification of agricultural operations and use on-site animal-derived services to offset external inputs (Bell et al., 2014; Garrett et al., 2017) and minimize detrimental impacts of agricultural intensification on soil properties critical to climate change adaptation (Lemaire et al., 2014; Russelle et al., 2007). Growing interest in utilizing cropland to sequester carbon may provide new opportunities to recouple crop and animal production and help achieve the ambitious climate mitigation targets set at the COP21 (UNFCCC, 2015). This is of particular importance in semi-arid regions, which contribute substantially to global crop and livestock production despite their high vulnerability to the impacts of global climate change (Guan et al., 2009). While semi-arid climatic and soil characteristics largely determine soil organic carbon (SOC) storage and turnover, grazing on cropland nevertheless impacts diverse agroecosystem dynamics such as landscape productivity, biodiversity, the adoption of on-farm conservation practices, and trophic interactions that are essential considerations for managing SOC (Salton et al., 2014; Sanderson et al., 2013).

Table 1: Characterization of predominant integrated crop-livestock systems

Key Production Services	**Land-based/within farm integration**	**Examples of ICL system**
• Source of animal feed • Labor reduction • Nutrient provision and cycling • Soil carbon deposition • Weed management • Resource conservation • Erosion control • Fire suppression	Grazing of crop residues	• Cotton stubble with sheep or cattle • Soy and grain stubble with sheep or cattle
	Grazing dual-purpose forage crop	• Early-season grazing of alfalfa crop with sheep or cattle
	Grazing of cover crops within cash-crop rotation	• Mixed legume-cereal cover crop grazing with small and large livestock
	Pasture rotation (phase farming)	• Cereal crop and forage rotation with sheep or cattle • Sod intercropping in corn-soy rotation with sheep or cattle
	Grazing of understory vegetation in perennial cropping systems	• Vineyards with sheep • Fruit and nut orchards with small and large livestock

This article explores how and to what extent grazing-based ICL practices, along with variable co-management components, may i) stimulate soil biological activity, ii) improve essential soil ecosystem processes, iii) accumulate additional SOC, and iv) provide co-benefits for climate change adaptation within semi-arid production systems. Globally, ICL systems remain understudied and, to the best of our knowledge, the underlying agroecosystem and soil biological mechanisms have not yet been shown. The body of ICL research is notably limited, and system design and agroecological components vary widely (Table 1). Thus, the lack of system-level ICL research included in this review is acknowledged. Nevertheless, we draw upon research from annual ICL systems – predominately represented by grazing of medium or large ruminants on pasture-phase rotations, cover crops, and crop residues – as well as rangeland systems to develop working hypotheses and better understand how edaphic, agroecological, and climatic factors may affect the regional potential of semi-arid ICL systems to store SOC and support essential soil ecosystem services. The emphasis of this review is less to predict specific ICL system outcomes and more to further develop mechanistic understanding of how various ICL management components could be utilized to maximize SOC persistence in semi-arid cropland. We specifically focus on ICL management practices that are instrumental to stimulating biological processes and long-term soil carbon sequestration, in order to inform the design of ICL systems that effectively support ecological intensification and agricultural production goals.

1.2 SEMI-ARID CROPLAND: AN UNDERUTILIZED SINK FOR SOIL CARBON

Semi-arid ecoregions cover ~15% of global land surface (Safriel et al., 2005) and climate change projections anticipate both substantial expansion of semi-arid global land area and increased dryland ecosystem degradation throughout the century (Huang et al., 2016). Semi-arid regions are ecological intermediates between desert and humid regions, with seasonal and highly variable mean annual precipitation that is usually below the regional evapotranspiration potential (Bailey, 1979). While gaps remain in understanding the primary drivers of SOC dynamics in semi-arid production systems, there is a large relative influence of environmental variables such as precipitation, temperature, geological parent material, and their compound impact on soil morphology and physicochemical characteristics such as soil pH and texture (Hoyle et al., 2016; Rabbi et al., 2014).

Temperature and soil moisture are the most significant factors regulating SOC dynamics in semi-arid agroecosystems (Wiesmeier et al., 2013), with annual precipitation rates very highly correlated to SOC storage potentials in non-irrigated landscapes (Liu et al., 2011; Rabbi et al., 2014). Both temperature and soil moisture partially shape broad ecological features that govern the quantity and quality of organic residue inputs, as well as a suite of microbial community processes related to litter decomposition and SOC transformation, stabilization, and mineralization (Conant et al., 2011; Thiessen et al., 2013). For example, soil moisture and temperature-driven decoupling of C, N, and P cycles with increasing aridity (Delgado-Baquerizo et al., 2013) place stoichiometric limitations on SOC formation and stabilization (Cleveland and Liptzin, 2007; Schmidt et al., 2011), especially in coarse-textured soils (Dlamini et al., 2016; Mcsherry and Ritchie, 2013). A sustained decline in soil moisture has been shown to reduce both labile and older, recalcitrant SOC fractions (X. Chen et al., 2015).

Climatic variables influence soil microbial communities and their regulation of ecosystem carbon storage and turnover in diverse and dynamic ways. For example, prolonged periods of both low and high soil water status may restrict microbial mineralization and SOC formation, due to poor carbon substrate and O_2 diffusion rates, respectively (Devêvre and Horwáth, 2000; Zheng et al., 2019). High mean annual temperatures are characteristic of many semi-arid ecoregions and are associated with expedited rates of enzymatic depolymerization and SOC turnover (Bond-Lamberty and Thomson, 2010; Giardina et al., 2014; Qi et al., 2016). While higher temperatures may increase microbial carbon use-efficiency (CUE) under specific soil microbial community and water status interactions, an increase in temperature is more often associated with declines in CUE (Conant et al., 2011; Devêvre and Horwáth, 2000; Manzoni et al., 2012; Zheng et al., 2019). Whereas high microbial CUE promotes microbial growth and SOC stabilization, lower CUE increases soil carbon losses with higher respiration and decreased investment in microbial biomass production (Manzoni et al., 2012).

The soil carbon sequestration potential of a given semi-arid cropland will ultimately be regulated by the most limiting accumulation factor for SOC formation (Hoyle et al., 2016). When precipitation limits biomass production, irrigation technologies are implemented to mitigate negative impacts on plant productivity and crop yield. While this may also provide SOC storage benefits (Wiesmeier et al., 2013), prolonged use of irrigation is often associated with increased salt deposition onto soil surfaces. According to UNEP (2014) estimates, nearly 50% of semi-arid irrigated landscapes are experiencing significant impacts of soil salinity. In addition to adverse impacts on plant productivity (Munns and Termaat, 1986) and subsequent residue deposition, salt-affected soils also tend to have lower microbial CUE (Rietz and Haynes, 2003) and enhanced aggregate dispersion (Wong et al., 2010) which can increase SOC accessibility to mineralization processes and further exacerbate the potential for SOC losses (Setia et al., 2013).

Land use and associated management practices are also large regulators of SOC within semi-arid systems (Conant et al., 2017) and designing agroecosystems that maximize carbon inputs and minimize management induced losses could thus enhance SOC storage (Tautges et al., 2019). While some semi-arid ICL systems integrate biodiverse perennial or high-residue annual forage rotations into cropland, others utilize grazing more simply as a termination methodology for crop residues and weeds (Garrett et al., 2017). These approaches can result in widely different system-level outcomes. The adoption of diversified systems with prolonged soil cover, high residue inputs, tightly-coupled C and N cycling, and low soil disturbance have been shown to improve soil carbon sequestration and the provision of ecosystem services within semi-arid irrigated cropland (Bowles et al., 2015; Garcia-Franco et al., 2018; Plaza-Bonilla et al., 2015; Schmidt et al., 2011). While implementation varies across agroecosystems, many ICL studies consider these components essential elements of successful integrated systems (Entz et al., 2005; Herrero et al., 2010; Lemaire et al., 2014; Russelle et al., 2007).

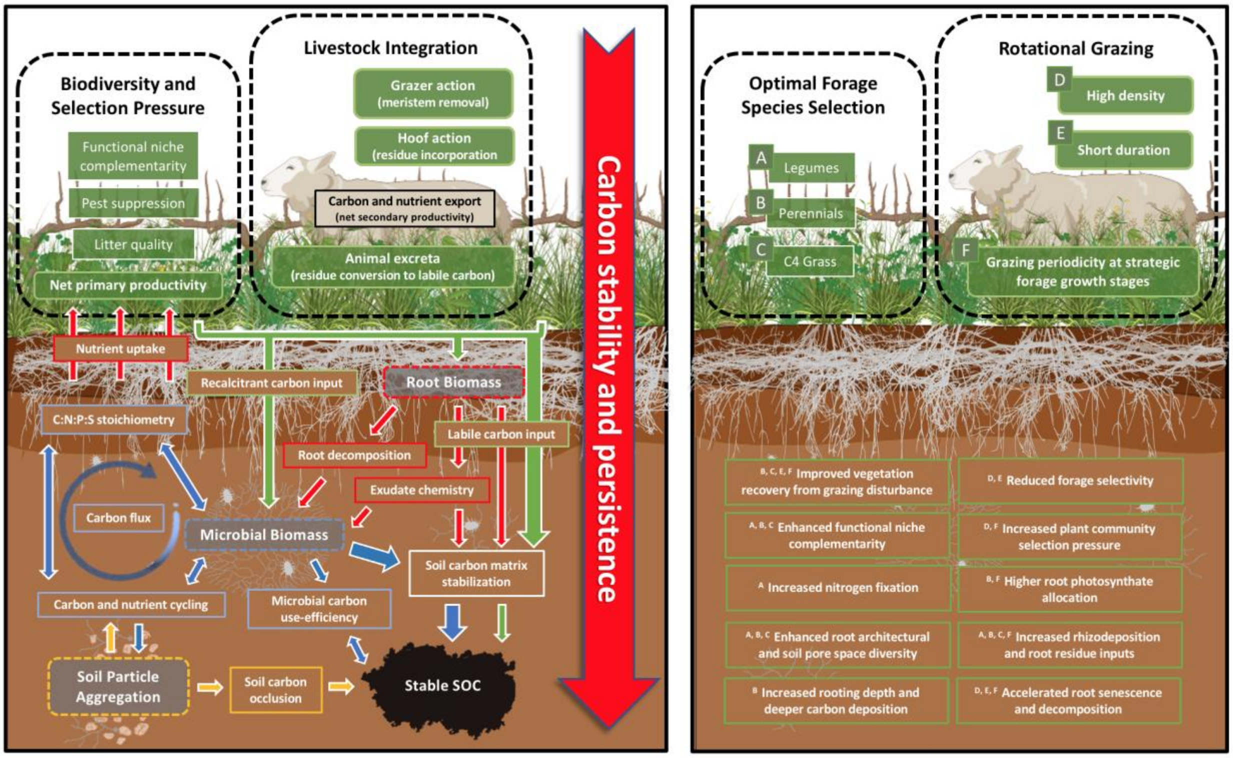
Although semi-arid ecoregions frequently approach climatic threshold limits for SOC storage capacity (Hoyle et al., 2013; Huang et al., 2016), SOC fluxes out of dry semi-arid soils are often small and residence time can be long-lasting when not exacerbated by management-induced losses (Booker et al., 2013). Given the extent of semi-arid agroecosystems across the globe (Safriel et al., 2005) and their significant historical SOC losses, these systems are likely far from soil carbon saturation (Ahlström et al., 2015) and provide a large opportunity for global atmospheric carbon mitigation through optimizing the SOC storage conditions in managed landscapes. While the rate at which SOC sequestration in these regions occurs is generally slow, ICL systems offer varying management approaches that may be a highly effective avenue for largescale carbon storage. This is particularly worthwhile when considering residence time and the potential ecosystem services and production co-benefits resulting from soil quality improvements in semi-arid regions.

1.3 PATHWAYS FOR SOIL ORGANIC CARBON ACCUMULATION IN CROP-LIVESTOCK SYSTEMS

Grazing alters numerous fundamental landscape dynamics and ecological relationships that regulate SOC storage potential. Variation in edaphic properties, co-management and their interactions with grazing means that SOC can increase, decrease, or remain unchanged under diverse grazing practices (Bardgett and Wardle, 2003; Lal, 2002; Orgill et al., 2017; Pineiro et al., 2010). However, most studies implementing grazing best management practices, across various climates and agroecosystems, have reported SOC accumulation in ICL systems relative to non-integrated, less diverse cropping systems (Acosta-Martínez et al., 2004; Assmann et al., 2014; Boeni et al., 2014; Carvalho et al., 2010; Da Silva et al., 2014; Fernández et al., 2011; Fultz et al., 2013b, 2013a; Muniz et al., 2011; Souza et al., 2010; Tian et al., 2010; Tracy and Zhang, 2008). Some ICL publications have attributed potential SOC accumulation to improved rotational complexity, biodiversity, and synergistic feedbacks among ICL production components (de Faccio Carvalho et al., 2010; Entz et al., 2005; Lemaire et al., 2014; Salton et al., 2014).

However, the specific mechanisms influencing SOC stabilization and persistence under ICL management remain unclear. This is especially true in semi-arid ICL systems, resulting from a lack of grazing-specific studies within cropland and large variation in co-management practices and site-specific agroecological processes. Literature from both systems-level studies and management-specific approaches, using examples from within and outside of semi-arid regions, offer insight into potential ICL agroecological and biogeochemical pathways underlying SOC control mechanisms. Pineiro et al. (2010) proposed several mechanistic pathways that could govern the grazing influence on SOC storage, including shifts in i) forage net primary productivity and carbon deposition; ii) N stocks and cycling; and iii) decomposition rates. Furthermore, grazing is proposed here to induce alterations in SOC through additional shifts in agroecosystem and biogeochemical mechanisms of iv) plant community composition and biodiversity; v) forage photosynthate allocation and input stoichiometry; and vi) soil physical structure (Figure 1a).

Figure 1: Potential agroecological outcomes of ICLS and the underlying soil biogeochemical mechanisms



(A) Potential changes in functional ecological and biogeochemical relationships with ICL adoption. Grazing directly influences plant community dynamics and organic carbon inputs (green) and indirectly alters root photosynthate allocation and decomposition (red), microbial community functioning (blue), and soil particle aggregation and physical structure (yellow) with feedbacks to soil organic carbon (SOC) formation and stabilization. SOC persistence is increased as residues and animal excreta are processed through microbial transformations and stabilized through the soil mineral matrix or within soil aggregates. Where grazing may decouple carbon from essential nutrients, increasing bioavailability and reactivity, alterations in plant and microbial productivity will influence recoupling of C and N. In tandem, these counteracting forces will determine ICL agroecosystem carbon and nutrient use-efficiency. (B) Schematic representation of the agroecological implications of livestock integration under best management. Ideal forage species mixtures are biodiverse and include legumes and high-residue C4 perennial grasses. Best grazing management utilizes high density, short duration rotational grazing practices at strategic and site-specific forage growth periods. When managed properly and in tandem, these practices provide a suite of aboveground agroecological and belowground productivity and SOC accumulation benefits. Letters on below text boxes represent influential practices (aboveground).

1.3.1 Net primary productivity and carbon deposition

The accumulation of SOC is a function of the balance between carbon deposition – from plant residues, animal excreta, root exudates, and external inputs – and microbial decomposition and SOC stabilization (Jastrow et al., 2007). Increases in landscape net primary productivity (NPP) deposit more organic carbon into the agroecosystem and are positively correlated with SOC accruement in semi-arid rangelands and croplands (Briske et al., 2011; Hoyle et al., 2013). Increases in soil carbon deposition stimulate belowground trophic networks (Hoyle et al., 2013; Peterson and Lajtha, 2013) and microbially-regulated mineralization processes that can enhance soil C-, N-, P-, and S- cycling rates and nutrient availability (Leff et al., 2012). In turn, these processes increase plant nutrient uptake (Baligar and Fageria, 2015) and positive plant-soil feedbacks on system productivity and SOC accumulation (Flavel and Murphy, 2006; Lal, 2002; Ryals and Silver, 2013; Ryals et al, 2015).

Grazing of cash crop residues, cover crops, and understory biomass provide an opportunity to enhance NPP by maintaining longer vegetation cover and managing for forage quality and composition, especially by promoting the use of forage legumes (Garrett et al., 2017; Lemaire et al., 2014; Reddy and Reddy, 2016; Rota and Sperandini, 2009). Additionally, grazing has been shown to impact NPP (Bardgett and Wardle, 2003; Briske and Noy-Meir, 1998) through i) shifting photosynthate allocation toward roots (Assmann et al., 2014; W. Chen et al., 2015; Pineiro et al., 2010); ii) defoliation, removal of senescent tissues and greater light availability for actively photosynthesizing vegetation (Klumpp et al., 2009; Reeder et al., 2001; Rumpel et al., 2015); iii) changes in litter C-to-N ratios (Pineiro et al., 2010) and residue transformation rates (Breland and Eltun, 1999; W. Chen et al., 2015; Shariff et al., 1994); and iv) shifts in plant and soil microbial community structure and biomass (Bardgett and Wardle, 2003; Hanke et al., 2014). While livestock integration into cropland will export a small percentage of C and nutrients, in the form of livestock gains and respiration (Sulc and Franzluebbers, 2014), precision management may increase nutrient turnover rates and bioavailability (de Faccio Carvalho et al., 2010) to the extent that subsequent crop yields have been shown to be maintained or increased (Bell et al., 2014; Peterson et al., 2020).

Whereas increases in NPP are essential for improving SOC, there is a diminishing soil carbon sequestration benefit of increasing NPP beyond a site-specific threshold. A 20-year trial that artificially doubled plant residue inputs within unmanaged systems found that bulk SOC storage did not significantly increase, especially in more protected and stable SOC pools with slower turnover periods (Lajtha et al., 2014). This may partially be explained by a priming effect, where the decomposition of older SOC is stimulated by low concentrations of microbially-accessible N, or excessive N mineralization from recently deposited low C-to-N litter causing increased microbial competition for substrate (Kuzyakov, 2002; Qiao et al., 2016; Zatta et al., 2014). The introduction of grazing may increase priming, as defoliation triggers root senescence and quick bursts of belowground N-rich residue deposition (Bardgett and Wardle, 2003). Adversely, where best grazing practices and species selection choices promote the proliferation of living roots, exudates and other rhizodeposits may contribute more to long-term SOC storage through preferential and efficient utilization by soil microbes (Sokol et al., 2019). While the stimulation of NPP and maintenance of residue inputs within semi-arid ICL systems are important for SOC regulation, further increases in SOC storage will further depend on short- and long-term variability in aboveground and belowground diversity, residue quality and input stoichiometry, and spatial distribution (Peterson and Lajtha, 2013; Qiao et al., 2016).

1.3.2 Forage composition and biodiversity

A growing body of literature has observed a positive relationship between plant composition richness and soil carbon sequestration (Cong et al., 2014; De Deyn et al., 2008; Fornara and Tilman, 2008; Lambers et al., 2004; Lange et al., 2015; Steinbeiss et al., 2008). This benefit is associated with improvements in NPP, exudate release rate and diversity, and microbial functioning (Cardinale et al., 2012; Dijkstra et al., 2006; Lange et al., 2015; Steinbeiss et al., 2008), which result from shifts in trophic interactions and resource use and allocation among multiple species (Fornara and Tilman, 2008; Hooper et al., 2005). For instance, increased plant species richness has been shown to increase root architectural diversity and belowground biomass production, altering the spatial and temporal deposition of belowground carbon inputs (Cong et al., 2014; DuPont et al., 2014; Lange et al., 2015) and promoting the formation of soil micropores that may partially determine the storage capacity of C inputs (Kravchenko et al., 2019). More diverse plant assemblies have also been shown to enhance soil pathogen suppression, which may partially drive diversity-productivity relationships (Maron et al., 2011).

The introduction of grazing alters forage biodiversity and quality through ecological selection pressures, resulting in shifts in plant functional niche relationships and biogeochemical cycling (Hanke et al., 2014; Rumpel et al., 2015; Rutherford and Powrie, 2013; Stahlheber and D’Antonio, 2013). Heavily stocked and continuously grazed systems tend to reduce plant species richness (Pavlů et al., 2006; Rutherford and Powrie, 2013) and might shift vegetation compositions toward annual and exotic forbs and grasses (Díaz et al., 2007; Stahlheber and D’Antonio, 2013; Waters et al., 2017). However, this does not necessarily translate to reductions in vegetation cover or biomass accumulation (Stahlheber and D’Antonio, 2013). Precision grazing practices, such as rotational grazing with managed exclusion periods, are common under ICL (de Faccio Carvalho et al., 2010) and have been shown to conserve or improve plant diversity within semi-arid landscapes (Bakoglu et al., 2009; Pineiro et al., 2010), especially under conditions of low precipitation (Abdalla et al., 2018).

Variation in grazing intensity and periodicity also exert unique selective pressures over specific plant functional groups (Hart, 2001; Reeder, J.D, Schuman, G.E, Morgan, J.A., Lecain, D.R, Hart, 2001; Reeder et al., 2004). The plant species composition and biodiversity of grazed lands may be controlled with proper grazing management (Sanderson et al., 2005; Stahlheber and D'Antonio, 2013). For example, persistence of annual species may be lowered by late season heavy grazing through direct hindrance of seed production (Briske and Noy-Meir, 1998), whereas perennial species tend to decrease in continuously grazed systems, as maturing buds are removed and tiller replacement is constrained (Briske and Noy-Meir, 1998; Gutman et al., 2002). Once established, perennial and C4-dominated grasslands appear more resilient to grazer-induced disturbances than annual and C3-dominated grasslands, in terms of maintaining biodiversity (Hanke et al., 2014; Reeder, J.D, Schuman, G.E, Morgan, J.A., Lecain, D.R, Hart, 2001), annual biomass production (Gutman et al., 2002; Zatta et al., 2014; Zheng et al., 2011), and SOC accumulation (Abdalla et al., 2018; Beniston et al., 2014).

1.3.3 Decomposition, nutrient cycling and stoichiometry

Reports throughout different pedoclimatic conditions outline the significance of the nitrogen cycle in regulating SOC formation and turnover processes (Oren et al., 2001; J. Six et al., 2002; Van Groenigen et al., 2006). The stability of these SOC pools, and resulting soil carbon storage potential, not only depends on the cycling of nutrients during formation and turnover processes, but the consistency and narrow range of C, N, P, and S ratios as well (Cleveland and Liptzin, 2007; Hessen et al., 2004; Kirkby et al., 2013, 2011; Schmidt et al., 2011). Consumption of plant biomass by grazers significantly alters stoichiometric relationships in agroecosystems (Elser and Urabe, 1999; Metcalfe et al., 2014), profoundly impacting N and P cycling mechanisms by i) removal, transformation, return, and redistribution of N and P through urine and dung deposition (Parsons et al., 2013; Pineiro et al., 2010; Rumpel et al., 2015); ii) decoupling of C with N and P through animal metabolic processes (Parsons et al., 2013; Soussana and Lemaire, 2014); iii) modification of NPP, forage root activity, and C input quality (Gao et al., 2008; Hamilton et al., 2008; Hamilton and Frank, 2001; Klumpp et al., 2009; Rumpel et al., 2015); and iv) changes in compaction and aeration of top soil from hoof action (Beukes and Cowling, 2003) that differentially alter denitrification and soil respiration rates (Sexstone et al., 1985). Understanding the impacts of livestock integration on agroecosystem nutrient dynamics is therefore necessary to manage ICL systems for greater SOC accumulation.

High intensity grazing in grasslands has been shown to increase soil C-to-N ratios, as N is exported by animal biomass and expedited litter decomposition rates alter soil C and N mineralization (Hassink, 1994; Klumpp et al., 2009; Tracy and Zhang, 2008). This increase in soil C-to-N may decrease microbial CUE (Manzoni et al., 2012), thereby decreasing the relative allocation of soil C toward microbial growth (Kallenbach et al., 2016) and therefore SOC storage. Additionally, spatially heterogeneous build-ups of reactive soil N, from patches of urine and dung deposition (Afzal and Adams, 1992), can accelerate the initial stages of microbial litter decomposition (Berg, 2000; Berg and Meentemeyer, 2002). This build-up of reactive soil N may also increase the potential for N losses through leaching, denitrification, and volatilization of NH_3 (Núñez et al., 2007; Pineiro et al., 2010). Alternatively, there may be significant agroecosystem N removal upon grazing (Parsons et al., 2013) and potential N limitation for SOC stabilization. Where this occurs, N fertility management is likely to mitigate constraints within ICL systems (Janssen, 2006; Zhu and Chen, 2002). Removal of residual inorganic N with the introduction of ICL management may actually help to improve N use-efficiency and environmental outcomes relative to continuous cropping (Janssen, 2006; Snyder et al., 2009).

This is achieved when ICL best management practices promote forage root biomass production and greater net ecosystem N uptake (Pineiro et al., 2009).

A majority of consumed biomass is returned to the soil as dung and urine, where carbon and nutrients are stoichiometrically decoupled and present in more labile and bioavailable forms (Eldridge et al., 2017; Rumpel et al., 2015). As stocking rates increase, nutrient decoupling by animals can outpace the C, N, and P coupling gained through greater NPP (Lemaire et al., 2014). However, significant increases in microbial biomass and enzymatic activity under ICL management (Acosta-Martínez et al., 2010, 2004; da Silva et al., 2015; Franzluebbers and Stuedemann, 2008; Muniz et al., 2011; Salton et al., 2014) may facilitate a recoupling and balancing of stoichiometric relationships (Drinkwater and Snapp, 2007; Rumpel et al., 2015). This stoichiometric balancing of C, N, and P is not only important for determining SOC ordination, quality and stability of freshly deposited carbon, but also for the mineralization of older, stable SOC stocks (Schmidt et al., 2011). The stoichiometric relationships of plant-grazer-soil interactions are mediated by species-specific herbivore metabolic processes and body size managed according to plant community composition and productivity. Whereas herbivore metabolic processes might exacerbate stoichiometric decoupling, other characteristics of ICL systems, such as enhanced agroecosystem NPP and microbial activity, can help recouple soil C with N and P and provide new avenues to prevent reactive soil N build-up and losses.

1.3.4 Soil physical structure and SOC occlusion

Physical protection of SOC, through intra-aggregate occlusion and mineral sorption, promotes stabilization longevity of SOC through reduced access to microbial mineralization and oxidation

(Brodowski et al., 2006; Dungait et al., 2012; Kaiser and Guggenberger, 2000; Schmidt et al., 2011; J. Six et al., 2002). The strength of mineral sorption is related to the collective surface area and bonding properties of the mineral phase and the lability and aromaticity of SOC compounds (J. Six et al., 2002). While conventional understanding suggested that recalcitrant, lignin-derived, and aromatic organic C inputs contribute more to mineral-associated organic carbon (MOC), a protected and persistent pool of soil C (Kaiser and Guggenberger, 2000; Lavallee et al., 2020; Smith et al., 1997), recent research emphasizes the contributions of labile and non-structural compounds toward MOC stabilization (Cotrufo et al., 2015; Kallenbach et al., 2016). Ruminant conversion of plant structural components, such as lignin, cellulose, and hemi-cellulose (Jung and Allen, 1995), into more labile carbon compounds (Rumpel et al., 2015) might enhance MOC accumulation (Cotrufo et al., 2015; Kallenbach et al., 2016) under ICL. There may be a positive feedback between MOC stabilization and soil aggregate formation, where physically occluded intra-aggregate SOC is composed predominantly of MOC, and is further protected from microbial degradation (Bongiovanni and Lobartini, 2006; Kallenbach et al., 2016, 2015; Lavallee et al., 2020).

While the existing literature is scarce, multiple ICL studies have shown improvements in aggregate stabilization (Acosta-Martínez et al., 2004; Fultz et al., 2013b; Maughan et al., 2009; Salton et al., 2014) and occluded intra-aggregate SOC (Boeni et al., 2014; Fultz et al., 2013b; Salton et al., 2014) relative to continuous cropping. However, other studies have found no increase in intra-aggregate SOC from ICL adoption (Assmann et al., 2014; Franzluebbers and Stuedemann, 2008). Souza et al. (2010) monitored three grazing intensities under integrated no-tillage soybean/pasture rotations and found that light and moderate grazing intensities substantially improved macroaggregate (4.67 to 9.52 mm) formation, while having a non-significant impact on microaggregates (<1 mm). They hypothesized that animal integration stimulated pasture root biomass and exudate release, resulting in higher soil particle aggregation and modest increases in total SOC content – corroborating recent findings on the relative contributions of living roots and rhizodeposits to SOC accumulation (Kallenbach et al., 2016; Sokol et al., 2019). Fultz et al. (2013a) observed significant relative increases in recalcitrant, intra-aggregate SOC pools within semi-arid ICL systems, further highlighting the potential soil carbon sequestration benefit with improved aggregate size and stability.

Aggregate formation is enhanced by biological activity, due to the particle binding dynamics of microbially-derived decomposition products (Chotte, 2005; Kallenbach et al., 2015) and the physical effects of roots and fungal hyphae (Rillig and Mummey, 2006; Tisdall et al., 1997). In addition to an increase in total microbial biomass and activity, ICL management may promote a shift toward more fungal dominated populations (Acosta-Martínez et al., 2010; Davinic et al., 2013). Improvements in particle aggregation and SOC physical protection under ICL management are also attributed to increases in organic inputs, reductions in mechanization, and increases in root growth due to forage integration into previously continuously cropped land (Acosta-Martínez et al., 2004; Salton et al., 2014; Souza et al., 2010).

The introduction of livestock to cropland does provide concern over soil compaction and associated decreases in water and air conductivity (Hamza and Anderson, 2005). Whereas some field studies (Lobry De Bruyn and Kingston, 1997) and modeling approaches (Kaine and Tozer, 2005) have shown reduced soil porosity and infiltration with increased livestock trampling, other studies have found no effects of increasing stocking rates on soil physical condition (Monaghan et al., 2005). Some studies suggest that higher earthworm abundances – that result from higher stocking densities and subsequent manure deposition – could partially counter the compaction impacts from trampling (Curry et al., 2008; Schon et al., 2008). While compaction has been observed in ICL systems with cattle integration (Tracy and Zhang, 2008), the extent of compaction is drastically reduced when animal traffic occurs during dry and thawed soil conditions, as compared to wet and frozen periods (Bell et al., 2011; Drewry et al., 2004). Additionally, increases in compaction under ICL management are generally isolated to shallow soil depths, may be ameliorated through root growth and conservative tillage (Bell et al., 2011; Tracy and Zhang, 2008), and do not appear to decrease subsequent crop yields (Bell et al., 2011; Rakkar et al., 2017; Tracy and Zhang, 2008). Although it remains unclear to what extent ICL displacement of mechanization, such as tillage, weed cultivation, and mowing, will contribute to improvements in subsurface soil compaction (Soane et al., 1982), the degree to which ICL itself contributes to soil compaction largely depends on grazing management and co-management practices.

1.4 MANAGING INTEGRATED CROP-LIVESTOCK SYSTEMS FOR SOIL ORGANIC CARBON SEQUESTRATION

Based on the fundamental understanding described above, there are various opportunities that exist to optimize ICL systems for enhanced SOC accumulation including management of i) grazer stocking intensity, frequency, and duration; ii) vegetation composition and coverage; and iii) soil disturbance levels (Figure 1b). While the potential impacts of ICL adoption on SOC storage remain inconclusive, much of the literature underscores the value of controlled grazing management and some of the co-management conservation practices frequently implemented within ICL systems (Da Silva et al., 2014; Ryschawy et al., 2017; Salton et al., 2014).

1.4.1 Stocking intensity and rotational grazing

Grazing intensity is a function of grazer density and duration and is one of the main management drivers of SOC accumulation or decline within grazed ecosystems (Holechek et al., 1995; Zhou et al., 2017). The response of plant communities and SOC to grazing is highly context specific and dependent on interacting agroecological, edaphic, and climatic conditions (Mcsherry and Ritchie, 2013; Pineiro et al., 2010; Stahlheber and D'Antonio, 2013). However, the magnitude of these impacts will largely be determined by management with respect to the timing (periodicity and frequency) and intensity with which livestock are grazed. ICL systems may utilize either continuous grazing, where livestock graze for extended periods of time with no or infrequent rest periods, or rotational grazing where livestock are rotated frequently amongst smaller sections, allowing for longer vegetation rest periods. When compared to grazing exclusion, some studies have found a positive relationship between stocking density and SOC accumulation under both continuous and rotational grazing regimens (Conant et al., 2003; Derner et al., 2006; Dubeux et al., 2006; Manley et al., 1995; Reeder et al., 2004; Schuman et al., 2002). However, there is a site-specific threshold at which stocking rates become inversely associated with SOC storage (W. Chen et al., 2015; Da Silva et al., 2014; Dlamini et al., 2016; Ernst and Siri-Prieto, 2009; Mcsherry and Ritchie, 2013; Plaza-Bonilla et al., 2015; Teague et al., 2011), especially for labile SOC fractions (Cao et al., 2013; Silveira et al., 2013). For instance, grasslands dominated by C3 and mixed C3-C4 species are more sensitive to SOC losses at higher grazing pressures (Frank et al., 1995; Mcsherry and Ritchie, 2013) than those dominated by C4 grasses.

Under continuous grazing, lower intensity may help maximize the potential SOC accumulation provided by animal integration while minimizing the detrimental impacts of heavier grazing intensities. High intensity, continuous duration grazing practices have been shown to reduce vegetation biodiversity (Teague et al., 2011; Waters et al., 2017) and landscape productivity (W. Chen et al., 2015; Plaza-Bonilla et al., 2015; Schönbach et al., 2011), while light or moderate intensity grazing can maintain or improve biodiversity and aboveground biomass productivity compared to grazing exclusion (Cui et al., 2005). Heavy stocking rates may enhance litter decomposition and turnover rates through (i) shifts in forage population toward fast-growing species with low lignin and high N content (Rumpel et al., 2015); (ii) return of carbon in more labile forms as dung and urine (Rumpel et al., 2015); and (iii) physical breakdown and incorporation of residues with animal traffic (Schuman et al., 2002, 1999). However, belowground productivity and carbon deposition appears to benefit from light to moderate grazing, relative to high intensity or grazing exclusion (W. Chen et al., 2015; Zhou et al., 2017). A meta-analysis by Zhou et al. (2017) found that, while heavy and moderate intensity grazing decreased SOC pools, light intensity grazing significantly increased microbial biomass and total SOC compared to grazing exclusion. The importance of grazing intensity management is even more pronounced in arid and semi-arid ecoregions, where sustained high intensity grazing may result in rapid SOC decline (Dlamini et al., 2016).

Depending on the type of ICL system, rotational grazing may be essential to maintain or improve SOC (Figure 1b). Within semi-arid agroecosystems the adoption of rotational grazing practices, which incorporate periods of rest between short and intensively stocked grazing periods, have been observed to increase SOC (Briske et al., 2011; Conant et al., 2003; Teague et al., 2011;

Waters et al., 2017) and maintain topsoil (Mcsherry and Ritchie, 2013; Sanjari et al., 2008; Teague et al., 2015) relative to continuous grazing. Though some experimental results are mixed (Briske et al., 2008). Intensive rotational grazing can result in reduced animal selectivity and more uniform and homogenous grazing (Dumont et al., 2007; Leigh and Holgate, 1978; Teague and Dowhower, 2003). When best management practices are utilized, this can result in a shift toward more beneficial pasture composition for SOC accumulation (W. Chen et al., 2015; Teague et al., 2011; Waters et al., 2017), with higher perennial grass content (Kemp et al., 2000) and soil coverage (Earl and Jones, 1996; Teague et al., 2011). Longer periods of rest can also enhance vegetation recovery (Sanderman et al., 2015), improve aboveground (Briske et al., 2011; Teague et al., 2011) and belowground productivity (W. Chen et al., 2015), enhance nutrient retention (W. Chen et al., 2015; Conant et al., 2003; Teague et al., 2011; Waters et al., 2017), and reduce soil erosion potential (Kemp et al., 2000; Sanjari et al., 2008).

1.4.2 Forage species selection

Forage species may be chosen to provide annual or short term-cover, such as through cover cropping, or as part of longer perennial understory or pasture-phase rotations. The adoption of pasture-phase rotations have been shown strong evidence to maintain or improve cropland SOC (Conant et al., 2017; Franzluebbers et al., 2014; Glover et al., 2010; Jarecki and Lal, 2003; Salton et al., 2014), especially under conservation tillage management (Da Silva et al., 2014; De Souza et al., 2008; Gamble et al., 2014). Pasture-phase rotations are also more efficient than crop phases at recycling and retaining residual crop nutrients (Lemaire et al., 2014; Rumpel et al., 2015; Russelle et al., 2007), providing direct benefits for subsequent crop yields (Maughan et al., 2009; Tracy and Zhang, 2008). Choice of forage species for pasture or cover cropping is an important consideration when implementing ICL systems (Figure 1b), as specific plant functional groups have been shown to strongly mediate SOC storage potentials (Lange et al., 2015; Oelmann et al., 2007; Steinbeiss et al., 2008; Temperton et al., 2007; Wu et al., 2017).

Pasture-phase rotations are often dominated by cool or warm-season perennial grasses, sometimes incorporating leguminous N-fixing species (Bell et al., 2014; Bell and Moore, 2012; Russelle et al., 2007). Perennial grasses have more extensive root development and prolonged soil cover compared to annual pastures or cropland (Beniston et al., 2014; Glover et al., 2010; Schipanski and Drinkwater, 2012). Studies have consistently shown that root-deposited C has a longer residence time than aboveground-derived carbon (Mazzilli et al., 2015; Rasse et al., 2005), potentially due to increased physico-chemical protection and sorption interactions during decomposition (Rasse et al., 2005). Additionally, increased biological activity from fine root development and rhizosphere exudation also promote microaggregate formation and subsequent enhancement of SOC physical occlusion within the soil matrix (Jastrow et al., 2007, 1998; Johan Six et al., 2002). Perennial pastures have also been shown to (i) mitigate soil carbon loss from erosion (Robertson et al., 2009; Russelle et al., 2007; Schipanski and Drinkwater, 2012); (ii) improve water holding capacity and use-efficiency (Bell et al., 2014; Tracy and Zhang, 2008); (iii) and increase microbial biomass and activity (Acosta-Martínez et al., 2010, 2004; Beniston et al., 2014; DuPont et al., 2014) relative to annual-dominated pastures and continuous cropland, potentially providing positive feedbacks for SOC accumulation.

While plant community composition strongly affects SOC storage processes, the influence of specific plant functional groups within more complex and diverse communities remains poorly understood. Introducing legumes may partially mediate belowground productivity and turnover as well as a suite of biogeochemical functions that benefit SOC storage. Semi-arid grassland communities containing legumes show increases in plant functional complementarity and facilitation that reduce competition for soil N (Wu et al., 2017), increase leaf N uptake (Temperton et al., 2007), and enhance P bioavailability (Drinkwater and Snapp, 2007). Drinkwater et al. (1998) found that even though leguminous mixtures did not increase aboveground biomass production, these systems still resulted in higher accumulation of new SOC compared to non-leguminous mixtures. However, other studies have found that predominately leguminous plant mixtures negatively affect SOC storage (Lange et al., 2015). This may be due to reduced root biomass production and rhizosphere activity (Bessler et al., 2009; Lange et al., 2015) or decreasing C-to-N ratios accelerating the decomposition of resident SOC (Kuzyakov, 2002; Qiao et al., 2016).

Different forage legumes do not perform equally to grazing disturbances (Kleen et al., 2011; Schwinning and Parsons, 1996) and species selection is therefore an important BMP consideration. Annual re-planting of red or white clovers may provide an optimal outcome, due to their preferential selection by grazers (Dumont et al., 2007) and positive performance under grazing pressure with respect to total forage productivity (Sanderson et al., 2005) and protein content (Kleen et al., 2011). The pairing of grass species, especially C4 grasses, with legumes appear to maximize ecosystem functional niche complementarity and SOC accumulation benefits, especially compared to monocultures (Fornara and Tilman, 2008). This is likely achieved through increased access and provision of N by legumes and greater N uptake and use-efficiency by C4 grasses, in both high and low diversity plant communities (Fornara and Tilman, 2008). In addition, landscapes dominated by C4 and perennial grasses show greater adaptation to heavier stocking rates. Their higher root-to-shoot ratios and subsequent increases in belowground carbon deposition have been shown to sequester additional SOC with grazing (Dubeux et al., 2006; Mcsherry and Ritchie, 2013; Orgill et al., 2017; Waters et al., 2017).

1.4.3 Tillage disturbance and residue retention

Heavy tillage co-management is likely to reduce the SOC accumulation potential of semi-arid ICL systems (de Faccio Carvalho et al., 2010; Franzluebbers and Stuedemann, 2008; Siri-Prieto et al., 2007; Sulc and Franzluebbers, 2014), especially at shallow soil depths (Acosta-Martínez et al., 2004; Fultz et al., 2013b). However, the use of controlled grazing and the introduction of forage plants can assist in noxious weed suppression and residue management (Schoofs and Entz, 2000; Schuster et al., 2016; Sean Clark and Gage, 1996; Tracy and Davis, 2009), potentially reducing the use of mechanical disturbance and better facilitating a transition to conservation tillage management within semi-arid cropland (Smith et al., 2015).

A decrease in mechanical cultivation abates the turnover of macro- and microaggregates that facilitate the physical occlusion and protection of SOC, thereby reducing the exposure of older, stable SOC to microbial decomposition (Mikha and Rice, 2004; Six et al., 2000). This is particularly critical for semi-arid ICL systems where increases in occluded intra-aggregate SOC are proposed to be a significant part of the SOC accumulation benefit. In addition to increasing SOC storage potential, conservation tillage practices can increase microbial biomass (Acosta-Martínez et al., 2004; Angers et al., 1993; Franzluebbers et al., 1995) and activity (Acosta-Martínez et al., 2010; Deng and Tabatabai, 1997) and promote the proliferation of soil fungi

(Frey et al., 1999) which have shown to be critical for stable SOC formation (Kallenbach et al., 2016; Liang et al., 2019). A 13-year study comparing the relative outcomes of different semi-arid annual cropping systems found 22% more SOC in the 0—15 cm depth fraction under no-till (NT) ICL management than conventional tillage (CT) continuous cropping, with significantly more SOC within occluded intra-aggregate pools (Fultz et al., 2013a). A study by Carvalho et al. (2010) also observed significantly higher SOC accumulation in multiple depth fractions down to 25cm under NT ICL management relative to both CT ICL and continuous cropping systems. Larger amounts of retained surface residues under NT also help reduce soil surface exposure, thereby improving soil water conservation and soil temperature regulation (Lal and Kimble, 1997; Ramakrishna et al., 2006) and reducing soil erosion potential (Lal and Kimble, 1997; Plaza-Bonilla et al., 2015).

1.5 ECOSYSTEM SERVICES AND CO-BENEFITS

The overwhelming thrust of agronomic research and technological development over the last half century has focused on improving the productivity and sustainability outcomes of agricultural systems that are increasingly specialized in crop or livestock production. Nevertheless, a growing body of literature suggests that reintegrating livestock at the farm-scale can provide economic and environmental benefits while reducing risks associated with manure nutrients and market and weather variability (Garrett et al., 2017). In the face of increasing resource scarcities, climate change, and societal demands for a broad set of sustainability outcomes, ICL systems offer the potential to advance agriculture toward several key sustainability goals that are essential for climate change resilience, including: (i) improved net landscape carbon sequestration; (ii) increased growth of total agricultural productivity per unit of land; (iii) significant gains in N and

P nutrient use-efficiency; (iv) improved erosion control; and (iv) reduced vulnerability to crop and livestock losses associated with environmental stresses. For instance, pasture-phase rotations in annual cropping system and prolonged maintenance of understory vegetation in perennial cropping systems enhance landscape NPP, reduce erosion and surface runoff, and increase nutrient recycling efficiency through deep and fibrous forage rooting that reintroduce leached nutrients back into the crop rooting zone. This further reduces groundwater contamination and external input requirements.

When managed properly, the introduction of forages and grazing have also been shown to suppress weed pressure, mitigating the use of mechanical and chemical pest control methods. Additionally, multiple ICL studies have observed the maintenance or improvement of subsequent crop yields following the introduction of grazing and pasture-phase integration (Maughan et al., 2009; Peterson et al., 2020; Tracy and Zhang, 2008). Improvements in soil structure increase infiltration rates and facilitate groundwater recharge while prolonging the period before initiation of seasonal irrigation requirements, with significant benefit for semi-arid producers. However, more ICL-specific research must be conducted to quantify the co-outcomes – including potential improvements in soil health, decreases in chemical inputs and labor, and potential tradeoffs such as compaction, stoichiometric nutrient decoupling and the build-up of reactive soil N.

1.6 CONCLUSION AND KNOWLEDGE GAPS

With a diversity of applications and management options, ICL systems have significant global adoption opportunity and climate change mitigation potential. Livestock re-integration may impact cropland SOC dynamics through modifying (i) above- and belowground biomass production; (ii) recycling of residual crop nutrients; (iii) biological activity and trophic networks complexity; (iv) soil structure and SOC physical protection; (v) accumulation of labile SOC fractions; and (vi) impacts on noxious weed cycles and subsequent use of mechanical cultivation (Lemaire et al., 2014; Salton et al., 2014; Vilela et al., 2011). The direction and magnitude of these impacts will largely be determined by climate and soils as well as interactions with other agroecosystem management components including plant species composition and cover, crop rotations, fertilization regimens, and soil disturbance.

Maximizing SOC accumulation potential under ICL management will require consideration of the important feedback between herbivory, soil microbial ecology, and forage species interactions (Figure 1a). While various findings of this overview were drawn from isolated management approaches, and may contradict or be altered over time, the existing body of research strongly supports the use of no-till management to capitalize on other potential SOC accumulation mechanisms of semi-arid ICL systems. Research also supports the utilization of C4 and perennial or high-residue annual forages, legumes, and light to moderate intensity rotational grazing practices for building SOC within semi-arid cropland (Figure 1b). Managing for enhanced biodiversity and tighter nutrient control will also assist in capitalizing on proposed SOC benefits of ICL.

However, specific knowledge gaps remain in optimizing plant-soil-grazer feedback and co-management practices to improve SOC quality and quantity. While much of the literature highlights potential changes in total SOC stoichiometry and quantity under ICL management, it is still unclear to what extent simply increasing SOC content provides short, medium, and long-term benefits. The accumulation of SOC may be central to realizing the climate change mitigation potential of agriculture, especially in semi-arid ecoregions where SOC storage potentials are rarely achieved (Ahlström et al., 2015) and often limit improvements in soil health and agroecosystem resilience to climate change. However, the utilization of SOC for its nutrients and energy to conduct microbial functions is an essential consideration. In this case, the quality of SOC may be much more important than the total quantity sequestered, and long-term persistence and stabilization of SOC, especially to mineral surfaces, may come as a trade-off for microbial accessibility.

As discussed, the integration of ruminant grazing into cropland may alter many SOC transformation pathways, and further research should focus on better understanding the mechanistic drivers of these outcomes, especially relating to semi-arid SOC quality, turnover, and stabilization dynamics. Additionally, the breadth of ICL research must expand across diverse climatic, edaphic, and agroecological conditions while placing a stronger emphasis on the biogeochemical outcomes of systems-level analyses. The extent to which specific ICL system practices, or combinations of management decisions, provide SOC benefits still remains unclear, and more long-term research is necessary to develop a comprehensive and interdisciplinary understanding of how these specific agroecological systems may benefit producers, the environment, and society at large.

Chapter 2: Long-term integrated crop-livestock grazing stimulates soil ecosystem carbon flux, increasing subsoil carbon storage in Mediterranean perennial agroecosystems

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ABSTRACT

The strategic use of ruminant grazing in perennial cropland is steadily increasing throughout Mediterranean perennial agroecosystems. Integrated sheep-vineyard (ISV) management, where small ruminant livestock graze on understory vegetation, is viewed by some practitioners as a feasible opportunity to transition toward less petrochemically intensive understory management paradigms. However, our knowledge of soil carbon dynamics associated with grazing in perennial integrated crop-livestock (ICL) agroecosystems is notably limited, especially within Mediterranean contexts. Here, we use a representative set of on-farm paired surveys to assess soil ecosystem habitat and resource conditions related to SOC flux and storage in vineyards utilizing sheep-integration (ISV) and conventional understory management techniques (CONV), with otherwise similar edaphic, climatic, and co-management characteristics. Our results show that long-term grazing increased the quantity of active, labile, and soluble carbon (C), nitrogen

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* A version of this chapter was submitted for publication as "Brewer, K.M., Muñoz-Araya, M., Martinez, I., Marshall, K.M, Gaudin, A.C.M., 2022. Long-term integrated crop-livestock grazing stimulates soil ecosystem carbon flux, increasing subsoil carbon storage in Mediterranean perennial agroecosystems" to the journal Geoderma and was under review at the time of writing.

(N), and phosphorus (P)within ISV soils. Vineyard soils with sheep grazing had much higher quantities of microbial biomass carbon (MBC) and phospholipid fatty acid (PLFA) biomarkers, particularly amongst core functional groups related to decomposition. Soil microbial communities under ISV showed higher C mineralization rates as well as higher carbon use-efficiency, as indicated by less CO_2-C respired relative to the size of the MBC pool. ISV microbial communities also showed altered metabolic investment strategies related to nutrient acquisition, with lower P-cycling enzyme activity and higher N-cycling enzyme activity. The ISV sites showed increases in SOC storage at subsoil depths, including increased physicochemical stabilization of mineral-associated organic carbon (MAOC) in the deepest measured subsoil layer (30–45 cm). We observed no differences in soil structure between treatments nor differences in the carbon fractions associated with four distinct aggregate size categories. We propose a framework to explain observed shifts in SOC dynamics of perennial ICL systems that include i) deposition of C and nutrient inputs with higher lability and solubility; ii) ruminant-induced decoupling of C from N and P, resulting in increased nutrient bioavailability; and iii) altered metabolic investment strategies of soil microbial communities toward more efficient biomass accumulation. These findings show strong potential of ICL grazing to enhance soil functioning and increase SOC storage in Mediterranean perennial agroecosystems.

2.1 INTRODUCTION

Agricultural resource conservation incentives, especially in utilizing cropland to sequester additional SOC, are providing new opportunities to explore underutilized farming methods for their potential agronomic and environmental benefits (Minasny et al., 2017). Perennial integrated crop-livestock (ICL) management, where ruminant livestock forage on understory plant communities during prolonged periods of vegetative growth, provide one such opportunity as a feasible agroecological alternative to current petrochemically-intensive understory management practices (such as mowing, herbicides, and tillage). Whereas much of the world's crop-livestock agroecosystem components are still managed in tandem, with animals providing diverse grazing-based services for crop production, the industrial intensification of U.S. agriculture has resulted in highly specialized and de-coupled farm-scale crop and livestock components (Entz et al., 2005; Garrett et al., 2020; Sanderson et al., 2013).

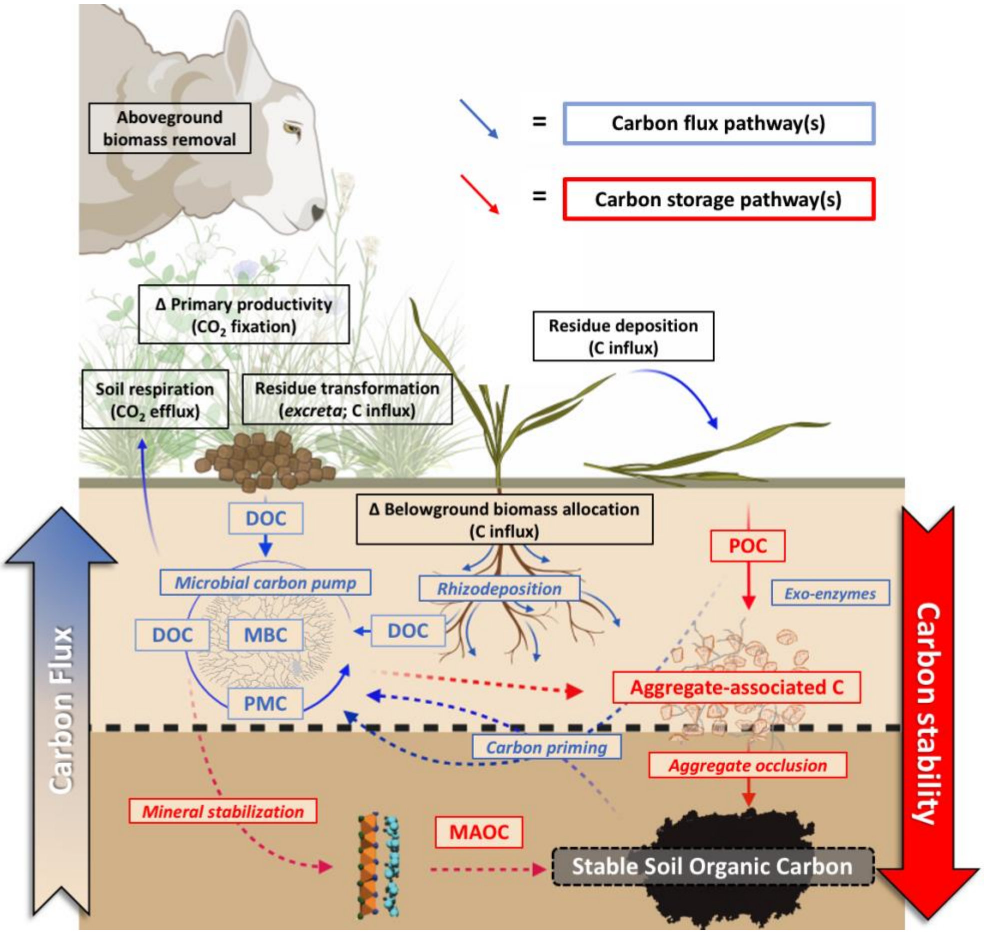
While more rigorous inquiry is necessary, crop-livestock de-coupling is currently understood to contribute to poor nutrient cycling within and between agricultural operations and an increased environmental footprint of both crop and livestock production (Garrett et al., 2017; Lemaire et al., 2014). As such, the re-integration of crop and livestock system components has been proposed as a strategy toward improving the environmental conservation and resource efficiency outcomes of agricultural landscapes (Russelle et al., 2007). However, the potential of this re-integration, with respect to the comparative benefits and/or trade-offs of this agroecological approach relative to conventional practices, is highly underexplored within industrial agricultural contexts (Garrett et al., 2017). Amongst several notable agronomic and environmental uncertainties, there are key knowledge gaps related to the impact of cropland grazing on ecological processes related to soil carbon dynamics.

A core proposition of agroecological farming models relate to efficiency increases in the utilization of externally-applied resources, through retention and (re)cycling processes that are endogenous to the agroecosystem's design and, therefore, *internally regulated* (Altieri et al., 2015; Garcia-Franco et al., 2018; Lipper et al., 2014; Lovell et al., 2010; Snapp, 2017; Wagg et al., 2020). This internal regulation of agroecosystems – defined as its capacity to tightly couple energy and nutrient (re)cycling (King and Hofmockel, 2017; Prommer et al., 2020; Tamburini et al., 2020) – depends upon the facilitation of critical ecosystem functions and their underlying biological processes, especially those related to energy and nutrient turnover (Lal, 2016; Power, 2010; Snapp, 2017; Tamburini et al., 2020; Xu et al., 2020). Soils play an essential role in agroecosystem internal regulation – most notably related to the flux of soil carbon (energy) and nutrients, as well as the eventual formation and stabilization of soil organic carbon (SOC).

The strategic integration of diverse plant and animal communities across multiple spatial (e.g., field, farm, and landscape) and temporal (e.g., inter- and intra-seasonal) scales have been shown to promote resource use-efficiency through internal regulation pathways (Altieri et al., 2015; Griesser et al., 2022; Lange et al., 2015; Prommer et al., 2020; Snapp, 2017; Wagg et al., 2020). This may occur in many forms related to increasing the presence of diverse carbon (C) and nutrient utilization pathways and, thereby, improving synchronicity in the utilization of deposited C and nutrients within soil ecosystems (Griesser et al., 2022; Lange et al., 2015; Prommer et al., 2020; Snapp, 2017; Wagg et al., 2020). Some key underlying mechanisms relate to the facilitation of interconnected ecological interactions that include, but are not limited to, niche partitioning and niche complementarity (Altieri et al., 2019; Garland et al., 2020; Petersen-Rockney et al., 2021; Ponisio et al., 2015; Snapp, 2017).

The impacts of grazing will affect multiple ecosystem processes related to nutrient utilization and the pathways regulating SOC flux and storage (Figure 1) (Brewer and Gaudin, 2020; de Faccio Carvalho et al., 2010; Jarvis, 2009; Lemaire et al., 2014; Rumpel et al., 2015). Specifically, animal re-integration into cropland can alter carbon and nutrient flows *directly* through (1) transformation of aboveground residues into soluble, nutrient-rich, and labile dung and urine, where carbon and nutrients are more stoichiometrically decoupled (Jarvis, 2009; Jung and Allen, 1995; Rumpel et al., 2015); (2) biomass removal that triggers shifts in forage productivity and the reallocation of resources above- and belowground (Dawson et al., 2009); and (3) residue deposition and incorporation due to the trampling effect and hoof action of animal traffic (Acosta-Martínez et al., 2004; Greenwood and McKenzie, 2001; Wei et al., 2021) (Figure 1). It may also alter carbon and nutrient flows *indirectly* via (4) inter- and intra-seasonal shifts in plant community composition (Chen et al., 2018) and (5) changes in soil structure, which alter transport and spatial distribution of soil carbon and nutrients as well as their physical protection from continual degradation through occlusion within aggregates (Erktan et al., 2020; Lavallee et al., 2020; Six et al., 2000).

Figure 1: Conceptual framework for soil carbon flux and storage pathways in perennial integrated crop-livestock systems



Potential direct mechanisms by which sheep grazing on understory forage alters carbon (C) flows into perennial cropland soils (black). Once deposited (C influx), labile and physically-accessible soil organic carbon (SOC) is fluxed (blue) through the soil ecosystem via the microbial carbon pump (MCP). Within the MCP, soil C is continually transformed and (re)cycled through assimilation within microbial biomass carbon (MBC), the release of dissolved organic carbon (DOC) substances and/or formation of microbial necromass, and re-assimilation back into MBC. This potentially mineralizable carbon (PMC) may continually cycle within the MCP or "leak" from the pump through either respiration (CO$_2$ efflux) or various soil carbon storage pathways (red). SOC storage pathways include mineral stabilization via formation of mineral-associated organic carbon (MAOC) or aggregate occlusion and physical protection as aggregate-associated C. Particulate organic carbon (POC) may also enter the MCP through fragmentation and depolymerization or may take a more direct storage pathway via aggregate occlusion. Storage pools may also re-mobilize into flux pools via soil carbon priming.

These modifications to agroecosystem carbon and nutrient inputs may also impact microbial ecological processes such as growth rates and community assembly, substrate utilization and resource acquisition, and investment strategies such as stress responses and the production of soil exo-enzymes (Malik et al., 2020). Since the partitioning of SOC into different biochemical and physical pools is mediated by the quantity, quality, and spatial distribution of substrates entering the soil ecosystem (Lavallee et al., 2020; Rasse et al., 2005; Schmidt et al., 2011; Sokol et al., 2019; Sokol and Bradford, 2019), it is likely that the plant-grazer-soil interactions associated with ICL adoption have significant implications for cropland carbon and nutrient dynamics. This partitioning will ultimately impact the fate of carbon within soil ecosystems – particularly with respect to how it will be utilized by soil microbes and if it will persist as long-term sequestered C (Cotrufo et al., 2013; Liang et al., 2019; Schmidt et al., 2011; Zhu et al., 2020).

The strategic design of ICL systems for improving SOC storage and other conservation outcomes will require heightened understanding and consideration of carbon and nutrient flows through the agroecosystem (Brewer and Gaudin, 2020) (Figure 1). Microbial communities largely drive these biogeochemical flows within soils, as they rely on energy from soil carbon decay channels to power nutrient cycling processes (Janzen, 2006; Kopittke et al., 2022; Zhu et al., 2020). Increasing the flux rate of carbon (energy) through soil ecosystems is therefore necessary in order to increase rates of ecological functioning. Since microbial utilization of SOC for biomass growth (anabolism) is generally associated with respiration and, therefore, CO_2 efflux (catabolism), it has been argued that storing soil carbon is inherently in tension with microbial functioning (Janzen, 2006). However, the accumulation of stable and long-term stabilized mineral-associated organic carbon (MAOC) has increasingly been shown to require the formation of microbial necromass, and is therefore dependent on the continual turnover of labile and accessible carbon (Dynarski et al., 2020; Lehmann and Kleber, 2015; J. Six et al., 2002; Six et al., 2004) – a concept known as the microbial carbon pump (MCP). In fact, recent studies have shown that the MCP and its microbially-derived anabolic compounds are the predominate source of stabilized MAOC (Basile-Doelsch et al., 2020; Kallenbach et al., 2016; Liang et al., 2019). Stabilized soil carbon may therefore be viewed predominately as a reservoir of previously processed microbial products, with stored chemical energy which may be accessed later by soil microbial communities when the habitat and resource conditions of the soil ecosystem are altered (Erktan et al., 2020) – a process understood as soil carbon priming (Kuzyakov, 2010). As such, the evaluation and interpretation of soil carbon storage as static and relatively inert *stocks* must be complimented by an understanding of soil carbon *flows* – as flux processes and an energy source for biological functions. These stocks and flows are of course related, as the production of microbial biomass and accumulation of microbial necromass is critical toward building long-term SOC storage.

The goal of this study was to evaluate the soil carbon flux dynamics and storage potential of perennial integrated crop-livestock systems within the context of working landscapes, with farmer implementation by early adopters who have integrated grazing for periods of multiple years. The use of precision grazing in perennial cropland is steadily increasing throughout California and beyond, particularly within Mediterranean integrated sheep-vineyard (ISV) systems (Ryschawy et al., 2021). However, mechanistic understandings of the legacy effects associated with grazing on nutrient cycling and SOC flux and storage within perennial cropland are lacking. This is especially true in semi-arid Mediterranean landscapes, which have unique features that regulate carbon flows and storage pathways (Brewer and Gaudin, 2020; Garcia-

Franco et al., 2018; Hoyle et al., 2016, 2013). Conducting on-farm studies across a representative sample of early-adopter ISV practitioners facilitates the important endeavor of evaluating the longer-term impacts of perennial cropland grazing practices within working landscapes (Garrett et al., 2017; Ryschawy et al., 2021) and deepens our understanding of the SOC storage potential associated with perennial crop-livestock re-integration.

We established an on-farm survey study across a spectrum of ISV early-adoption systems to evaluate the longer-term impacts of perennial cropland grazing practices on SOC fluxes and measurable benefits and/or trade-offs related to soil carbon storage. We explored the hypotheses that sheep grazing of winter soil covers will ***1) increase the quantity of carbon most readily available for processing by the soil food web***; and ***2) increase soil carbon flux indicators related to organic carbon turnover***; which should ***3) increase soil organic carbon storage dynamics, especially the fraction stored stably to the soil mineral matrix as mineral-associated organic carbon (MAOC).*** Better understanding of grazing impacts on SOC and biogeochemical processes will facilitate the development of best management practices (Garrett et al., 2017; Niles et al., 2018), inform widespread adoption of beneficial perennial ICL practices, and our understanding of the climate change mitigation and soil C sequestration potential of perennial cropland grazing (Brewer and Gaudin, 2020).

2.2 MATERIALS AND METHODS

Ethics statement

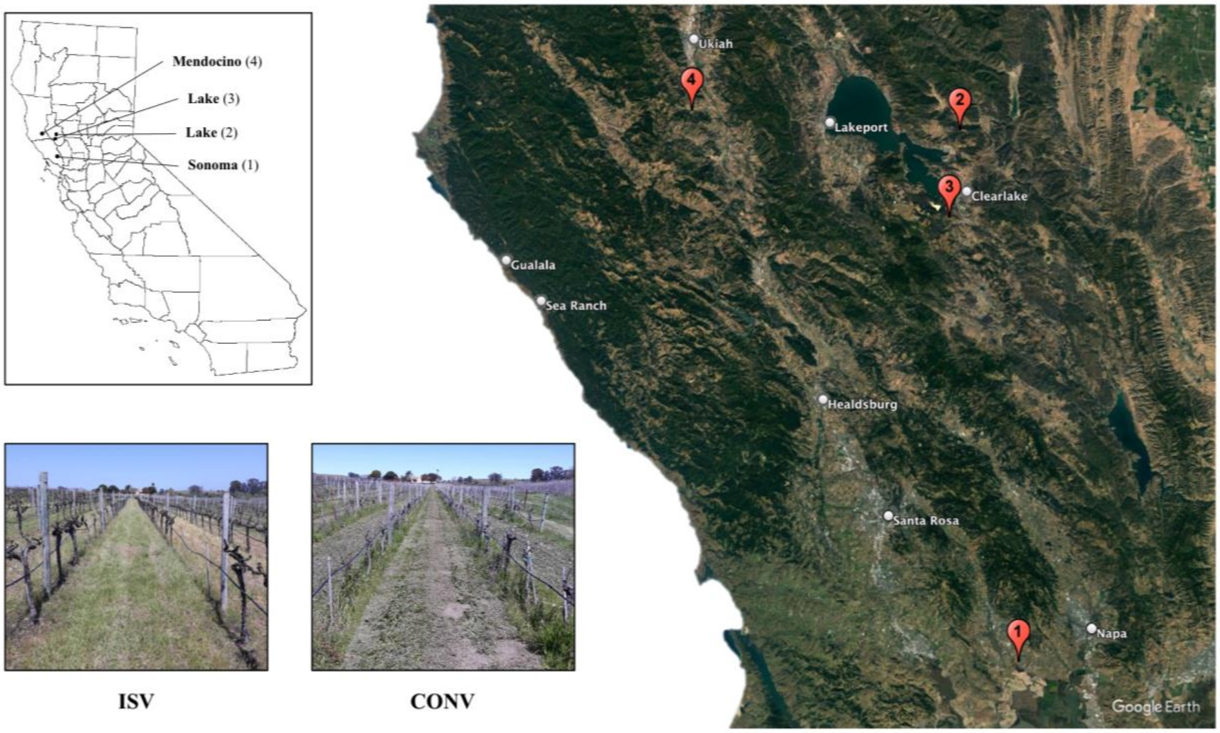
Permission for site access was previously granted by landowners. All sites were privately owned and no permits were required.

2.2.1 Study region and management characteristics

A soil survey of paired vineyard sites was conducted in the Northern California coastal foothills at three locations in 2018 and one location in 2021, between the months of January and March (Figure 2). The paired sites sampled in 2021 were added to strengthen and validate the initial findings from the 2018 sampling. Paired vineyard sites at each sampling location consisted of one '*non-integrated*' vineyard (understory vegetation managed through mowing; CONV) and one adjacent '*integrated*' vineyard (understory vegetation managed through grazing for 10+ years; ISV) – with one location in Sonoma County (home to Wappo and Patwin native peoples), two in Lake County (home to Pomo, Lake Miwok, and Patwin native peoples), and one in southern Mendocino County (home to Pomo and Yuki native peoples) (8 paired vineyards across 4 locations) (Figure 2). This Mediterranean climate is classified as a semi-arid Köppen-type *Csc* (Beck et al., 2018). It is characterized by mild cool winters, warm and dry summers, and seasonal mean annual precipitation that is lower than the regional evapotranspiration (ET) potential. The annual regional precipitation for sites in 2017 and 2020 was 739 mm and 368 mm, respectively. The mean maximum and minimum temperatures were 21.9°C and 5.7°C in 2017 and 25.8°C and 5.3°C in 2020, respectively. This contributed to an annual potential evapotranspiration (ET_o) of 1145 mm (2017) and 1406 mm (2020) and, therefore, a 1.5x (2017) and 3.8x (2020) higher potential water demand than the regional precipitation supply.

As was the case for all vineyard sites within this study, the vast majority of Northern California regional vineyard systems utilize micro-irrigation, especially surface drip systems (Tindula et al., 2013), to match vine ET demand during the warm, dry vine growing season (Prichard, 2000). This growing season generally begins in March (bud break) and goes throughout August to October (harvest), depending on the winegrape varietal. Irrigation was not applied to the interrow space, where ISV grazing predominately occurs (Niles et al., 2018; Ryschawy et al., 2021). The understory vegetation growing season is instead limited to periods of sustained precipitation, which typically occurs between November and April, during which 91% of all regional rainfall has occurred over the last 20 years (http://www.cimis.water.ca.gov/). This is also the period in which the vast majority of sheep grazing in regional vineyards occurs, including the ISV sites utilized within this study.

Figure 2: Map of study region



Paired vineyard sites (4 locations) consisted of one '*non-integrated*' vineyard (understory vegetation managed through mowing; CONV) and one adjacent '*integrated*' vineyard (understory vegetation managed through grazing; ISV), with one location in Sonoma County (1), two in Lake County (2 & 3), and one in southern Mendocino County (4), California, USA. Photos show vineyard comparisons immediately after occurrence of grazing (ISV) and mowing (CONV) events. Aerial imagery of the study area was derived from Google Earth Pro.

Most typically, sheep-vineyard grazing within this region is used as an understory plant growth termination methodology, similarly to the application of mowing, and is most often implemented immediately before vine bud break (Niles et al., 2018; Ryschawy et al., 2021). Though less common, sheep grazing sometimes occurs multiple times across the understory growing (vine dormancy) and vine growing seasons, where it is strategically applied to achieve additional management benefits such as vine leaf thinning and removal of suckering trunks (Niles et al., 2018; Ryschawy et al., 2021). The grazing strategies on all four of the integrated vineyards in this study were characterized as *high-density, short-duration rotational grazing* management (de Faccio Carvalho et al., 2010). This rotational grazing strategy incorporate small paddocks that are grazed with high animal density and rotated frequently amongst larger sections of the overall landscape. This strategy facilitates longer forage rest periods and increased competition amongst grazing ruminants (Teague et al., 2008). This has been found to lower the duration of grazing per unit of land area and reduce grazing selectivity and the spatial heterogeneity of grazing pressure (Teague et al., 2008; Teague and Dowhower, 2003).

Briefly described, temporary electrical fencing was erected to establish 1-acre sized grazing paddocks, where ~250 ewes were grazed for 1-2 days within each paddock before rotating to the next temporary paddock. Grazing generally occurred once during vine dormancy. The timing of grazing events varied with precipitation and understory plant growth rates, but generally occurred sometime between early March through late April, before vine bud break and a coinciding decrease in regional precipitation rates. Each grazing event aims to remove roughly 80% of understory biomass from the vineyard as a seasonal “termination” of the vineyard understory plant community, which remained dormant throughout the warm, dry vineyard growing season. In some years, grazing occurred two or more times throughout the dormant season (November to April), during periods of higher precipitation and forage productivity. In the years before transitioning to sheep grazing of understory vegetation, sites were managed by mowing, which generally occurred at the same time of year as grazing. Beyond the grazing (ISV) and mowing (CONV) treatments, there were some differences in management across sites. The undervine row of all four CONV vineyards and one ISV vineyard (Site 3) were managed using synthetic herbicide applications (Table 1). Both the ISV and CONV vineyards at Site 1 used conservation tillage, with shallow (<10 cm depth) tillage of every other row in alternating years (Table 1).

Table 1: ISV survey site characteristics of 8 paired vineyards in Sonoma, Lake, and Mendocino Counties, California, USA

Site	Understory management treatment	Length of current management (years)	Vine [varietal/rootstock] (vineyard plant date)	Soil texture[a] (% clay)	Soil type[b] (% slope)	Soil disturbance[c]	Synthetic herbicide application[d]	CCOF[e] organic certification status
1	ISV	17	Pinot Noir [UCD 12 / 1103P] (2001)	Loam (22%)	Haire (0-9%)	High	No	Yes
	CONV	21	Pinot Noir [UCD 13 / 1103P] (1997)	Loam (21%)	Haire (0-9%)	High	Yes	No
2	ISV	14	Cabernet Sauvignon [337 / 1103] (2001)	Clay Loam (28%)	Benridge-Sodabay (15-30%)	Moderate	No	No
	CONV	8	Cabernet Sauvignon [15 / 1103] (1998)	Clay Loam (28%)	Benridge-Sodabay (15-30%)	Low	Yes	No
3	ISV	14	Cabernet Sauvignon [08 / 110R] (1992)	Clay Loam (33%)	Sobrante-Guenoc-Hambright (15-30%)	Moderate	Yes	No
	CONV	21	Cabernet Sauvignon [CS7 /110R] (1996)	Clay Loam (29%)	Sobrante-Guenoc-Hambright (15-30%)	Low	Yes	No
4	ISV	17	Chardonnay [76 / 5C] (2001)	Loam (25%)	Cole (2-5%)	Low	No	Yes
	CONV	10	Chardonnay [76 / 5C] (2003)	Loam (27%)	Cole (2-5%)	Low	Yes	No

[a] Based from hydrometer measured sand, silt, and clay particle content (0–15 cm)

[b] Haire clay loam (0 to 9% slope): clayey, mixed, thermic Typic Haploxerults; Benridge-Sodabay loams (15 to 30% slope): (Benridge) fine, mixed, thermic Mollic Palexeralfs / (Sodabay) fine-loamy, mixed, thermic Mollic Haploxeralfs; Sobrante-Guenoc-Hambright complex (15 to 30% slope): (Sobrante) fine-loamy, mixed, thermic Mollic Haploxeralfs / (Gueonic) fine, kaolinitic, thermic Typic Rhodoxeralfs / (Hambright) loamy-skeletal, mixed, thermic Lithic Haploxerolls. Collected from the USDA-NRCS *SoilWeb* app (https://casoilresource.lawr.ucdavis.edu/)

[c] Soil disturbance is categorized as *Low* (infrequent mow or graze), *Moderate* (combination of infrequent mow + graze), and *High* (combination of infrequent mow or graze + conservation tillage [i.e. shallow tillage of every other row in alternating years])

[d] Applications occurring in vineyard interrow (not undervine row)

[e] California Certified Organic Farmers (CCOF) – United States Department of Agriculture certifying agency

[*] *No vineyards contained either organic or synthetic fertilizer amendments within vineyard interrow*

2.2.2 Site selection and participatory engagement

Study sites were first selected based on identifying early adopters of ISV management – vineyards that had a long-term legacy of grazing sheep – and selection of participating vineyards was confined to the Northern California coastal foothill region to reduce climate and soil variability (Table 1). While perceptions of ISV management are increasingly favorable among adopters and non-adopters alike (Ryschawy et al., 2021), vineyard grazing is still considered a niche production system compared to the dominant technological regimes (Garrett et al., 2020; Ryschawy et al., 2021) and early adopters of ISV practices in California are rare. Producers utilizing ISV management were identified using directories from the *LandSmart* collaborative (http://landsmart.org) and grower networks from the Community Alliance with Family Farmers (CAFF). Four integrated vineyards (ISV) were selected based on grower knowledge of long-term sheep grazing and co-management legacy. These ISV growers expressed interest in participating and worked with the study's authors to identify the adjacent non-integrated vineyards (CONV) for comparison. A participatory survey was conducted to collect management information for each vineyard (vine/rootstock varietal, understory vegetation management, external amendments, irrigation, and tillage) to assess and minimize variability between paired sites (Table 1). Soil type and topography data was collected from the USDA-NRCS *SoilWeb* app (https://casoilresource.lawr.ucdavis.edu). At the time of the study, two of the ISV vineyards (Site 1 & 4) were organic certified through the California Certified Organic Farmers (CCOF) program.

Sampling plots (2 ha) within each paired integrated (ISV) and non-integrated (CONV) vineyard site were selected to maximize the edaphic and co-management similarity of paired sites and isolate the impact of sheep grazing. Wine vineyards provide a unique opportunity for soil surveying, in that tightly controlling management variability, especially related to water and soil fertility, is essential for improving wine grape quality. Vineyard growers strategically limit irrigation and N uptake at certain stages of vine phenology to control vegetative growth and mitigate various perceived tradeoffs between vine vigor and wine grape quality (Spayd et al., 1994; Wheeler and Pickering, 2003; White et al., 2007). As such, excessive water and N availability is generally avoided by reducing inputs (Gaiotti et al., 2017; Lazcano et al., 2020). When inputs are utilized they are most often applied in small doses, timed only during when vine demand is highest, and delivered directly under the vine (Peter Christensen et al., 1994; Spayd et al., 1994). Consequently, while cover crops are increasingly utilized to prevent soil erosion and stabilize soil quality (Novara et al., 2019; Rodrigo-Comino, 2018), wine vineyards are otherwise often low-input agroecosystems, especially within the vineyard interrow, and thus have less co-management variability than other perennial agroecosystems.

2.2.3 Soil collection and processing

Soil sampling occurred once per vineyard site and was timed before the seasonal understory forage termination event(s) to maximize the soil acclimation period between the last graze or mow events. Soil samples were collected from eight randomly selected points per 2 ha plot in a "W" pattern (Moebius-Clune et al., 2016). Sub-plots (1 m^2) were set-up at each sampling point, surface residues were removed, and three soil cores (5 cm diameter) were taken at three depths (0–15 cm, 15–30 cm, and 30–45 cm) in the vine interrow. Samples were weighed in the field, homogenized and composited for each sub-plot, and placed in a cooler for transport. Soils were processed promptly through 4 mm sieves and stored at 4 °C until further analysis, except for ~75 g of soil that was separated and stored at −80°C for PLFA and enzyme assays. Approximately 10 g of field moist soil was sieved (2 mm) and oven dried (105°C) to a constant weight to determine soil gravimetric water content (GWC). Surface soil (0–15 cm) bulk density (BD) was determined for each soil core using mass of oven-dried soil (105 °C, 24 h or until consistent weight) and total volume of each soil core (Blake and Hartge, 1986). Another 250 g of soil was subsampled for chemical analysis and ~100 g was used to determine texture and soil aggregate characteristics.

2.2.4 Soil chemical properties

A subsample of ~300 g was sent to a certified laboratory (Ward Laboratories – Kearney, NE) for analyses of soil texture (sand:silt:clay) by hydrometer; pH (1:1 v/v method); soil salinity by electrical conductivity (EC; dS/m); available P (mg kg^{-1}) via Olsen bicarbonate extraction; and cation exchange capacity (CEC) (Meq 100 g^{-1}) based on ammonium acetate extraction and pH. All soil depth fractions were dried to constant mass, ball-milled, and weighed for total elemental C and N using combustion (Costech ESC 4010 Elemental Analyzer – Valencia, CA, USA). Soil

NH_4^+ and NO_3^- were extracted from 5 g of fresh soil with 20 ml 2 M KCl solution and measured using colorimetric assays on a BioTek Synergy HTX (BioSPX B.V. – The Netherlands) microplate reader. Mineral nitrogen is the sum of soil NH_4^+ and NO_3^-. Soil organic carbon (SOC) and nitrogen (SON) were measured by subtracting HCl inorganic C extraction measurements and inorganic N pools (NO_3^- and NH_4^+) from total elemental C and N analyses described above.

2.2.5 Soil aggregate size distribution and aggregate-associated carbon

Aggregate size categorization was performed on air-dried soils by wet sieving to separate water-stable aggregates into four size categories: large macro-aggregates (2000 µm), small macro-aggregates (250-2000 µm), micro-aggregates (530-250 µm), and the silt and clay fraction (<53 µm) (Cambardella and Elliott, 1993; Kemper and Rosenau, 1986). Each soil was submerged in deionized water for 10 minutes before wet-sieving, and a sub-sample was taken to assess soil gravimetric water content (g g^{-1}) after saturation. A 40 g sub-sample of saturated soil was then transferred to a vibratory sieving tower with rainfall simulator (Fritsch Analysette 3 Pro – Idar-Oberstein, Germany), with vibration amplitude set at 0.1 µm and frequency at 50 Hz. Sieving lasted until the deionized water used to wash soils on the sieve was flowing clear, which was generally around 60 seconds. The remaining fractions on each sieve (2000, 250, and 53 µm), as well as the soil-water suspension passed through the 53 µm sieve (<53 µm), were dried at 60° C to dry until reaching constant weight. The mass recovery threshold was set between 0.98 – 1.02% and was calculated as follows **(1)**:

$$(1)\ \textbf{Mass recovery}\ (\%) = \frac{\textbf{bulk soil}\ (\textbf{g}) - (\textbf{bulk soil}\ (\textbf{g})\ \cdot \textbf{GWC}\ (\textbf{g}\ \textbf{g}^{-1}))}{\sum_{i=1}^{4} \boldsymbol{A_i}\ (\textbf{g})} \cdot \textbf{100}$$

where bulk soil (g) is the mass of the soil used for wet-sieving of each sample; GWC (g g^{-1}) is the gravimetric water content of the soil used for wet-sieving; and A_i is the oven-dry weight (g) of each aggregate fraction. When samples did not meet the mass recovery threshold, the samples were repeated. Mean weight diameter (MWD), a weighted-average index of aggregate stability (van Bavel, 1950), was calculated as follows **(2)**:

$$(2)\ \mathbf{MWD} = \sum_{i=4}^{4} \bar{X}_i \cdot A_i$$

where X_i is the average diameter (µm) for particles of each *i*-level aggregate fraction and A_i is the weight percentage of the fraction in the bulk soil. SOC content was measured for each aggregate fraction using combustion analysis (Costech ESC 4010 Elemental Analyzer – Valencia, CA, USA). The proportional concentration of SOC in each aggregate fraction was calculated as follows **(3)**:

$$(3)\ \mathbf{M}_i = \frac{\mathbf{A}_i \cdot \mathbf{SOC}_i}{\sum_{i=1}^{4} A_i \cdot \mathbf{SOC}_i}$$

where M_i is the relative SOC concentration of each *i*-level aggregate fraction (%); A_i is the oven-dry weight (g) of each aggregate fraction; and SOC_i is the relative SOC concentration of each *i*-level aggregate fraction. The SOC stock for each aggregate fraction was calculated as follows **(4)**:

$$(4)\ \mathbf{M}_i = \mathbf{C}_i \cdot \mathbf{SOC}_i \cdot \mathbf{BD} \cdot \mathbf{H} \cdot 10^{-1}$$

where M_i is the SOC stock of each i-level aggregate fraction (t hm^{-2}); C_i and SOC_i are the relative fraction and SOC concentration each of i-level aggregate fraction, respectively; BD is the soil bulk density (g cm^{-3}) and H is the thickness of soil layer, which was 15 cm for this measurement.

2.2.6 Soil organic carbon size fractionation

Soil organic carbon was separated into particulate organic carbon (POC), and mineral-associated organic carbon (MAOC) using aggregate dispersion, wet sieving, and particle-size fractionation method (Six et al., 1998). In short, 20 g of air-dried soil was dispersed with 100 ml of 5% (w/v) sodium hexametaphosphate ($Na_6(PO_3)_6$) and an 18-hour rotary shaking for sufficient dispersion. Dispersed soils were washed through a 53 µm sieve on a vibratory sieve shaker (Fritsch Analysette 3 Pro – Idar-Oberstein, Germany) as described in Section 2.5. The fraction retained on the sieve was considered as POC, while the finer fraction that passed through the sieve was considered as MAOC. Both POC and MAOC fractions were dried at 60° C until reaching constant weight, then ground, and analyzed for total C on an elemental analyzer (Costech ESC 4010 Elemental Analyzer – Valencia, CA, USA). The final content of POC or MAOC in bulk soil was calculated based on the recovered mass. For example, POC (mg C g^{-1} bulk soil) was calculated with two formulas as follows **(5)** and **(6)**:

$$(5)\ \mathbf{Mass\ recovery}\ (\%) = [(\mathbf{POC}\ (\mathbf{g}) + \mathbf{MAOC}\ (\mathbf{g}))\ /\ \mathbf{bulk\ soil}\ (\mathbf{g})] \times \mathbf{100}$$

$$(6)\ \mathbf{POC}\ (\mathbf{mg\ C\ g^{-1}\ bulk\ soil}) = \frac{\mathbf{POC}\ (\mathbf{g}) \cdot \mathbf{POC}\ (\mathbf{mg\ C\ g^{-1}})}{\mathbf{bulk\ soil}\ (\mathbf{g}) \cdot (\mathbf{mass\ recovery} \cdot \mathbf{0.01})}$$

where bulk soil (g) is the mass of the soil used for wet-sieving of each sample; POC and MAOC (g) are the masses of the POC and MAOC fractions recovered after the wet-sieving, respectively; and POC (mg C g^{-1}) is the C concentration measured in the POC fraction.

2.2.7 Soil microbial biomass and dissolved organic carbon

Soil microbial biomass carbon (MBC) was measured using the fumigation-extraction method (Horwath and Paul, 1994). Fresh soil was sieved to 4 mm and two replicates of 6 g were weighed into glass vials. One replicate was fumigated for 24 h with chloroform ($CHCl_3$) and the other sample (unfumigated) was immediately extracted using 30 ml 0.5 M K_2SO_4. After chloroform fumigation, the fumigated sample was also extracted using 30 ml 0.5 M K_2SO_4. The extracted solutions were filtered with Q5 filter paper and then analyzed for TOC and TN (Elementar TOC/TNb – Ronkonkoma, NY, USA). Microbial biomass C was calculated as the difference in dissolved C concentration between fumigated and unfumigated samples, using a K_e conversion factor of 0.35. The dissolved C content in the unfumigated samples represent the dissolved organic C (DOC) fraction (Jones and Willett, 2006). The microbial quotient (Q_{mic}) represents the ratio of MBC relative to SOC (ug MBC/ug SOC) (Sun et al., 2020).

2.2.8 Carbon mineralization

A 35-day (Haney et al., 2008) incubation was conducted to determine C mineralization (C_{min}) over time, as well as potentially mineralizable C (PMC; the flush of CO_2 during a 72-hour incubation (Wade et al., 2018)) using rewetted air-dried soils. Three technical replicates were run per sample to account for potential methodological variability (Wade et al., 2018). Briefly, 15g of air-dried soil (0-15 cm depth) was sieved (4 mm) and weighed into 50-ml glass beakers. Each sample was rewetted from above to 50% water-filled pore space, placed inside a 0.4 L mason jar, capped with a metal lid and a rubber septum, and incubated at 25 °C for 35 days. Respired CO_2 was determined by sampling the headspace gas using a continuous-flow CO_2/H_2O gas analyzer (LI850 – LI-COR Biosciences, Lincoln, NE, USA) at 1, 3, 7, 14, 21, 28, and 35 days. Respiration for each sampling date was calculated as the difference between a sample and a control, using the ideal gas law and adjusting for the total headspace. Net respiration was calculated as the sum of the respiration measurements up to each sampling date. Jars were opened every 7 days to equilibrate with the atmosphere and allow replenishment of oxygen, but otherwise remained sealed with no air flow. The water loss by evaporation was added at days 14 and 21 by re-weighing soils and adding deionized water accordingly. The metabolic quotient (Q_{met}) represents the ratio of microbial respiration to microbial biomass, and was determined by dividing the 24-hour basal respiration (M_{resp}; ug CO_2-C g^{-1} dry soil) by MBC (ug MBC g^{-1} dry soil) (Anderson and Domsch, 1993).

2.2.9 Microbial community structure and exocellular soil enzymes

Soil microbial community structure was characterized using phospholipid fatty acid (PLFA) analysis (Ward Laboratories – Kearney, NE) using a chloroform-methanol extraction and gas chromatograph with a 25 m Ultra 2 (5%-phenyl)-methylpolysiloxane column (Bossio and Scow, 1998). Community structure biomarkers for PLFA were distinguished into bacterial groups including Gram-positive (Gram(+)) and Gram-negative (Gram(-)) bacteria, actinomycetes, and fungal groups including saprophytic fungi and arbuscular mycorrhizal fungi (AMF) using methods outlined in Hamel et al. (2006). The Gram(+)/Gram(-) and fungal/bacterial (F/B) ratios represent the relative distribution of Gram(+)-to-Gram(-) bacterial biomass and fungal-to-bacterial biomass, respectively.

Exocellular enzyme potentials included BG: β-Glucosidase (glycoside hydrolysis), CB: β-D-cellubiosidase (cellulose decomposition), LAP: L-aminopeptidase (peptide hydrolysis), and PHOS: Alkaline-Phosphatase (phosphate hydrolysis) were measured using fluorescence microplate assays (Bell et al., 2013). Briefly, 2.75g of soil was blended with 91 ml of 50 mM sodium acetate buffer and pH adjusted to the average pH of soil samples from a given vineyard. The soil slurry was then mixed on a stir plate as 800 µl were transferred into a deep 96-well plates. Substrate concentrations and incubation time were determined based on calibration tests to capture the maximum potential enzyme activity. 600 µM of fluorescently labeled substrates were added for all enzymes assayed, except LAP, where 400µM were added. A 200 µL aliquot of substrate was pipetted into the sample and incubated for 3 h at 25°C. Standard curves were prepared for each sample using 4-methylumbelliferone or 7-amino-4-methylcoumarin for LAP. After incubation, assays were centrifuged for 3 min at 1500 rpm and 250 µL of supernatant was pipetted into black 96-well plates. Substrate fluorescence was measured on a BioTek Synergy HTX microplate reader (BioSPX B.V. – The Netherlands) at wavelengths 365 nm (excitation) and 450 nm (emission). Urease (urea hydrolysis) was measured using a standard colorimetric assay method (Kandeler and Gerber, 1988). The enzyme activity was calculated based on the soil dry weight and incubation time (unit: nmol g^{-1} h^{-1}).

2.2.10 Statistical analysis and mixed model selection

Statistical analyses were conducted using the statistical software R, version 3.6.3 (R Core Team, 2021) Linear mixed-effect regression models were used to measure univariate treatment effects across all vineyard pairs, as well as difference between treatments within each vineyard pair. Models were fit using fixed effects for ‘treatment’ (ISV vs. CONV) and ‘location’ as well as their interaction term (treatment(*x*)location) to estimate differing treatment effects on response variables across locations with the *lmer* and *lmerTest* packages (Bates et al., 2015; Kuznetsova et al., 2017). We accounted for our sampling design by using a nested ‘plot’ (vineyard sampling zone nested within location) as a random effect, which yielded the lowest Akaike information criterion (AIC) score when included. Depth was not included as a factor in the model. Instead, each depth was analyzed independently using the model described above. Given the degree of multiple comparison testing associated with this univariate approach, MANOVA was conducted for soil carbon response variables as a false discovery rate (FDR) controlling approach using the *dplyr* package, in order to correct for random events that falsely appear significant as revealed by our univariate assessments (Benjamini and Hochberg, 1995). Before conducting MANOVA, the *mvnormtest* package was used to conduct a Shapiro-Wilk test for multivariate normality and the absence of multicollinearity was checked by conducting correlations among the response variables, which all measured $R^2 \leq 0.80$ and therefore presented no concern. Our MANOVA revealed similar patterns in soil carbon response variables to our univariate approach.

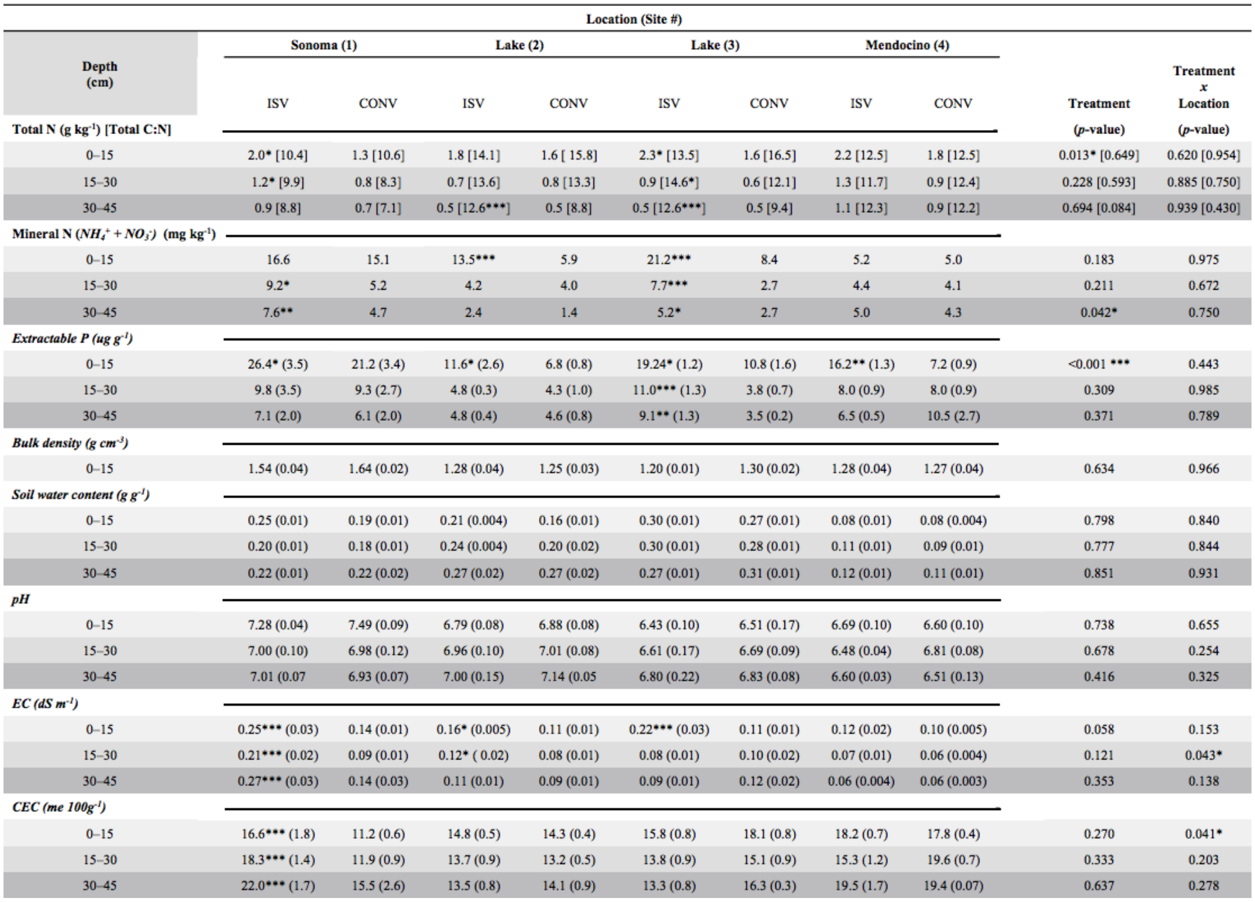
We further tested factors associated with the climatic and edaphic differences (i.e., MAP, MAT, %clay) among vineyards as covariates. These covariates were left out from final models as none of the environmental factors were significant or strongly influenced our main model effects. Residuals were checked for normality and homogeneity of variance. When variables were non-normally distributed or had unequal variance, data were log or square root transformed prior to calculation of means and back-transformed for visualization. Fixed effects were investigated with means comparisons and considered *p*-value < 0.001(***) as highly significant, *p*-value < 0.01(**) as significant, and *p*-value < 0.05(*) as marginally significant. Non-significant means comparisons with *p*-value < 0.10 were considered as a *'trend'* (Hurlbert and Lombardi, 2009; Wasserstein et al., 2019). Tukey's pairwise comparisons were used to assess differences between each treatment within each of the four study locations. Values in tables and graphs are reported as comparisons within each site, whereas values reported in the results section are averages across sites. Box plots were graphed using the *ggplot2* package in R. The horizontal line is the mean, and upper and lower sectors are the first and third quartiles, respectively. Upper and lower 'whiskers' extend to the highest or lowest value, respectively, within 1.5 times the inter-quartile range (the distance between the first and third quartiles).

2.3 RESULTS

2.3.1 Soil physicochemical habitat

Management treatment (ISV vs. CONV) had a significant effect on several key soil physicochemical parameters (Table 2). On average across all vineyards, the ISV treatment increased dissolved P (19.8±1.7 vs. 11.5±1.3 ug g^{-1}; $p<0.001$), Total N (TN;2.1±0.08 vs. 1.6±0.06 g kg^{-1}; $p=0.013$), and salt content (EC; 0.21±0.02 vs. 0.12±0.006 dS m^{-1}; $p=0.058$) in surface soils (0–15 cm) compared to CONV management. The increase in P was significant in all four paired vineyards and EC values were significantly higher in three out of four of the paired vineyard surface soils. Dissolved P, TN, and EC were not significantly different in subsoil depth zones (15–30 and 30–45 cm). The mineral N fraction ($NH_4^+ + NO_3^-$) was significantly higher under ISV management at subsoil depth (30–45 cm) (5.1±0.4 vs. 3.3±0.3; $p=0.042$). While mineral N values reported higher under ISV in the 0–15 cm (14.1±1.2 vs. 8.6±0.8; $p=0.183$) and 15–30 cm (6.3±0.5 vs. 4.1±0.3; $p=0.211$) depths, these increases were non-significant. Grazing did not significantly affect soil pH or CEC at any depth zone, although treatment effects for CEC varied between locations (treatment(*x*)location *p*=0.041).

Table 2: Physicochemical properties from integrated sheep-vineyard (ISV) and conventional understory (CONV) managed soils



	Location (Site #)									
	Sonoma (1)		**Lake (2)**		**Lake (3)**		**Mendocino (4)**			
Depth (cm)	ISV	CONV	ISV	CONV	ISV	CONV	ISV	CONV	**Treatment**	**Treatment *x* Location**
Total N ($g\ kg^{-1}$) [Total C:N]									**(*p*-value)**	**(*p*-value)**
0–15	2.0* [10.4]	1.3 [10.6]	1.8 [14.1]	1.6 [15.8]	2.3* [13.5]	1.6 [16.5]	2.2 [12.5]	1.8 [12.5]	0.013* [0.649]	0.620 [0.954]
15–30	1.2* [9.9]	0.8 [8.3]	0.7 [13.6]	0.8 [13.3]	0.9 [14.6*]	0.6 [12.1]	1.3 [11.7]	0.9 [12.4]	0.228 [0.593]	0.885 [0.750]
30–45	0.9 [8.8]	0.7 [7.1]	0.5 [12.6***]	0.5 [8.8]	0.5 [12.6***]	0.5 [9.4]	1.1 [12.3]	0.9 [12.2]	0.694 [0.084]	0.939 [0.430]
Mineral N ($NH_4^+ + NO_3^-$) ($mg\ kg^{-1}$)										
0–15	16.6	15.1	13.5***	5.9	21.2***	8.4	5.2	5.0	0.183	0.975
15–30	9.2*	5.2	4.2	4.0	7.7***	2.7	4.4	4.1	0.211	0.672
30–45	7.6**	4.7	2.4	1.4	5.2*	2.7	5.0	4.3	0.042*	0.750
Extractable P ($ug\ g^{-1}$)										
0–15	26.4* (3.5)	21.2 (3.4)	11.6* (2.6)	6.8 (0.8)	19.24* (1.2)	10.8 (1.6)	16.2** (1.3)	7.2 (0.9)	<0.001 ***	0.443
15–30	9.8 (3.5)	9.3 (2.7)	4.8 (0.3)	4.3 (1.0)	11.0*** (1.3)	3.8 (0.7)	8.0 (0.9)	8.0 (0.9)	0.309	0.985
30–45	7.1 (2.0)	6.1 (2.0)	4.8 (0.4)	4.6 (0.8)	9.1** (1.3)	3.5 (0.2)	6.5 (0.5)	10.5 (2.7)	0.371	0.789
Bulk density ($g\ cm^{-3}$)										
0–15	1.54 (0.04)	1.64 (0.02)	1.28 (0.04)	1.25 (0.03)	1.20 (0.01)	1.30 (0.02)	1.28 (0.04)	1.27 (0.04)	0.634	0.966
Soil water content ($g\ g^{-1}$)										
0–15	0.25 (0.01)	0.19 (0.01)	0.21 (0.004)	0.16 (0.01)	0.30 (0.01)	0.27 (0.01)	0.08 (0.01)	0.08 (0.004)	0.798	0.840
15–30	0.20 (0.01)	0.18 (0.01)	0.24 (0.004)	0.20 (0.02)	0.30 (0.01)	0.28 (0.01)	0.11 (0.01)	0.09 (0.01)	0.777	0.844
30–45	0.22 (0.01)	0.22 (0.02)	0.27 (0.02)	0.27 (0.02)	0.27 (0.01)	0.31 (0.01)	0.12 (0.01)	0.11 (0.01)	0.851	0.931
pH										
0–15	7.28 (0.04)	7.49 (0.09)	6.79 (0.08)	6.88 (0.08)	6.43 (0.10)	6.51 (0.17)	6.69 (0.10)	6.60 (0.10)	0.738	0.655
15–30	7.00 (0.10)	6.98 (0.12)	6.96 (0.10)	7.01 (0.08)	6.61 (0.17)	6.69 (0.09)	6.48 (0.04)	6.81 (0.08)	0.678	0.254
30–45	7.01 (0.07	6.93 (0.07)	7.00 (0.15)	7.14 (0.05	6.80 (0.22)	6.83 (0.08)	6.60 (0.03)	6.51 (0.13)	0.416	0.325
EC ($dS\ m^{-1}$)										
0–15	0.25*** (0.03)	0.14 (0.01)	0.16* (0.005)	0.11 (0.01)	0.22*** (0.03)	0.11 (0.01)	0.12 (0.02)	0.10 (0.005)	0.058	0.153
15–30	0.21*** (0.02)	0.09 (0.01)	0.12* (0.02)	0.08 (0.01)	0.08 (0.01)	0.10 (0.02)	0.07 (0.01)	0.06 (0.004)	0.121	0.043*
30–45	0.27*** (0.03)	0.14 (0.03)	0.11 (0.01)	0.09 (0.01)	0.09 (0.01)	0.12 (0.02)	0.06 (0.004)	0.06 (0.003)	0.353	0.138
CEC ($me\ 100g^{-1}$)										
0–15	16.6*** (1.8)	11.2 (0.6)	14.8 (0.5)	14.3 (0.4)	15.8 (0.8)	18.1 (0.8)	18.2 (0.7)	17.8 (0.4)	0.270	0.041*
15–30	18.3*** (1.4)	11.9 (0.9)	13.7 (0.9)	13.2 (0.5)	13.8 (0.9)	15.1 (0.9)	15.3 (1.2)	19.6 (0.7)	0.333	0.203
30–45	22.0*** (1.7)	15.5 (2.6)	13.5 (0.8)	14.1 (0.9)	13.3 (0.8)	16.3 (0.3)	19.5 (1.7)	19.4 (0.07)	0.637	0.278

Soils were sampled across 8 paired vineyards (4 locations). Soils cores were separated into three depths zones (0–15 cm, 15–30 cm, and 30–45 cm) and measured for total N (TN), mineral N (NH_4^+-N plus NO_3^-N), extractable phosphorous (P), bulk density, soil water content, pH, electrical conductivity (EC), and cation exchange capacity (CEC). Means are followed by standard error in parentheses. Shown are the treatment and treatment(x)location statistical significance across sites (n=64). For each location, a Tukey-Kramer means (n=16) comparison was used to evaluate significant pairwise difference between each treatment. Asterisks (*) denote significant treatment differences at each depth increment.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

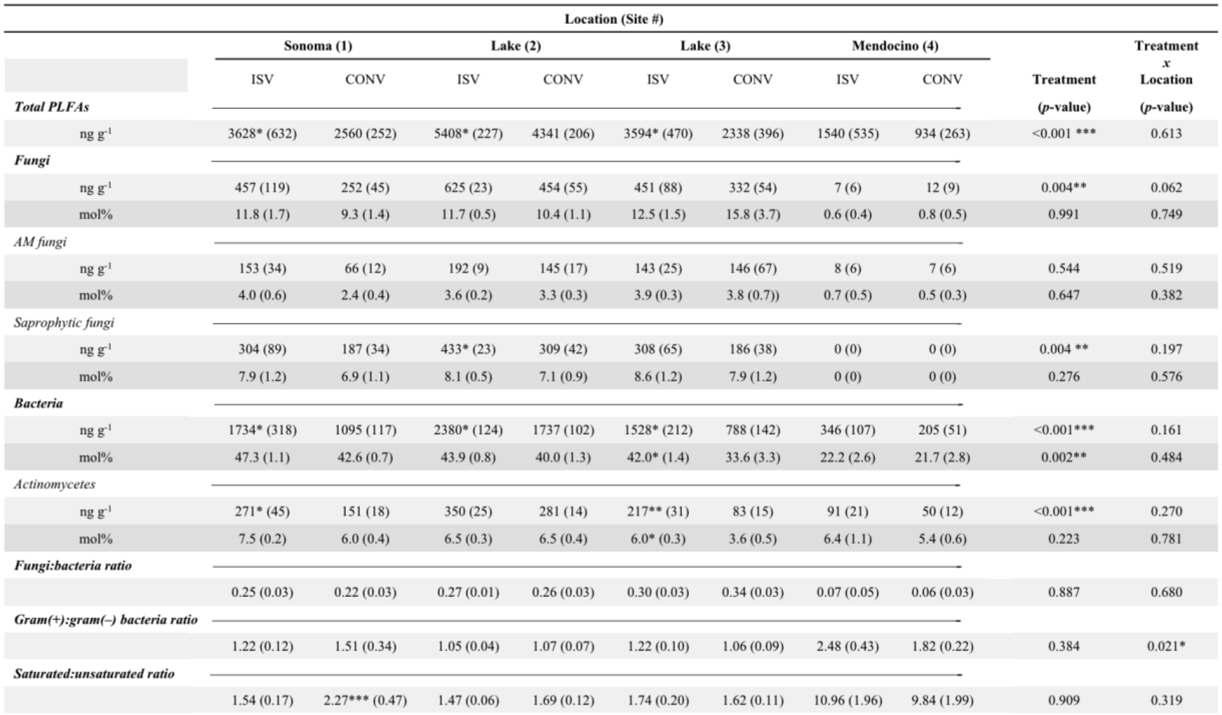
The physical characteristics of surface soils (0–15 cm) as indicated by compaction (BD; 1.32±0.03 vs. 1.37±0.03 g cm^{-3}; *p*=0.634; Table 2) and aggregate stability (MWD; 1.47±0.13 vs. 1.44±0.12; *p*=0.953; Supplementary Figure 1) were not affected by management across any of the four locations. There was also no difference in the relative size distribution of surface soil (0–15 cm) aggregates (Supplementary Figure 1) between ISV and CONV treatments for *macroaggregates* (>2000 um; 21.2±2.5% vs. 19.9±2.3%; *p*=0.959), *large microaggregates* (250–2000 um; 32.6±2.4% vs. 36.4±2.7%; *p*=0.791), *small microaggregates* (53–250 um; 22.5±1.9% vs. 20.2±1.6%; *p*=0.835), or the *silt and clay* fraction (<53 um; 23.7±2.3% vs. 23.5±2.4%; *p*=0.635). Soil water content at the time of sampling was also alike in both treatments, indicating similarities in hydrological cycling characteristics in all depth zones: 0–15 cm (0.21±0.01 vs. 0.18±0.1 g g^{-1}; *p*=0.798), 15–30 cm (0.21±0.01 vs. 0.19±0.01 g g^{-1}; *p*=0.777), and 30–45 cm (0.22±0.01 vs. 0.23±0.01 g g^{-1}; *p*=0.851).

2.3.2 Soil microbial community structure and enzymatic activity

The surface soil (0–15 cm) abundance (ng g^{-1}) of total phospholipid fatty acid (PLFA) biomarkers, an indicator of viable microbial biomass, significantly responded to long-term grazing (Table 3; *p*<0.001). Individual vineyard pairs ranged from 24.6% to 64.9% higher total PLFA abundance under ISV (3543±304) than CONV (2543±234) management, with significantly higher total PLFA abundance in three out four paired vineyards. Community structural biomarkers showed higher abundance of both bacterial (1497±149 vs. 956±102; *p*<0.001) and fungal (385±49 vs. 263±33; *p*=0.004) biomass in ISV vineyards across sites. Mole percent distribution (mol%) also indicated an increase in bacteria abundance (38.9±1.8% vs. 34.5±1.6%; *p*<0.001), but no changes for fungi under long-term grazing (9.1±1.0% vs.

9.1±1.2%; *p*=0.991). While total bacterial biomarkers increased under ISV in three out of four paired vineyards, total fungal biomarkers treatment response did not differ across locations (Table 3), despite a significant main treatment effect. One location (Site 4) showed very low total fungal biomarker abundance values in both the ISV (7±6 ng g^{-1}) and CONV (12±9 ng g^{-1}) treatments. The relative abundance of bacterial and fungal groups was not affected by grazing (F/B; 0.22±0.02 vs. 0.22±0.02; *p*=0.887).

Table 3: PLFA biomarkers and biological ratios from integrated sheep-vineyard (ISV) and conventional understory (CONV) surface soils (0–15 cm depth)



	Location (Site #)									
	Sonoma (1)		**Lake (2)**		**Lake (3)**		**Mendocino (4)**			**Treatment *x* Location**
	ISV	CONV	ISV	CONV	ISV	CONV	ISV	CONV	**Treatment**	
Total PLFAs									**(*p*-value)**	**(*p*-value)**
ng g^{-1}	3628* (632)	2560 (252)	5408* (227)	4341 (206)	3594* (470)	2338 (396)	1540 (535)	934 (263)	<0.001 ***	0.613
Fungi										
ng g^{-1}	457 (119)	252 (45)	625 (23)	454 (55)	451 (88)	332 (54)	7 (6)	12 (9)	0.004**	0.062
mol%	11.8 (1.7)	9.3 (1.4)	11.7 (0.5)	10.4 (1.1)	12.5 (1.5)	15.8 (3.7)	0.6 (0.4)	0.8 (0.5)	0.991	0.749
AM fungi										
ng g^{-1}	153 (34)	66 (12)	192 (9)	145 (17)	143 (25)	146 (67)	8 (6)	7 (6)	0.544	0.519
mol%	4.0 (0.6)	2.4 (0.4)	3.6 (0.2)	3.3 (0.3)	3.9 (0.3)	3.8 (0.7))	0.7 (0.5)	0.5 (0.3)	0.647	0.382
Saprophytic fungi										
ng g^{-1}	304 (89)	187 (34)	433* (23)	309 (42)	308 (65)	186 (38)	0 (0)	0 (0)	0.004 **	0.197
mol%	7.9 (1.2)	6.9 (1.1)	8.1 (0.5)	7.1 (0.9)	8.6 (1.2)	7.9 (1.2)	0 (0)	0 (0)	0.276	0.576
Bacteria										
ng g^{-1}	1734* (318)	1095 (117)	2380* (124)	1737 (102)	1528* (212)	788 (142)	346 (107)	205 (51)	<0.001***	0.161
mol%	47.3 (1.1)	42.6 (0.7)	43.9 (0.8)	40.0 (1.3)	42.0* (1.4)	33.6 (3.3)	22.2 (2.6)	21.7 (2.8)	0.002**	0.484
Actinomycetes										
ng g^{-1}	271* (45)	151 (18)	350 (25)	281 (14)	217** (31)	83 (15)	91 (21)	50 (12)	<0.001***	0.270
mol%	7.5 (0.2)	6.0 (0.4)	6.5 (0.3)	6.5 (0.4)	6.0* (0.3)	3.6 (0.5)	6.4 (1.1)	5.4 (0.6)	0.223	0.781
Fungi:bacteria ratio										
	0.25 (0.03)	0.22 (0.03)	0.27 (0.01)	0.26 (0.03)	0.30 (0.03)	0.34 (0.03)	0.07 (0.05)	0.06 (0.03)	0.887	0.680
Gram(+):gram(–) bacteria ratio										
	1.22 (0.12)	1.51 (0.34)	1.05 (0.04)	1.07 (0.07)	1.22 (0.10)	1.06 (0.09)	2.48 (0.43)	1.82 (0.22)	0.384	0.021*
Saturated:unsaturated ratio										
	1.54 (0.17)	2.27*** (0.47)	1.47 (0.06)	1.69 (0.12)	1.74 (0.20)	1.62 (0.11)	10.96 (1.96)	9.84 (1.99)	0.909	0.319

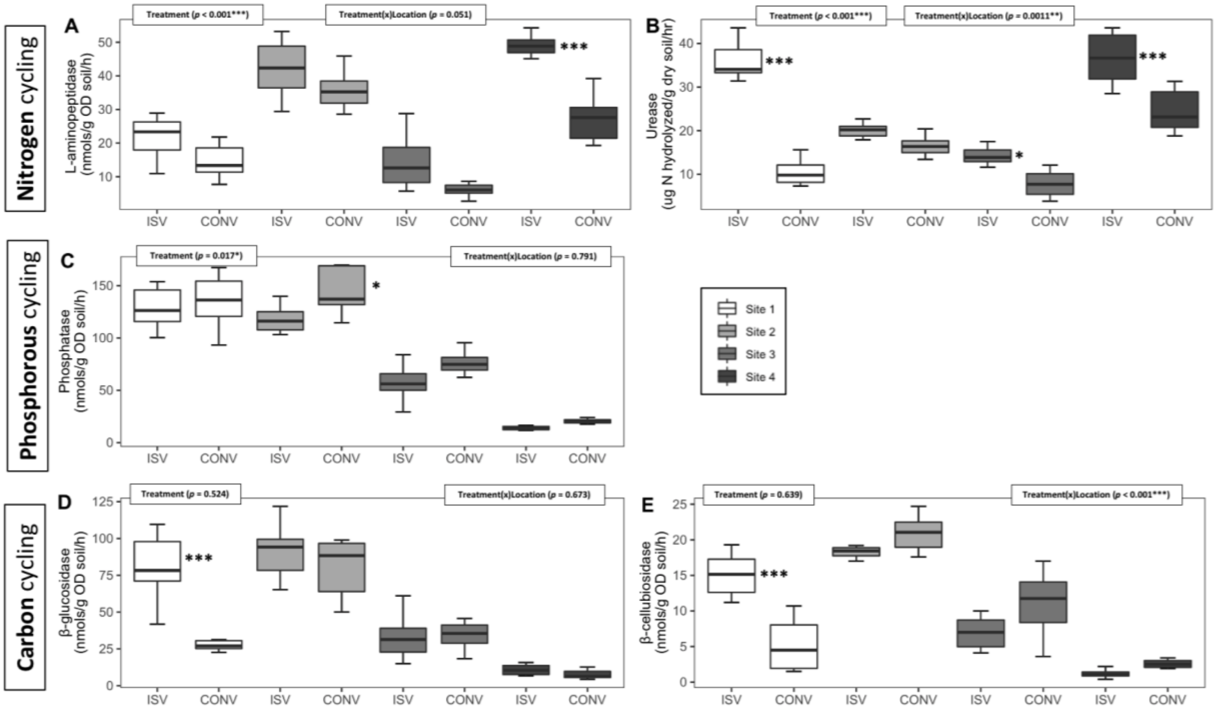
Phospholipid fatty acid (PLFA) profiles indicative of fungi, arbuscular mycorrhizal (AM) fungi, saprophytic fungi, bacteria, and actinomycetes, as well as the relative ratios of fungi-to-bacteria and stress indicator ratios Gram(+)-to-Gram(-) bacteria and saturated-to-unsaturated fatty acids. Ratios are unitless, while PLFAs are given in both ng g soil^{-1} *and mole percent distribution (mol%). Means are followed by standard error in parentheses. Shown are the treatment and treatment(x)location statistical significance across sites (n=64). For each location, a Tukey-Kramer* *means (n=16) comparison was used to evaluate significant pairwise difference between each treatment. Asterisks (*) denote significant treatment differences at each depth increment.*

** $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.*

The main treatment effect varied for specific fungal and bacterial functional groups, with higher abundances under ISV for saprophytic fungi (261±35 vs. 170±23; $p=0.004$) and actinomycete (232±21 vs. 141±16; $p<0.001$), but no significant difference between ISV and CONV for arbuscular mycorrhizal (AM) fungi (124±15 vs. 91±17; $p=0.544$). There was also no significant main treatment effect between ISV and CONV for Gram(+)/Gram(-) ratio (1.49±0.13 vs. 1.37±0.10; $p=0.384$) and saturated/unsaturated fatty acid ratio (3.93±0.79 vs. 3.85±0.72; $p=0.909$), although the saturated-to-unsaturated fatty acid ratio treatment(*x*)location interaction ($p=0.021$) indicated variability in the treatment response between paired vineyards.

The surface soil (0-15 cm) exocellular enzymatic activity potentials (nmols g OD soil^{-1} hour^{-1}; Figure 3) related to nitrogen cycling were higher under ISV compared to CONV management for both L-aminopeptidase (peptide hydrolysis) (30.9±2.6 vs. 21.1±2.1; $p<0.001$; Figure 3A) and Urease (urea hydrolysis) (26.6±1.8 vs. 14.7±1.2; $p=0.001$; Figure 3B). Pairwise comparisons for Urease activity showed significant treatment effects at three out of four paired vineyards, while L-aminopeptidase was higher in the ISV treatment at only one paired vineyard. Phosphatase (phosphate hydrolysis) was lower under ISV management compared to CONV (79.2±8.1 vs. 94.9±8.8; $p=0.017$; Figure 3C), with significant effects at only one site. There was no significant treatment effect for enzymes related to carbon cycling – β-Glucosidase (glycoside hydrolysis) (54.1±6.1 vs. 38.0±4.8; $p=0.524$; Figure 3D) and β-D-cellubiosidase (cellulose decomposition) (10.3±1.2 vs. 9.8±1.2; $p=0.639$; Figure 3E).

Figure 3: Management impact on soil exo-enzyme activity potential from surface soil (0–15 cm depth)



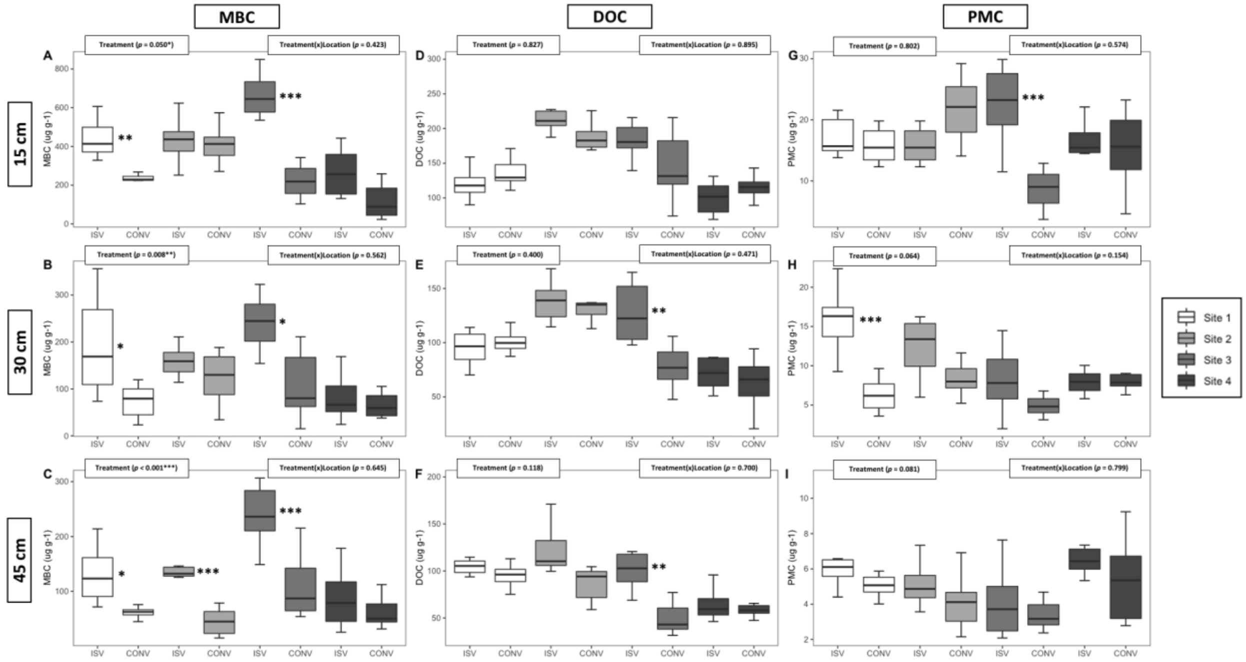
Impact of integrated sheep-vineyard (ISV) and conventional vineyard understory (CONV) management on surface soil (0 – 15 cm depth) exo-enzyme synthesis potential for (A) L-aminopeptidase, (B) urease, (C) phosphatase, (D) ß-glucosidase, and (E) ß-cellubiosidase. Shown are the treatment and treatment(x)location statistical significance across sites (n=64). For each location, a Tukey-Kramer means (n=16) comparison was used to evaluate significant pairwise difference between each treatment. Error bars represent standard error. Asterisks (*) denote significant treatment differences at each depth increment.

** $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.*

2.3.3 Soil carbon flux pools and metabolic activity indicators

Soil carbon flux pools, indicative of labile and active soil carbon (Figure 1), were strongly impacted by animal grazing. Although soil carbon flux pool values were generally highest in surface soils (0–15 cm) across both treatments, ISV management was most significantly impactful in subsoil depths (Figure 4). Microbial biomass C (MBC; ug g^{-1}) was significantly higher under ISV management compared to CONV at all depth zones: 0–15 cm (454±30 vs. 245±22; *p*=0.050; Figure 4A), 15–30 cm (174±15 vs. 94±9; *p*=0.008; Figure 4B), and 30–45 cm (150±12 vs. 70±7; *p*<0.001; Figure 4C). While there was no significant main treatment variation in dissolved organic C (DOC; ug g^{-1}) or potentially mineralizable C (PMC; ug g^{-1}) at all depths, DOC contents trended higher in the 30–45 cm depth of the ISV treatment (98±5 vs. 76±5; *p*=0.118; Figure 4F). PMC also trended higher at both the 15–30 cm (10.9±0.8 vs. 6.7±0.3; *p*=0.064) and 30–45 cm (5.5±0.3 vs. 4.4±0.3; *p*=0.081) depths (Figure 4H-I).

Figure 4: Soil carbon flux pools in integrated sheep-vineyard (ISV) and conventional understory (CONV) managed soils

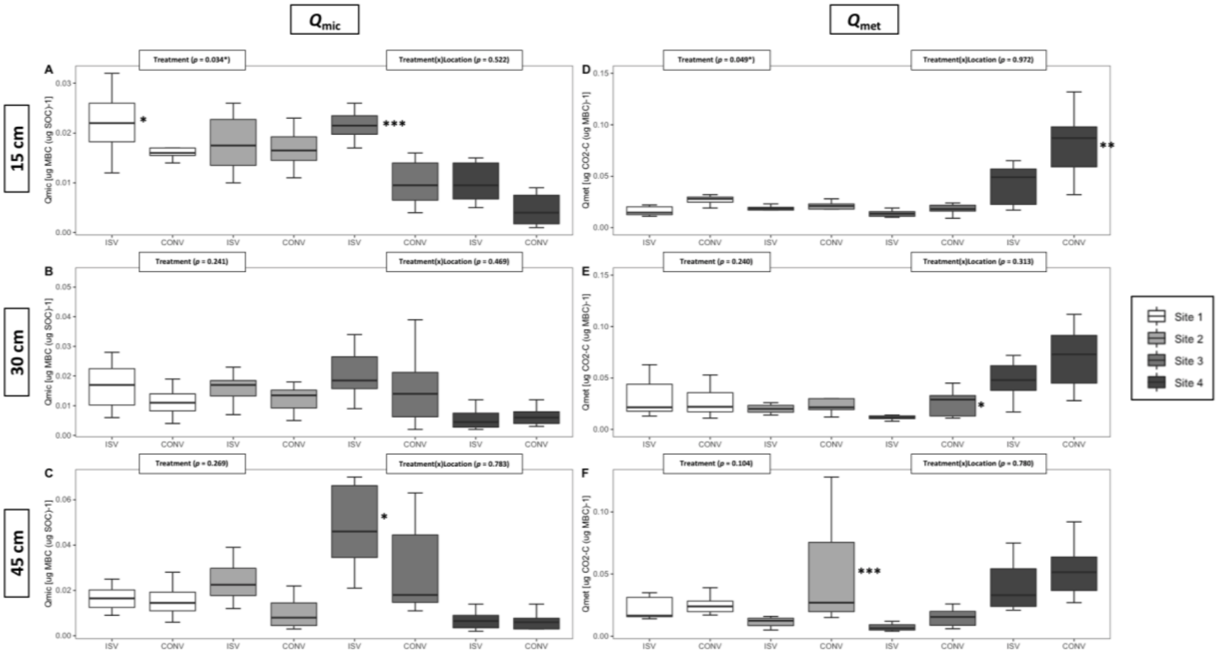


(A-C) Microbial biomass C (MBC), (D-F) dissolved organic C (DOC), and (G-I) 3-day potentially mineralizable C (PMC) were measured at three depths zones (0–15cm, 15–30cm, and 30–45cm) from integrated sheep-vineyard (ISV) and conventional vineyard understory (CONV) managed soils. Shown are the treatment and treatment(x)location statistical significance across sites (n=64). For each location, a Tukey-Kramer means (n=16)

comparison was used to evaluate significant pairwise difference between each treatment. Error bars represent standard error. Asterisks (*) denote significant treatment differences at each depth increment.
** $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.*

The soil microbial quotient (Q_{mic}; MBC:SOC) was significantly higher in ISV surface soils (0–15 cm) compared to CONV (0.018±0.001 vs. 0.012±0.001; p=0.034; Figure 5A). The Q_{mic} main treatment effect was non-significant in both subsoil depths: 15–30 cm (0.016±0.002 vs. 0.011±0.001; p=0.241; Figure 5B) and 30–45 cm (0.024±0.003 vs. 0.016±0.002; p=0.269; Figure 5C). The soil metabolic quotient (Q_{met}; M_{resp}:MBC) was also impacted by long-term grazing similarly across sites. ISV management significantly lowered Q_{met} values compared to CONV in 0–15 cm surface soils (0.023±0.003 vs. 0.056±0.019; p=0.049; Figure 5D). While Q_{met} values also trended lower in the 30–45 cm subsoil depth of ISV vineyards (0.021±0.003 vs. 0.036±0.005; p=0.104), Q_{met} was not significantly affected by treatment in the 15–30 cm depth 0.038±0.020 vs. 0.44±0.006; p=0.240) (Figure 5E-F). Soil carbon mineralization (C_{min}) rates, measured via respiration over a 35-day incubation period, showed similar trends between ISV and CONV in surface soils (0–15 cm) with a cumulative rate of 1.28±0.11 vs. 1.09±0.12 ug CO_2-C g soil^{-1} day^{-1}, respectively (p=0.853; Figure 6A). The C_{min} rate was significantly higher under ISV in the 15–30 cm subsoil depth (1.89±0.29 vs. 1.46±0.18 ug CO_2-C g soil^{-1} day^{-1}; p=0.048; Figure 6B), though not significantly different at 30–45 cm (0.37±0.04 vs. 0.33±0.03 ug CO_2-C g soil^{-1} day^{-1}; p=0.397; Figure 6C).

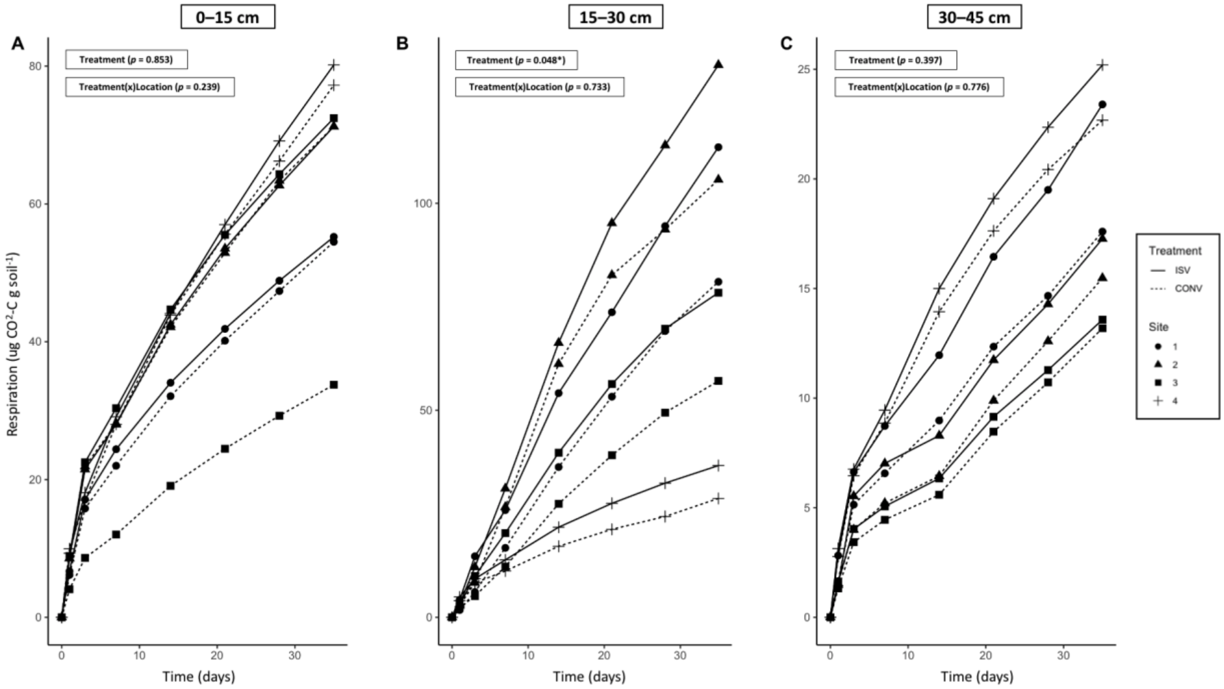
Figure 5: Microbial quotient (Q_{mic}) and metabolic quotient (Q_{met}) of integrated sheep-vineyard (ISV) and conventional understory (CONV) managed soils



(A-C) Microbial quotient (Q_{mic}) and (D-F) metabolic quotient (Q_{met}) were measured at three depths zones (0–15cm, 15–30cm, and 30–45cm) from integrated sheep-vineyard (ISV) and conventional vineyard understory (CONV) managed soils. Shown are the treatment and treatment(x)location statistical significance across sites (n=64). For each location, a Tukey-Kramer means (n=16) comparison was used to evaluate significant pairwise difference between each treatment. Error bars represent standard error. Asterisks (*) denote significant treatment differences at each depth increment.

** $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.*

Figure 6: Soil carbon mineralization rates over a 35-day incubation from integrated sheep-vineyard (ISV) and conventional understory (CONV) managed soils



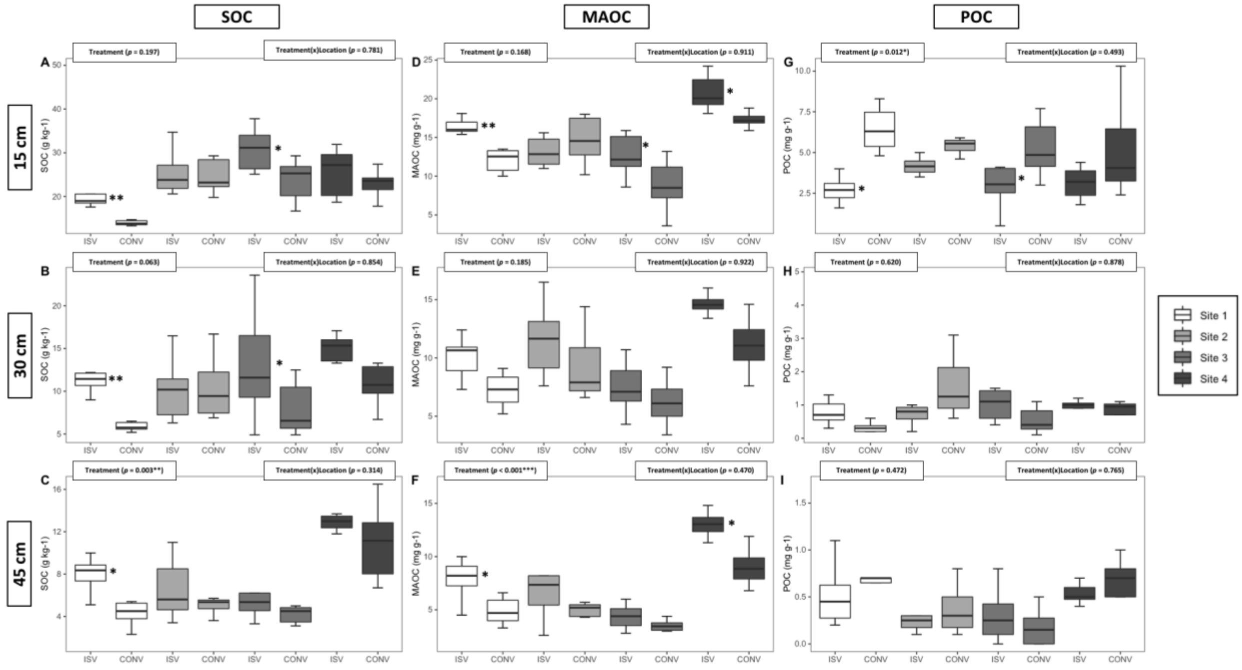
Soils were incubated and measured for C mineralization (C_{min}) via microbial respiration rates (umol CO_2 g soil^{-1}) at seven time points (1, 3, 7, 14, 21, 28, and 35 days) in soils from three depth zones (A) 0–15cm, (B) 15–30cm, and (C) 30–45cm. Treatment and treatment(x)location significance was calculated across sites (n=64). Asterisks (*) denote significant treatment differences within a time point.

** $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.*

2.3.4 Soil carbon stabilization and storage pools

Total SOC (g kg^{-1}) was highest in the surface soils (0–15 cm) and decreased in total quantity with increasing depth in both ISV and CONV treatments, (Figure 7A-C). The main treatment effect on soil carbon storage pools was generally most significantly impactful in subsoil depths (15–30 and 30–45 cm) and we observed no significant differences in total SOC content of surface soils (0–15 cm; 26.1±1.2 vs. 21.4±0.9; p=0.197; Figure 7A). Within subsoils, SOC content trended higher in the 15–30 cm depth (12.4±0.6 vs. 8.9±0.5; p=0.063) and was significantly higher at 30–45 cm (8.3±0.6 vs. 6.2±0.6; *p*=0.003) under ISV management (Figure 7B-C). The main treatment effect followed a similar pattern for MAOC, with no significant variation between ISV and CONV treatments at both 0–15 cm (15.8±0.6 vs. 13.3±0.6; *p*=0.168; Figure 7D) and the 15–30 cm subsoil depth (11.0±0.5 vs. 8.6±0.5; *p*=0.185; Figure 7E) but significant increases under ISV management in the 30–45 cm subsoil depth (8.1±0.6 vs. 5.9±0.5; *p*<0.001; Figure 7F). The POC fraction showed opposite trends with a significant main treatment effect at 0–15 cm and higher surface soil POC under CONV management (3.5±0.3 vs. 6.2±0.5; *p*=0.012; Figure 7G), but no significant effects in either the 15–30 (1.0±0.1 vs. 1.0±0.2; *p*=0.620) or 30–45 cm (0.4±0.04 vs. 0.5±0.06; *p*=0.472) subsoil depths (Figure 7H-I).

Figure 7: Soil carbon stabilization and storage pools in integrated sheep-vineyard (ISV) and conventional understory (CONV) managed soils



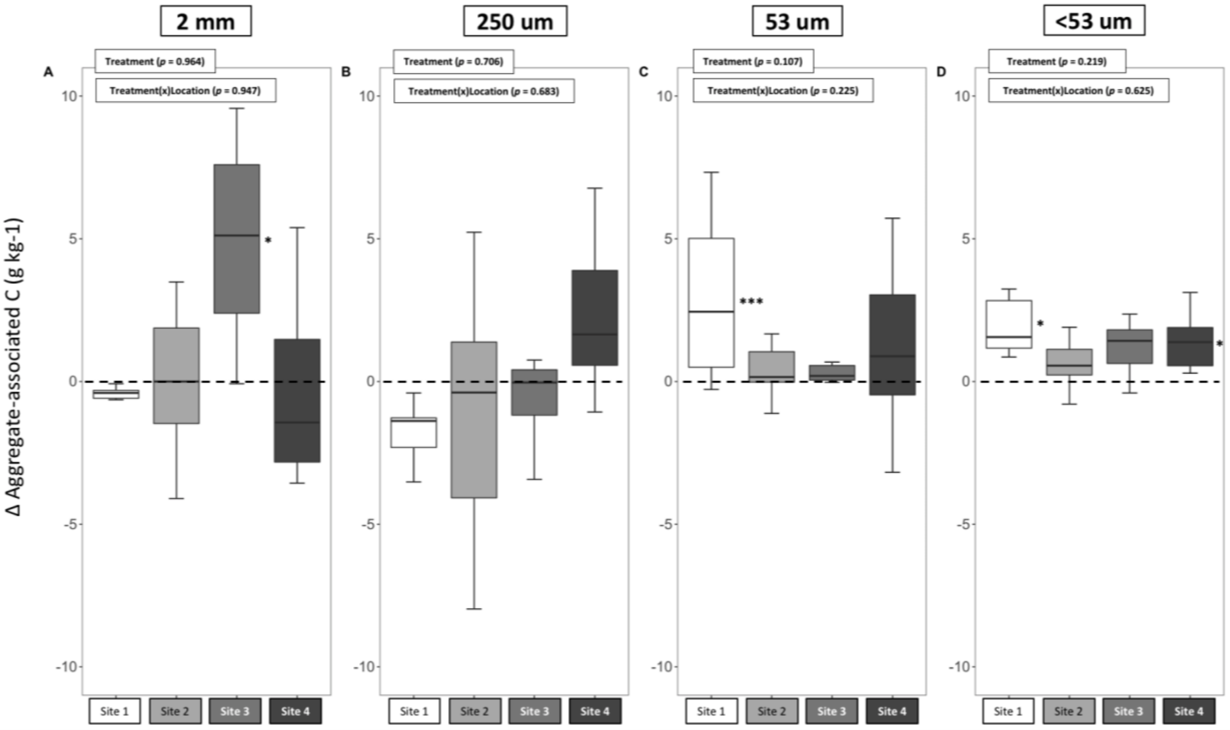
(A-C) Total soil organic C (SOC), (D-F) mineral-associated organic C (MAOC), and (G-I) particulate organic C (POC) were measured at three depths zones (0–15 cm, 15–30 cm, and 30–45 cm) from integrated sheep-vineyard

(ISV) and conventional vineyard understory (CONV) managed soils. Shown are the treatment and treatment(x)location statistical significance across sites (n=64). For each location, a Tukey-Kramer means (n=16) comparison was used to evaluate significant pairwise difference between each treatment. Error bars represent standard error. Asterisks (*) denote significant treatment differences at each depth increment.

** p <0.05; ** p <0.01; *** p < 0.001.*

There was no impact of long-term ISV grazing on absolute SOC values (g kg^{-1}) in surface soils (0–15 cm) for the macroaggregate (>2 mm; 6.7±0.9 vs. 5.7±0.8; *p*=0.964; Figure 8A), large microaggregate (250–2000 um; 8.6±0.7 vs. 8.6±0.7; *p*=0.706; Figure 8B), and silt and clay fractions (<53 um; 5.4±0.4 vs. 4.2±0.3; *p*=0.219; Figure D) across sites. The ISV treatment did trend higher than CONV for the aggregate-associated C content within small microaggregates (53–250 um; 5.1±0.5 vs. 3.4±0.3; *p*=0.107; Figure 8C). Management treatment also did not shift the relative distribution (% of total C; Supplemental Figure 2) of surface soil (0–15 cm) SOC across *macroaggregates* (>2000 um; 25.3±2.9% vs. 21.8±2.2%; *p*=0.447), *large microaggregates* (250–2000 um; 31±2.4% vs. 39.7±2.1%; *p*=0.621), *small microaggregates* (53–250 um; 20.9±2.1% vs. 15.9±1.2%; *p*=0.149), and the *silt and clay* fraction (<53 um; 22.6±2.3% vs. 22.6±2.6%; *p*=0.871).

Figure 8: Aggregate-associated C pools in integrated sheep-vineyard (ISV) and conventional understory (CONV) managed surface soils (0–15 cm depth)



Surface soils (0–15 cm depth) were measured for the total C content associated with four soil aggregate physical size fractions (>2000um, 250-2000um, 53-250um, and <53um; A-D). For A-D, the dashed bar represents the CONV treatment mean for each paired site. Boxes above or below the line represent the relative increase or decrease in ISV values (Δ) for each site. Shown are the treatment and treatment(x)location statistical significance across sites (n=64). For each location, a Tukey-Kramer means (n=16) comparison was used to evaluate significant pairwise difference between each treatment. Error bars represent standard error. Asterisks (*) denote significant treatment differences within site at each size fraction.

** p <0.05; ** p <0.01; *** p < 0.001.*

2.4 DISCUSSION

This study sought to evaluate the soil carbon flux dynamics and storage potential of long-term perennial integrated crop-livestock management. We were particularly interested if, and to what degree, ICL in perennial systems affects the partitioning of SOC into distinct biochemical and physical pools. Further, we sought to understand whether long-term perennial ICL legacy effects impact microbial ecological characteristics such as community structure, soil carbon utilization, and investment strategies related to biomass accumulation, stress tolerance, and the production of soil exo-enzymes. We provide here strong supporting evidence that small ruminant grazing can increase stable carbon storage within perennial cropland soils, especially when accounting for subsoil depth zones. Further, our findings show that the continuous year-after-year use of perennial cropland grazing altered soil carbon quality, with a higher total quantity and greater relative proportion of soil carbon allocated toward biologically active carbon flux pools – the carbon most readily available and utilized by soil microbial communities. We argue that this stimulation in soil carbon flux is likely to be the dominant driver of potential SOC accumulation in perennial ICL systems, due to enhanced production of microbial necromass and increased stabilization as MAOC. These results indicate strong potential of perennial ICL management to invigorate internal agroecosystem processes, with significant relevance for climate change mitigation and adaptation goals in Mediterranean perennial croplands.

2.4.1 Perennial cropland grazing increased the active flux of soil carbon throughout the soil profile

Our study shows that the introduction of sheep grazing increased the pool of actively fluxed soil carbon across four distinct paired vineyards. This was the case both in terms of the concentration of total SOC and the relative proportion (% of total SOC) allocated toward labile carbon flux pools, especially within the microbial biomass carbon (MBC) pool. This corroborates findings from other studies across ICL systems, where positive impacts of cropland grazing on the size of soil microbial communities are commonly reported (Acosta-Martínez et al., 2004; Bansal et al., 2022; da Silva et al., 2015; Franzluebbers and Stuedemann, 2008; Sekaran et al., 2021; Silva et al., 2022; Tracy and Zhang, 2008). The benefits of sheep grazing for soil microbial growth were observed at all depths, with an average MBC increase of 82%, 65%, and 99% at the 0–15, 15–30, and 30–45 cm depths, respectively (Figure 4B-C). While the MBC pool comprised a notably higher relative proportion of total SOC at the surface soil (0–15 cm) under ISV (+49% *Qmic*; Figure 5A), the MBC pool was otherwise most significantly impacted by ISV management at deeper subsoil layers.

Increases in MBC may be attributed to shifts in the grazed plant community's composition, productivity, and the allocation of energy and nutrients above- and belowground (Bardgett and Wardle, 2003; Cong et al., 2014; Dawson et al., 2009; Rumpel et al., 2015; Tian et al., 2016). While cropland-specific impacts are less understood, research throughout diverse grazed ecosystems show that feedbacks between grazing *intensity* (density and duration) and *periodicity* (seasonality and frequency) exert unique selective pressure on plant communities and the rate and quality of carbon influxes (Figure 1). Numerous studies have documented higher rates of rhizodeposition immediately following high-intensity grazing events (Dawson et al., 2009; Gavrichkova et al., 2008; Hamilton et al., 2008; Hamilton and Frank, 2001), which increases the availability of labile and soluble carbon substrates and facilitates preferential and efficient utilization by soil microbial communities (Cheng and Kuzyakov, 2015; Gavrichkova et al., 2008; Ota et al., 2013; Wilson et al., 2018). Observed increases in MBC under ISV management may also be facilitated by the mineralization of aboveground plant residues within the ruminant of grazing animals – where significant quantities of recalcitrant plant structural compounds such as cellulose and lignin are fragmented, depolymerized, and returned to the soil as more labile, soluble, and nutrient-dense excreta (dung and urine) (Faissal et al., 2017; Jarvis, 2009; Soussana and Lemaire, 2014). Ruminant mineralization and trampling of plant residues also likely explain the lower quantities of POC found in the surface soils of the ISV treatment (Figure 7G).

The effects of ISV management on the availability and active microbial utilization of labile soil carbon were generally most pronounced in deeper subsoil layers, which may result from increased leaching of soluble DOC compounds into deeper subsoil layers. This assumption is supported by our observations of increased trends in dissolved organic carbon (DOC) content (Figure 4F) and potentially mineralizable carbon (PMC; Figure 4H-I) in subsurface soil depths under ISV relative to CONV understory management, as well as other studies reporting higher DOC concentrations under various ICL management systems (Sekaran et al., 2021; Tian et al., 2010). Due to their heightened transport within soil solution, compounds in the DOC pool are generally more spatially accessible to microbial processing (Erktan et al., 2020; Nakhavali et al., 2021; Neff and Asner, 2001; Ota et al., 2013; Rumpel and Kögel-Knabner, 2011). The lower molecular weight and activation energy requirements of compounds in the DOC pool also facilitate quick microbial assimilation and utilization than the complex and less nutrient-rich structural compounds associated with the POC pool (Blagodatskaya et al., 2011; Kallenbach et al., 2016, 2015; Kok et al., 2022; Lavallee et al., 2020; Shahbaz et al., 2017; Weiss et al., 1991). The relevancy of this concept is supported by increased soil carbon mineralization (C_{min}) rates measured in the 15–30 cm subsoils depth under ISV management (Figure 6B). The larger MBC pool within the ISV treatment may further be more primed to quickly utilize deposited DOC compounds compared to the CONV managed soils (Geyer et al., 2020). This, along with leaching, may partially explain the lack of observed differences in DOC content between treatments at shallow soil depths, despite the presumably large quantities of soluble excreta deposited through grazing.

Whereas nutrients from excreta may be more readily transformed and assimilated by soil microbes than ungrazed plant residues (Kooch et al., 2020; Wang et al., 2018), ruminant mineralization of plant residues has also been shown to increase the bioavailability of soil N and P for plant and microbial uptake as a result of high-intensity grazing disturbance events (Costa et al., 2014; Tracy and Frank, 1998; Wu et al., 2011; Zhang et al., 2020). We observed substantially higher quantities of extractable P at surface soil depths and soluble mineral N content (NH_4 and NO_3) in subsoils at all ISV sites (Table 2), reflecting differences in solubility between N and P and their physical transport pathways within soil solution. The increased bioavailability of soil N and P, coupled with intra-ruminal conversion of POC (*celluloses, hemi-celluloses, lignin, etc.*) to DOC and altered C influx pulses from rhizodeposition, are potential mechanisms underlying observed increases in soil microbial biomass and their rates of carbon mineralization under ISV management.

2.4.2 Grazing shifted the resource investment strategy of surface soil microbial communities toward efficient biomass accumulation

Our results showed that perennial cropland grazing increased the size of soil microbial communities, which may occur through ameliorating soil habitat conditions that would otherwise orient metabolic investment strategies toward stress tolerance and/or acquisition of limited resources (Malik et al., 2020). In addition to higher MBC in ISV surface soils, the total quantity of PLFA biomarkers was also remarkably higher – with a 47% increase compared to the CONV treatment (Table 3). We further observed a 41% reduction in metabolic quotient (Q_{met}) values (Figure 5C) in surface soils of grazed vineyards, which indicates higher microbial carbon use-efficiency (CUE) as less CO_2-C is respired relative to the size of the MBC pool (Dilly and Munch, 1998; Sinsabaugh et al., 2017). Increased availability of soil N and P have been shown to lower Q_{met} values across climatic and soil management gradients (Xu et al., 2017). Increased microbial growth efficiency and investment in biomass accumulation under ISV management is further supported by the substantially higher proportion of MBC relative to total SOC (+49% *Qmic*) within the 0–15 cm depth (Figure 5A). Higher Q_{mic} values are associated with a greater potential for soil microbes to transform energy sources via increased availability of soil carbon and nutrients (Sparling, 1992; Sun et al., 2020). Trends toward higher PMC values are also indicative of increased energy source availability in the grazed vineyards, as this pool measures the reservoir of readily available soil carbon that drives microbial functions (catabolism) and biomass accumulation (anabolism) (Levi-Minzi et al., 1990). These findings corroborate another recent ICL study, which showed higher microbial biomass in grazed cropland that was similarly attributed to increased availability of carbon and nutrient substrates (Sekaran et al., 2021). Given the role of microbial necromass in the formation of stable MAOC, these efficiency and growth indicators suggest a higher net SOC storage potential under ISV management.

As another indicator of microbial investment, the production of metabolically-costly extra-cellular enzymes represent shifts in resource acquisition strategies in response to growth factor limitations through altering energy and nutrient availability within the near-cell soil environment (Nannipieri et al., 2002; Zheng et al., 2020). While the availability of soil P was higher in surface soils of the ISV treatment (Table 2), we observed significantly lower enzymatic activity related to P cycling (phosphatase; Figure 3C). The composition of sheep excreta has high inorganic P content (Arnuti et al., 2020) and soil applications of inorganic P have been shown to reduce phosphatase activity (Oshima et al., 1996), as this enzyme cleaves phosphate (PO_4) groups from proteins and becomes an increasingly unnecessary investment under high P availability conditions. These observations indicate an increased accessibility of soil P and reduced microbial investment in P acquisition (Nannipieri et al., 2011) in perennial croplands with grazing. At the same time, we observed significantly higher N cycling enzymatic activity in the ISV treatment as measured by aminopeptidase (peptide hydrolysis) and urease (urea hydrolysis) enzymes (Figure 3A-B). The increase in urease activity corroborates previous findings across various grazed ecosystems (Acosta-Martínez et al., 2010; McNaughton et al., 1997; Sekaran et al., 2021) as a result of urea degradation, the dominant N constituent found in urine (Bristow et al., 1992). The release of aminopeptidase enzymes could indicate potential limitation in microbial N availability and an increased metabolic investment in N acquisition (Schimel and Bennett, 2004). However, both the mineral N (NO_3 and NH_4) pool and the higher total N content of ISV surface soils (0–15 cm) do not indicate reduced availability of soil N (Table 2). Alternatively, recent research has suggested that soil microbial communities also use aminopeptidase enzymes as a means to access protein-derived carbon – a potent energetic resource for cellular growth (Norman et al., 2020).

Shifts in microbial processes may reflect differences in the abundance of core functional groups such as those related to decomposition (Bhatti et al., 2017; Setälä and McLean, 2004), which were higher in the ISV treatment across both fungal (+53% saprophytic fungi) and bacterial (+64% actinomycete) groups (Table 3). While neither fungal/bacterial ratios nor the mole percent distribution (mol%) of fungal PLFAs were significantly different between treatments, we did observe a significant increase in mol% of bacterial PLFAs. Although we observed benefit for both bacteria and fungi with vineyard grazing, relative increases in bacterial groups under ISV nevertheless suggest a soil ecosystem (habitat and/or resource) shift that preferentially benefit consumers of labile substrates and fast energy channels. Traditional soil food web models assume distinct and preferential utilization of recalcitrant (slow energy channel) and labile (fast energy channel) carbon substrates by fungal and bacterial groups, respectively (Hunt et al., 1987). Under this view, changes in the quantity and quality of organic inputs should therefore induce shifts in soil fungal/bacterial ratios (Wardle et al., 2004). Alternatively, emerging empirical evidence has shown that multi-channel omnivores are the dominant constituency of both fungal and bacterial communities and the presence of these omnivores help to stabilize soil food web communities (Kramer et al., 2016; Wolkovich, 2016). There may also be instances in which these trophic relationships do not behave consistently, with conceptual models also indicating that fungal and bacterial communities can coexist in a stable state under the presence of large labile carbon pulse inputs, such as the input of dung and urine over the course of a grazing event (de Vries and Caruso, 2016). Nevertheless, empirical evidence indicates that bacteria still likely hold a competitive advantage in utilizing these substrates (Ho et al., 2017; Xun et al., 2018).

Within bacterial communities, the Gram(+)/Gram(-) ratio is thought a useful indicator of environmental disturbance along the r-K-strategist spectrum. Gram(+) bacteria are generally more adapted to heavily disturbed soil environments (habitat and/or resource limitation) and often less dependent than Gram(-) bacteria on the continuous input of labile carbon compounds

(De Vries and Shade, 2013; Fanin et al., 2019). We observed no significant variation in the Gram(+)/Gram(-) ratio between treatments which, when analyzed in tandem with fungal/bacterial ratios, suggests no variation in the stress response of soil microbial communities as a result of cropland grazing. This is further supported by other measured soil physicochemical indicators such soil water content, pH, and compaction (bulk density; BD) – which were similar amongst treatments and indicate physical habitat conditions that are relatively alike (Table 2).

2.4.3 Integrated crop-livestock grazing increased perennial cropland soil carbon storage in subsoils

Total SOC storage trended higher in the ISV treatment at both subsurface depth zones. The treatment effect was more significant with increasing depth and resulted in a 39% and 34% increase in SOC under ISV compared to the CONV treatment at 15–30 and 30–45 cm, respectively (Figure 7B-C). The introduction of sheep grazing into perennial cropland increased the physicochemical stabilization of soil carbon within the mineral matrix (MAOC) of the deepest measured subsoil layer (30–45 cm) by 37% compared to the CONV treatment (Figure 7F). The larger soil carbon storage response in subsoil depths with grazing reflect changes in soil carbon flux pools and are likely related to the increased solubility of deposited animal excreta and deeper spatial distribution of DOC and nutrient substrates (Gross and Harrison, 2019; Rumpel and Kögel-Knabner, 2011). The higher CUE of grazed soils, as indicated by lower Q_{met} values under ISV in the 0–15 and 30–45 cm depths (Figure 5E-F), should theoretically build the capacity for SOC storage. Where both the rate and efficiency of microbial carbon utilization is higher for labile urine and manure inputs than plant structural compounds (POC) (Cai et al., 2016; Hossain et al., 2017), these properties have been shown to facilitate a more direct pathway toward long-term MAOC stabilization and persistence (Cotrufo et al., 2015, 2013; Dynarski et al., 2020; Haddix et al., 2016; Lavallee et al., 2020; Liebmann et al., 2020). The incorporation of litter-derived POC by animal trampling has also recently been shown to increase its microbial utilization, expediting its decomposition rate and promoting increased physiochemical stabilization of MAOC (Wei et al., 2021).

However, the introduction of ruminant grazers did not result in significant alterations to surface soil (0–15 cm) aggregation (Figure 3), despite both the physical disturbance of animal trampling and grazing-induced reductions in POC content (Figure 7G). This is notable, given that POC is essential as a nucleus in the formation and stability of soil macroaggregates (Six et al., 2000). We also did not show significant differences in surface soil (0–15 cm) aggregate-associated C between ISV and CONV treatments, as represented by both the total C content (g kg^{-1}) associated with soil aggregate size fractions (Figure 8A-D) and the relative distribution (% of total C) across those size fractions (Supplementary Figure 2). As a measurement of the SOC pool associated with four distinct aggregate size categories, aggregate-associated C is an indicator of SOC physical protection via occlusion within aggregates. As such, this study does not indicate that aggregate occlusion of SOC is strongly impacted by perennial ICL grazing.

Our results corroborate some previous ICL research findings, where increases in SOC have been reported under crop-livestock integration across a spectrum of crop production systems (Acosta-Martínez et al., 2010, 2004; Bansal et al., 2022; Da Silva et al., 2014; de Faccio Carvalho et al., 2010; Franzluebbers et al., 2014; Fultz et al., 2013a; Maughan et al., 2009). Given the variability in ICL grazing intensity (density and duration) and its interactions with climatic, edaphic, and co-management components across agricultural systems, other studies across diverse ICL systems have also found negligible (Fernández et al., 2011; Liebig et al., 2020; Tian et al., 2010) and even negative (Tobin et al., 2020) SOC storage benefits associated with cropland grazing. As empirical evidence increasingly shows the positive relationship between soil microbial growth and SOC formation and stabilization (Bradford et al., 2013; Kallenbach et al., 2016, 2015; Wang et al., 2021), agroecosystem design and management characteristics that stimulate microbial biomass formation and necromass preservation may be central toward increasing SOC storage (Lange et al., 2015; Liang et al., 2019; Prommer et al., 2020; Wilson et al., 2018). When metabolic investment trade-offs (i.e. less energy to invest elsewhere) are satisfied through ameliorating soil habitat and nutrient limitations, this may facilitate efficient microbial biomass accumulation strategies (Malik et al., 2020). The increased allocation of soil carbon toward active microbial pools, with higher use-efficiency, may indicate a determinant mechanism necessary for increasing SOC accumulation within grazed perennial cropland (Figure (9).

Chapter 3: Short-term integrated crop-livestock grazing increases carbon cycling activity in the rhizosphere of three distinct forage species with minimal impact on bulk soil

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ABSTRACT

The adoption of sheep grazing in perennial vineyard systems is steadily increasing throughout multiple regions of California. A partial driver of adoption is the perception of improved agronomic and environmental outcomes associated with integrated sheep-vineyard (ISV) management, especially related to potential soil carbon storage benefits. While ISV systems are receiving more scientific interest, processes and outcomes of these perennial integrated crop-livestock (ICL) systems have yet to be investigated under an experimental monitoring approach. Here, we used a multi-year monitoring trial with coupled factorial design to evaluate, across multiple spatial (bulk vs. rhizosphere soil) and temporal (intra- vs. inter-seasonal) scales, the use of integrated sheep-vineyard (ISV) grazing as contrasted against conventional vineyard mowing practices (CONV). We measured indicators of root morphology and rhizosphere carbon (C) cycling for three understory forage plants species (A. *sativa*, T. *aestivum*, and G. *dissectum*) throughout the course of a single season (intra-seasonal), in tandem with C cycling indicators in bulk soils across multiple seasons (inter-seasonal). Whole-soil ecosystem respiration (CO_2-C efflux) was also measured multiple times throughout a single season (intra-seasonal) and surveys of the understory plant community were conducted (intra- and inter-seasonal) to evaluate shifts in community composition and structural diversity over time. Our results show that ISV grazing induced substantial intra-seasonal shifts in rhizosphere C cycling across all plant species – including increases in microbial biomass carbon (MBC), dissolved organic carbon (DOC), potentially mineralizable carbon (PMC), and carbon mineralization rates (C_{min}) though decreases in rhizosphere carbon use-efficiency (CUE; as indicated by increased CO_2-C respired relative to MBC pool size). There was minimal divergence between the rhizosphere C cycling responses of individual species to management treatments. Further, increases in rhizosphere C cycling indicators under ISV did not translate to substantial alterations in inter-seasonal bulk soil C cycling. Although we observed inter-seasonal shifts in bulk soil organic carbon (SOC) storage, differences between treatments largely depended on the year with not a clear trend over time. We also observed reductions in intra-seasonal understory plant community total canopy cover (total%) and increases in bare soil exposure (bare%) under ISV grazing. While overall biodiversity of the understory forage community did not differ between treatments, the relative canopy area of forage species (species%) shifted intra-seasonally with increasing prevalence of A. *sativa* grasses over time. These outcomes support findings from Chapter 2, which indicate enhanced rates of carbon (energy) and nutrient flows and potential SOC storage benefits with the adoption of perennial ICL grazing. Our findings also highlight the heterogeneity of carbon pools and processes when evaluated at diverse spatial and temporal scales.

3.1 INTRODUCTION

The introduction of ruminant grazing into agroecosystems is well understood to facilitate novel disturbances that both directly and indirectly impact energy and nutrient flows, with potential consequence for soil organic carbon (SOC) formation and stabilization outcomes. Several grazing disturbance mechanisms are linked to defoliation, including removal of both actively photosynthesizing vegetation and senescent tissues, as well as alterations in light availability and absorption (Wade and Carvalho, 2009). These mechanisms directly impact net primary productivity (NPP) while also introducing selective pressures over forage plant species community structure and functional trait assembly (Bardgett and Wardle, 2003; Chen et al., 2018; Dawson et al., 2009). Given that the accumulation of SOC is fundamentally a function of the balance between carbon (C) influx (inward flow) and efflux (outward flow) processes, landscape NPP and plant functional traits are strong drivers of SOC accruement in cropland soils (Cong et al., 2014; De Deyn et al., 2008; Fornara and Tilman, 2008; Hoyle et al., 2013; Jastrow et al., 2007).

Another crucial grazing disturbance mechanism is the intra-ruminal transformation of recalcitrant, particulate materials from aboveground biomass into soluble, labile, and nutrient-dense animal dung and urine. Through this process, dissolved organic carbon (DOC) and nutrients are stoichiometrically decoupled relative to their plant material origins, and are more easily diffused and transported throughout the soil profile (de Faccio Carvalho et al., 2010; Eldridge et al., 2017; Rumpel et al., 2015). This has functional relevance for soil microbial communities, both in terms of the physical accessibility of substrates and the energy investment requirements necessary for microbial processing. The energy required to depolymerize and assimilate simple, soluble, and labile substrates is much less than that of complex and recalcitrant compounds (e.g. cellulose, lignin, etc.). As such, grazing-induced alterations in the quality of inputs into the soil ecosystem may trigger shifts in the microbial community’s energy investment strategies (Kallenbach et al., 2015; Kravchenko et al., 2019; Malik et al., 2020; Schimel et al., 2007) and their carbon use-efficiency (CUE) (Cotrufo et al., 2013; Kallenbach et al., 2015; Kirkby et al., 2013; Manzoni et al., 2012), with downstream impacts on the accumulation of SOC.

An additional category of grazing disturbance mechanisms relate to process shifts in the allocation of carbon (energy) and nutrients between above- and belowground plant fractions (Dawson et al., 2009; Lemaire and Agnusdei, 2009; Pineiro et al., 2010). The belowground plant fraction is composed of both root litter (e.g., root hairs, root residues) and living root inputs known as rhizodeposits (e.g., root exudates, secretions) (Rasse et al., 2005). Grazing-induced defoliation and alterations in soil nutrient availability are strongly associated with response shifts in belowground investment strategies related to root morphology and architecture (Dawson et al., 2009; Klumpp et al., 2009), which are compensated through changes in specific root length (SRL), diameter, and/or root branching (Poorter et al., 2012). Grazing is also documented to impact rates of rhizodeposition and root senescence and turnover in the period immediately after disturbance (Dawson et al., 2009; Hamilton et al., 2008; Hamilton and Frank, 2001). However, the prolonged effects of grazing on rhizodeposition throughout the course of a season are less understood. These rhizodeposits are diverse and dynamic in composition and can be either water-soluble – such as sugars, amino acids, and organic acids – or water-insoluble – such as cell well components, lipids, and mucilage (Canarini et al., 2019). It is estimated that 5 to 20% of all photosynthetically fixed carbon is transferred to the rhizosphere in the form of root exudates (Walker et al., 2003). A growing body of literature has recently highlighted how plant controls over metabolite rhizodeposition may also regulate the composition of rhizosphere microorganisms, recruiting from throughout the bulk soil to improve essential rhizosphere functions and plant fitness in response to environmental conditions (de Vries and Wallenstein, 2017; Zhalnina et al., 2018).

All of the aforementioned mechanisms have potential downstream impacts on soil stoichiometric (C:N:P) ratios (Bardgett and Wardle, 2003; Pineiro et al., 2010; Rumpel et al., 2015), the physical accessibility of organic substrates (Erktan et al., 2020), and rates and efficiency of carbon and nutrient transformations (Lemaire and Agnusdei, 2009; Wang et al., 2018). The importance of roots, in particular, is highlighted by recent research showing that, relative to carbon inputs from aboveground plant materials, the presence of living roots may increase stabilization between belowground SOC inputs and soil mineral surfaces (Sokol et al., 2019; Sokol and Bradford, 2019), promote greater accumulation of particulate organic carbon (POC) (Mazzilli et al., 2015), and therefore improve longer-term persistence of SOC (Jackson et al., 2017; Schmidt et al., 2011). While still a current topic of scientific exploration, this may relate to the deposition of aliphatic and nutrient-rich DOC substances (such as root exudates and arbuscular mycorrhizal fungi (AMF) cytoplasm) directly into the rhizosphere and adjacent soil mineral matrix regions (Farrar et al., 2003; Sokol and Bradford, 2019), with less physical transport and a more abundant microbial community that can directly stabilize these lower molecular weight compounds (Cotrufo et al., 2015; Lajtha et al., 2014). In particular, soluble rhizodeposits such as exudated sugar and organic acids have shown quick soil carbon stabilization pathways, through direct sorption to mineral surfaces (Angst et al., 2021; Liang et al., 2017; Sokol et al., 2019). Various plant-soil-microbe interactions within the rhizosphere may also impact nutrient availability (Dotaniya and Meena, 2015) and the microbial assimilation efficiency of carbon inputs relative to the bulk soil at-large (Rasse et al., 2005; Schmidt et al., 2011; Sokol et al., 2019).

A growing body of literature has explored the comparative impacts of agricultural management on bulk soil relative to the rhizosphere. Whereas agricultural management may be a dominant factor for determining outcomes in both bulk and rhizosphere soils, biogeochemical processes occur dynamically at different spatial (bulk vs. rhizosphere soil) and temporal (intra-seasonal vs. inter-seasonal) scales, which require distinct experimental approaches in order to detect and untangle (Goss-Souza et al., 2020; Saliendra et al., 2018; Yang et al., 2013). For instance, the biogeochemical cycling rates of rhizosphere microbial communities have been shown to occur much quicker, and with differing magnitudes, than those of bulk soil communities (Liu et al., 2022). As such, different sampling schemes are required to capture dynamic shifts in these varying communities. This is particularly notable within ecosystems with biodiverse plant community compositions, in which each individual species may illicit distinct rhizosphere responses to agricultural management disturbances (Schmidt et al., 2019).

We established an integrated sheep-vineyard (ISV) monitoring trial and utilized *in-situ* and laboratory methods to analyze if and how grazing alters intra-seasonal (within season) whole-soil C efflux patterns, as well as root and rhizosphere functional traits related to C cycling across three dominant forage plant species. We further conducted two years of inter-seasonal (across season) monitoring within the same ISV trial to analyze shifts in plant community structure and bulk soil characteristics related to C cycling. We aimed to explore the hypotheses that sheep grazing in vineyards will ***1) increases the size of labile C pools within rhizosphere soils (intra-***

seasonally) and bulk soils (inter-seasonally) and ***2) increases the rate of C flux throughout the soil ecosystem (intra-seasonally)***, with the assumption that this ***3) increases bulk soil carbon storage (inter-seasonally) across longer time periods***. We also had the objectives of understanding if potential changes in C cycling occurred in the presence of ***4) shifts in soil microbial C substrate utilization patterns (intra-seasonally)*** and/or whether ISV grazing ***5) alters the understory forage plant community's composition (intra- and inter-seasonally) and/or root morphological development patterns across each forage species' lifespan (intra-seasonally)***. Developing our understanding of perennial integrated crop-livestock (ICL) system outcomes and mechanisms related to understory forage community dynamics and biogeochemical cycling will work to address critical knowledge gaps. These knowledge gaps currently inhibit the adoption of ICL management, our understanding of its potential strategic applications, and the development of best management practices across diverse agricultural contexts.

3. 2 MATERIALS AND METHODS

3.2.1 Study region climate characteristics

Our study was conducted in the Northern California coastal foothills at a location in Napa, CA. This Mediterranean climate is classified as a semi-arid Köppen-type *Csc* (Beck et al., 2018). It is characterized by mild cool winters, warm and dry summers, and seasonal mean annual precipitation that is lower than the regional evapotranspiration (ET) potential. The average annual precipitation for years one and two of the inter-seasonal experimental period was 271 mm and 222 mm, respectively (http://www.cimis.water.ca.gov/). The mean maximum and minimum temperatures were 22.0°C and 6.4°C in year one and 23.1°C and 6.0°C in year 2, respectively.

This contributed to an annual potential evapotranspiration (ET_o) of 1284 mm (year 1) and 1215 mm (year 2) and, therefore, a 4.7x (year 1) and 5.5x (year 2) higher potential water demand than the regional precipitation supply.

The average daily air temperature throughout the intra-seasonal experimental period (February through April) was 10.5±0.3 °C (Supplementary Figure 1A) and total precipitation was low (Supplementary Figure 1B; 47.0 mm). The potential evapotranspiration (ETo) was fairly consistent across throughout the season, averaging 3.4±0.1 mm day^{-1} (Supplementary Figure 1B). Low precipitation and consistent ETo resulted in a decline of the climate ratio over time, ranging between 1.33 to 0.49 (Supplementary Figure 1C). This culminated in a 269% reduction in the moisture balance from beginning to end of the 65 day experimental period. Accordingly, while the rhizosphere GWC did not vary across treatments, it steadily declined over time from 0.31±0.01 to 0.06±0.01 g H_20 g^{-1} soil over the intra-seasonal experimental period (Supplementary Figure 1B; Time, *P*<0.0001).

3.2.2 Field trial design and study system characteristics

Our ISV field trial began in November 2018 on previously ungrazed vineyard blocks at the Huichica Creek Sustainable Demonstration Vineyard in Napa, CA. The vineyard was planted in 1991 with Chardonnay (Old Wente (101-14)) and has since been managed homogenously with no-till, the maintenance of self-recruiting winter resident vegetation (with no planted species) in the interrow, and mowing used to terminate resident vegetation in all areas of the vineyard. The field trial was established using a three-step factorial strip-plot design to control for spatial variability of soil conditions (Dutta et al., 2009; Tanaka et al., 2008). Two farm management treatments were applied to four replicated and randomized 1-acre plots (4 experimental units): grazed (ISV) or mowed (CONV) management of understory plant communities within the vineyard interrow space. Five sub-plots were randomly selected from with each plot (30m x 10m; 20 sub-plots total), from which all plant and soil sampling occurred. Each sub-plot was then subdivided into three sections (sub-sub-plots; 10m x 10m; 60 sub-sub-plots total), with each sub-sub-plot assigned to one of three different forage plant species (*Avena sativa*, *Triticum aestivum*, and *Geranium dissectum*) from amongst the mixed vineyard understory community. These three forage plant species were part of the resident, naturally-occurring vineyard understory plant community and were selected based on their ubiquity and representation of distinct plant morphological categories (one forb and two C3 grasses). Other species within these plant community mixtures were not individually sampled, but their presence was noted and categorized as 'other species' for use in later plant community analyses. This experimental design allowed us to investigate responses to farm management (ISV or CONV) over seasons (inter-seasonal), as well as the interaction of management across three different understory plant species (A. *sativa*, T. *aestivum*, and G. *dissectum*) within seasons (intra-seasonal).

For the ISV treatment, rotational grazing occurred twice annually through the vine dormancy period, during the regional precipitation period when understory growth reaches peak productivity. One grazing occurred during the understory mid-growing season and the second graze was conducted as an understory plant termination method. Briefly described, temporary electrical fencing was erected to establish ~2-acre sized grazing paddocks, where ~250 ewes were grazed for 0.5–1.0 days within each paddock before rotating to the next paddock. This grazing strategy has been found to lower the duration of grazing per unit of land area and reduce grazing selectivity and the spatial heterogeneity of grazing pressure (Teague et al., 2008; Teague and Dowhower, 2003). The timing of both grazing events varied with precipitation and understory plant growth rates, but always occurred between mid-January and early-April (before vine bud break) for the duration of the trial. Grazing of experimental plots in the ISV treatment generally took 3–4 days to completion. The understory vegetation in the CONV plots were mowed once annually at termination, which occurred during the same period as the ISV termination graze. For the final year of this study (2021), the two grazing events occurred from 2/26/21–3/1/21 and 4/5/21–4/8/21. The mowing termination event occurred on 4/9/21. The inter-seasonal monitoring occurred from trial establishment in 2018 through 2021, while the intra-seasonal monitoring occurred during a 65-day period from 2/21/21 to 4/28/21.

3.2.3 Understory forage community survey

A quadrat sampling method was used to monitor vineyard understory forage plant communities from 2019–2021 (Barbour et al., 1987; Cox, 1990). Briefly described, quadrats (1 m^2) were established randomly within sub-plots to delimit an area in which forage species ID (i.e. A. *sativa*, T. *aestivum*, and G. *dissectum*), total number of individuals per forage species, area cover per forage species (species%), and total area cover (total%) were measured. Understory forage community sampling occurred in January, February, and March of each year. Quadrat sampling was conducted independently by two or more people, and the average estimates for a given area was calculated to obtain a more accurate census. Area cover per forage species (species%) was defined as the percentage of quadrat area covered by the canopy of a given species when viewing from an overhead aerial perspective. When overlap of two or more species occurred, the cover of only the overlying species was recorded (Barbour et al., 1987). For areas without canopy cover, bare soil exposure (bare%) and residue coverage (residue%) were measured. The total dry weight (g) of forage biomass was also taken from quadrats during each sampling time. Briefly, the biomass within each quadrat was cut and removed, placed in a cooler for transport, and promptly oven-dried (60°C) to a constant weight and recorded. Forage species richness (R_p) was calculated as the total number of species present. Forage community diversity and evenness were calculated using the Shannon index (H_p) and Simpson index (D_p), respectively, as follows:

$$\textbf{Shannon Index (H)} = -\sum \boldsymbol{p_i} \ln \boldsymbol{p_i}$$

$$\textbf{Simpson Index (D)} = \mathbf{1} - \sum \boldsymbol{p_i^2}$$

where ***p*** is the proportion (n/N) of individuals for a species (n) divided by the total number of individual plants found (N). The species diversity (H) is a measure based on the number of species present (richness; R) and the number of individuals per species (abundance), whereas the evenness (D) is a measure of the degree to which species composition is equally distributed (i.e. dominance).

3.2.4 Soil and root sampling scheme

We measured bulk soil physicochemical properties (inter-seasonal) in November, 2018 at trial establishment (baseline; Year 0) and twice annually thereafter during the months of March/early-April and July/early-August. The first sampling (Year 0.5) occurred in July, 2019 and the last sampling (Year 2) occurred in March, 2021. The winter season annual soil sampling (Year 1 and 2) occurred quickly after the forage termination (vine dormancy) to capture immediate impacts of grazing or mowing, whereas the summer sampling (Year 0.5 and 1.5) occurred during vine growing season to represent bulk soil conditions after an acclimation period. One soil sample (each a composite of 3 individual soil cores) was taken in the vineyard interrow of each sub-sub-plot (n=60). Samples were taken to a depth of 15 cm and divided into two depth increments (0-7 and 7-15 cm). Samples were weighed in the field, homogenized and composited for each sub-sub-plot, and placed in a chilled cooler for transport. Bulk soils were processed promptly and stored at 4 °C until further analysis, except for ~75 g of soil that was separated and stored at −80°C for PLFA.

Roots and rhizosphere soil (intra-seasonal) were sampled four times throughout the vine dormant season in 2021 (65-day period from 2/21/21 to 4/28/21) within the same sub-sub-plots to reduce spatial heterogeneity. Samples were taken 3 days before (T1-/T2-) and 3 days after (T1+/T2+) the occurrence of two separate 3-day vineyard grazing events (day(s) 1, 9, 41, and 50 of experimental trial). Whole root and soil profile transects (~0.5 m^3) were removed from randomly selected areas of the vineyard interrow within each sub-sub-plot using a destructive sampling broadfork technique. Briefly described, two broadforks (Meadow Creature – Washington, USA) with 50 cm tines were driven into the soil profile and simultaneously leveraged to lift out a 50(length)x50(width)x50(depth) cm transect that contained both roots and soil (bulk and rhizosphere). Transects were processed in the field and whole plant samples (shoot and root) for each distinct species (*A. sat.*, *T. aes.*, and *G. dis.*) were carefully separated. Only the soil adhering to the roots was considered as rhizosphere soil (Nazih et al., 2001), which was collected by shaking off loose soil before gently brushing off the attached rhizosphere soil from roots. Rhizosphere soil samples for each species were sieved to remove rocks and large roots (>2mm), homogenized and composited for each sub-sub-plot, and placed in a chilled cooler for transport. Immediately following the *in*-situ collection of rhizosphere soil, shoots were cut off and the roots were immediately stored in 50ml Falcon Tubes with a 65% ethanol solution. Rhizosphere soils were processed promptly and stored at −80°C until further analysis, except for ~45 g of soil that was subsampled for chemical analysis.

Figure A: Photo of whole root and soil profile transect being extracted

3.2.5 Bulk soil microbial community structure

Bulk soil microbial community structure was characterized using phospholipid fatty acid (PLFA) analysis (Ward Laboratories – Kearney, NE) using a chloroform-methanol extraction and gas chromatograph with a 25 m Ultra 2 (5%-phenyl)-methylpolysiloxane column (Bossio and Scow, 1998). PLFA community structure bioindicators were used to distinguish major fungal and bacterial groups including saprophytic fungi, arbuscular mycorrhizal fungi (AMF), Gram-positive (Gram(+)) bacteria, Gram-negative (Gram(-)) bacteria and actinomycetes. The Gram(+)/Gram(-) and fungal/bacterial (F/B) ratios represent the relative distribution of Gram(+)-to-Gram(-) bacterial biomass and fungal-to-bacterial biomass, respectively.

3.2.6 Biogeochemical properties of bulk and rhizosphere soils

Soil properties were measured for both bulk (inter-seasonal) and rhizosphere (intra-seasonal) soil samples. Approximately 10 g of field moist soil was sieved (2 mm) and oven dried (105°C) to a constant weight to determine soil gravimetric water content (GWC). A subsample of 10 g was sent to a certified laboratory (Ward Laboratories – Kearney, NE) and used for analyses of available P (mg kg^{-1}) via Mehlich-III extraction. Soil NH_4^+ and NO_3^- were extracted from 5 g of fresh soil with 20 ml 2 M KCl solution and measured using colorimetric assays on a BioTek Synergy HTX (BioSPX B.V. – The Netherlands) microplate reader. Mineral nitrogen is the sum of soil NH_4^+ and NO_3^-. Soil microbial biomass carbon (MBC) was measured using the fumigation-extraction method (Horwath and Paul, 1996). Fresh soil was sieved to 4 mm and two replicates of 6 g were weighed into glass vials. One replicate was fumigated for 24 h with chloroform ($CHCl_3$) to kill all soil microorganisms and the other (unfumigated) was immediately extracted using 30 ml 0.5 M K_2SO_4. After chloroform fumigation, the fumigated sample was also extracted using 30 ml 0.5 M K_2SO_4. The extracted solutions were filtered with Q5 filter paper and then analyzed for TOC and TN (Elementar TOC/TNb – Ronkonkoma, NY, USA). Microbial biomass C was calculated as the difference in dissolved C content between fumigated and unfumigated samples, using a K_e conversion factor of 0.35. The extracted C content in the unfumigated samples represent the dissolved organic C (DOC) fraction (Jones and Willett, 2006).

3.2.7 Rhizosphere soil carbon mineralization

A 35-day incubation was conducted for both bulk and rhizosphere soils to determine C mineralization (C_{min}) over time (Haney et al., 2008), as well as potentially mineralizable C (PMC; the flush of CO_2 during both a 72-hour (Wade et al., 2018)) using rewetted air-dried soils. Three technical replicates were run per sample to account for higher potential methodological variability (Wade et al., 2018). Briefly, a 15g portion of air-dried soil (0-15 cm depth) was sieved (4 mm) and weighed into 50-ml glass beakers. Bulk density and the standard particle density of 2.65 g cm^{-3} were used to calculate the pore space. Each sample was rewetted from above to 50% water-filled pore space and placed into 0.4 L mason jars with a metal lid and a rubber septum before being incubated at 25 °C for 35 days. All jars additionally had 20 mL of water added to the base of the 50-ml beakers to reduce the vapor pressure deficit between the wetted soils and air within the jar. Respired CO_2 was determined by sampling the headspace gas using a continuous-flow CO_2/H_2O gas analyzer (LI850 – LI-COR Biosciences, Lincoln, NE, USA) at 1, 3, 7, 14, 21, 28, and 35 days. Respiration for each sampling date was calculated as the difference between a sample and a control (empty jar with 20 mL of water), using the ideal gas law and adjusting for the total headspace. Net respiration was calculated as the sum of the respiration measurements up to each sampling date. Jars were opened every 7 days to equilibrate with the atmosphere and allow replenishment of oxygen. The water loss by evaporation was added at days 14 and 21 by re-weighing soils and adding deionized water accordingly. The metabolic quotient (Q_{met}) represents the ratio of microbial respiration to microbial biomass, and was determined by dividing the 24-hour basal respiration (ug CO_2-C g^{-1} dry soil) by MBC (ug MBC g^{-1} dry soil) (Anderson and Domsch, 1993).

3.2.8 Rhizosphere community-level physiological profiling

Rhizosphere soil samples were analyzed on Biolog® EcoPlate™ microplates to quantify carbon utilization of 31 distinct carbon sources. To prepare the samples for microplates, 5 g of soil frozen to -80°C was shaken in a tube with 50 mL 1.8% sterile sodium pyrophosphate solution ($Na_4P_2O_7{\cdot}10H_2O$) for 30 min. After incubating at 4°C overnight, the tubes were shaken again for 30 min and left to settle at 25°C for another 30 min. The solution was diluted 10-to-2 using sterile saline solution, pipetted into the microplates, and left to incubate in the darkness at 25°C. Microplate readings were taken every 12 h at wavelengths of 590 nm and 750 nm using a microplate reader (BioTek Synergy HTX multimode reader). Absorbances at 144 h were chosen for all samples as the peak absorbance values were found at that time increment. Each Biolog® EcoPlate™ has 3 replicates of the 31 carbon sources with water used as a control blank. The blank value was subtracted from all values to minimize background noise. Optical densities (C_i) for each carbon source were calculated by subtracting the absorbance value measured at 750 nm from the absorbance value measured at 590 nm. EcoPlates were analyzed for their different rates of color development after a specific incubation period (144 h), expressed as average well color development (AWCD). Each of the 31 carbon sources were categorized into one of six different metabolic functional groups (amines, amino acids, carbohydrates, carboxylic acids, phenolic acids, or polymers) and substrate utilization richness (R_s; # of wells with avg C_i values > 0.25), Shannon diversity (H_s), and Simpson evenness (D_s) indices were calculated.

3.2.9 Root functional traits

After washing to remove soil particles, root image analysis was conducted using WinRhizo software (Pro version, Regent Instruments Inc., Québec City, QC, Canada) at a resolution of 1200 dpi on an Epson Expression 10000XL scanner (Tokyo, Japan). WinRhizo was used to measure root morphological characteristics including total root length (cm), surface area (cm^2), average diameter (mm), and volume (cm^3) for each plant root system (Arsenault et al., 2019; Chassot et al., 2001). Roots were then dried at 60°C until reaching constant weight (g). Specific root length (SRL; $m\ g^{-1}$) and specific root surface area (SRA; $m^2\ g^{-1}$) were calculated by dividing root length and surface area by their root dry mass, respectively (Lõhmus et al., 1989; Ostonen et al., 2007). Root tissue density (RTD; $g\ cm^{-3}$) was calculated by dividing each root system dry mass by its root volume (Birouste et al., 2014).

3.2.10 Whole-soil carbon flux

In-situ whole-soil respiration (intra-seasonal) was measured eight times between 2/21/21 and 4/23/21 – occurring on days(s) 1, 8, 11, 22, 41, 50, 53, and 65 from the start of the first measurement. Respired CO_2 was determined by sampling the headspace gas of a closed dynamic chamber system using a portable CO_2/H_2O gas analyzer (LI850 – LI-COR Biosciences, Lincoln, NE, USA). Briefly described, an opaque chamber (10 cm in diameter by 24.4 cm tall) connected to the gas analyzer was placed on PVC collars 10 cm diameter by 10 cm tall using an air-tight rubberized band (Rochette et al., 1997). Each sub-plot was equipped with three collars permanently embedded to a depth of 5 cm previous to trial establishment to minimize CO_2 efflux induced artificially by soil disturbance. CO_2 in the collar headspace was measured for four to six minutes, depending on the CO_2 flux rate (Hicks Pries et al., 2017). The CO_2 flux was calculated using the rate of change of CO_2 concentration (umol CO2 m^{-2} s^{-1}) in the chamber over time under a closed-loop continuous gas flow (Heinemeyer and McNamara, 2011). The CO_2 flux was converted to its equivalent quantity CO_2-C flux (F_c) using a conversion factor of 0.273. The LI850 gas analyzer also collected real-time data for temperature (°C), pressure (kPa), and water vapor (mmol H_2O mol^{-1}) within the chamber, which was used to calibrate CO_2 efflux measurements using the calculation:

$$\mathbf{F}_{\boldsymbol{c}} = \frac{\mathbf{V} \cdot \mathbf{P_0}}{\mathbf{R} \cdot \mathbf{S} \cdot \mathbf{T_0}} \cdot \frac{\mathbf{dC}}{\mathbf{dt}}$$

where F_c is the soil CO_2 flux; V is the volume of air (cm^3); P_0 is the initial pressure (kPa); R is the gas constant; S is the surface area (cm^2); T_0 is the initial temperature (K); and dC/dt is the initial rate of change in CO_2 mol fraction.

3.2.11 Statistical analyses

Statistical analyses were conducted using the statistical package R, version 3.6.3 (http://cran.r-project.org/). For *inter-seasonal* effects (bulk soil and forage community variables), we analyzed the effect of 'farm management' (ISV vs CONV), 'time,' and the response of each treatment across time ('treatment(x)time' interaction) using a linear mixed-effect regression model with *lme4* and *lmerTest* packages (Bates et al., 2015; Kuznetsova et al., 2017). This model was fit to account for our experimental design, which included the use of ‘plot,’ ‘sub-plot,’ and ‘sub-sub-plot’ as random effects. A similar model was used to evaluate *intra-seasonal* effects of treatment and time on whole-soil carbon efflux. A separate model was created to analyze other intra-seasonal effects (rhizosphere soil and roots), which considered the impact of ‘farm management’ (ISV vs CONV), ‘species’ (*A. sat.*, *T. aes.*, and *G. dis*), ‘time’, as well as their two-way (‘treatment(x)time,’ ‘treatment(x)species,’ and ‘species(x)time) and three-way (‘treatment(x)species(x)time’) interaction terms, as fixed effects. We again used ‘plot,’ ‘sub-plot,’ and ‘sub-sub-plot’ as random effects for this model.

An analysis of variance (ANOVA) for each model was conducted using type II Wald Chi-square tests on the *car* package (Fox and Weisberg, 2019). Tukey’s pairwise comparisons were conducted using the *emmeans* package to assess differences between combinations of treatments and species across each time point (Midway et al., 2020). Residuals were checked for normality and homogeneity of variance. When variables were non-normally distributed or had unequal variance, data were log or square root transformed prior to calculation of means and back-transformed for visualization. Fixed effects were investigated with means comparisons and considered p-value < 0.001(***) as highly significant, p-value < 0.01(**) as significant, and p-value < 0.05(*) as marginally significant. A Pearson’s correlation analysis was also conducted to evaluate coefficients (r^2) between some select variables (Rodgers and Nice Wander, 1988). Box plots and line plots were graphed using the *ggplot2* package and heatmaps were constructed using the *reshape* and *ggplot2* packages.

3.3 RESULTS

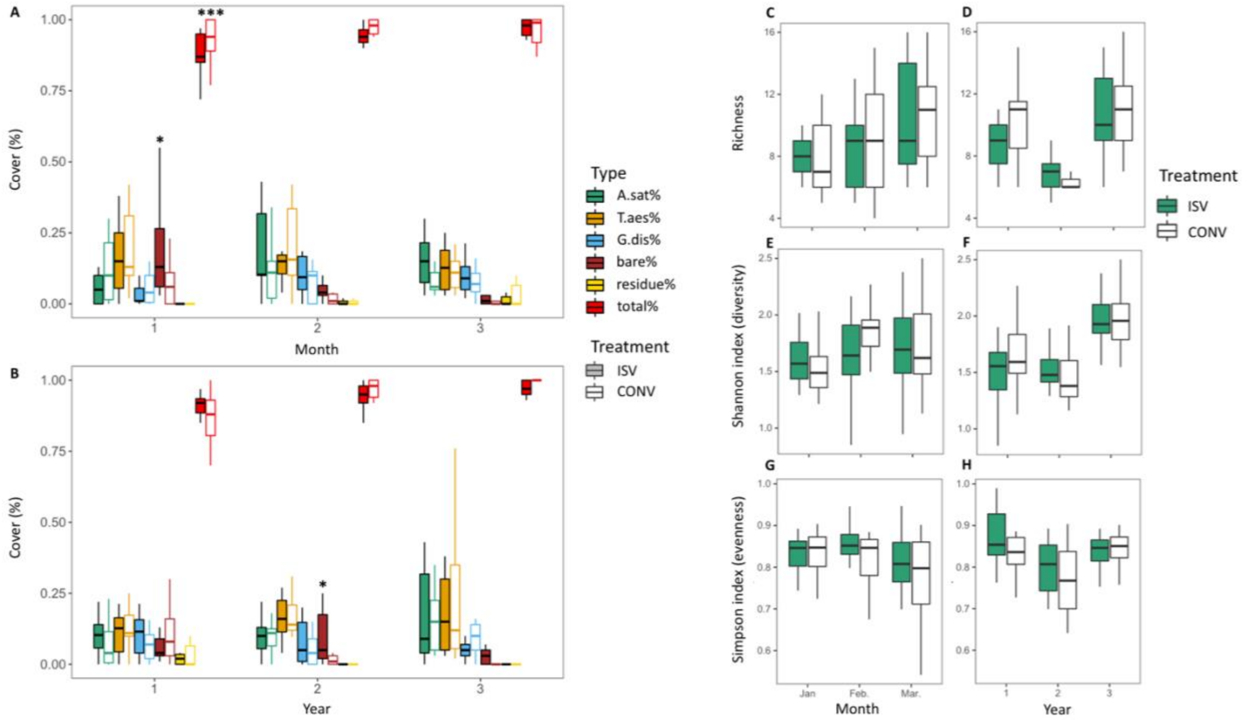
3.3.1 Plant response to grazing

3.3.1.1 Plant community structural diversity (intra- and inter-seasonal)

While there was high annual variability in total canopy cover (total%; Year, *P*<0.001) and the relative canopy cover distribution of different plant species (species%;Year, *P*=0.003), this variability was similar between management treatments across the inter-seasonal experimental period (Supplementary Table 1). On the other hand, management significantly altered total% across the intra-seasonal timescale (Figure 1A; Treatment*(x)*Month, *P*<0.001). On average, the month-to-month total% under ISV decreased between January to February by 5% and increased between February to March by 11%. This differed from the CONV treatment, which saw increases in total% of 11% and 4% over the same time periods, respectively. Shifts in species% across months were also significantly different between treatments (Treatment*(x)*Species*(x)* Month, *P*=0.029). In particular, the relative shift in distribution of A. *sativa* (A.sat%) across the intra-seasonal experimental period (between the months of January and March) was 59% higher under ISV compared to CONV management (Figure 1A; Treatment*(x)*Month, *P*=0.015). There were also significant intra-seasonal treatment differences for bare soil exposure (bare%; Treatment*(x)*Month, *P*=0.008). This was particularly notable during the month of January, which showed 11% higher bare% under ISV compared to CONV (Figure 1A). Significant shifts in plant community structure, residue coverage (residue%), and bare% were not observed between management treatments (ISV vs. CONV) across the inter-seasonal experimental period (Figure 1B).

Forage community richness, diversity, and evenness were not affected by management treatment across either months or years (Supplemental Table 1). Across management treatments, the understory plant community richness (R_p) did increase from month-to-month (Figure 1C; Time, P=0.001), though it remained steady across years (Figure 1D). The Shannon diversity index (H_p) also shifted across months (Figure 1E; Time, P=0.009) as well as years (Figure 1F; Year, P<0.001), with a 33% increase from the beginning to end of the inter-seasonal experimental period (3 years) across both treatments. Otherwise, the Simpson index (Figure 1G-H) did not significantly change across either intra-seasonal or inter-seasonal timescales.

Figure 1: Understory plant community composition and structural diversity (intra- and inter-seasonal)



The composition and structural diversity of understory plant communities were evaluated for three years, during the months of January, February, and March. Understory plant communities were measured in the vineyard interrow space of two treatments (ISV vs. CONV) for total canopy cover area (total%) and canopy cover area per forage species (species%). Where no canopy cover was present, the area of soil with residue coverage (residue%) and bare soil exposure (bare%) were measured. Figure 1A-B show the total canopy cover (total%) as well as the distribution of A. sativa (A.sat%), T. aestivum (T.aes%), and G dissectum (G.dis%) as their relative proportion(s) of total%. Where total% is <100, the area of bare soil (bare%) and soil covered by residues (residue%) are shown such that *the sum of total%, bare%, and residue% are equal to 100%. Species richness (B-C), Shannon index (D-E) and Simpson index (F-G) were also calculated. For each sampling time, a Tukey-Kramer means comparison was used to evaluate significant pairwise difference between treatments.*

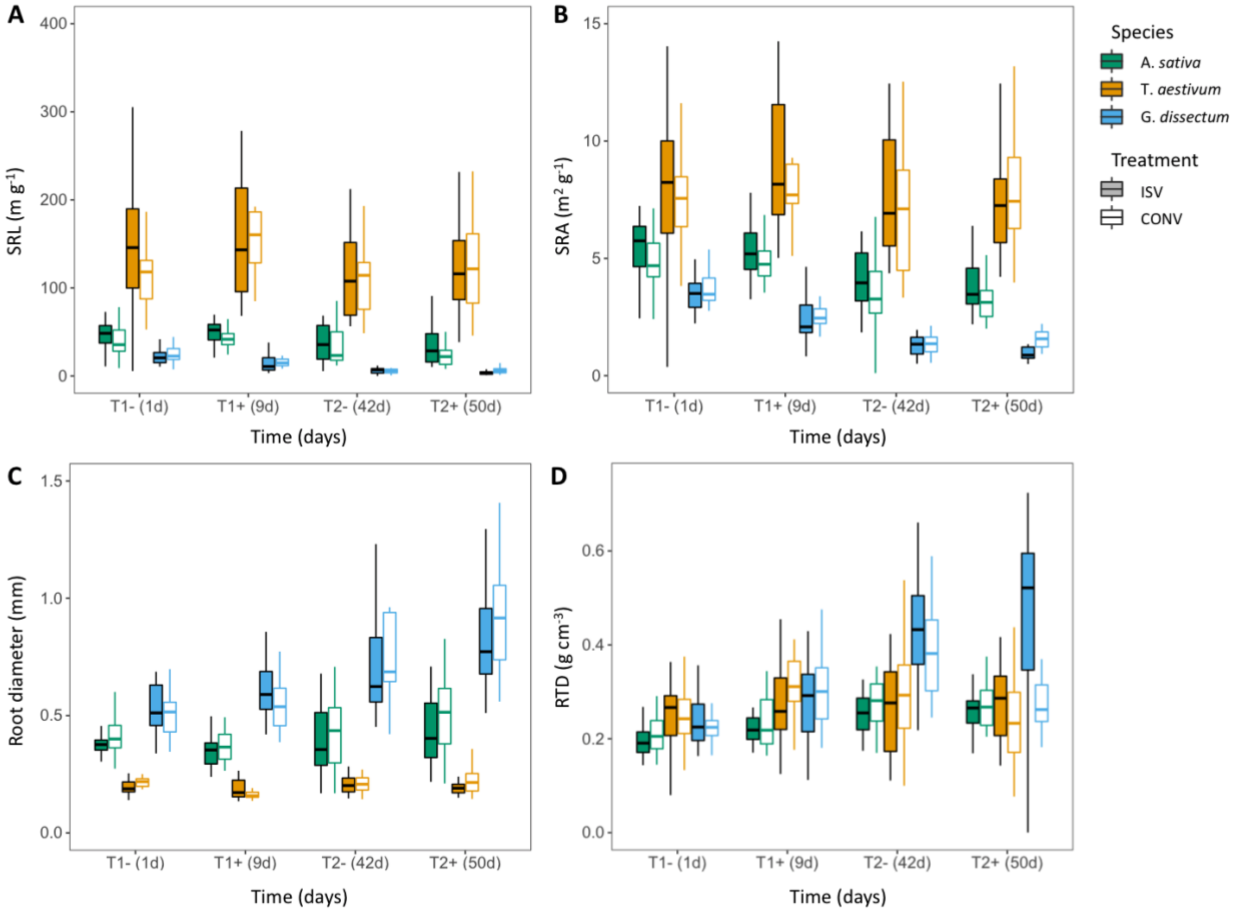
** p <0.05; ** p <0.01; *** p < 0.001.*

3.3.1.2 Plant root morphological diversity (intra-seasonal)

Management had minimal impacts on the root morphological development of species over time (Supplementary Table 1). While we did observe a divergent management effect on the specific root area (SRA) of each species (Figure 1A; Treatment*(x)*Species, *P*=0.011), there was no significant pairwise variation in SRA between treatments for A. *sativa* (Tukey's Treatment, *P*=0.56), G. *dissectum* (Tukey's Treatment, *P*=0.79), or T. *aestivum* (Tukey's Treatment, *P*=0.98). Though non-significant, there was also a notable divergent management trend for the specific root length (SRL) of each species (Figure 1B; Treatment(*x*)Species, *P*=0.094). However, there was again no significant pairwise variation between treatments for the SRL of A. *sativa* (Tukey's Treatment, *P*=0.94), T. *aestivum* (Tukey's Treatment, *P*=0.39), or G. *dissectum* (Tukey's Treatment, *P*=0.99). These treatment effects were also not found to significantly alter intra-seasonal species responses across time (Treatment*(x)*Species*(x)*Time), and there were otherwise no variations in the response of management across species or time (Supplementary Table 1).

Root morphological characteristics of each species nevertheless showed substantial diversity in their developmental patterns throughout the intra-seasonal period, with significant variation in specific root area (SRA; Figure 2A; Species*(x)*Time, *P*<0.001), specific root length (SRL; Figure 2B; Species*(x)*Time, *P*<0.001), root diameter (Figure 2C; Species*(x)*Time, *P*=0.007), and root tissue density (RTD; Figure 2D; Species*(x)*Time, *P*=0.039). For SRA, values were much higher for T. *aestivum* (8.5±0.4 m^2 g^{-1}) than A. *sativa* (4.6±0.3 m^2 g^{-1}) and G. *dissectum* (2.2±0.4 m^2 g^{-1}) across treatments (Figure 2A). The SRL values showed similar trends (Figure 2B) with values in descending order: T. *aestivum* (143.3±7.8 m g^{-1}) > A. *sativa* (41.7±3.8 m g^{-1}) > G. *dissectum* (12.4±2.8 m g^{-1}). The average root diameter (Figure 2C) followed an opposing trend, with values in descending order: G. *dissectum* (0.75±0.07 mm) > A. *sativa* (0.41±0.02 mm) > T. *aestivum* (0.22±0.02 mm). As for the RTD, we observed higher values for G. *dissectum* (0.35±0.04 g cm^{-3}) and T. *aestivum* (0.31±0.03 g cm^{-3}) than for A. *sativa* (0.24±0.01 g cm^{-3}) (Figure 2D). We also found a strong linear correlation between SRL and SRA (Supplementary Figure 2A; $P<0.001$; $r^2 = 0.90$), and a logarithmic correlation between SRL and root diameter (Supplementary Figure 2B $P<0.001$; $r^2 = 0.72$). This provides support for the methodological rigor of root sampling and imaging analysis (Khan et al., 2021; Kramer-Walter et al., 2016).

Figure 2: Root morphological characteristics (intra-seasonal)



The (A) specific root length (SRL), (B) specific root area (SRA), (C) root diameter, and (D) root tissue density (RTD) of understory plant species were measured four times throughout a 65-day time period (intra-seasonal) across three species (A. sativa, T. aestivum, and G dissectum) and two treatments (ISV vs. CONV). The times (T1/T2) represent the occurrence of the first graze and second graze/termination mow event(s), respectively. The (-/+) represent 3-days before and 3-days after the graze/mow event(s), respectively. For each sampling time, a Tukey-Kramer means comparison was used to evaluate significant pairwise difference between treatment(x)species interactions. No significant pairwise differences were found.

3.3.2 Rhizosphere soil response to grazing (intra-seasonal)

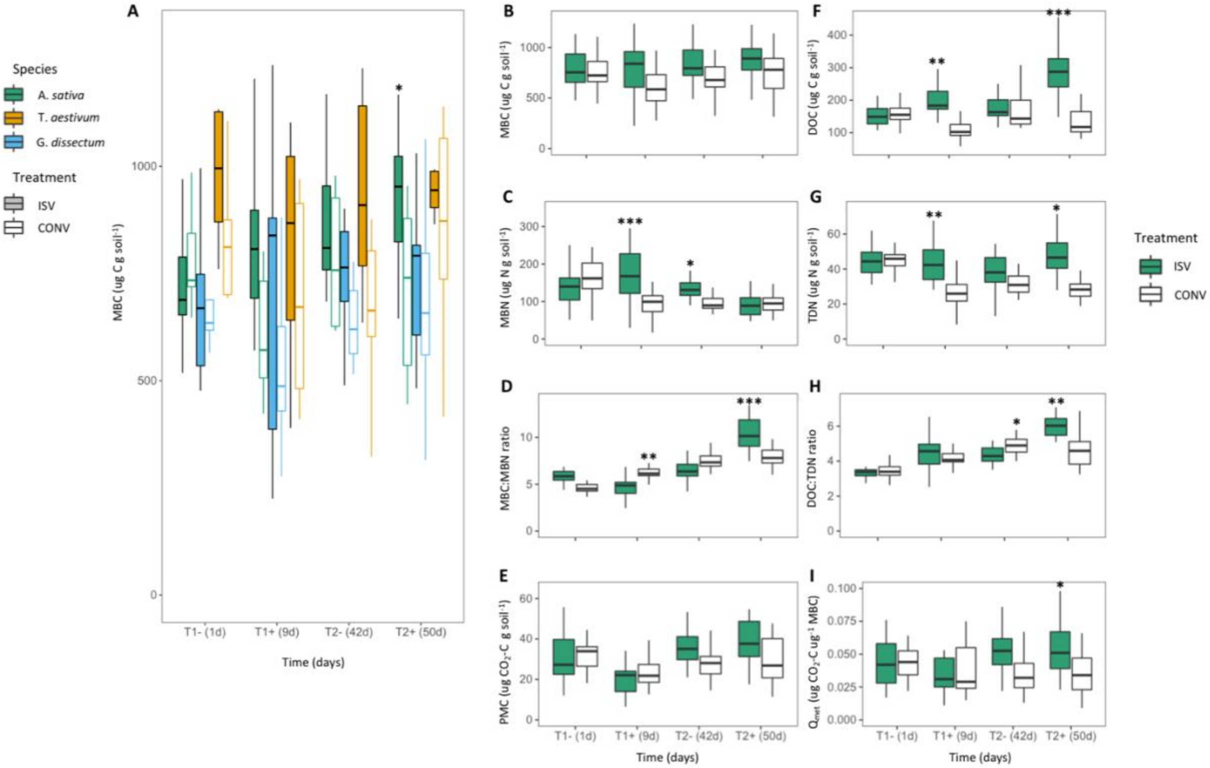
3.3.2.1 Size of rhizosphere microbial communities

The intra-seasonal rhizosphere microbial biomass carbon (MBC) pool was significantly higher under ISV relative to CONV management (Supplementary Table 2; Treatment, *P*<0.001). The rhizosphere MBC pool trended higher under ISV across time (Treatment*(x)*Time, *P*=0.102), with an 81% (T1) and 14% (T2) more positive response to intra-seasonal grazing events relative to the CONV treatment (Figure 3B). However, there was significant variation between rhizosphere soils of each species (Species, *P*<0.001), with divergent trends in their immediate responses over time (Species*(x)*Time, *P*=0.100) and their responses to management treatments over time (Figure 3A; Treatment*(x)*Species*(x)*Time, *P*=0.121). While high in variability, we observed a substantial MBC increase in rhizosphere soils of A. *sativa* during the immediate period following ISV grazing at both T1 (+234±85 ug g^{-1}) and T2 (+280±136 ug g^{-1}) (Tukey's Treatment, *P*=0.088). We observed an opposing trend in the rhizosphere soils of T. *aestivum*, with decreases in MBC at both T1 (-71±109 ug g^{-1}) and T2 (-115±89 ug g^{-1}) in the period immediately following ISV grazing (Tukey's Treatment, *P*=0.073). The MBC management response was most variable in rhizosphere soils of G. *dissectum*, with an increase at T1 (+164±109 ug g^{-1}) and decrease at T2 (-73±82 ug g^{-1}) under ISV that was non-significant in pairwise treatment comparisons (Tukey's Treatment, *P*=0.74).

Rhizosphere microbial biomass nitrogen (MBN) pools also diverged under ISV compared to CONV (Supplementary Table 2; Treatment, *P*<0.001), though they did not show consistent patterns throughout the intra-seasonal experimental period (Figure 3C). The MBN response did not significantly differ across species throughout the intra-seasonal experimental period

(Supplemental Table 2). Otherwise, while the rhizosphere MBC:N ratio significantly increased across time across all rhizosphere soils (Figure 3D), by an average of 71% from beginning to end of the experimental period (5.4±0.3 vs. 9.3±0.4; Time, *P*<0.001), no significant variation was observed across treatments or species (Supplemental Table 2).

Figure 3: Rhizosphere soil biogeochemical indicators (intra-seasonal)



The rhizosphere soil (A-B) microbial biomass carbon (MBC), (C) microbial biomass nitrogen (MBN), (D) MBC:MBN ratio, (E) potentially mineralizable carbon (PMC), (F) dissolved organic carbon (DOC), (G) total dissolved nitrogen (TDN), (H) DOC:TDN ratio, and the (I) metabolic quotient (Q_{met}) of understory plant species were measured four times throughout a 65-day time period (intra-seasonal) across three species (A. sativa, T. aestivum, and G dissectum) and two treatments (ISV vs. CONV). Results for (A) MBC are shown with significant species interaction, whereas results for (B-I) are averages across species. For each sampling time, a Tukey-Kramer means comparison was used to evaluate significant pairwise difference between treatments or treatment(x)species interactions.

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

3.3.2.2 Rhizosphere carbon and nitrogen pools

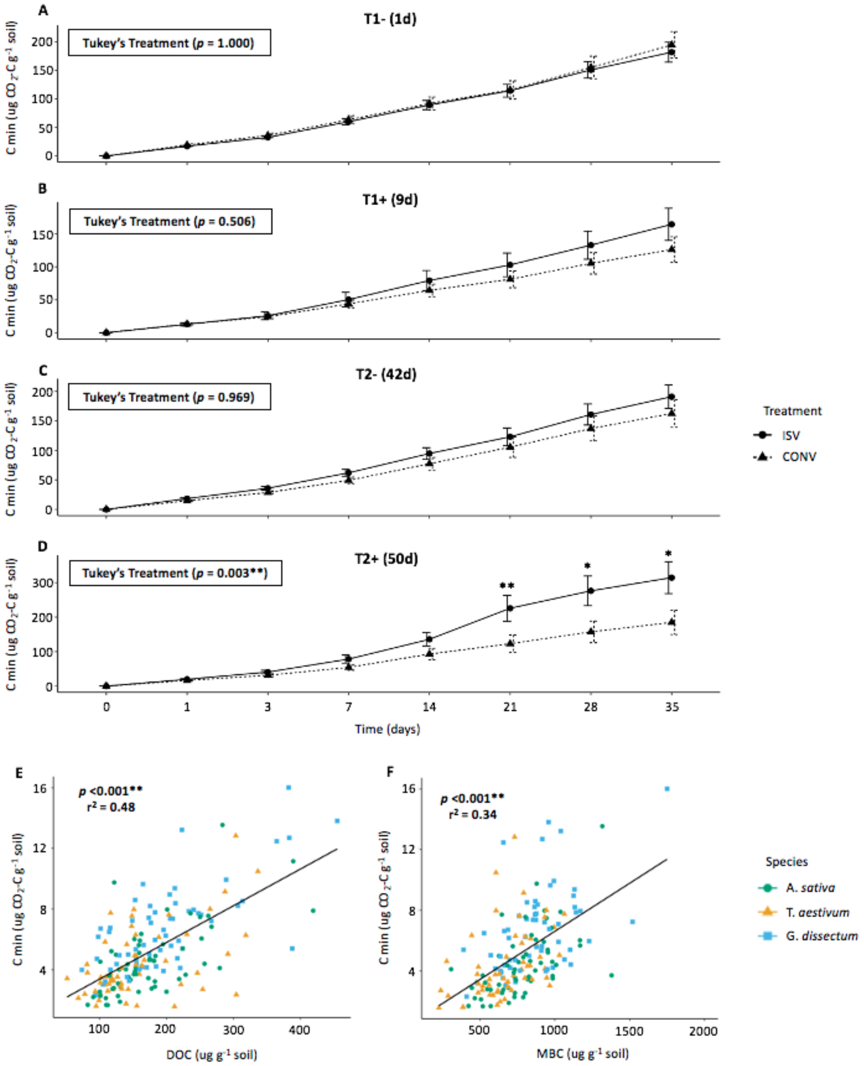
Intra-seasonal rhizosphere soil organic carbon flux pools were higher under ISV compared to CONV management, including increases in dissolved organic carbon (DOC) and potentially mineralizable carbon (PMC) over time. However, there were no significant management treatment differences in rhizosphere soil carbon and nutrient pools across forage species (Supplementary Table 2). The PMC pool increased by 82% under ISV relative to CONV management from beginning to end of the experimental period (Figure 3E; Treatment*(x)*Time, P=0.001). The rhizosphere DOC pool also shifted over time (Treatment*(x)*Time, P<0.0001), with significant increases in immediate response to grazing at both T1 (+103±15 ug g^{-1}; Tukey's Treatment P=0.008) and T2 (+142±9 ug g^{-1}; Tukey's Treatment P<0.001) time points (Figure 3F). Further, the intra-seasonal rhizosphere pool of total dissolved nitrogen (TDN) increased with ISV grazing (Treatment*(x)*Time, P=0.018), including significant pairwise increases after grazing at T1 (+75%; Tukey's Treatment P<0.001) relative to the CONV treatment (Figure 3G). Overall, the rhizosphere DOC:TDN ratio increased over time under ISV relative to CONV (Figure 3H; Treatment*(x)*Time, P=0.011).

3.3.2.3 Rhizosphere carbon mineralization and use-efficiency

The efficiency of the rhizosphere microbial community (metabolic quotient, Q_{met}) decreased under ISV over the intra-seasonal experimental period (Figure 3I; Treatment*(x)*Time, P<0.001), with more CO_2-C respired relative to the size of the MBC pool (Dilly and Munch, 1998; Xu et al., 2017) over time. Simultaneously, the intra-seasonal ISV treatment increased the rate of carbon mineralization (C_{min}) in rhizosphere soils across species and over time (Figure 4A-D;

Treatment*(x)*Time, *P*<0.001), especially in period immediately after T2 grazing (Figure 4D; Tukey's Treatment, *P*=0.003). On average across T1 and T2, the rate of rhizosphere C_{min} increased under ISV by 74% compared to CONV for soils sampled immediately after grazing occurred (4.94±0.76 vs. 8.59±1.16 ug CO_2-C g soil^{-1} day^{-1}). Notably, there was also a significantly positive relationship between C_{min} and the size of both the rhizosphere DOC (Figure 4E; $P<0.001$; $r^2 = 0.48$) and MBC (Figure 4F; $P<0.001$; $r^2 = 0.34$) pools over the course of the intra-seasonal experimental period.

Figure 4: Soil carbon mineralization (intra-seasonal)



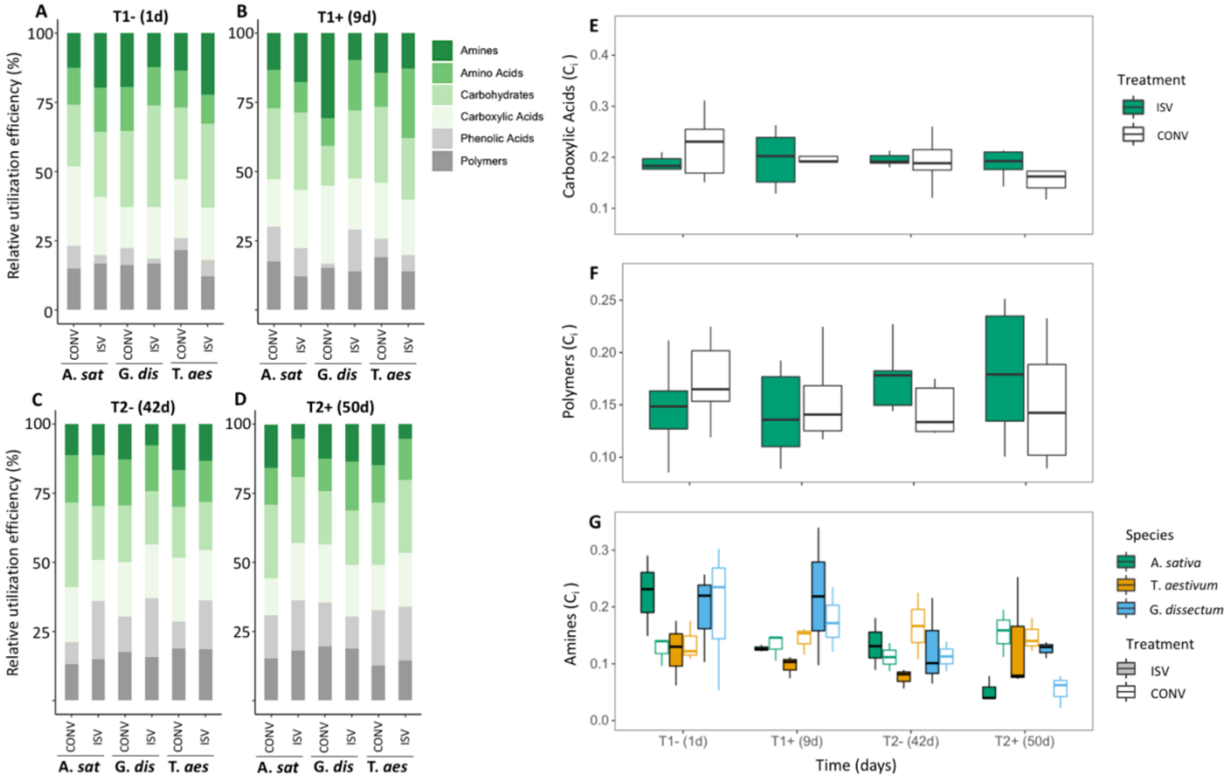
(A-D) Rhizosphere soils were incubated and measured for C mineralization (C_{min}) via microbial respiration rates (umol CO_2 g soil^{-1}) at four time points (T1(-/+) and T2(-/+)). For each sampling time, a Tukey-Kramer means comparison was used to evaluate significant pairwise difference between treatments.

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

3.3.2.4 Rhizosphere microbial metabolic diversity

The intra-seasonal metabolic capacities of rhizosphere microbial communities, assessed via the relative utilization efficiency of six biochemical categories (amines, amino acids, carbohydrates, carboxylic acids, phenolic acids, and polymers), did not considerably differ across species though did vary in their treatment responses over time (Supplemental Table 3). The relative utilization amino acids, phenolic acids, and carbohydrates showed no significant treatment responses throughout the intra-seasonal experimental period (Figure 5A-D). Alternatively, comparisons from beginning to end of the experimental period showed increased utilization of carboxylic acids (+61%; Treatment*(x)*Time, P=0.041) and polymers (+37%; Treatment*(x)*Time, P=0.050) under ISV relative to CONV management (Figure 5E-F). The utilization of amines also significantly differed over time, with diverging species responses to management (Treatment*(x)*Species*(x)*Time p=0.004) though no pairwise significance amongst individual species (Figure 5G). We observed no significant treatment variation in pairwise comparisons between pre-graze (-) vs. post-graze (+) values for any biochemical category in either T1 and T2 grazing events.

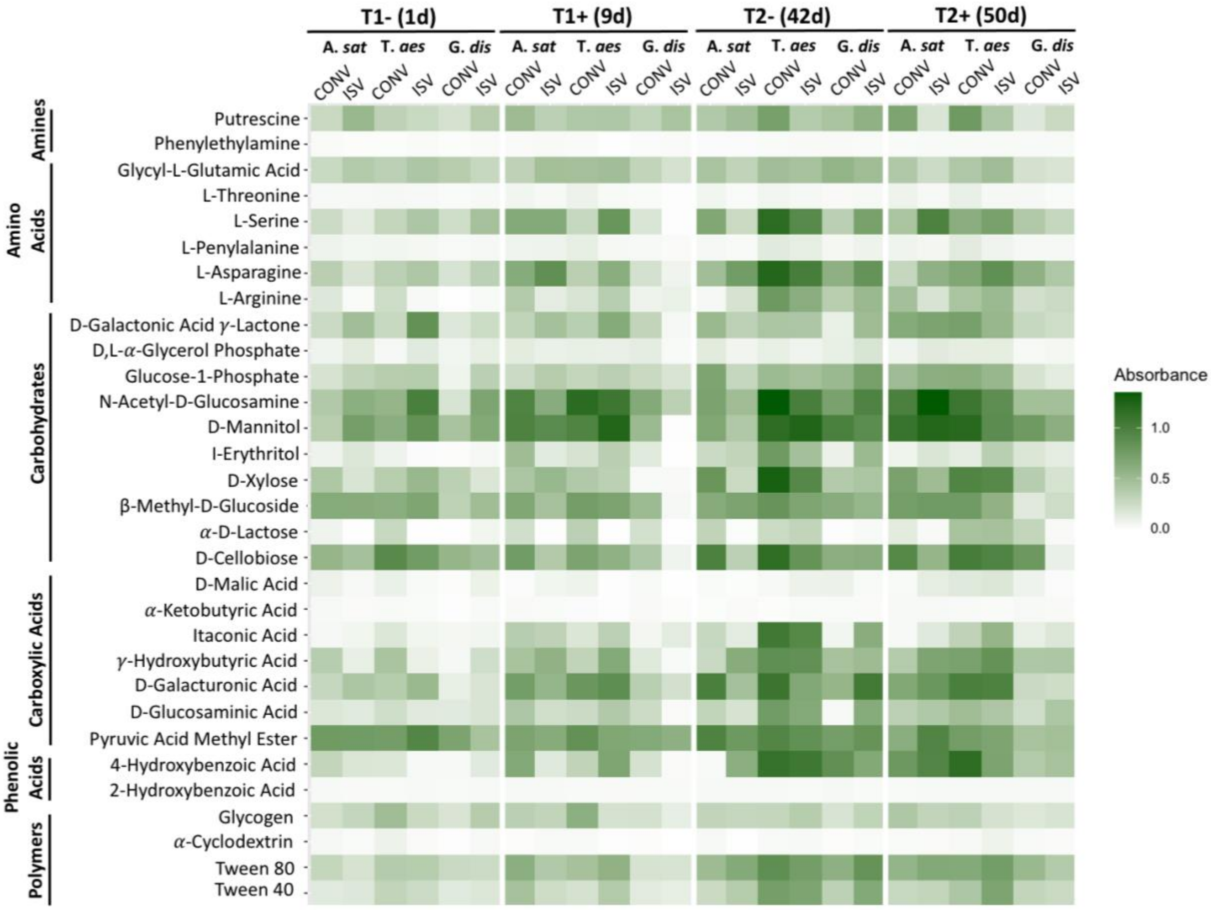
Figure 5: Rhizosphere microbial substrate utilization of six carbon biochemical categories (intra-seasonal)



Rhizosphere soils were incubated and measured for microbial metabolic diversity via community-level physiological profiling (Biolog EcoPlate). (A-D) The relative utilization efficiency (%) of six biochemical substrate categories calculated at four time points (T1(-/+) and T2(-/+)). Shown are also optical density (C_i) measurements for (E) carboxylic acids, (F) polymers, and (G) amines. Results for (G) amines are shown with significant species interaction. For each sampling time, a Tukey-Kramer means comparison was used to evaluate significant pairwise difference between treatments or treatment(x)species interactions. No significant pairwise differences were found.

There was no significant treatment variation amongst any one of the 31 unique substrates. Further, the utilization of all 31 individual substrates was generally similar with rhizosphere soils of each species over time. Out of all substrates, only Putrescine (amino acid; Species, *P*=0.033*) and Threonine (amine; Species, *P* =0.048*) showed significant species variation in microbial utilization (Figure 6). Average well color development (AWCD) values also generally followed the same pattern across time, and did not differ based on treatment or species (Supplemental Table 5). Otherwise, while the Shannon index (H_s), the Simpson index (D_s), and substrate richness (R_s) all varied across species and time, there was no significant treatment variation in the intra-seasonal metabolic diversity of rhizosphere communities (Supplemental Table 4).

Figure 6: Rhizosphere microbial substrate utilization of 31 carbon substrates (intra-seasonal)

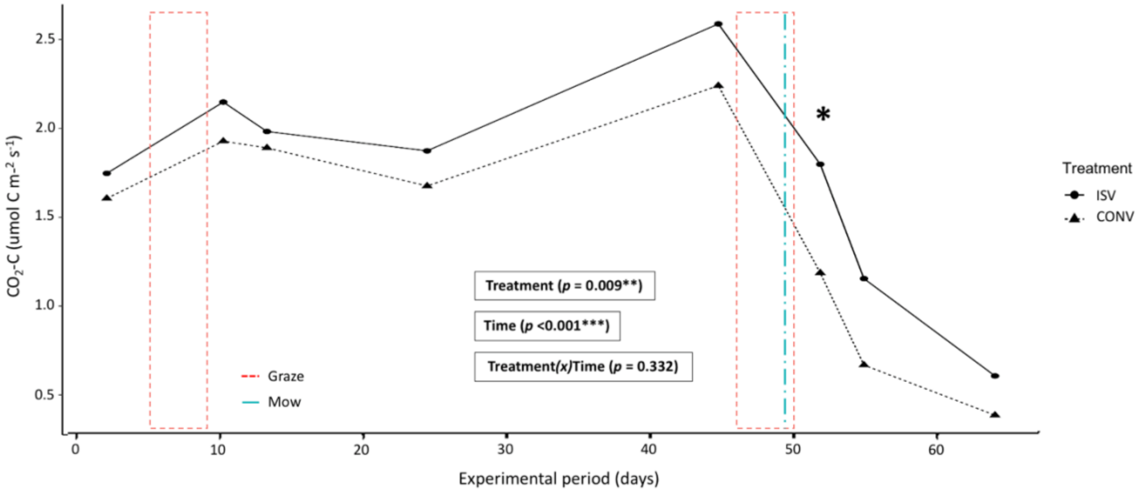


Heat map based on Biolog EcoPlate carbon source utilization patterns of rhizosphere microbial communities. The optical density (C_i) absorbance readings of all 31 carbon substrates for the final incubation time point (144 hours) were calculated at four time points (T1(-/+) and T2(-/+)).

3.3.3 Whole-soil carbon efflux (intra-seasonal)

Intra-seasonal patterns of *in-situ* soil carbon efflux were highly variable throughout the season (Figure 7; Time, *P*<0.001), with higher treatment values (Treatment, *P*=0.009) though similar treatment response patterns throughout the experimental period (Treatment*(x)*Time, *P*=0.660). Nevertheless, the ISV treatment showed higher CO_2-C flux rates (umol C m-^{2} s^{-1}) under ISV for all measured time points. Notably, we also observed significantly higher soil carbon flux under ISV (1.80±0.16 umol C m-^{2} s^{-1}) compared to CONV (1.19±0.14 umol C m-^{2} s^{-1}) on day 51 of the experimental period (Figure 7; Tukey's Treatment, *P*=0.032) – one day after the final graze and mow events for both ISV and CONV treatments, respectively.

Figure 7: Whole-soil ecosystem carbon efflux (intra-seasonal)



Whole-soil CO_2 production rates were collected from chamber measurements on days(s) 1, 8, 11, 22, 41, 50, 53, and 65 of the intra-seasonal experimental period. Total CO_2-C production corresponds to CO_2 efflux rates from the soil surface. Dashed lines represent the occurrence and duration of graze (red) and mow (blue) events. For each sampling time, a Tukey-Kramer means comparison was used to evaluate significant pairwise difference between treatments.

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001

3.3.4 Bulk soil response to grazing (inter-seasonal)

3.3.4.1 Size of bulk soil microbial communities

The bulk soil MBC pool (Figure 8A) did not significantly change throughout the inter-seasonal experiment period (Supplementary Table 3), nor did the MBN pool (Figure 8B) or MBC:N ratio (Figure 8C). Management (ISV vs. CONV) also did not significantly shift MBC and MBN pools, nor the MBC:N ratio over time. Similarly, while the total inter-seasonal abundance (ng g^{-1}) of phospholipid fatty acid (PLFA) biomarkers, an indicator of viable microbial biomass, did change over the inter-seasonal experiment period (Supplementary Table 6; Time, *P*=0.041), it did not significantly respond to the management treatment across seasons (Figure 9A).

3.3.4.2 Bulk soil carbon and nitrogen pools

There were no significant shifts in inter-seasonal bulk soil DOC pools (Figure 8E) across treatments or time (Supplementary Table 6), nor for the TDN pool (Figure 8F) and DOC:TDN ratio (Figure 8G). However, there were significant differences between treatment responses for inter-seasonal bulk soil SOC concentrations (Figure 8D; Treatment*(x)*Time, *P*=0.011). While SOC did show a 31% increase across the entire intra-seasonal experimental period under ISV relative to CONV (-4.3 vs. +4.4 mg C g $soil^{-1}$, respectively), differences between treatments largely depended on the year with not a clear trend of the treatments over time.

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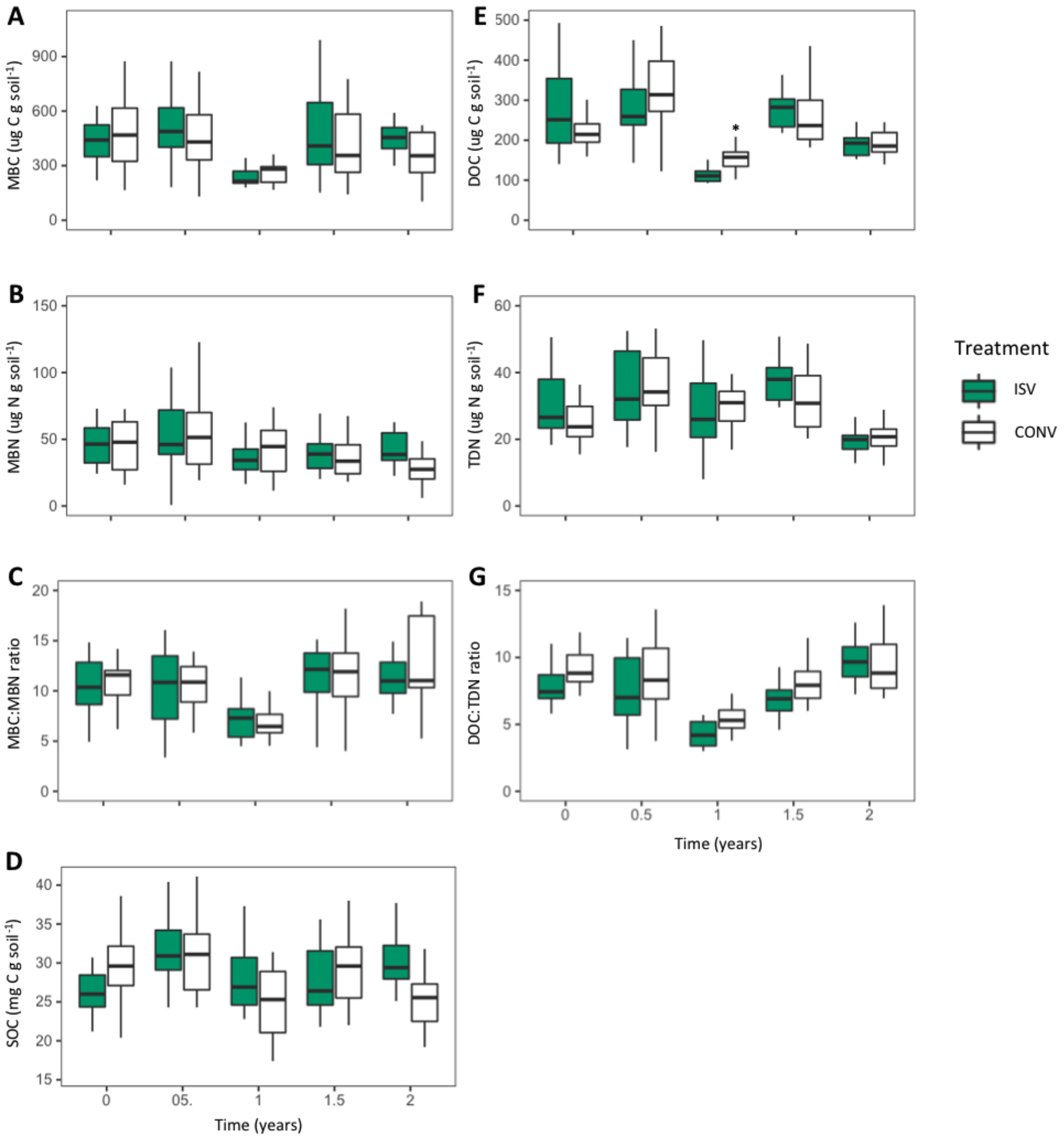
Figure 8: Bulk soil biogeochemical indicators (inter-seasonal)



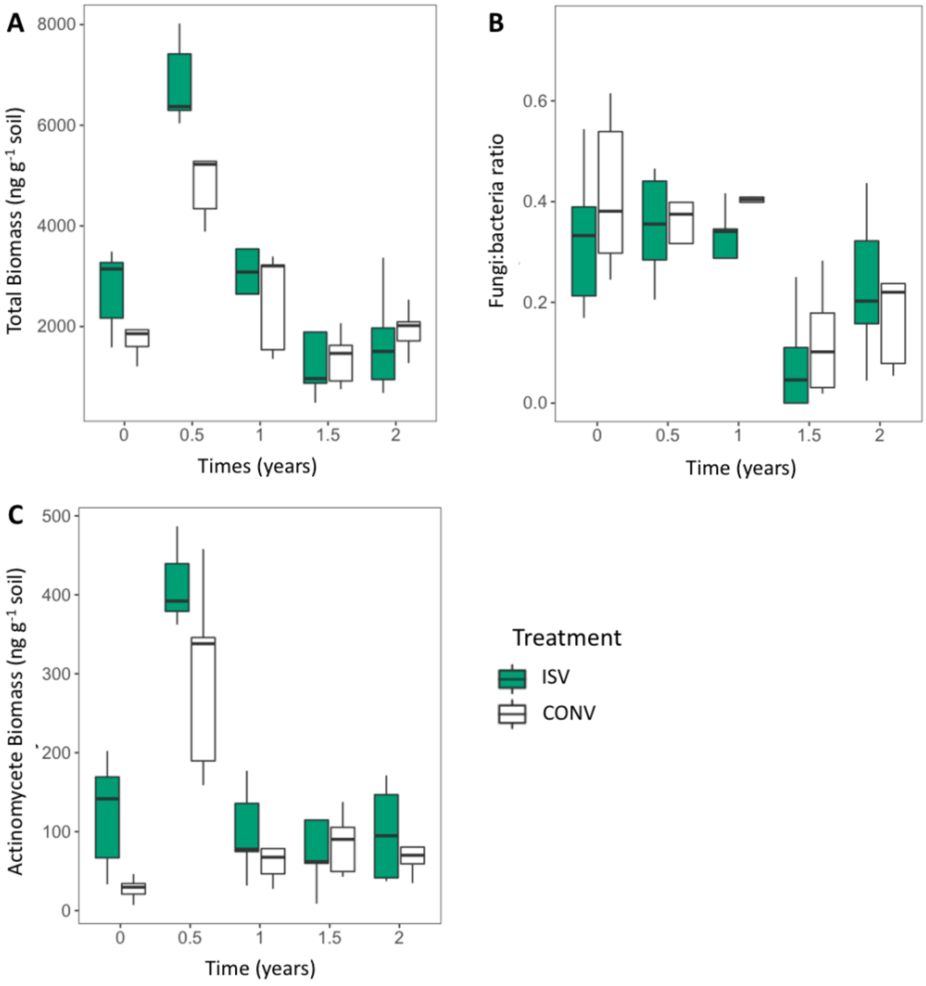
The bulk soil (A) microbial biomass carbon (MBC), (B) microbial biomass nitrogen (MBN), (C) MBC:MBN ratio, (D) total soil organic carbon (SOC), (E) dissolved organic carbon (DOC), (F) total dissolved nitrogen (TDN), and (G) DOC:TDN ratio were measured twice per year across two treatments (ISV vs. CONV). For each sampling time, a Tukey-Kramer means comparison was used to evaluate significant pairwise difference between treatments.

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001

3.3.4.3 Bulk soil microbial community structural diversity

Inter-seasonal bulk soil PLFA structural biomarkers showed similar trends over time and across management treatments (Supplementary Table 7). Structural biomarkers showed similar abundances of both total bacterial and fungal groups under ISV and CONV management. There were also no significant treatment effects across seasons for the fungi:bacteria ratio (Figure 9B) or the Gram(+):Gram(-) ratio (Supplementary Table 4). The only significant differences in functional groups between management treatments was for actinomycetes, with higher abundances (ng g^{-1}) under ISV (Figure 9C; Treatment, P=0.035). While the actinomycete treatment response also trended differently over time, it was not significant (Treatment*(x)*Time, P=0.099). Otherwise, there was no significant treatment effects for any other fungal or bacterial functional group (Supplementary Table 7).

Figure 9: Bulk soil PLFA biomarkers (inter-seasonal)



Phospholipid fatty acid (PLFA) indicators indicative of (A) total biomass, (B) fungi-to-bacteria ratio, and (C) actinomycete biomass. Ratios are unitless, while PLFAs are given in ng g soil^{-1}*. For each sampling time, a Tukey-Kramer means comparison was used to evaluate significant pairwise difference between treatments. No significant pairwise differences were found.*

3.4 DISCUSSION

This study aimed to identify whether the introduction of grazing into vineyards (ISV) would substantially alter soil C cycling patterns relative to the conventional method of mowing vineyard understory plant communities (CONV). To do so, we monitored SOC pool and process shifts at distinct temporal and spatial scales (i.e. rhizosphere soil within a single season (intra-seasonal) and bulk soil across multiple seasons (inter-seasonal)) with goal of understanding the extent of potential shifts, the timescale at which they may occur, and whether these shifts translated similarly across these distinct scales. We also sought to evaluate some drivers and linkages between potential outcomes, namely whether microbial community composition and C utilization patterns, forage community composition, and/or root morphological traits shift in response to management treatments. We hypothesized that the size of labile SOC pools and the rate of C fluxes would increase under ISV, and that this would translate to early indications of increases in SOC storage.

3.4.1 Grazing decreases forage canopy cover with minimal impact on plant community structure and root morphology

Structural indicators of community composition in the vineyard understory shifted significantly over time, with distinct developmental patterns amongst forage plant species across both months and years. However, the understory community composition mostly shifted in similar ways under ISV relative to CONV management. Notably, we observed significant intra-seasonal treatment differences in total forage canopy cover (total%) with a higher coverage under CONV, especially in earlier months of the productive forage season. (Figure 1A). We also observed higher intra-seasonal bare soil exposure (bare%) under ISV within the early months of the forage growth period, as well as an increasing trend in more bare% exposure in grazed vineyards across years (Figure 1B). While this study did not measure biomass production, other studies have observed notable effects of grazing on forage productivity (Lemaire and Agnusdei, 2009; Matches, 1992). These grazer-plant-soil interactions may result in positive, negative, or in many cases neutral impacts on forage productivity that are often contextualized within specific grazing intensities and edaphic, climatic, and forage community composition dynamics (Bardgett and Wardle, 2003; Dawson et al., 2009; Matches, 1992).

Experimental studies have shown relative similarities in the productivity of forage species subjected to similar intensities of grazing and mowing disturbances (Cuykendall and Marten, 1968; Mládková et al., 2015). On the other hand, where nutrients within forage residues undergo intra-ruminal mineralization and deposition back into soil ecosystems in soluble and bioavailable forms via animal excreta, this may improve forage productivity up to certain animal densities and under low soil nutrient availability contexts (Rumpel et al., 2015). Amongst studies that compare forage biomass production under different grazing intensities, both forage productivity and bare ground exposure are often linked to the frequency and magnitude of grazing disturbances (Patton et al., 2007; Schönbach et al., 2011; Teague et al., 2011; Teague and Dowhower, 2003). While these grazer-forage productivity dynamics are phenotype-specific, underling mechanisms may be most directly linked to defoliation intensity. When surpassing a context-specific threshold of animal densities, higher grazing pressure may trigger longer forage recovery intervals and therefore reduce forage accumulation rates (Martins et al., 2020). Observed reductions in total% and increases in bare% within grazed vineyard plots may relate more directly to the presence of two grazing events (under ISV) relative to one mowing event (under CONV) within our study design. In this case, hindrance of forage recovery responses from the increased quantity of disturbance events may be most plausible rather than inherent differences in dynamics between the two types of disturbance events.

While our study showed similar responses of T. *aestivum* (T.aes%) and G *dissectum* (G.dis%) against both grazing and mowing disturbances throughout both the intra- and inter-seasonal timescales (Supplementary Table 1), we observed a distinct increase in the distribution of A. *sativa* (A.sat%) grasses from beginning to end of the intra-seasonal experimental period (Figure 1A). However, this did not translate to significant shifts in the presence of each species across multiple seasons. Further, forage community diversity indicators – which account for the presence of all forage species amongst the entire community composition during the time of sampling – did not significantly shift across either measured timescale (Figure 1). Previous studies have concluded that grazing and mowing act as similar ecological filters, with equivalent capacities to maintain or improve grassland biodiversity when applied in analogous ways (McKenzie et al., 2016; Ren et al., 2012). On the other hand, empirical studies have shown strong evidence that grazing supports the dominance of grasses while mowing favors that of forb phenotypes, which potentially result from preferential and selective grazing of legumes and forbs as well as short rather than tall vegetation (Díaz et al., 2007; Dumont et al., 2007; Mládková et al., 2015; Schuman et al., 1999). Our results corroborate both these assumptions, as we observed a slight shift toward increasing dominance of grass species under ISV grazing but minimal impact to the overall diversity of the vineyard understory plant community.

Observed values for traits related to root length, area, diameter, and density trended parallel to forage structural dynamics, with notably distinct intra-seasonal development patterns amongst plant species but otherwise similar responses across management treatments (Figure 2). Our sampling scheme – which measured root traits in the period immediately before and after grazing and mowing events – gives strong indication that intra-seasonal morphological strategies did not vary either in immediate response to management disturbances nor after longer periods of recovery and acclimation. Whereas root morphological traits and growth patterns are shaped by many interacting ecosystem properties – especially in response to the density and architecture of neighboring plant species' roots – it is notable that similarities in forage community composition may further explain observed parallel root development responses between management treatments (Chen et al., 2020; Garlick et al., 2021).

Another potential driver of root trait development is in response to soil nutrient availability (Grossman and Rice, 2012; Mommer et al., 2012). Under the root economic spectrum (RES) model, increases in specific root length (SRL; increased root length-to-mass ratio) and specific root area (SRA; increased root areas-to-mass ratio) are considered to optimize biomass investment for nutrient capture (especially in low soil P and N conditions), as higher surface area increases the capacity for nutrient absorption (Dawson et al., 2009; Kramer-Walter et al., 2016). As such, relative shifts in SRL and SRA are often considered to occur in response to plant nutrient availability, with increased fine root development in low nutrient conditions (Ostonen et al., 2007; Paterson and Sim, 1999). While the availability of rhizosphere inorganic P did not change across the intra-seasonal experimental period (though was continuously higher throughout), the intra-seasonal availability of both TDN (Figure 3G) and inorganic N (Supplementary Table 2) increased over time under ISV. However, we did not observe relative shifts in root length or area measurements between management treatments. Under the RES model, traits positively associated with nutrient uptake capacity (i.e. SRL) should correlate negatively with tissue investment (i.e. RTD) and positively with rhizosphere metabolic activity (Bardgett et al., 2014; Kramer-Walter et al., 2016). Higher investment in fine root development has also been associated with increased rhizodeposition (Dawson et al., 2009). While we observed a relationship between SRL and RTD across species (Supplementary Figure 2C), we did not observe a correlation between SRL and rhizosphere microbial metabolic activity (i.e. C_{min}; Supplementary Figure 3A) nor between SRL and DOC (Supplementary Figure 3B).

3.4.2 Grazing quickly increases rhizosphere carbon flux across forage species while bulk soil carbon dynamics remain stable

Our results show that, despite similarities between treatments in root morphological traits over time, rhizosphere activity related to C cycling was substantially higher under ISV and shifted quickly in response to grazing disturbances across forage species. Overall, the quantity of dissolved organic carbon (DOC), potentially mineralizable carbon (PMC), microbial biomass carbon (MBC) and nitrogen (MBN), and total dissolved nitrogen (TDN) were all higher in the rhizosphere soil of grazed vineyard plots. Notably, we observed substantial and rapid relative increases in DOC (Figure 3F) and TDN (Figure 3G) across forage species during the 6-day period between both pre-graze and post-graze sampling events (T1-/+ and T2-/+, respectively). While mowing (CONV) also occurred during the T2 sampling period, we did not observe a comparable increase in active rhizosphere SOC pools or C cycling activity relative to grazing (ISV).

Grazing is well documented to impact rates of rhizodeposition in the period immediately following defoliation (Hamilton et al., 2008; Hamilton and Frank, 2001). While the allocation of carbon above- and belowground depends on forage phenotypes and interacting growing conditions, it is estimated that grasses (i.e. A. *sativa* and T. *aestivum*) allocate roughly 30–40%

of photosynthetically-fixed carbon belowground, of which 5–10% is deposited as root exudates in the rhizosphere (Farrar et al., 2003; Pausch and Kuzyakov, 2018). The allocation of belowground C may even proportionally increase in response to low nutrient availability, conditions commonly found in soils within the low-input interrow space of vineyards (Jones et al., 2004; Paterson and Sim, 1999; Whitehead, 2020). Notably for our study, defoliation from grazing has consistently been found to increase root exudation of soluble DOC compounds (Dawson et al., 2009; Hamilton et al., 2008; Henry et al., 2008). One study observed this occurrence for periods of 3–5 days following defoliation events (Paterson and Sim, 1999). This defoliation effect has recently been found to increase both the quantity and stability of newly assimilated belowground carbon in soils under moderate grazing intensity (Zhao et al., 2022).

Although the MBC pool trended higher over time under ISV, it was less responsive to grazing disturbance (Figure 3B) and further showed divergent patterns amongst species (Figure 3A). Overall, A. *sativa* showed increases in MBC over time, especially in response to the T2 grazing event, while patterns for T. *aestivum* and G. *dissectum* were less clear. Stimulation of rhizosphere microbial biomass upon defoliation is well documented, especially in grass species, and is generally correlated with increased exudation of soluble, labile C and nutrient substrates (Hamilton et al., 2008; Hamilton and Frank, 2001; L. Mawdsley, R. D. Bardgett, 1996). It has been shown that fungal communities are less affected by rhizodeposition from defoliation, which has been taken to indicate that defoliation promotes fast carbon cycles that preferentially favor bacterial growth (Bardgett et al., 1998; Grayston et al., 2001; L. Mawdsley, R. D. Bardgett, 1996). While our study did not indicate shifts in bulk soil fungi:bacteria ratios across the longer inter-seasonal experiment period, we did observe significantly higher quantities of actinomycete bacteria under ISV over the same time span (Figure 9D). Actinomycetes, a quick-cycling functional group related to decomposition (Bhatti et al., 2017; Setälä and McLean, 2004), were the only PLFA biomarker to show a significant treatment response over time.

Overall, soil C fluxes were much larger and more rapid under ISV relative to CONV. In addition to increases in SOC pools, microbial carbon mineralization (C_{min}) rates were higher under ISV and substantially increased in quick response to grazing disturbances (Figure 4A-D). This may be directly linked to higher rhizodeposition of exudates, which are composed of relatively simple sugars, amino acids, phenolics, and organic acids that may be quickly processed and assimilated by soil microbes (Farrar et al., 2003; Guo et al., 2016). Intuitively, carbon mineralization (C_{min}) rates were correlated with the availability of C sources (DOC; Figure 4E) and the size of microbial communities (MBC; Figure 4F). We observed congruent patterns during intra-seasonal whole-soil CO_2 efflux monitoring, with higher rates in ISV plots throughout the entire season, but especially during the sampling point immediately after T2 graze and mow events on day 52 (Figure 7). While CO_2 efflux rates were higher under ISV at all measured timepoints, the efflux patterns were similar between treatments across time and tended to follow patterns of environmental conditions throughout the intra-seasonal experimental period (Supplementary Figure 1).

Whereas we did observe higher deposition of rhizosphere DOC in response to ISV grazing, the composition of this soluble C pool remains unknown. Community-level physiological profiling (via Biolog EcoPlate) revealed relatively similar microbial utilization of carbon substrates amongst different forage species, with some variation between treatments (Supplementary Table

3). Amongst six biochemical substrate categories, the utilization of carboxylic acids (Figure 5E) and polymers (Figure 5F) responded differently over time with higher rates observed under ISV management. Compared to other carbon source functional groups in this analysis, carboxylic acids and polymers are considered relatively complex and recalcitrant compounds (Teng et al., 2020), which generally indicate higher utilization of stabilized SOC substrates rather than freshly-deposited exudates (Grayston et al., 2001, 1998, 1997; Teng et al., 2020). We also observed forage species-dependent alterations in the utilization of amines (Figure 5G), with higher metabolic rates over time for G. *dissectum* (forb) and lower rates for A. *sativa* and T. *aestivum* (grasses) under ISV relative to CONV management. Enhanced utilization of polymers and amines have been shown to correlate in another study, which was interpreted as a heightened potential capacity of soil microbes to process recalcitrant materials (Brandstaetter et al., 2022). One potential explanation for the higher utilization of carboxylic acids, polymers, and amines in grazed vineyard plots is the bolstered capacity of rhizosphere microbes to process structural compounds and materials associated with root senescence and biomass turnover (Horwath, 2007; Iyyemperumal and Shi, 2008). While measurements of root traits in our study were not suitable to determine root turnover dynamics, increased rates of root senescence are commonly associated with defoliation from grazing (Dawson et al., 2009; Hamilton et al., 2008; Hamilton and Frank, 2001).

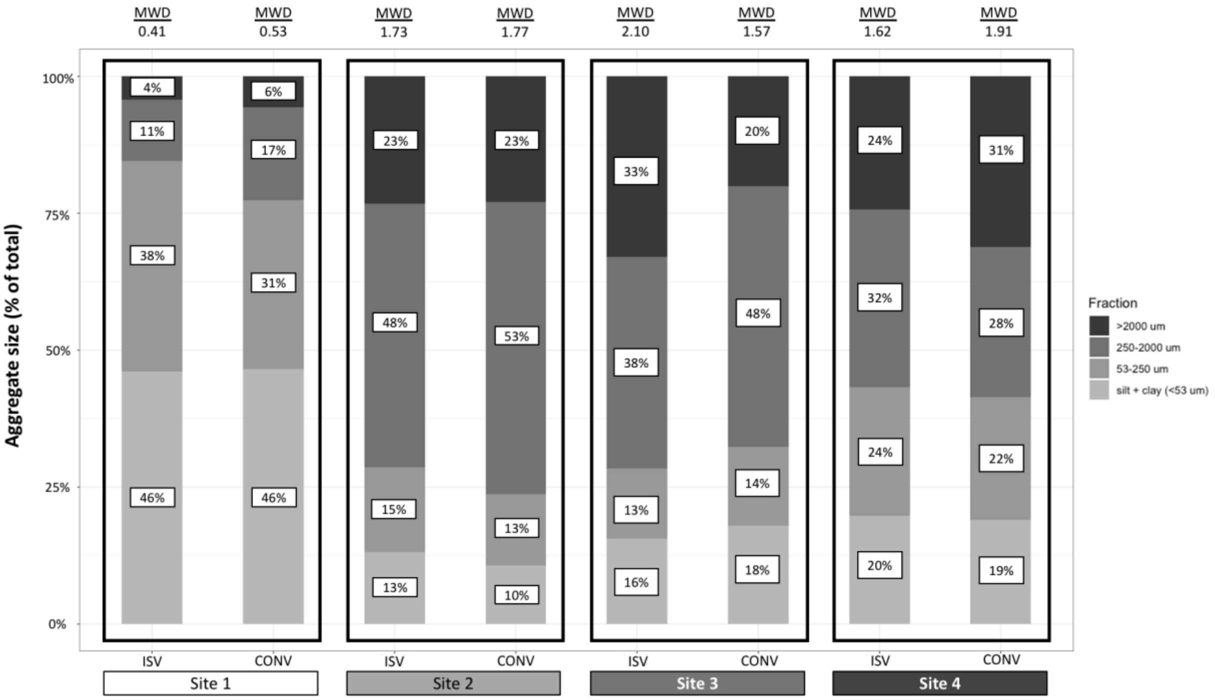
Whereas the soil carbon flux in rhizosphere soils was very responsive to grazing disturbances, inter-seasonal SOC pool measurements in bulk soils were relatively stable, showing fluctuation over time but similar trends between management treatments across seasons (Supplementary Table 6). For instance, increases in intra-seasonal rhizosphere DOC content under ISV did not translate to changes in the size of inter-seasonal bulk soil DOC pools (Figure 8E). There were also no significant inter-seasonal shifts in the size of soil microbial communities, as represented by similar quantities of bulk soil MBC (Figure 8A) and total PLFA biomarkers (Figure 9A) between treatments over time. While we did not observe significant variation in bulk soil C flux pools at the inter-seasonal temporal scale (with two samplings per year), we did observe significantly distinct management responses for total SOC (Figure 8D). While SOC showed a relative increasing trend under ISV compared to CONV, differences between treatments largely depended on the year – with not a clear trend of the treatments nor an adequate experiment duration period to observe meaningful shifts in SOC. Nevertheless, previous research has concluded that grazing may be more beneficial for SOC accumulation compared to mowing, up to a certain animal density and depending on soil type and pedoclimatic context (Rumpel et al., 2015). This is potential is considered especially plausible under low-input contexts, in which grazing may work to liberate additional nutrients necessary for SOM formation processes.

Notably, these neutral to moderately positive SOC outcomes were observed in ISV plots despite higher intra-seasonal whole-soil CO_2-C efflux patterns – a predominate SOC loss pathway – as well as observed reductions in intra-seasonal rhizosphere microbial carbon use-efficiency (CUE; as indicated by higher Q_{met}) under ISV (Figure 3I). This is a notable finding, as it indicates potential neutral-to-positive SOC retention outcomes in grazed vineyards, despite substantially more soil C efflux throughout the course of a single grazing season. This may be associated with increases in rhizosphere C inputs within grazed vineyard plots, which have been linked to improved SOC storage (Angst et al., 2021; Lange et al., 2015) and especially under lower soil fertility contexts (Whitehead, 2020). It may also relate to the temporal dynamics of soil C inputs, where belowground carbon deposition occurs as both *pulse* (more but infrequent, such as root biomass turnover) and *drip* (less but frequent, such as mucilage and exudates) delivery, with differing outcomes for SOC stabilization and destabilization (de Vries and Caruso, 2016; Sokol et al., 2019).

While our study provides meaningful initial insight into grazer-plant-soil dynamics of perennial integrated crop-livestock systems, more experimentation will be required to validate these findings and unravel the underlying mechanisms. Ultimately, given the similarities in nutrient input levels and co-management characteristics, the interrow space of ISV vineyard plots within this study appear to have responded similarly to previous literature from grazing studies in less intensively managed grassland systems. As such, where moderate intensity grazing has been shown potential to improve SOC outcomes in grassland systems, the positive soil C cycling and increases in P and N availability observed here indicate that ISV grazing may offer a notable transition opportunity away from petrochemical-intensive alternative understory vineyard management regimes such as mowing and/or herbicides. This may be particularly beneficial when accounting for: (i) externalities in the environmental and GHG footprints associated with alternative management options; (ii) potential increases and diversification of income streams associated with integrating vineyard and livestock production components; and (iii) improved multifunctionality of land-use and potential benefit for reducing grazing pressure on adjacent grassland and pasture systems (Niles et al., 2018; Ryschawy et al., 2021).

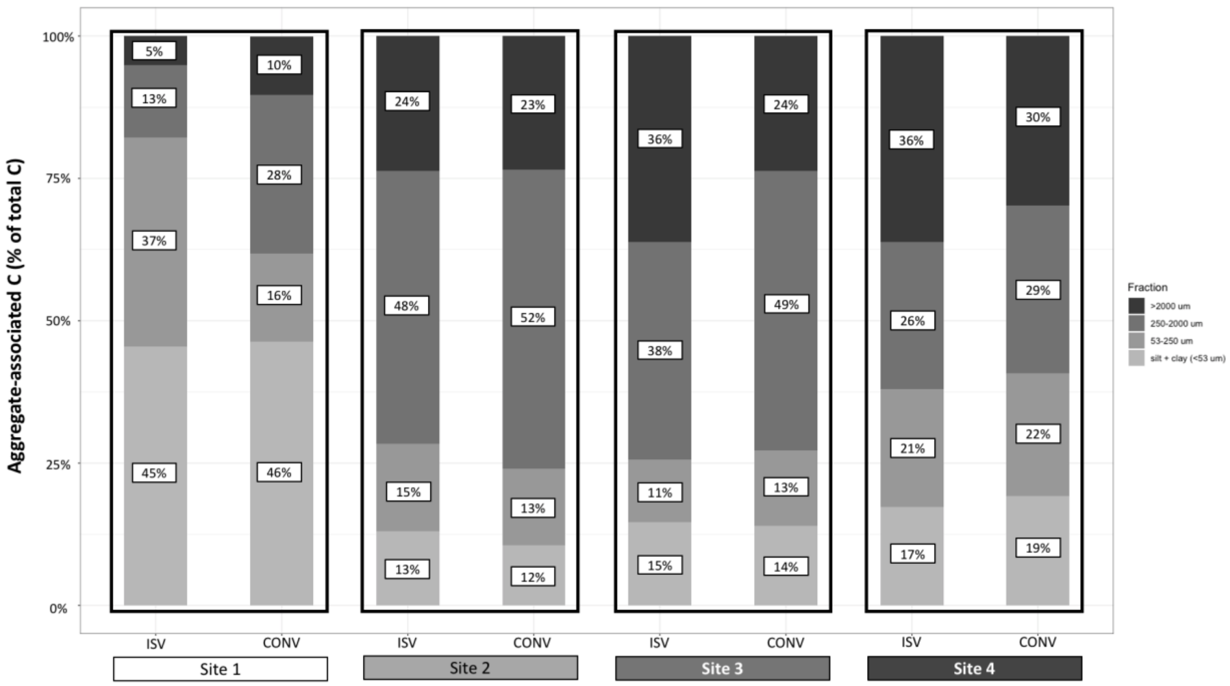
Appendix 1: Supplementary information for Chapter 2

Supplemental Figure 1: Aggregate size distribution from integrated sheep-vineyard (ISV) and conventional understory (CONV) managed surface soils (0–15 cm depth)



Relative distribution of four soil aggregate physical size fractions (>2000um, 250-2000um, 53-250um, and <53um). Shown are mean values for each size category and the mean weight diameter (MWD). For each site, a Tukey-Kramer means (n=16) comparison was used to evaluate significant pairwise difference between each treatment. Treatment and treatment(x)location significance was also calculated across sites (n=64). For MWD, both the Treatment (p=0.953) and treatment(x)location interaction (p=0.979) effects were non-significant. Treatment and treatment(x)location effects were also non-significant for all size fractions.

Supplemental Figure 2: Relative distribution of aggregate-associated C pools in integrated sheep-vineyard (ISV) and conventional understory (CONV) managed surface soils (0–15 cm depth)



The relative distribution (% of total C) across four surface soil (0–15 cm depth) aggregate physical size fractions (>2000um, 250-2000um, 53-250um, and <53um). For each site, a Tukey-Kramer means (n=16) comparison was used to evaluate significant difference between each treatment. Treatment and treatment(x)location significance was also calculated across sites (n=64). Treatment and treatment(x)location effects were non-significant for all size fractions.

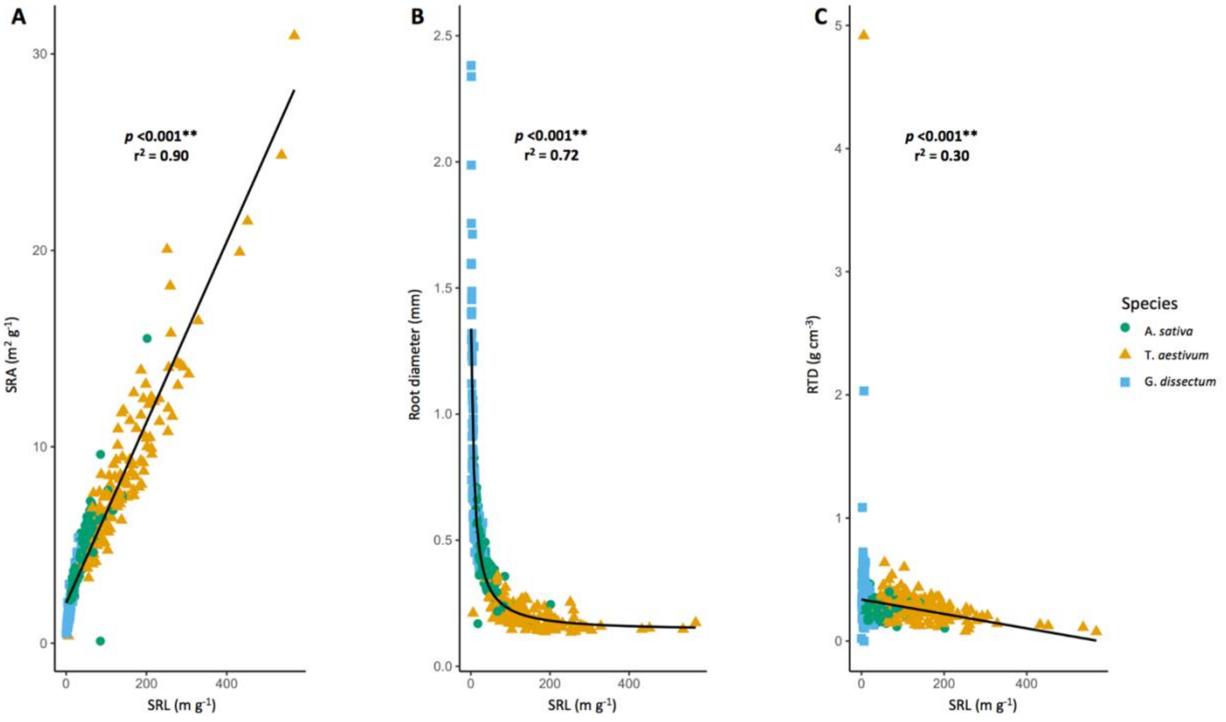
Appendix 2: Supplementary information for Chapter 3

Supplementary Table 1: Model p-value output for the effects of explanatory variables on intra-and inter-seasonal plant community structure and intra-seasonal root morphology

Explanatory variable	Intra-seasonal													
	Root morphological traits				Plant community structure									
	SRL	SRA	RTD	Diameter	species%	total%	A.sat%	T.aes%	G.dis%	bare%	residue%	Richness	H_p	D_p
Treatment	0.991	0.928	0.692	0.501	0.320	**<0.001*****	0.357	0.188	0.343	0.053	0.328	0.743	0.470	0.241
Species	**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****	**0.010***	--	--	--	--	--	--	--	--	--
Month	**<0.001*****	**<0.001*****	0.081	**<0.001*****	0.877	0.060	0. 226	**0.029***	0.135	**<0.001*****	**<0.001*****	**0.001****	**0.009****	0.151
Treatment *x* Species	0.093	**0.011***	0.314	0.576	0.280	--	--	--	--	--	--	--	--	--
Species *x* Month	**<0.001*****	**<0.001*****	**0.039***	**0.007****	911	--	--	--	--	--	--	--	--	--
Treatment *x* Month	0.777	0.502	0.682	0.559	0.485	**<0.001*****	**0.015***	0.319	0.265	**0.008****	0.334	0.999	0.382	0.378
Treatment *x* Species *x* Month	0.642	0.305	0.613	0.818	**0.029***	--	--	--	--	--	--	--	--	--
	Inter-seasonal													
Year	--	--	--	--	**0.003****	**<0.001*****	**0.011***	**0.013***	0.970	**0.003****	**<0.001*****	0.157	**<0.001*****	0.563
Treatment *x* Year	--	--	--	--	0.644	0.295	0.594	0.731	0.168	0.112	0.440	0.687	0.262	0.081
Species *x* Year	--	--	--	--	0.078	--	--	--	--	--	--	--	--	--
Treatment *x* Species *x* Year	--	--	--	--	0.307	--	--	--	--	--	--	--	--	--

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Supplementary Figure 2: Correlation curves between root morphological traits



Supplementary Table 2: Model p-value output for the effects of explanatory variables on intra-seasonal rhizosphere soil properties

Explanatory variable	DOC	MBC	TDN	MBN	DOC/TDN ratio	MBC/N ratio	C_{min}	PMC	Q_{met}	Inorganic N	Inorganic P
Treatment	**<0.001*****	**<0.001*****	**<0.001*****	**0.004****	0.674	0.949	**<0.001*****	0.353	**0.019***	0.873	**0.029***
Species	**0.011***	**0.001****	0.165	**0.004****	0.179	0.893	0.430	0.288	0.170	0.180	**0.001****
Time	**<0.001*****	**0.015***	**0.004****	**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****	**0.026***	0.609	**<0.001*****	**<0.001*****
Treatment *x* Species	0.585	0.214	0.886	0.707	0.693	0.591	0.937	0.507	0.962	0.073	0.412
Species *x* Time	0.945	0.100	0.634	0.821	0.888	0.313	0.805	0.229	0.794	0.681	0.145
Treatment *x* Time	**<0.001*****	0.102	**0.018***	0.735	**0.008**	0.241	**<0.001*****	**0.001****	**<0.001*****	0.085	0.960
Treatment *x* Species *x* Time	0.995	0.121	0.804	0.363	0.702	0.685	0.839	0.516	0.263	0.796	0.958

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001

Supplementary Table 3: Model p-value output for the effects of explanatory variables on intra-seasonal rhizosphere utilization of six biochemical categories

Explanatory variable	Amines	Amino acids	Carbohydrates	Carboxylic acids	Phenolic acids	Polymers
Treatment	0.769	0.226	0.413	0.995	0.847	0.907
Species	0.554	0.414	0.201	0.701	0.544	0.287
Time	**0.001****	0.748	**0.037***	0.258	**<0.001*****	0.850
Treatment *x* Species	0.067	0.377	0.653	0.905	0.274	0.350
Species *x* Time	0.423	0.646	0.519	0.094	0.551	0.674
Treatment *x* Time	0.278	0.934	0.067	**0.012***	0.995	**0.040***
Treatment *x* Species *x* Time	**0.004****	0.870	0.618	0.617	0.162	0.550

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Supplementary Table 4: Model p-value output for the effects of explanatory variables on rhizosphere carbon-source utilization diversity indices for three plant species and two treatments

Explanatory variable	AWCD	Shannon index (diversity)	Simpson index (evenness)	Substrate richness (#C_i>0.25)
Treatment	0.904	0.759	0.786	0.950
Species	**0.034***	**0.029***	**0.031***	**0.024***
Time	**0.003****	**0.002****	**0.018***	**0.001****
Treatment *x* Species	0.416	0.541	0.881	0.486
Species *x* Time	0.615	0.773	0.554	0.640
Treatment *x* Time	0.847	0.524	0.533	0.498
Treatment *x* Species *x* Time	0.979	0.715	0.184	0.700

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Supplementary Table 5: Intra-seasonal rhizosphere carbon-source utilization diversity indices for three plant species and two treatments

Species	Time	Treatment	AWCD	Shannon index (diversity)	Simpson index (evenness)	Substrate richness ($\#C_i>0.25$)
A. *sativa*	T1-	ISV	0.23 ± 0.04	2.79 ± 0.09	0.92 ± 0.01	11.3 ± 1.9
		CONV	0.23 ± 0.14	2.57 ± 0.29	0.86 ± 0.05	7.3 ± 5.3
	T1+	ISV	0.32 ± 0.15	2.88 ± 0.11	0.93 ± 0.01	13.3 ± 4.6
		CONV	0.40 ± 0.11	2.96 ± 0.09	0.94 ± 0.01	17.0 ± 3.6
	T2-	ISV	0.30 ± 0.04	2.90 ± 0.02	0.94 ± 0.00	14.3 ± 0.9
		CONV	0.60 ± 0.02	3.05 ± 0.04	0.95 ± 0.00	21.5 ± 0.5
	T2+	ISV	0.44 ± 0.09	2.90 ± 0.06	0.93 ± 0.01	16.0 ± 2.6
		CONV	0.40 ± 0.08	2.99 ± 0.02	0.94 ± 0.00	17.0 ± 1.0
T. *aestivum*	T1-	ISV	0.30 ± 0.10	2.69 ± 0.10	0.91 ± 0.01	11.0 ± 2.5
		CONV	0.29 ± 0.12	2.86 ± 0.15	0.92 ± 0.01	12.0 ± 5.7
	T1+	ISV	0.41 ± 0.07	2.91 ± 0.01	0.94 ± 0.00	17.33 ± 1.2
		CONV	0.36 ± 0.10	2.86 ± 0.16	0.93 ± 0.02	15.3 ± 4.8
	T2-	ISV	0.54 ± 0.16	2.96 ± 0.19	0.94 ± 0.01	19.33 ± 3.7
		CONV	0.44 ± 0.29	2.86 ± 0.26	0.93 ± 0.03	14.5 ± 7.5
	T2+	ISV	0.49 ± 0.21	2.96 ± 0.16	0.93 ± 0.02	17.0 ± 6.0
		CONV	0.52 ± 0.08	3.09 ± 0.02	0.95 ± 0.00	19.3 ± 1.5
G. *dissectum*	T1-	ISV	0.22 ± 0.06	2.84 ± 0.12	0.93 ± 0.01	11.0 ± 2.5
		CONV	0.15 ± 0.07	2.54 ± 0.11	0.88 ± 0.02	6.3 ± 2.9
	T1+	ISV	0.09 ± 0.02	2.30 ± 0.15	0.83 ± 0.03	3.7 ± 1.2
		CONV	0.21 ± 0.10	2.74 ± 0.17	0.91 ± 0.03	9.7 ± 4.8
	T2-	ISV	0.47 ± 0.07	2.99 ± 0.06	0.94 ± 0.00	18.3 ± 1.9
		CONV	0.33 ± 0.10	2.82 ± 0.08	0.93 ± 0.01	13.0 ± 2.0
	T2+	ISV	0.21 ± 0.07	2.78 ± 0.13	0.92 ± 0.01	10.7 ± 3.3
		CONV	0.26 ± 0.11	2.70 ± 0.34	0.87 ± 0.07	11.7 ± 4.8

Supplementary Table 6: Model p-value output for the effects of explanatory variables on inter-seasonal bulk soil properties

Explanatory variable	SOC	DOC	MBC	TDN	MBN	DOC/TDN ratio	MBC/N ratio
Treatment	0.481	0.616	0.203	0.280	0.497	0.060	0.646
Time	0.290	**0. 003****	**0.035***	**0.007****	**0.002****	0.767	0.098
Treatment *x* Time	**0.010***	0. 591	0.630	0.644	0.690	0.909	0.553

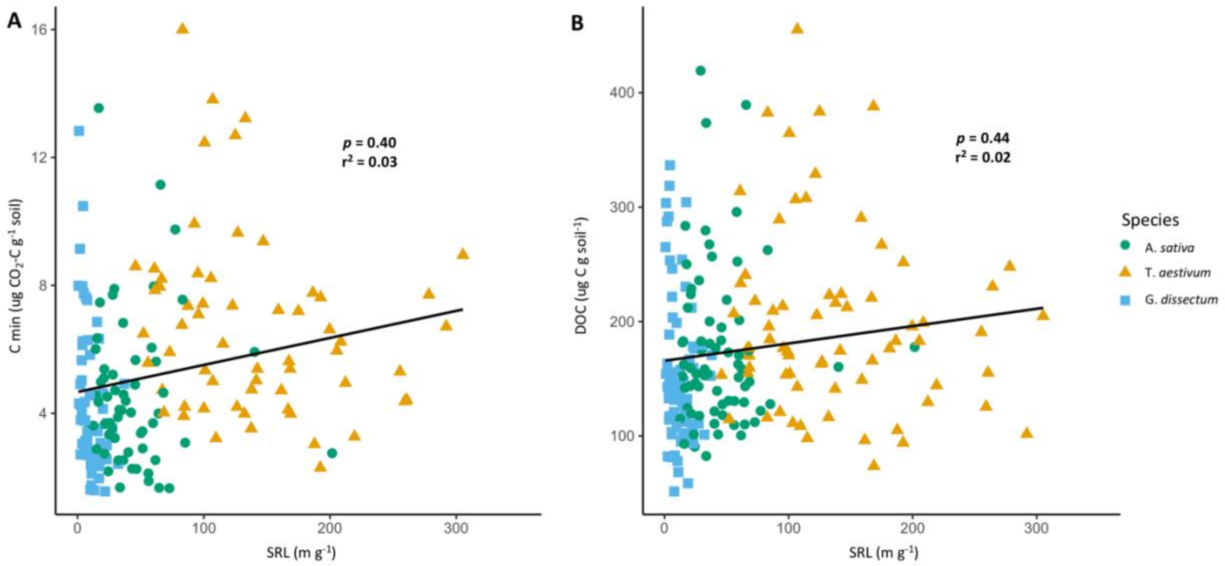
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Supplementary Table 7: Inter-seasonal bulk soil PLFA properties and model p-value output for the effects of explanatory variables

	Baseline (T0)		**T1**		**T2**		**T3**		**T4**		***p*-value**		
	ISV	**CONV**	**ISV**	**CONV**	**ISV**	**CONV**	**ISV**	**CONV**	**ISV**	**CONV**	**Treatment**	**Time**	**Treatment x Time**
Total biomass	2731	2210	6829	5173	3473	2543	1367	1789	1694	1927	0.521	**<0.001*****	0.285
Shannon index	1.39	1.33	1.51	1.50	1.36	1.41	1.22	1.09	1.37	1.37	0.803	**0.059***	0.456
F:B ratio	0.33	0.42	0.35	0.36	0.31	0.40	0.12	0.14	0.23	0.27	0.244	**0.002****	0.834
Bacteria biomass (mol%)	1160 (42.4)	690 (40.7)	2773 (40.7)	2024 (39.1)	1454 (40.6)	1037 (41.6)	506 (35.9)	678 (34.7)	620 (35.0)	424 (22.0)	0.235 **(0.033*)**	**<0.001***** **(<0.001***)**	0.501 (0.678)
Actinomycete biomass (mol%)	123 (4.8)	28 (1.4)	412 (6.1)	298 (5.6)	100 (3.2)	77 (3.2)	110 (8.0)	85 (4.8)	98 (5.7)	82 (4.2)	**0.009**** (0.103)	0.503 (0.072)	**0.035*** (0.253)
Gram-positive biomass (mol%)	573 (21.4)	361 (16.7)	1559 (23.0)	1086 (20.8)	656 (18.7)	447 (17.8)	344 (25.1)	458 (25.7)	359 (21.2)	269 (13.6)	0.156 **(0.032*)**	**0.001**** (0.971)	0.503 (0.683)
Gram-negative biomass (mol%)	587 (21.0)	329 (17.1)	1213 (17.7)	938 (18.2)	798 (21.9)	590 (23.8)	162 (10.8)	220 (8.9)	346 (13.9)	165 (8.4)	0.085 (0.528)	**<0.001***** **(<0.001***)**	0.452 (0.895)
Gram(+):Gram(-) ratio	1.78	1.36	1.31	1.15	0.86	0.75	2.78	3.58	1.80	1.58	0.475	**<0.001*****	0.776
Fungi biomass (mol%)	378 (13.6)	302 (13.6)	960 (14.2)	767 (14.2)	490 (12.8)	415 (16.5)	71 (4.6)	106 (3.2)	176 (8.5)	108 (5.1)	0.326 (0.829)	**<0.001***** **(<0.001***)**	0.789 (0.587)
Arbuscular mycorrhizae biomass (mol%)	103 (3.6)	70 (3.4)	319 (4.7)	237 (4.3)	155 (4.0)	138 (5.5)	24 (1.5)	45 (1.5)	65 (3.6)	67 (3.1)	0.315 (0.856)	**0.008** (0.102)	0.538 (0.938)
Saprophyte biomass (mol%)	274 (10.0)	231 (10.3)	642 (9.4)	434 (7.7)	335 (8.9)	277 (11.0)	47 (3.0)	61 (1.8)	111 (4.9)	41 (2.0)	0.363 (0.834)	**<0.001***** **(<0.001***)**	0.917 (0.461)
Undifferentiated biomass (mol%)	1190 (43.9)	1219 (52.6)	3061 (44.6)	2346 (46.1)	1524 (46.5)	1090 (41.9)	764 (55.9)	1027 (57.4)	898 (56.5)	1385 (72.9)	0.475 (0.177)	**0.021** **(<0.001***)**	0.398 (0.575)

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Supplementary Figure 3: Correlation curves between specific root length (SRL) and rhizosphere carbon flux indicators



*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001

REFERENCES

Abdalla, M., Hastings, A., Chadwick, D.R., Jones, D.L., Evans, C.D., Jones, M.B., Rees, R.M., Smith, P., 2018. Critical review of the impacts of grazing intensity on soil organic carbon storage and other soil quality indicators in extensively managed grasslands. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2017.10.023

Acosta-Martínez, V., Bell, C.W., Morris, B.E.L., Zak, J., Allen, V.G., 2010. Long-term soil microbial community and enzyme activity responses to an integrated cropping-livestock system in a semi-arid region. Agric. Ecosyst. Environ. 137, 231–240. https://doi.org/10.1016/j.agee.2010.02.008

Acosta-Martínez, V., Zobeck, T.M., Allen, V., 2004. Soil Microbial, Chemical and Physical Properties in Continuous Cotton and Integrated Crop-Livestock Systems. Soil Sci. Soc. Am. J. 68, 1875–1884. https://doi.org/10.2136/sssaj2004.1875

Afzal, M., Adams, W.A., 1992. Heterogeneity of Soil Mineral Nitrogen in Pasture Grazed by Cattle. Soil Sci. Soc. Am. J. 56, 1160–1166. https://doi.org/10.2136/sssaj1992.03615995005600040026x

Ahlström, A., Raupach, M.R., Schurgers, G., Smith, B., Arneth, A., Jung, M., Reichstein, M., Canadell, J.G., Friedlingstein, P., Jain, A.K., Kato, E., Poulter, B., Sitch, S., Stocker, B.D., Viovy, N., Wang, Y.P., Wiltshire, A., Zaehle, S., Zeng, N., 2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink. Science (80-.). 348, 895–899. https://doi.org/10.1126/science.aaa1668

Altieri, M.A., Farrell, J.G., Hecht, S.B., Liebman, M., Magdoff, F., Murphy, B., Norgaard, R.B., Sikor, T.O., Altieri, M.A., Farrell, J.G., Hecht, S.B., Liebman, M., Magdoff, F., Murphy, B., Norgaard, R.B., Sikor, T.O., 2019. The Agroecosystem: Determinants, Resources, Processes, and Sustainability, in: Agroecology. https://doi.org/10.1201/9780429495465-3

Altieri, M.A., Nicholls, C.I., Henao, A., Lana, M.A., 2015. Agroecology and the design of climate change-resilient farming systems. Agron. Sustain. Dev. https://doi.org/10.1007/s13593-015-0285-2

Anderson, T.H., Domsch, K.H., 1993. The metabolic quotient for CO2 (qCO2) as a specific activity parameter to assess the effects of environmental conditions, such as ph, on the microbial biomass of forest soils. Soil Biol. Biochem. https://doi.org/10.1016/0038-0717(93)90140-7

Angers, D.A., N'dayegamiye, A., Côté, D., 1993. Tillage-Induced Differences in Organic Matter of Particle-Size Fractions and Microbial Biomass. Soil Sci. Soc. Am. J. 57, 512–516. https://doi.org/10.2136/sssaj1993.03615995005700020035x

Angst, G., Mueller, K.E., Nierop, K.G.J., Simpson, M.J., 2021. Plant- or microbial-derived? A review on the molecular composition of stabilized soil organic matter. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2021.108189

Arnuti, F., Luiz, L.G., Pedro, P.A., Alves, L.A., Cecagno, D., De Assis, J., Da S. Schaidhauer, W., Anghinoni, I., Chabbi, A., Paulo, P.C., 2020. Sheep dung composition and phosphorus and potassium release affected by grazing intensity and pasture development stage in an integrated cr op-livestock system. Agronomy. https://doi.org/10.3390/agronomy10081162

Arsenault, J.-L., Poulcur, S., Messier, C., Guay, R., 2019. WinRHlZO™, a Root-measuring System with a Unique Overlap Correction Method. HortScience. https://doi.org/10.21273/hortsci.30.4.906d

Assmann, J.M., Anghinoni, I., Martins, A.P., Costa, S.E.V.G. de A., Cecagno, D., Carlos, F.S., Carvalho, P.C. de F., 2014. Soil carbon and nitrogen stocks and fractions in a long-term integrated crop-livestock system under no-tillage in southern Brazil. Agric. Ecosyst. Environ. 190, 52–59. https://doi.org/10.1016/j.agee.2013.12.003

Bailey, H.P., 1979. Semi-Arid Climates: Their Definition and Distribution. pp. 73–97. https://doi.org/10.1007/978-3-642-67328-3_3

Bakoglu, A., Bagci, E., Erkovan, H.I., Koc, A., Kocak, A., 2009. Seed stocks of grazed and ungrazed rangelands on Palandoken Mountains of Eastern Anatolia. J. Food, Agric. Environ. 7, 674–678.

Baligar, V.C., Fageria, N.K., 2015. Nutrient Use Efficiency in Plants: An Overview, in: Nutrient Use Efficiency: From Basics to Advance. pp. 1–14. https://doi.org/10.1007/978-81-322-2169-2_2

Bansal, S., Chakraborty, P., Kumar, S., 2022. Crop–livestock integration enhanced soil aggregate-associated carbon and nitrogen, and phospholipid fatty acid. Sci. Rep. 12, 2781. https://doi.org/10.1038/s41598-022-06560-6

Barbour, M.G., Burk, J.H., Gilliam, F.S., Schwartz, M.W., 1987. Terrestrial Plant Ecology, 3rd Edition., Terrestrial Plant Ecology.

Bardgett, R.D., Mommer, L., De Vries, F.T., 2014. Going underground: Root traits as drivers of ecosystem processes. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2014.10.006

Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology. https://doi.org/10.1890/02-0274

Bardgett, R.D., Wardle, D.A., Yeates, G.W., 1998. Linking above-ground and below-ground interactions: How plant responses to foliar herbivory influence soil organisms. Soil Biol. Biochem. https://doi.org/10.1016/S0038-0717(98)00069-8

Basile-Doelsch, I., Balesdent, J., Pellerin, S., 2020. Reviews and syntheses: The mechanisms underlying carbon storage in soil. Biogeosciences. https://doi.org/10.5194/bg-17-5223-2020

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. https://doi.org/10.18637/jss.v067.i01

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future köppen-geiger climate classification maps at 1-km resolution. Sci. Data. https://doi.org/10.1038/sdata.2018.214

Bell, C.W., Fricks, B.E., Rocca, J.D., Steinweg, J.M., McMahon, S.K., Wallenstein, M.D., 2013. High-throughput fluorometric measurement of potential soil extracellular enzyme activities. J. Vis. Exp. https://doi.org/10.3791/50961

Bell, L.W., Kirkegaard, J.A., Swan, A., Hunt, J.R., Huth, N.I., Fettell, N.A., 2011. Impacts of soil damage by grazing livestock on crop productivity. Soil Tillage Res. 113, 19–29. https://doi.org/10.1016/j.still.2011.02.003

Bell, L.W., Moore, A.D., 2012. Integrated crop-livestock systems in Australian agriculture: Trends, drivers and implications. Agric. Syst. https://doi.org/10.1016/j.agsy.2012.04.003

Bell, L.W., Moore, A.D., Kirkegaard, J.A., 2014. Evolution in crop-livestock integration systems that improve farm productivity and environmental performance in Australia. Eur. J. Agron. 57, 10–20. https://doi.org/10.1016/j.eja.2013.04.007

Beniston, J.W., DuPont, S.T., Glover, J.D., Lal, R., Dungait, J.A.J., 2014. Soil organic carbon dynamics 75 years after land-use change in perennial grassland and annual wheat agricultural systems. Biogeochemistry 120, 37–49. https://doi.org/10.1007/s10533-014-9980-3

Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. J. R. Stat. Soc. Ser. B.

https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manage. 133, 13–22. https://doi.org/10.1016/S0378-1127(99)00294-7

Berg, B., Meentemeyer, V., 2002. Litter quality in a north European transect versus carbon storage potential, in: Plant and Soil. pp. 83–92. https://doi.org/10.1023/A:1019637807021

Bessler, H., Temperton, V.M., Roscher, C., Buchmann, N., Schmid, B., Schulze, E.D., Weisser, W.W., Engels, C., 2009. Aboveground overyielding in grassland mixtures is associated with reduced biomass partitioning to belowground organs. Ecology 90, 1520–1530. https://doi.org/10.1890/08-0867.1

Beukes, P.C., Cowling, R.M., 2003. Non-selective grazing impacts on soil-properties of the Nama Karoo. J. Range Manag. 56, 547–552. https://doi.org/10.2307/4003849

Bhatti, A.A., Haq, S., Bhat, R.A., 2017. Actinomycetes benefaction role in soil and plant health. Microb. Pathog. https://doi.org/10.1016/j.micpath.2017.09.036

Birouste, M., Zamora-Ledezma, E., Bossard, C., Pérez-Ramos, I.M., Roumet, C., 2014. Measurement of fine root tissue density: A comparison of three methods reveals the potential of root dry matter content. Plant Soil. https://doi.org/10.1007/s11104-013-1874-y

Blagodatskaya, E., Yuyukina, T., Blagodatsky, S., Kuzyakov, Y., 2011. Turnover of soil organic matter and of microbial biomass under C3-C4 vegetation change: Consideration of 13C fractionation and preferential substrate utilization. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2010.09.028

Blake, G.R., Hartge, K.H., 1986. Bulk density. In Methods of Soil Analysis, Part 1—Physical and Mineralogical Methods. Agron. Monogr. 9, Am. Soc. Agron. Sci. Soc. Am.

Boeni, M., Bayer, C., Dieckow, J., Conceição, P.C., Dick, D.P., Knicker, H., Salton, J.C., Macedo, M.C.M., 2014. Organic matter composition in density fractions of Cerrado Ferralsols as revealed by CPMAS 13C NMR: Influence of pastureland, cropland and integrated crop-livestock. Agric. Ecosyst. Environ. 190, 80–86. https://doi.org/10.1016/j.agee.2013.09.024

Bond-Lamberty, B., Thomson, A., 2010. Temperature-associated increases in the global soil respiration record. Nature 464, 579–582. https://doi.org/10.1038/nature08930

Bongiovanni, M.D., Lobartini, J.C., 2006. Particulate organic matter, carbohydrate, humic acid contents in soil macro- and microaggregates as affected by cultivation. Geoderma 136, 660–665. https://doi.org/10.1016/j.geoderma.2006.05.002

Booker, K., Huntsinger, L., Bartolome, J.W., Sayre, N.F., Stewart, W., 2013. What can ecological science tell us about opportunities for carbon sequestration on arid rangelands in the United States? Glob. Environ. Chang. 23, 240–251. https://doi.org/10.1016/j.gloenvcha.2012.10.001

Bossio, D.A., Scow, K.M., 1998. Impacts of carbon and flooding on soil microbial communities: Phospholipid fatty acid profiles and substrate utilization patterns. Microb. Ecol. https://doi.org/10.1007/s002489900082

Bowles, T.M., Hollander, A.D., Steenwerth, K., Jackson, L.E., 2015. Tightly-coupled plant-soil nitrogen cycling: Comparison of organic farms across an agricultural landscape. PLoS One 10. https://doi.org/10.1371/journal.pone.0131888

Bradford, M.A., Keiser, A.D., Davies, C.A., Mersmann, C.A., Strickland, M.S., 2013. Empirical evidence that soil carbon formation from plant inputs is positively related to microbial growth. Biogeochemistry. https://doi.org/10.1007/s10533-012-9822-0

Brandstaetter, C., Fricko, N., Rahimi, M.J., Fellner, J., Ecker-Lala, W., Druzhinina, I.S., 2022.

The microbial metabolic activity on carbohydrates and polymers impact the biodegradability of landfilled solid waste. Biodegradation. https://doi.org/10.1007/s10532-021-09967-6

Breland, T.A., Eltun, R., 1999. Soil microbial biomass and mineralization of carbon and nitrogen in ecological, integrated and conventional forage and arable cropping systems. Biol. Fertil. Soils 30, 193–201. https://doi.org/10.1007/s003740050608

Brewer, K.M., Gaudin, A.C.M., 2020. Potential of crop-livestock integration to enhance carbon sequestration and agroecosystem functioning in semi-arid croplands. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2020.107936

Briske, D.D., Derner, J.D., Brown, J.R., Fuhlendorf, S.D., Teague, W.R., Havstad, K.M., Gillen, R.L., Ash, A.J., Willms, W.D., 2008. Rotational grazing on rangelands: Reconciliation of perception and experimental evidence. Rangel. Ecol. Manag. 61, 3–17. https://doi.org/10.2111/06-159R.1

Briske, D.D., Noy-Meir, I., 1998. Plant responses to grazing: a comparative evaluation of annual and perennial grasses. Ecol. basis Livest. grazing Mediterr. Ecosyst. 13, 26.

Briske, D.D., Sayre, N.F., Huntsinger, L., Fernandez-Gimenez, M., Budd, B., Derner, J.D., 2011. Origin, persistence, and resolution of the rotational grazing debate: Integrating human dimensions into rangeland research. Rangel. Ecol. Manag. https://doi.org/10.2111/REM-D-10-00084.1

Bristow, A.W., Whitehead, D.C., Cockburn, J.E., 1992. Nitrogenous constituents in the urine of cattle, sheep and goats. J. Sci. Food Agric. https://doi.org/10.1002/jsfa.2740590316

Brodowski, S., John, B., Flessa, H., Amelung, W., 2006. Aggregate-occluded black carbon in soil. Eur. J. Soil Sci. 57, 539–546. https://doi.org/10.1111/j.1365-2389.2006.00807.x

Cai, A., Xu, H., Shao, X., Zhu, P., Zhang, W., Xu, M., Murphy, D. V., 2016. Carbon and nitrogen mineralization in relation to soil particle-size fractions after 32 years of chemical and manure application in a continuous maize cropping system. PLoS One. https://doi.org/10.1371/journal.pone.0152521

Cambardella, C.A., Elliott, E.T., 1993. Carbon and Nitrogen Distribution in Aggregates from Cultivated and Native Grassland Soils. Soil Sci. Soc. Am. J. https://doi.org/10.2136/sssaj1993.03615995005700040032x

Canarini, A., Kaiser, C., Merchant, A., Richter, A., Wanek, W., 2019. Root exudation of primary metabolites: Mechanisms and their roles in plant responses to environmental stimuli. Front. Plant Sci. https://doi.org/10.3389/fpls.2019.00157

Cao, J., Wang, X., Sun, X., Zhang, L., Tian, Y., 2013. Effects of grazing intensity on soil labile organic carbon fractions in a desert steppe area in Inner Mongolia. Springerplus 2. https://doi.org/10.1186/2193-1801-2-S1-S1

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Carvalho, J.L.N., Raucci, G.S., Cerri, C.E.P., Bernoux, M., Feigl, B.J., Wruck, F.J., Cerri, C.C., 2010. Impact of pasture, agriculture and crop-livestock systems on soil C stocks in Brazil. Soil Tillage Res. 110, 175–186. https://doi.org/10.1016/j.still.2010.07.011

Chassot, A., Stamp, P., Richner, W., 2001. Root distribution and morphology of maize seedlings as affected by tillage and fertilizer placement. Plant Soil. https://doi.org/10.1023/A:1010335229111

Chen, B.J.W., Xu, C., Liu, M.S., Huang, Z.Y.X., Zhang, M.J., Tang, J., Anten, N.P.R., 2020. Neighbourhood-dependent root distributions and the consequences on root separation in arid ecosystems. J. Ecol. https://doi.org/10.1111/1365-2745.13360

Chen, T., Nan, Z., Kardol, P., Duan, T., Song, H., Wang, J., Li, C., Hou, F., 2018. Effects of interspecific competition on plant-soil feedbacks generated by long-term grazing. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2018.08.029

Chen, W., Huang, D., Liu, N., Zhang, Y., Badgery, W.B., Wang, X., Shen, Y., 2015. Improved grazing management may increase soil carbon sequestration in temperate steppe. Sci. Rep. 5. https://doi.org/10.1038/srep10892

Chen, X., Zhang, D., Liang, G., Qiu, Q., Liu, J., Zhou, G., Liu, S., Chu, G., Yan, J., 2015. Effects of precipitation on soil organic carbon fractions in three subtropical forests in southern China. J. Plant Ecol. 9, 10–19. https://doi.org/10.1093/jpe/rtv027

Cheng, W., Kuzyakov, Y., 2015. Root Effects on Soil Organic Matter Decomposition. pp. 119–143. https://doi.org/10.2134/agronmonogr48.c7

Chotte, J.-L., 2005. Importance of Microorganisms for Soil Aggregation, in: Microorganisms in Soils: Roles in Genesis and Functions. pp. 107–119. https://doi.org/10.1007/3-540-26609-7_5

Cleveland, C.C., Liptzin, D., 2007. C:N:P stoichiometry in soil: Is there a “Redfield ratio” for the microbial biomass? Biogeochemistry 85, 235–252. https://doi.org/10.1007/s10533-007-9132-0

Conant, R.T., Cerri, C.E.P., Osborne, B.B., Paustian, K., 2017. Grassland management impacts on soil carbon stocks: A new synthesis: A. Ecol. Appl. 27, 662–668. https://doi.org/10.1002/eap.1473

Conant, R.T., Ryan, M.G., Ågren, G.I., Birge, H.E., Davidson, E.A., Eliasson, P.E., Evans, S.E., Frey, S.D., Giardina, C.P., Hopkins, F.M., Hyvönen, R., Kirschbaum, M.U.F., Lavallee, J.M., Leifeld, J., Parton, W.J., Megan Steinweg, J., Wallenstein, M.D., Martin Wetterstedt, J.Å., Bradford, M.A., 2011. Temperature and soil organic matter decomposition rates - synthesis of current knowledge and a way forward. Glob. Chang. Biol. https://doi.org/10.1111/j.1365-2486.2011.02496.x

Conant, R.T., Six, J., Paustian, K., 2003. Land use effects on soil carbon fractions in the southeastern United States. I. Management-intensive versus extensive grazing. Biol. Fertil. Soils 38, 386–392. https://doi.org/10.1007/s00374-003-0652-z

Cong, W.F., van Ruijven, J., Mommer, L., De Deyn, G.B., Berendse, F., Hoffland, E., 2014. Plant species richness promotes soil carbon and nitrogen stocks in grasslands without legumes. J. Ecol. 102, 1163–1170. https://doi.org/10.1111/1365-2745.12280

Costa, S.E.V.G.A., Souza, E.D., Anghinoni, I., Carvalho, P.C.F., Martins, A.P., Kunrath, T.R., Cecagno, D., Balerini, F., 2014. Impact of an integrated no-till crop-livestock system on phosphorus distribution, availability and stock. Agric. Ecosyst. Environ. 190, 43–51. https://doi.org/10.1016/j.agee.2013.12.001

Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H., Parton, W.J., 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. Nat. Geosci. 8, 776–779. https://doi.org/10.1038/ngeo2520

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? Glob. Chang. Biol. https://doi.org/10.1111/gcb.12113

Cox, G., 1990. Labratory manual of general ecology, 6th Ed. ed. Dubuque, Iowa: William C. Brown.

Cui, X., Wang, Y., Niu, H., Wu, J., Wang, S., Schnug, E., Rogasik, J., Fleckenstein, J., Tang, Y., 2005. Effect of long-term grazing on soil organic carbon content in semiarid steppes in Inner Mongolia. Ecol. Res. 20, 519–527. https://doi.org/10.1007/s11284-005-0063-8

Curry, J.P., Doherty, P., Purvis, G., Schmidt, O., 2008. Relationships between earthworm populations and management intensity in cattle-grazed pastures in Ireland. Appl. Soil Ecol. 39, 58–64. https://doi.org/10.1016/j.apsoil.2007.11.005

Cuykendall, C.H., Marten, G.C., 1968. Defoliation by Sheep-Grazing Versus Mower-Clipping for Evaluation of Pasture 1 . Agron. J. https://doi.org/10.2134/agronj1968.00021962006000040022x

da Silva, A.S., Colozzi Filho, A., Nakatani, A.S., Alves, S.J., de Andrade, D.S., Guimarães, M. de F., 2015. Atributos microbiológicos do solo em sistema de integração. Rev. Bras. Cienc. do Solo 39, 40–48. https://doi.org/10.1590/01000683rbcs20150185

Da Silva, F.D., Amado, T.J.C., Ferreira, A.O., Assmann, J.M., Anghinoni, I., Carvalho, P.C. de F., 2014. Soil carbon indices as affected by 10 years of integrated crop-livestock production with different pasture grazing intensities in Southern Brazil. Agric. Ecosyst. Environ. 190, 60–69. https://doi.org/10.1016/j.agee.2013.12.005

Davinic, M., Moore-Kucera, J., Acosta-Martínez, V., Zak, J., Allen, V., 2013. Soil fungal distribution and functionality as affected by grazing and vegetation components of integrated crop-livestock agroecosystems. Appl. Soil Ecol. 66, 61–70. https://doi.org/10.1016/j.apsoil.2013.01.013

Dawson, L.A., Grayston, S.J., Paterson, E., 2009. Effects of grazing on the roots and rhizosphere of grasses., in: Grassland Ecophysiology and Grazing Ecology. https://doi.org/10.1079/9780851994529.0061

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11, 516–531. https://doi.org/10.1111/j.1461-0248.2008.01164.x

de Faccio Carvalho, P.C., Anghinoni, I., de Moraes, A., de Souza, E.D., Sulc, R.M., Lang, C.R., Flores, J.P.C., Terra Lopes, M.L., da Silva, J.L.S., Conte, O., de Lima Wesp, C., Levien, R., Fontaneli, R.S., Bayer, C., 2010. Managing grazing animals to achieve nutrient cycling and soil improvement in no-till integrated systems. Nutr. Cycl. Agroecosystems 88, 259–273. https://doi.org/10.1007/s10705-010-9360-x

De Souza, E.D., De Andrade Costa, S.E.V.G., De Lima, C.V.S., Anghinoni, I., Meurer, E.J., De Faceio Carvalho, P.C., 2008. Carbono orgânico e fósforo microbiano em sistema de integração agricultura-pecuária submetido a diferentes intensidades de pastejo em plantio direto. Rev. Bras. Cienc. do Solo 32, 1273–1282. https://doi.org/10.1590/s0100-06832008000300035

de Vries, F.T., Caruso, T., 2016. Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2016.06.023

De Vries, F.T., Shade, A., 2013. Controls on soil microbial community stability under climate change. Front. Microbiol. https://doi.org/10.3389/fmicb.2013.00265

de Vries, F.T., Wallenstein, M.D., 2017. Below-ground connections underlying above-ground food production: a framework for optimising ecological connections in the rhizosphere. J. Ecol. https://doi.org/10.1111/1365-2745.12783

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M.A., Wallenstein, M.D., Quero, J.L., Ochoa, V., Gozalo, B., García-Gómez, M., Soliveres, S., García-Palacios, P., Berdugo, M., Valencia, E., Escolar, C., Arredondo, T., Barraza-Zepeda, C., Bran, D., Carreira, J.A., Chaieb, M., Conceicao, A.A., Derak, M., Eldridge, D.J., Escudero, A., Espinosa, C.I., Gaitán, J., Gatica, M.G., Gómez-González, S., Guzman, E., Gutiérrez, J.R., Florentino, A., Hepper, E., Hernández, R.M., Huber-Sannwald, E., Jankju, M., Liu, J., Mau, R.L., Miriti, M., Monerris, J., Naseri, K., Noumi, Z., Polo, V., Prina, A., Pucheta, E., Ramírez, E., Ramírez-Collantes, D.A., Romao, R., Tighe, M., Torres, D., Torres-Díaz, C., D. Ungar, E., Val, J., Wamiti, W., Wang, D., Zaady, E., 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature 502, 672–676. https://doi.org/10.1038/nature12670

Deng, S.P., Tabatabai, M.A., 1997. Effect of tillage and residue management on enzyme activities in soils: III. Phosphatases and arylsulfatase. Biol. Fertil. Soils 24, 141–146. https://doi.org/10.1007/s003740050222

Derner, J.D., Boutton, T.W., Briske, D.D., 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant Soil 280, 77–90. https://doi.org/10.1007/s11104-005-2554-3

Devêvre, O.C., Horwáth, W.R., 2000. Decomposition of rice straw and microbial carbon use efficiency under different soil temperatures and moistures. Soil Biol. Biochem. 32, 1773–1785. https://doi.org/10.1016/S0038-0717(00)00096-1

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., Campbell, B.D., 2007. Plant trait responses to grazing - A global synthesis. Glob. Chang. Biol. 13, 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Dijkstra, F.A., Hobbie, S.E., Reich, P.B., 2006. Soil Processes Affected by Sixteen Grassland Species Grown under Different Environmental Conditions. Soil Sci. Soc. Am. J. 70, 770–777. https://doi.org/10.2136/sssaj2005.0088

Dilly, O., Munch, J.C., 1998. Ratios between estimates of microbial biomass content and microbial activity in soils. Biol. Fertil. Soils. https://doi.org/10.1007/s003740050446

Dlamini, P., Chivenge, P., Chaplot, V., 2016. Overgrazing decreases soil organic carbon stocks the most under dry climates and low soil pH: A meta-analysis shows. Agric. Ecosyst. Environ. 221, 258–269. https://doi.org/10.1016/j.agee.2016.01.026

Dotaniya, M.L., Meena, V.D., 2015. Rhizosphere Effect on Nutrient Availability in Soil and Its Uptake by Plants: A Review. Proc. Natl. Acad. Sci. India Sect. B - Biol. Sci. https://doi.org/10.1007/s40011-013-0297-0

Drewry, J.J., Paton, R.J., Monaghan, R.M., 2004. Soil compaction and recovery cycle on a Southland dairy farm: Implications for soil monitoring. Aust. J. Soil Res. 42, 851–856. https://doi.org/10.1071/SR03169

Drinkwater, L.E., Snapp, S.S., 2007. Nutrients in Agroecosystems: Rethinking the Management Paradigm. Adv. Agron. https://doi.org/10.1016/S0065-2113(04)92003-2

Drinkwater, L.E., Wagoner, P., Sarrantonio, M., 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. Nature 396, 262–265. https://doi.org/10.1038/24376

Dubeux, J.C.B., Sollenberger, L.E., Comerford, N.B., Scholberg, J.M., Ruggieri, A.C., Vendramini, J.M.B., Interrante, S.M., Portier, K.M., 2006. Management intensity affects density fractions of soil organic matter from grazed bahiagrass swards. Soil Biol. Biochem. 38, 2705–2711. https://doi.org/10.1016/j.soilbio.2006.04.021

Dumont, B., Rook, A.J., Coran, C., Röver, K.U., 2007. Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 2. Diet selection. Grass Forage Sci. 62, 159–171. https://doi.org/10.1111/j.1365-2494.2007.00572.x

Dungait, J.A.J., Hopkins, D.W., Gregory, A.S., Whitmore, A.P., 2012. Soil organic matter turnover is governed by accessibility not recalcitrance. Glob. Chang. Biol. https://doi.org/10.1111/j.1365-2486.2012.02665.x

DuPont, S.T., Beniston, J., Glover, J.D., Hodson, A., Culman, S.W., Lal, R., Ferris, H., 2014. Root traits and soil properties in harvested perennial grassland, annual wheat, and never-tilled annual wheat. Plant Soil 381, 405–420. https://doi.org/10.1007/s11104-014-2145-2

Dutta, G., Das, P., Mandal, N.K., 2009. Optimum covariate designs in split-plot and strip-plot design set-ups. J. Appl. Stat. https://doi.org/10.1080/02664760802520777

Dynarski, K.A., Bossio, D.A., Scow, K.M., 2020. Dynamic Stability of Soil Carbon: Reassessing the “Permanence” of Soil Carbon Sequestration. Front. Environ. Sci. https://doi.org/10.3389/fenvs.2020.514701

Earl, J., Jones, C., 1996. The Need for a New Approach to Grazing Management - Is Cell Grazing the Answer? Rangel. J. 18, 327. https://doi.org/10.1071/rj9960327

Eldridge, D.J., Delgado-Baquerizo, M., Travers, S.K., Val, J., Oliver, I., 2017. Do grazing intensity and herbivore type affect soil health? Insights from a semi-arid productivity gradient. J. Appl. Ecol. 54, 976–985. https://doi.org/10.1111/1365-2664.12834

Elser, J.J., Urabe, J., 1999. The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. Ecology 80, 735–751. https://doi.org/10.1890/0012-9658(1999)080[0735:TSOCDN]2.0.CO;2

Entz, M.H., Bellotti, W.D., Powell, J.M., Angadi, S. V., Chen, W., Ominski, K.H., Boelt, B.,

2005. Evolution of integrated crop-livestock production systems. Grassl. A Glob. Resour. 137–148. https://doi.org/10.3920/978-90-8686-551-2

Erktan, A., Or, D., Scheu, S., 2020. The physical structure of soil: Determinant and consequence of trophic interactions. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2020.107876

Ernst, O., Siri-Prieto, G., 2009. Impact of perennial pasture and tillage systems on carbon input and soil quality indicators. Soil Tillage Res. 105, 260–268. https://doi.org/10.1016/j.still.2009.08.001

Faissal, A., Ouazzani, N., Parrado, J.R., Dary, M., Manyani, H., Morgado, B.R., Barragán, M.D., Mandi, L., 2017. Impact of fertilization by natural manure on the microbial quality of soil: Molecular approach. Saudi J. Biol. Sci. https://doi.org/10.1016/j.sjbs.2017.01.005

Fanin, N., Kardol, P., Farrell, M., Nilsson, M.C., Gundale, M.J., Wardle, D.A., 2019. The ratio of Gram-positive to Gram-negative bacterial PLFA markers as an indicator of carbon availability in organic soils. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2018.10.010

Farrar, J., Hawes, M., Jones, D., Lindow, S., 2003. How roots control the flux of carbon to the rhizosphere. Ecology. https://doi.org/10.1890/0012-9658(2003)084[0827:HRCTFO]2.0.CO;2

Fernández, P.L., Alvarez, C.R., Taboada, M.A., 2011. Assessment of topsoil properties in integrated crop-livestock and continuous cropping systems under zero tillage. Soil Res. 49, 143–151. https://doi.org/10.1071/SR10086

Flavel, T.C., Murphy, D. V., 2006. Carbon and Nitrogen Mineralization Rates after Application of Organic Amendments to Soil. J. Environ. Qual. 35, 183–193. https://doi.org/10.2134/jeq2005.0022

Fornara, D.A., Tilman, D., 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. J. Ecol. 96, 314–322. https://doi.org/10.1111/j.1365-2745.2007.01345.x

Fox, J., Weisberg, S., 2019. An {R} Companion to Applied Regression, Third Edition. Thousand Oaks CA Sage.

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. J. Range Manag. 48, 470–474. https://doi.org/10.2307/4002255

Franzluebbers, A.J., Hons, F.M., Zuberer, D.A., 1995. Tillage and Crop Effects on Seasonal Soil Carbon and Nitrogen Dynamics. Soil Sci. Soc. Am. J. 59, 1618–1624. https://doi.org/10.2136/sssaj1995.03615995005900060016x

Franzluebbers, A.J., Sawchik, J., Taboada, M.A., 2014. Agronomic and environmental impacts of pasture-crop rotations in temperate North and South America. Agric. Ecosyst. Environ. 190, 18–26. https://doi.org/10.1016/j.agee.2013.09.017

Franzluebbers, A.J., Stuedemann, J.A., 2008. Early Response of Soil Organic Fractions to Tillage and Integrated Crop-Livestock Production. Soil Sci. Soc. Am. J. 72, 613–625. https://doi.org/10.2136/sssaj2007.0121

Frey, S.D., Elliott, E.T., Paustian, K., 1999. Bacterial and fungal abundance and biomass in conventional and no-tillage agroecosystems along two climatic gradients. Soil Biol. Biochem. 31, 573–585. https://doi.org/10.1016/S0038-0717(98)00161-8

Fultz, L.M., Moore-Kucera, J., Zobeck, T.M., Acosta-Martínez, V., Allen, V.G., 2013a. Aggregate Carbon Pools after 13 Years of Integrated Crop-Livestock Management in Semiarid Soils. Soil Sci. Soc. Am. J. 77, 1659–1666. https://doi.org/10.2136/sssaj2012.0423

Fultz, L.M., Moore-Kucera, J., Zobeck, T.M., Acosta-Martínez, V., Wester, D.B., Allen, V.G., 2013b. Organic carbon dynamics and soil stability in five semiarid agroecosystems. Agric. Ecosyst. Environ. 181, 231–240. https://doi.org/10.1016/j.agee.2013.10.004

Gaiotti, F., Marcuzzo, P., Belfiore, N., Lovat, L., Fornasier, F., Tomasi, D., 2017. Influence of compost addition on soil properties, root growth and vine performances of Vitis vinifera cv Cabernet sauvignon. Sci. Hortic. (Amsterdam). https://doi.org/10.1016/j.scienta.2017.06.052

Gamble, A. V., Howe, J.A., Wood, C.W., Watts, D.B., van Santen, E., 2014. Soil Organic Carbon Dynamics in a Sod-Based Rotation on Coastal Plain Soils. Soil Sci. Soc. Am. J. 78, 1997–2008. https://doi.org/10.2136/sssaj2014.05.0217

Gao, Y.Z., Giese, M., Lin, S., Sattelmacher, B., Zhao, Y., Brueck, H., 2008. Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. Plant Soil 307, 41–50. https://doi.org/10.1007/s11104-008-9579-3

Garcia-Franco, N., Hobley, E., Hübner, R., Wiesmeier, M., 2018. Climate-Smart Soil Management in Semiarid Regions, in: Soil Management and Climate Change: Effects on Organic Carbon, Nitrogen Dynamics, and Greenhouse Gas Emissions. pp. 349–368. https://doi.org/10.1016/B978-0-12-812128-3.00023-9

Garland, G., Banerjee, S., Edlinger, A., Miranda Oliveira, E., Herzog, C., Wittwer, R., Philippot, L., Maestre, F.T., van der Heijden, M.G.A., 2020. A closer look at the functions behind ecosystem multifunctionality: A review. J. Ecol. https://doi.org/10.1111/1365-2745.13511

Garlick, K., Drew, R.E., Rajaniemi, T.K., 2021. Root responses to neighbors depend on neighbor identity and resource distribution. Plant Soil. https://doi.org/10.1007/s11104-021-05083-9

Garrett, R.D., Niles, M.T., Gil, J.D.B., Gaudin, A., Chaplin-Kramer, R., Assmann, A., Assmann, T.S., Brewer, K., de Faccio Carvalho, P.C., Cortner, O., Dynes, R., Garbach, K., Kebreab, E., Mueller, N., Peterson, C., Reis, J.C., Snow, V., Valentim, J., 2017. Social and ecological analysis of commercial integrated crop livestock systems: Current knowledge and remaining uncertainty. Agric. Syst. https://doi.org/10.1016/j.agsy.2017.05.003

Garrett, R.D., Ryschawy, J., Bell, L.W., Cortner, O., Ferreira, J., Garik, A.V.N., Gil, J.D.B., Klerkx, L., Moraine, M., Peterson, C.A., Dos Reis, J.C., Valentim, J.F., 2020. Drivers of decoupling and recoupling of crop and livestock systems at farm and territorial scales. Ecol. Soc. https://doi.org/10.5751/ES-11412-250124

Gavrichkova, O., Moscatelli, M.C., Grego, S., Valentini, R., 2008. Soil carbon mineralization in a Mediterranean pasture: Effect of grazing and mowing management practices. Agrochimica.

Geyer, K., Schnecker, J., Grandy, A.S., Richter, A., Frey, S., 2020. Assessing microbial residues in soil as a potential carbon sink and moderator of carbon use efficiency. Biogeochemistry. https://doi.org/10.1007/s10533-020-00720-4

Giardina, C.P., Litton, C.M., Crow, S.E., Asner, G.P., 2014. Warming-related increases in soil CO2 efflux are explained by increased below-ground carbon flux. Nat. Clim. Chang. 4, 822–827. https://doi.org/10.1038/nclimate2322

Glover, J.D., Culman, S.W., DuPont, S.T., Broussard, W., Young, L., Mangan, M.E., Mai, J.G., Crews, T.E., DeHaan, L.R., Buckley, D.H., Ferris, H., Turner, R.E., Reynolds, H.L., Wyse, D.L., 2010. Harvested perennial grasslands provide ecological benchmarks for agricultural sustainability. Agric. Ecosyst. Environ. 137, 3–12. https://doi.org/10.1016/j.agee.2009.11.001

Goss-Souza, D., Mendes, L.W., Rodrigues, J.L.M., Tsai, S.M., 2020. Ecological Processes

Shaping Bulk Soil and Rhizosphere Microbiome Assembly in a Long-Term Amazon Forest-to-Agriculture Conversion. Microb. Ecol. https://doi.org/10.1007/s00248-019-01401-y

Grayston, S.J., Griffith, G.S., Mawdsley, J.L., Campbell, C.D., Bardgett, R.D., 2001. Accounting for variability in soil microbial communities of temperate upland grassland ecosystems. Soil Biol. Biochem. https://doi.org/10.1016/S0038-0717(00)00194-2

Grayston, S.J., Vaughan, D., Jones, D., 1997. Rhizosphere carbon flow in trees, in comparison with annual plants: The importance of root exudation and its impact on microbial activity and nutrient availability. Appl. Soil Ecol. https://doi.org/10.1016/S0929-1393(96)00126-6

Grayston, S.J., Wang, S., Campbell, C.D., Edwards, A.C., 1998. Selective influence of plant species on microbial diversity in the rhizosphere. Soil Biol. Biochem. https://doi.org/10.1016/S0038-0717(97)00124-7

Greenwood, K.L., McKenzie, B.M., 2001. Grazing effects on soil physical properties and the consequences for pastures: A review. Aust. J. Exp. Agric. https://doi.org/10.1071/EA00102

Griesser, M., Steiner, M., Pingel, M., Uzman, D., Preda, C., Giffard, B., Tolle, P., Memedemin, D., Forneck, A., Reineke, A., Leyer, I., Bacher, S., 2022. General trends of different inter-row vegetation management affecting vine vigor and grape quality across European vineyards. Agric. Ecosyst. Environ. 338, 108073. https://doi.org/https://doi.org/10.1016/j.agee.2022.108073

Gross, C.D., Harrison, R.B., 2019. The case for digging deeper: Soil organic carbon storage, dynamics, and controls in our changing world. Soil Syst. https://doi.org/10.3390/soilsystems3020028

Grossman, J.D., Rice, K.J., 2012. Evolution of root plasticity responses to variation in soil nutrient distribution and concentration. Evol. Appl. https://doi.org/10.1111/j.1752-4571.2012.00263.x

Guan, X., Huang, J., Guo, N., Bi, J., Wang, G., 2009. Variability of soil moisture and its relationship with surface albedo and soil thermal parameters over the Loess Plateau. Adv. Atmos. Sci. 26, 692–700. https://doi.org/10.1007/s00376-009-8198-0

Guo, J., McCulley, R.L., Phillips, T.D., McNear, D.H., 2016. Fungal endophyte and tall fescue cultivar interact to differentially affect bulk and rhizosphere soil processes governing C and N cycling. Soil Biol. Biochem. 101, 165–174. https://doi.org/https://doi.org/10.1016/j.soilbio.2016.07.014

Gutman, M., Noy-Meir, I., Pluda, D., Seligman, N., Rothman, S., Sternberg, M., 2002. Biomass partitioning following defoliation of annual and perennial mediterranean grasses. Ecol. Soc. 5. https://doi.org/10.5751/es-00308-050201

Haddix, M.L., Paul, E.A., Cotrufo, M.F., 2016. Dual, differential isotope labeling shows the preferential movement of labile plant constituents into mineral-bonded soil organic matter. Glob. Chang. Biol. https://doi.org/10.1111/gcb.13237

Hamel, C., Hanson, K., Selles, F., Cruz, A.F., Lemke, R., McConkey, B., Zentner, R., 2006. Seasonal and long-term resource-related variations in soil microbial communities in wheat-based rotations of the Canadian prairie. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2006.01.011

Hamilton, E.W., Frank, D.A., 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82, 2397–2402. https://doi.org/10.1890/0012-9658(2001)082[2397:CPSSMA]2.0.CO;2

Hamilton, E.W., Frank, D.A., Hinchey, P.M., Murray, T.R., 2008. Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. Soil Biol. Biochem. 40, 2865–2873. https://doi.org/10.1016/j.soilbio.2008.08.007

Hamza, M.A., Anderson, W.K., 2005. Soil compaction in cropping systems: A review of the nature, causes and possible solutions. Soil Tillage Res. https://doi.org/10.1016/j.still.2004.08.009

Haney, R.L., Brinton, W.H., Evans, E., 2008. Estimating soil carbon, nitrogen, and phosphorus mineralization from short-term carbon dioxide respiration. Commun. Soil Sci. Plant Anal. https://doi.org/10.1080/00103620802358862

Hanke, W., Böhner, J., Dreber, N., Jürgens, N., Schmiedel, U., Wesuls, D., Dengler, J., 2014. The impact of livestock grazing on plant diversity: An analysis across dryland ecosystems and scales in southern Africa. Ecol. Appl. 24, 1188–1203. https://doi.org/10.1890/13-0377.1

Hart, R.H., 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. Plant Ecol. 155, 111–118. https://doi.org/10.1023/A:1013273400543

Hassink, J., 1994. Effects of soil texture and grassland management on soil organic C and N and rates of C and N mineralization. Soil Biol. Biochem. 26, 1221–1231. https://doi.org/10.1016/0038-0717(94)90147-3

Heinemeyer, A., McNamara, N.P., 2011. Comparing the closed static versus the closed dynamic chamber flux methodology: Implications for soil respiration studies. Plant Soil. https://doi.org/10.1007/s11104-011-0804-0

Henry, F., Vestergård, M., Christensen, S., 2008. Evidence for a transient increase of rhizodeposition within one and a half day after a severe defoliation of Plantago arenaria grown in soil. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2007.12.015

Herrero, M., Thornton, P.K., Notenbaert, A.M., Wood, S., Msangi, S., Freeman, H.A., Bossio, D., Dixon, J., Peters, M., Van De Steeg, J., Lynam, J., Rao, P., MacMillan, S., Gerard, B., McDermott, J., Seré, C., Rosegrant, M., 2010. Smart investments in sustainable food production: Revisiting mixed crop-livestock systems. Science (80-.). https://doi.org/10.1126/science.1183725

Hessen, D.O., Ågren, G.I., Anderson, T.R., Elser, J.J., De Ruiter, P.C., 2004. Carbon sequestration in ecosystems: The role of stoichiometry. Ecology 85, 1179–1192. https://doi.org/10.1890/02-0251

Hicks Pries, C.E., Castanha, C., Porras, R.C., Torn, M.S., 2017. The whole-soil carbon flux in response to warming. Science (80-.). https://doi.org/10.1126/science.aal1319

Ho, A., Di Lonardo, D.P., Bodelier, P.L.E., 2017. Revisiting life strategy concepts in environmental microbial ecology. FEMS Microbiol. Ecol. https://doi.org/10.1093/femsec/fix006

Holechek, J.L., Pieper, R.D., Herbel, C.H., 1995. Range management: principles and practices. Prentice-Hall, Englewood Cliffs, New Jersey.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol. Monogr. 75, 3–35. https://doi.org/10.1890/04-0922

Horwath, W., 2007. 12 - Carbon cycling and formation of soil organic matter, in: PAUL Ecology and Biochemistry (Third Edition), E.A.B.T.-S.M. (Ed.), . Academic Press, San Diego, pp. 303–339. https://doi.org/https://doi.org/10.1016/B978-0-08-047514-1.50016-0

Horwath, W.R., Paul, E.A., 1996. Microbial Biomass, in: Methods of Soil Analysis. Part 2 -

Microbiological and Biochemical Properties. pp. 753–773.

Horwath, W.R., Paul, E.A., 1994. Microbial Biomass. https://doi.org/10.2136/sssabookser5.2.c36

Hossain, M.B., Rahman, M.M., Biswas, J.C., Miah, M.M.U., Akhter, S., Maniruzzaman, M., Choudhury, A.K., Ahmed, F., Shiragi, M.H.K., Kalra, N., 2017. Carbon mineralization and carbon dioxide emission from organic matter added soil under different temperature regimes. Int. J. Recycl. Org. Waste Agric. https://doi.org/10.1007/s40093-017-0179-1

Hoyle, F.C., D'Antuono, M., Overheu, T., Murphy, D. V., 2013. Capacity for increasing soil organic carbon stocks in dryland agricultural systems. Soil Res. 51, 657–667. https://doi.org/10.1071/SR12373

Hoyle, F.C., O'Leary, R.A., Murphy, D. V., 2016. Spatially governed climate factors dominate management in determining the quantity and distribution of soil organic carbon in dryland agricultural systems. Sci. Rep. 6. https://doi.org/10.1038/srep31468

Huang, J., Ji, M., Xie, Y., Wang, S., He, Y., Ran, J., 2016. Global semi-arid climate change over last 60 years. Clim. Dyn. 46, 1131–1150. https://doi.org/10.1007/s00382-015-2636-8

Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., Rose, S.L., Reid, C.P.P., Morley, C.R., 1987. The detrital food web in a shortgrass prairie. Biol. Fertil. Soils. https://doi.org/10.1007/BF00260580

Hurlbert, S.H., Lombardi, C.M., 2009. Final collapse of the Neyman-Pearson decision theoretic framework and rise of the neoFisherian. Ann. Zool. Fennici. https://doi.org/10.5735/086.046.0501

Iyyemperumal, K., Shi, W., 2008. Soil enzyme activities in two forage systems following application of different rates of swine lagoon effluent or ammonium nitrate. Appl. Soil Ecol.

https://doi.org/10.1016/j.apsoil.2007.10.001

Jackson, R.B., Lajtha, K., Crow, S.E., Hugelius, G., Kramer, M.G., Piñeiro, G., 2017. The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls. Annu. Rev. Ecol. Evol. Syst. https://doi.org/10.1146/annurev-ecolsys-112414-054234

Janssen, B.H., 2006. Agriculture and the nitrogen cycle, Assessing the impact of fertilizer use on food production and the environment. Geoderma 134, 233–234. https://doi.org/10.1016/j.geoderma.2005.11.001

Janzen, H.H., 2006. The soil carbon dilemma: Shall we hoard it or use it? Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2005.10.008

Jarecki, M.K., Lal, R., 2003. Crop management for soil carbon sequestration. CRC. Crit. Rev. Plant Sci. https://doi.org/10.1080/713608318

Jarvis, S.C., 2009. Soil-plant-animal interactions and impact on nitrogen and phosphorus cycling and recycling in grazed pastures., in: Grassland Ecophysiology and Grazing Ecology. https://doi.org/10.1079/9780851994529.0317

Jastrow, J.D., Amonette, J.E., Bailey, V.L., 2007. Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. Clim. Change 80, 5–23. https://doi.org/10.1007/s10584-006-9178-3

Jastrow, J.D., Miller, R.M., Lussenhop, J., 1998. Contributions of interacting biological mechanisms to soil aggregate stabilization in restored prairie. Soil Biol. Biochem. 30, 905–916. https://doi.org/10.1016/S0038-0717(97)00207-1

Jones, D.L., Hodge, A., Kuzyakov, Y., 2004. Plant and mycorrhizal regulation of rhizodeposition. New Phytol. https://doi.org/10.1111/j.1469-8137.2004.01130.x

Jones, D.L., Willett, V.B., 2006. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2005.08.012

Jung, H.G., Allen, M.S., 1995. Characteristics of plant cell walls affecting intake and digestibility of forages by ruminants. J. Anim. Sci. 73, 2774–2790. https://doi.org/10.2527/1995.7392774x

Kaine, G.W., Tozer, P.R., 2005. Stability, resilience and sustainability in pasture-based grazing systems. Agric. Syst. 83, 27–48. https://doi.org/10.1016/j.agsy.2004.03.001

Kaiser, K., Guggenberger, G., 2000. The role of DOM sorption to mineral surfaces in the preservation of organic matter in soils, in: Organic Geochemistry. pp. 711–725. https://doi.org/10.1016/S0146-6380(00)00046-2

Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2016. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. Nat. Commun. 7. https://doi.org/10.1038/ncomms13630

Kallenbach, C.M., Grandy, A.S., Frey, S.D., Diefendorf, A.F., 2015. Microbial physiology and necromass regulate agricultural soil carbon accumulation. Soil Biol. Biochem. 91, 279–290. https://doi.org/10.1016/j.soilbio.2015.09.005

Kandeler, E., Gerber, H., 1988. Short-term assay of soil urease activity using colorimetric determination of ammonium. Biol. Fertil. Soils. https://doi.org/10.1007/BF00257924

Kemp, D.R., Michalk, D.L., Virgona, J.M., 2000. Towards more sustainable pastures: Lessons learnt. Aust. J. Exp. Agric. 40, 343–356. https://doi.org/10.1071/EA99001

Kemper, W.D., Rosenau, R.C., 1986. Aggregate Stability and Size Dlstributlon’. Methods soil Anal. Part 1 Phys. Mineral. Methods.

Khan, A., Zarif, N., Yang, L., Clothier, B., Rewald, B., 2021. Correlation of leaf and root traits of two angiosperm tree species in northeast China under contrasting light and nitrogen availabilities. Forests. https://doi.org/10.3390/f12050596

King, A.E., Hofmockel, K.S., 2017. Diversified cropping systems support greater microbial cycling and retention of carbon and nitrogen. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2017.01.040

Kirkby, C.A., Kirkegaard, J.A., Richardson, A.E., Wade, L.J., Blanchard, C., Batten, G., 2011. Stable soil organic matter: A comparison of C:N:P:S ratios in Australian and other world soils. Geoderma 163, 197–208. https://doi.org/10.1016/j.geoderma.2011.04.010

Kirkby, C.A., Richardson, A.E., Wade, L.J., Batten, G.D., Blanchard, C., Kirkegaard, J.A., 2013. Carbon-nutrient stoichiometry to increase soil carbon sequestration. Soil Biol. Biochem. 60, 77–86. https://doi.org/10.1016/j.soilbio.2013.01.011

Kleen, J., Taube, F., Gierus, M., 2011. Agronomic performance and nutritive value of forage legumes in binary mixtures with perennial ryegrass under different defoliation systems. J. Agric. Sci. 149, 73–84. https://doi.org/10.1017/S0021859610000456

Klumpp, K., Fontaine, S., Attard, E., Le Roux, X., Gleixner, G., Soussana, J.F., 2009. Grazing triggers soil carbon loss by altering plant roots and their control on soil microbial community. J. Ecol. 97, 876–885. https://doi.org/10.1111/j.1365-2745.2009.01549.x

Kok, D.D., Scherer, L., de Vries, W., Trimbos, K., van Bodegom, P.M., 2022. Relationships of priming effects with organic amendment composition and soil microbial properties. Geoderma 422, 115951. https://doi.org/https://doi.org/10.1016/j.geoderma.2022.115951

Kooch, Y., Moghimian, N., Wirth, S., Noghre, N., 2020. Effects of grazing management on leaf litter decomposition and soil microbial activities in northern Iranian rangeland. Geoderma. https://doi.org/10.1016/j.geoderma.2019.114100

Kopittke, P.M., Berhe, A.A., Carrillo, Y., Cavagnaro, T.R., Chen, D., Chen, Q.-L., Román Dobarco, M., Dijkstra, F.A., Field, D.J., Grundy, M.J., He, J.-Z., Hoyle, F.C., Kögel-Knabner, I., Lam, S.K., Marschner, P., Martinez, C., McBratney, A.B., McDonald-Madden, E., Menzies, N.W., Mosley, L.M., Mueller, C.W., Murphy, D. V, Nielsen, U.N., O'Donnell, A.G., Pendall, E., Pett-Ridge, J., Rumpel, C., Young, I.M., Minasny, B., 2022. Ensuring planetary survival: the centrality of organic carbon in balancing the multifunctional nature of soils. Crit. Rev. Environ. Sci. Technol. 1–17. https://doi.org/10.1080/10643389.2021.2024484

Kramer-Walter, K.R., Bellingham, P.J., Millar, T.R., Smissen, R.D., Richardson, S.J., Laughlin, D.C., 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. J. Ecol. https://doi.org/10.1111/1365-2745.12562

Kramer, S., Dibbern, D., Moll, J., Huenninghaus, M., Koller, R., Krueger, D., Marhan, S., Urich, T., Wubet, T., Bonkowski, M., Buscot, F., Lueders, T., Kandeler, E., 2016. Resource partitioning between bacteria, fungi, and protists in the detritusphere of an agricultural soil. Front. Microbiol. https://doi.org/10.3389/fmicb.2016.01524

Kravchenko, A.N., Guber, A.K., Razavi, B.S., Koestel, J., Quigley, M.Y., Robertson, G.P., Kuzyakov, Y., 2019. Microbial spatial footprint as a driver of soil carbon stabilization. Nat. Commun. 10. https://doi.org/10.1038/s41467-019-11057-4

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. J. Stat. Softw. https://doi.org/10.18637/JSS.V082.I13

Kuzyakov, Y., 2010. Priming effects: Interactions between living and dead organic matter. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2010.04.003

Kuzyakov, Y., 2002. Review: Factors affecting rhizosphere priming effects, in: Journal of Plant Nutrition and Soil Science. pp. 382–396. https://doi.org/10.1002/1522-2624(200208)165:4<382::aid-jpln382>3.0.co;2-%23

L. Mawdsley, R. D. Bardgett, J., 1996. Continuous defoliation of perennial ryegrass (Lolium perenne) and white clover (Trifolium repens) and associated changes in the composition and activity of the microbial population of an upland grassland soil. Biol. Fertil. Soils. https://doi.org/10.1007/s003740050207

Lajtha, K., Bowden, R.D., Nadelhoffer, K., 2014. Litter and Root Manipulations Provide Insights into Soil Organic Matter Dynamics and Stability. Soil Sci. Soc. Am. J. 78, S261–S269. https://doi.org/10.2136/sssaj2013.08.0370nafsc

Lal, R., 2016. Climate Change and Agriculture, in: Climate Change: Observed Impacts on Planet Earth: Second Edition. pp. 465–489. https://doi.org/10.1016/B978-0-444-63524-2.00028-2

Lal, R., 2002. Soil carbon dynamics in cropland and rangeland, in: Environmental Pollution. pp. 353–362. https://doi.org/10.1016/S0269-7491(01)00211-1

Lal, R., Kimble, J.M., 1997. Conservation tillage for carbon sequestration. Nutr. Cycl. Agroecosystems 49, 243–253. https://doi.org/10.1023/A:1009794514742

Lambers, J.H.R., Harpole, W.S., Tilman, D., Knops, J., Reich, P.B., 2004. Mechanisms responsible for the positive diversity-productivity relationship in Minnesota grasslands. Ecol. Lett. 7, 661–668. https://doi.org/10.1111/j.1461-0248.2004.00623.x

Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B.C., Trumbore, S.E., Gleixner, G., 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nat. Commun. 6. https://doi.org/10.1038/ncomms7707

Lavallee, J.M., Soong, J.L., Cotrufo, M.F., 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Glob. Chang. Biol. 26, 261–273. https://doi.org/10.1111/gcb.14859

Lazcano, C., Decock, C., Wilson, S.G., 2020. Defining and Managing for Healthy Vineyard Soils, Intersections With the Concept of Terroir. Front. Environ. Sci. https://doi.org/10.3389/fenvs.2020.00068

Lee Rodgers, J., Alan Nice Wander, W., 1988. Thirteen ways to look at the correlation coefficient. Am. Stat. 42. https://doi.org/10.1080/00031305.1988.10475524

Leff, J.W., Wieder, W.R., Taylor, P.G., Townsend, A.R., Nemergut, D.R., Grandy, A.S., Cleveland, C.C., 2012. Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. Glob. Chang. Biol. 18, 2969–2979. https://doi.org/10.1111/j.1365-2486.2012.02749.x

Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature. https://doi.org/10.1038/nature16069

Leigh, J., Holgate, M., 1978. Effects of pasture availability on the composition and quality of the diet selected by sheep grazing native, degenerate and improved pastures in the Upper Shoalhaven Valley, New South Wales. Aust. J. Exp. Agric. 18, 381. https://doi.org/10.1071/ea9780381

Lemaire, G., Agnusdei, M., 2009. Leaf tissue turnover and efficiency of herbage utilization., in: Grassland Ecophysiology and Grazing Ecology. https://doi.org/10.1079/9780851994529.0265

Lemaire, G., Franzluebbers, A., Carvalho, P.C. de F., Dedieu, B., 2014. Integrated crop-livestock systems: Strategies to achieve synergy between agricultural production and environmental quality. Agric. Ecosyst. Environ. 190, 4–8. https://doi.org/10.1016/j.agee.2013.08.009

Levi-Minzi, R., Riffaldi, R., Saviozzi, A., 1990. Carbon mineralization in soil amended with different organic materials. Agric. Ecosyst. Environ. https://doi.org/10.1016/0167-8809(90)90231-2

Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial necromass contribution to soil organic matter. Glob. Chang. Biol. 25, 3578–3590. https://doi.org/10.1111/gcb.14781

Liang, C., Schimel, J.P., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. Nat. Microbiol. https://doi.org/10.1038/nmicrobiol.2017.105

Liebig, M.A., Faust, D.R., Archer, D.W., Kronberg, S.L., Hendrickson, J.R., Tanaka, D.L., 2020. Integrated crop-livestock effects on soil carbon and nitrogen in a semiarid region. Agrosystems, Geosci. Environ. https://doi.org/10.1002/agg2.20098

Liebmann, P., Wordell-Dietrich, P., Kalbitz, K., Mikutta, R., Kalks, F., Don, A., Woche, S.K., Dsilva, L.R., Guggenberger, G., 2020. Relevance of aboveground litter for soil organic matter formation - A soil profile perspective. Biogeosciences. https://doi.org/10.5194/bg-17-3099-2020

Lipper, L., Thornton, P., Campbell, B.M., Baedeker, T., Braimoh, A., Bwalya, M., Caron, P., Cattaneo, A., Garrity, D., Henry, K., Hottle, R., Jackson, L., Jarvis, A., Kossam, F., Mann, W., McCarthy, N., Meybeck, A., Neufeldt, H., Remington, T., Sen, P.T., Sessa, R., Shula, R., Tibu, A., Torquebiau, E.F., 2014. Climate-smart agriculture for food security. Nat. Clim. Chang. https://doi.org/10.1038/nclimate2437

Liu, S., He, F., Kuzyakov, Y., Xiao, H., Hoang, D.T.T., Pu, S., Razavi, B.S., 2022. Nutrients in the rhizosphere: A meta-analysis of content, availability, and influencing factors. Sci. Total

Environ. https://doi.org/10.1016/j.scitotenv.2022.153908

Liu, Z., Shao, M., Wang, Y., 2011. Effect of environmental factors on regional soil organic carbon stocks across the Loess Plateau region, China. Agric. Ecosyst. Environ. 142, 184–194. https://doi.org/10.1016/j.agee.2011.05.002

Lobry De Bruyn, L.A., Kingston, T.J., 1997. Effects of summer irrigation and trampling in dairy pastures on soil physical properties and earthworm number and species composition. Aust. J. Agric. Res. 48, 1059–1079. https://doi.org/10.1071/a94132

Lõhmus, K., Oja, T., Lasn, R., 1989. Specific root area: A soil characteristic. Plant Soil. https://doi.org/10.1007/BF02370415

Lovell, S.T., DeSantis, S., Nathan, C.A., Olson, M.B., Ernesto Méndez, V., Kominami, H.C., Erickson, D.L., Morris, K.S., Morris, W.B., 2010. Integrating agroecology and landscape multifunctionality in Vermont: An evolving framework to evaluate the design of agroecosystems. Agric. Syst. https://doi.org/10.1016/j.agsy.2010.03.003

Malik, A.A., Martiny, J.B.H., Brodie, E.L., Martiny, A.C., Treseder, K.K., Allison, S.D., 2020. Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. ISME J. https://doi.org/10.1038/s41396-019-0510-0

Manley, J.T., Schuman, G.E., Reeder, J.D., Hart, R.H., 1995. Rangeland soil carbon and nitrogen responses to grazing. J. Soil Water Conserv. 50, 294–298.

Manzoni, S., Taylor, P., Richter, A., Porporato, A., Ågren, G.I., 2012. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytol. https://doi.org/10.1111/j.1469-8137.2012.04225.x

Maron, J.L., Marler, M., Klironomos, J.N., Cleveland, C.C., 2011. Soil fungal pathogens and the relationship between plant diversity and productivity. Ecol. Lett. 14, 36–41.

https://doi.org/10.1111/j.1461-0248.2010.01547.x

Marshall, K., Brewer, K.M., 2020. A New Vision for American Agriculture: The Just and Equitable Transition Toward Agroecology. Sci. People 23, 50–53.

Martins, C.D.M., Schmitt, D., Duchini, P.G., Miqueloto, T., Sbrissia, A.F., 2020. Defoliation intensity and leaf area index recovery in defoliated swards: Implications for forage accumulation. Sci. Agric. https://doi.org/10.1590/1678-992x-2019-0095

Matches, A.G., 1992. Plant Response to Grazing: A Review. J. Prod. Agric. https://doi.org/10.2134/jpa1992.0001

Maughan, M.W., Flores, J.P.C., Anghinoni, I., Bollero, G., Fernández, F.G., Tracy, B.F., 2009. Soil quality and corn yield under crop-livestock integration in Illinois. Agron. J. 101, 1503–1510. https://doi.org/10.2134/agronj2009.0068

Mazzilli, S.R., Kemanian, A.R., Ernst, O.R., Jackson, R.B., Piñeiro, G., 2015. Greater humification of belowground than aboveground biomass carbon into particulate soil organic matter in no-till corn and soybean crops. Soil Biol. Biochem. 85, 22–30. https://doi.org/10.1016/j.soilbio.2015.02.014

McKenzie, S.C., Goosey, H.B., O’Neill, K.M., Menalled, F.D., 2016. Impact of integrated sheep grazing for cover crop termination on weed and ground beetle (Coleoptera:Carabidae) communities. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2015.11.018

McNaughton, S.J., Zuniga, G., McNaughton, M.M., Banyikwa, F.F., 1997. Ecosystem Catalysis: Soil Urease Activity and Grazing in the Serengeti Ecosystem. Oikos. https://doi.org/10.2307/3546619

Mcsherry, M.E., Ritchie, M.E., 2013. Effects of grazing on grassland soil carbon: A global review. Glob. Chang. Biol. 19, 1347–1357. https://doi.org/10.1111/gcb.12144

Metcalfe, D.B., Asner, G.P., Martin, R.E., Silva Espejo, J.E., Huasco, W.H., Farfán Amézquita, F.F., Carranza-Jimenez, L., Galiano Cabrera, D.F., Baca, L.D., Sinca, F., Huaraca Quispe, L.P., Taype, I.A., Mora, L.E., Dávila, A.R., Solórzano, M.M., Puma Vilca, B.L., Laupa Román, J.M., Guerra Bustios, P.C., Revilla, N.S., Tupayachi, R., Girardin, C.A.J., Doughty, C.E., Malhi, Y., 2014. Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. Ecol. Lett. 17, 324–332. https://doi.org/10.1111/ele.12233

Midway, S., Robertson, M., Flinn, S., Kaller, M., 2020. Comparing multiple comparisons: practical guidance for choosing the best multiple comparisons test. PeerJ. https://doi.org/10.7717/peerj.10387

Mikha, M.M., Rice, C.W., 2004. Tillage and Manure Effects on Soil and Aggregate-Associated Carbon and Nitrogen. Soil Sci. Soc. Am. J. 68, 809–816. https://doi.org/10.2136/sssaj2004.8090

Minasny, B., Malone, B.P., McBratney, A.B., Angers, D.A., Arrouays, D., Chambers, A., Chaplot, V., Chen, Z.S., Cheng, K., Das, B.S., Field, D.J., Gimona, A., Hedley, C.B., Hong, S.Y., Mandal, B., Marchant, B.P., Martin, M., McConkey, B.G., Mulder, V.L., O’Rourke, S., Richer-de-Forges, A.C., Odeh, I., Padarian, J., Paustian, K., Pan, G., Poggio, L., Savin, I., Stolbovoy, V., Stockmann, U., Sulaeman, Y., Tsui, C.C., Vågen, T.G., van Wesemael, B., Winowiecki, L., 2017. Soil carbon 4 per mille. Geoderma. https://doi.org/10.1016/j.geoderma.2017.01.002

Mládková, P., Mládek, J., Hejduk, S., Hejcman, M., Cruz, P., Jouany, C., Pakeman, R.J., 2015. High-nature-value grasslands have the capacity to cope with nutrient impoverishment induced by mowing and livestock grazing. J. Appl. Ecol. https://doi.org/10.1111/1365-

2664.12464

Moebius-Clune, B.N., Moebius-Clune, D.J., Gugino, B.K., Idowu, O.J., Schindelbeck, R.R., Ristow, A.J., van Es, H.M., Thies, J.E., Shayler, H.A., McBride, M.B., Wolfe, D.W., Abawi, G.S., 2016. Comprehensive Assessment of Soil Health – The Cornell Framework Manual, Edition 3.1. Cornell Univ. Geneva, NY.

Mommer, L., van Ruijven, J., Jansen, C., van de Steeg, H.M., de Kroon, H., 2012. Interactive effects of nutrient heterogeneity and competition: Implications for root foraging theory? Funct. Ecol. https://doi.org/10.1111/j.1365-2435.2011.01916.x

Monaghan, R.M., Paton, R.J., Smith, L.C., Drewry, J.J., Littlejohn, R.P., 2005. The impacts of nitrogen fertilisation and increased stocking rate on pasture yield, soil physical condition and nutrient losses in drainage from a cattle-grazed pasture. New Zeal. J. Agric. Res. 48, 227–240. https://doi.org/10.1080/00288233.2005.9513652

Muniz, L.C., Madari, B.E., de Freitas Trovo, J.B., de Lima Cantanhêde, I.S., de Almeida Machado, P.L.O., Cobucci, T., de Souza França, A.F., 2011. Atributos biológicos do solo em pastagens de diferentes idades no sistema de integração lavoura-pecuária. Pesqui. Agropecu. Bras. 46, 1262–1268. https://doi.org/10.1590/S0100-204X2011001000021

Munns, R., Termaat, A., 1986. Whole-plant responses to salinity. Aust. J. Plant Physiol. 13, 143–160. https://doi.org/10.1071/PP9860143

Nakhavali, M., Lauerwald, R., Regnier, P., Guenet, B., Chadburn, S., Friedlingstein, P., 2021. Leaching of dissolved organic carbon from mineral soils plays a significant role in the terrestrial carbon balance. Glob. Chang. Biol. https://doi.org/10.1111/gcb.15460

Nannipieri, P., Giagnoni, L., Landi, L., Renella, G., 2011. Role of Phosphatase Enzymes in Soil - Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling, in: Bünemann, E., Oberson, A., Frossard, E. (Eds.), . Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 215–243. https://doi.org/10.1007/978-3-642-15271-9_9

Nannipieri, P., Kandeler, E., Ruggiero, P., 2002. Enzyme activities and microbiological and biochemical processes in soil. Enzym. Environ. 1–34.

Nations, U., Programme, E., 2013. YEAR UNEP YEAR BOOK 2013 Emerging issues in our global environment. Emerg. issues our Glob. Environ. 78.

Nazih, N., Finlay-Moore, O., Hartel, P.G., Fuhrmann, J.J., 2001. Whole soil fatty acid methyl ester (FAME) profiles of early soybean rhizosphere as affected by temperature and matric water potential. Soil Biol. Biochem. https://doi.org/10.1016/S0038-0717(00)00197-8

Neff, J.C., Asner, G.P., 2001. Dissolved organic carbon in terrestrial ecosystems: Synthesis and a model. Ecosystems. https://doi.org/10.1007/s100210000058

Niles, M.T., Garrett, R.D., Walsh, D., 2018. Ecological and economic benefits of integrating sheep into viticulture production. Agron. Sustain. Dev. 38. https://doi.org/10.1007/s13593-017-0478-y

Norman, J.S., Smercina, D.N., Hileman, J.T., Tiemann, L.K., Friesen, M.L., 2020. Soil aminopeptidase induction is unaffected by inorganic nitrogen availability. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2020.107952

Novara, A., Minacapilli, M., Santoro, A., Rodrigo-Comino, J., Carrubba, A., Sarno, M., Venezia, G., Gristina, L., 2019. Real cover crops contribution to soil organic carbon sequestration in sloping vineyard. Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2018.10.247

Núñez, P., Demanet, R., Matus, F., Mora, M., 2007. Grazing Management, Ammonia and Nitrous Oxide Emissions: a General View. Rev. la Cienc. del suelo y Nutr. Veg. 7, 61–99. https://doi.org/10.4067/S0718-27912007000300006

Oelmann, Y., Wilcke, W., Temperton, V.M., Buchmann, N., Roscher, C., Schumacher, J., Schulze, E.-D., Weisser, W.W., 2007. Soil and Plant Nitrogen Pools as Related to Plant Diversity in an Experimental Grassland. Soil Sci. Soc. Am. J. 71, 720–729. https://doi.org/10.2136/sssaj2006.0205

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schäfer, K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G., Katul, G.G., 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. Nature 411, 469–472. https://doi.org/10.1038/35078064

Orgill, S.E., Waters, C.M., Melville, G., Toole, I., Alemseged, Y., Smith, W., 2017. Sensitivity of soil organic carbon to grazing management in the semi-arid rangelands of south-eastern Australia. Rangel. J. 39, 153–167. https://doi.org/10.1071/RJ16020

Oshima, Y., Ogawa, N., Harashima, S., 1996. Regulation of phosphatase synthesis in Saccharomyces cerevisiae - A review. Gene. https://doi.org/10.1016/S0378-1119(96)00425-8

Ostonen, I., Püttsepp, Ü., Biel, C., Alberton, O., Bakker, M.R., Lõhmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A.F.M., Pronk, A., Vanguelova, E., Weih, M., Brunner, I., 2007. Specific root length as an indicator of environmental change. Plant Biosyst. https://doi.org/10.1080/11263500701626069

Ota, M., Nagai, H., Koarashi, J., 2013. Root and dissolved organic carbon controls on subsurface soil carbon dynamics: A model approach. J. Geophys. Res. Biogeosciences. https://doi.org/10.1002/2013JG002379

Parsons, A.J., Thornley, J.H.M., Newton, P.C.D., Rasmussen, S., Rowarth, J.S., 2013. Soil carbon dynamics: The effects of nitrogen input, intake demand and off-take by animals. Sci.

Total Environ. 465, 205–215. https://doi.org/10.1016/j.scitotenv.2013.02.019

Paterson, E., Sim, A., 1999. Rhizodeposition and C-partitioning of Lolium perenne in axenic culture affected by nitrogen supply and defoliation. Plant Soil. https://doi.org/10.1023/a:1004789407065

Patton, B.D., Dong, X., Nyren, P.E., Nyren, A., 2007. Effects of grazing intensity, precipitation, and temperature on forage production. Rangel. Ecol. Manag. https://doi.org/10.2111/07-008R2.1

Pausch, J., Kuzyakov, Y., 2018. Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale. Glob. Chang. Biol. https://doi.org/10.1111/gcb.13850

Pavlů, V., Hejcman, M., Pavlů, L., Gaisler, J., Nežerková, P., 2006. Effect of continuous grazing on forage quality, quantity and animal performance. Agric. Ecosyst. Environ. 113, 349–355. https://doi.org/10.1016/j.agee.2005.10.010

Peter Christensen, L., Bianchi, M.L., Peacock, W.L., Hirschfelt, D.J., 1994. Effect of nitrogen fertilizer timing and rate on inorganic nitrogen status, fruit composition, and yield of grapevines. Am. J. Enol. Vitic.

Petersen-Rockney, M., Baur, P., Guzman, A., Bender, S.F., Calo, A., Castillo, F., De Master, K., Dumont, A., Esquivel, K., Kremen, C., LaChance, J., Mooshammer, M., Ory, J., Price, M.J., Socolar, Y., Stanley, P., Iles, A., Bowles, T., 2021. Narrow and Brittle or Broad and Nimble? Comparing Adaptive Capacity in Simplifying and Diversifying Farming Systems. Front. Sustain. Food Syst. https://doi.org/10.3389/fsufs.2021.564900

Peterson, C.A., Deiss, L., Gaudin, A.C.M., 2020. Commercial integrated crop-livestock systems achieve comparable crop yields to specialized production systems: A meta-analysis. PLoS

One 15. https://doi.org/10.1371/journal.pone.0231840

Peterson, F.S., Lajtha, K.J., 2013. Linking aboveground net primary productivity to soil carbon and dissolved organic carbon in complex terrain. J. Geophys. Res. Biogeosciences 118, 1225–1236. https://doi.org/10.1002/jgrg.20097

Pineiro, G., Paruelo, J.M., Jobbágy, E.G., Jackson, R.B., Oesterheld, M., 2009. Grazing effects on belowground C and N stocks along a network of cattle exclosures in temperate and subtropical grasslands of South America. Global Biogeochem. Cycles 23. https://doi.org/10.1029/2007GB003168

Pineiro, G., Paruelo, J.M., Oesterheld, M., Jobbágy, E.G., 2010. Pathways of grazing effects on soil organic carbon and nitrogen. Rangel. Ecol. Manag. 63, 109–119. https://doi.org/10.2111/08-255.1

Plaza-Bonilla, D., Arrúe, J.L., Cantero-Martínez, C., Fanlo, R., Iglesias, A., Álvaro-Fuentes, J., 2015. Carbon management in dryland agricultural systems. A review. Agron. Sustain. Dev. https://doi.org/10.1007/s13593-015-0326-x

Ponisio, L.C., M’gonigle, L.K., Mace, K.C., Palomino, J., Valpine, P. De, Kremen, C., 2015. Diversification practices reduce organic to conventional yield gap. Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2014.1396

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. New Phytol. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Power, A.G., 2010. Ecosystem services and agriculture: Tradeoffs and synergies. Philos. Trans. R. Soc. B Biol. Sci. https://doi.org/10.1098/rstb.2010.0143

Prichard, T., 2000. Vineyard Irrigation Systems. Raisin Prod. Man.

Prommer, J., Walker, T.W.N., Wanek, W., Braun, J., Zezula, D., Hu, Y., Hofhansl, F., Richter, A., 2020. Increased microbial growth, biomass, and turnover drive soil organic carbon accumulation at higher plant diversity. Glob. Chang. Biol. https://doi.org/10.1111/gcb.14777

Qi, R., Li, J., Lin, Z., Li, Z., Li, Y., Yang, X., Zhang, J., Zhao, B., 2016. Temperature effects on soil organic carbon, soil labile organic carbon fractions, and soil enzyme activities under long-term fertilization regimes. Appl. Soil Ecol. 102, 36–45. https://doi.org/10.1016/j.apsoil.2016.02.004

Qiao, N., Xu, X., Hu, Y., Blagodatskaya, E., Liu, Y., Schaefer, D., Kuzyakov, Y., 2016. Carbon and nitrogen additions induce distinct priming effects along an organic-matter decay continuum. Sci. Rep. 6. https://doi.org/10.1038/srep19865

Rabbi, S.M.F., Tighe, M., Cowie, A., Wilson, B.R., Schwenke, G., Mcleod, M., Badgery, W., Baldock, J., 2014. The relationships between land uses, soil management practices, and soil carbon fractions in South Eastern Australia. Agric. Ecosyst. Environ. 197, 41–52. https://doi.org/10.1016/j.agee.2014.06.020

Rakkar, M.K., Blanco-Canqui, H., Drijber, R.A., Drewnoski, M.E., MacDonald, J.C., Klopfenstein, T., 2017. Impacts of Cattle Grazing of Corn Residues on Soil Properties after 16 Years. Soil Sci. Soc. Am. J. 81, 414–424. https://doi.org/10.2136/sssaj2016.07.0227

Ramakrishna, A., Tam, H.M., Wani, S.P., Long, T.D., 2006. Effect of mulch on soil temperature, moisture, weed infestation and yield of groundnut in northern Vietnam. F. Crop. Res. 95, 115–125. https://doi.org/10.1016/j.fcr.2005.01.030

Rasse, D.P., Rumpel, C., Dignac, M.F., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation, in: Plant and Soil. pp. 341–356. https://doi.org/10.1007/s11104-004-

0907-y

Reddy, P.P., Reddy, P.P., 2016. Integrated Crop–Livestock Farming Systems, in: Sustainable Intensification of Crop Production. pp. 357–370. https://doi.org/10.1007/978-981-10-2702-4_23

Reeder, J.D, Schuman, G.E, Morgan, J.A., Lecain, D.R, Hart, R.H., 2001. Impact of grazing management strategies on carbon sequestration in a semi-arid rangeland, USA, Proceedings of the XIX International Grassland Congress.

Reeder, J.D., Schuman, G.E., Morgan, J.A., Lecain, D.R., 2004. Response of organic and inorganic carbon and nitrogen to long-term grazing of the shortgrass steppe, in: Environmental Management. pp. 485–495. https://doi.org/10.1007/s00267-003-9106-5

Ren, H., Schönbach, P., Wan, H., Gierus, M., Taube, F., 2012. Effects of Grazing Intensity and Environmental Factors on Species Composition and Diversity in Typical Steppe of Inner Mongolia, China. PLoS One 7. https://doi.org/10.1371/journal.pone.0052180

Rietz, D.N., Haynes, R.J., 2003. Effects of irrigation-induced salinity and sodicity on soil microbial activity. Soil Biol. Biochem. 35, 845–854. https://doi.org/10.1016/S0038-0717(03)00125-1

Rillig, M.C., Mummey, D.L., 2006. Mycorrhizas and soil structure. New Phytol. https://doi.org/10.1111/j.1469-8137.2006.01750.x

Robertson, M., Bathgate, A., Moore, A., Lawes, R., Lilley, J., 2009. Seeking simultaneous improvements in farm profit and natural resource indicators: A modelling analysis. Anim. Prod. Sci. 49, 826–836. https://doi.org/10.1071/AN09008

Rochette, P., Ellert, B., Gregorich, E.G., Desjardins, R.L., Pattey, E., Lessard, R., Johnson, B.G., 1997. Description of a dynamic closed chamber for measuring soil respiration and its comparison with other techniques, in: Canadian Journal of Soil Science. https://doi.org/10.4141/S96-110

Rodrigo-Comino, J., 2018. Five decades of soil erosion research in “terroir”. The State-of-the-Art. Earth-Science Rev. https://doi.org/10.1016/j.earscirev.2018.02.014

Rota, A., Sperandini, S., 2009. Livestock and pastoralists, Livestock Thematic Papers.

Rumpel, C., Crème, A., Ngo, P.T., Velásquez, G., Mora, M.L., Chabbi, A., 2015. The impact of grassland management on biogeochemical cycles involving carbon, nitrogen and phosphorus. J. Soil Sci. Plant Nutr. 15, 353–371. https://doi.org/10.4067/s0718-95162015005000034

Rumpel, C., Kögel-Knabner, I., 2011. Deep soil organic matter-a key but poorly understood component of terrestrial C cycle. Plant Soil. https://doi.org/10.1007/s11104-010-0391-5

Russelle, M.P., Entz, M.H., Franzluebbers, A.J., 2007. Reconsidering integrated crop-livestock systems in North America, in: Agronomy Journal. pp. 325–334. https://doi.org/10.2134/agronj2006.0139

Rutherford, M.C., Powrie, L.W., 2013. Impacts of heavy grazing on plant species richness: A comparison across rangeland biomes of South Africa. South African J. Bot. 87, 146–156. https://doi.org/10.1016/j.sajb.2013.03.020

Ryals, R., Hartman, M.D., Parton, W.J., DeLonge, M.S., Silver, W.L., 2015. Long-term climate change mitigation potential with organic matter management on grasslands. Ecol. Appl. 25, 531–545. https://doi.org/10.1890/13-2126.1

Ryals, R., Silver, W.L., 2013. Effects of organic matter amendments on net primary productivity and greenhouse gas emissions in annual grasslands. Ecol. Appl. 23, 46–59. https://doi.org/10.1890/12-0620.1

Ryschawy, J., Liebig, M.A., Kronberg, S.L., Archer, D.W., Hendrickson, J.R., 2017. Integrated Crop-Livestock Management Effects on Soil Quality Dynamics in a Semiarid Region: A Typology of Soil Change over Time. Appl. Environ. Soil Sci. 2017. https://doi.org/10.1155/2017/3597416

Ryschawy, J., Tiffany, S., Gaudin, A., Niles, M.T., Garrett, R.D., 2021. Moving niche agroecological initiatives to the mainstream: A case-study of sheep-vineyard integration in California. Land use policy. https://doi.org/10.1016/j.landusepol.2021.105680

Safriel, U., Adeel, Z., Niemeijer, D., Puigdefabregas, J., White, R., Lal, R., Winslow, M., Ziedler, J., Prince, S., Archer, E., King, C., Shapiro, B., Wessels, K., Nielsen, T., Portnov, B., Reshef, I., Thonell, J., Lachman, E., Mcnab, D., 2005. Chapter 22: Dryland Systems, in: Ecosystems and Human Well-Being: Current State and Trends, Volume 1. pp. 625–664.

Saliendra, N.Z., Liebig, M.A., Kronberg, S.L., 2018. Carbon use efficiency of hayed alfalfa and grass pastures in a semiarid environment. Ecosphere. https://doi.org/10.1002/ecs2.2147

Salton, J.C., Mercante, F.M., Tomazi, M., Zanatta, J.A., Concenço, G., Silva, W.M., Retore, M., 2014. Integrated crop-livestock system in tropical Brazil: Toward a sustainable production system. Agric. Ecosyst. Environ. 190, 70–79. https://doi.org/10.1016/j.agee.2013.09.023

Sanderman, J., Reseigh, J., Wurst, M., Young, M.A., Austin, J., 2015. Impacts of rotational grazing on soil carbon in native grass-based pastures in southern Australia. PLoS One 10. https://doi.org/10.1371/journal.pone.0136157

Sanderson, M.A., Archer, D., Hendrickson, J., Kronberg, S., Liebig, M., Nichols, K., Schmer, M., Tanaka, D., Aguilar, J., 2013. Diversification and ecosystem services for conservation agriculture: Outcomes from pastures and integrated crop-livestock systems. Renew. Agric. Food Syst. 28, 129–144. https://doi.org/10.1017/S1742170512000312

Sanderson, M.A., Soder, K.J., Muller, L.D., Klement, K.D., Skinner, R.H., Goslee, S.C., 2005. Forage mixture productivity and botanical composition in pastures grazed by dairy cattle. Agron. J. 97, 1465–1471. https://doi.org/10.2134/agronj2005.0032

Sanjari, G., Ghadiri, H., Ciesiolka, C.A.A., Yu, B., 2008. Comparing the effects of continuous and time-controlled grazing systems on soil characteristics in Southeast Queensland. Aust. J. Soil Res. 46, 348–358. https://doi.org/10.1071/SR07220

Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial stress-response physiology and its implications for ecosystem function. Ecology. https://doi.org/10.1890/06-0219

Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: Challenges of a changing paradigm. Ecology. https://doi.org/10.1890/03-8002

Schipanski, M.E., Drinkwater, L.E., 2012. Nitrogen fixation in annual and perennial legume-grass mixtures across a fertility gradient. Plant Soil 357, 147–159. https://doi.org/10.1007/s11104-012-1137-3

Schmidt, J.E., Kent, A.D., Brisson, V.L., Gaudin, A.C.M., 2019. Agricultural management and plant selection interactively affect rhizosphere microbial community structure and nitrogen cycling. Microbiome. https://doi.org/10.1186/s40168-019-0756-9

Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56. https://doi.org/10.1038/nature10386

Schon, N.L., Mackay, A.D., Minor, M.A., Yeates, G.W., Hedley, M.J., 2008. Soil fauna in grazed New Zealand hill country pastures at two management intensities. Appl. Soil Ecol. 40, 218–228. https://doi.org/10.1016/j.apsoil.2008.04.007

Schönbach, P., Wan, H., Gierus, M., Bai, Y., Müller, K., Lin, L., Susenbeth, A., Taube, F., 2011. Grassland responses to grazing: Effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. Plant Soil 340, 103–115. https://doi.org/10.1007/s11104-010-0366-6

Schoofs, A., Entz, M.H., 2000. Influence of annual forages on weed dynamics in a cropping system. Can. J. Plant Sci. 80, 187–198. https://doi.org/10.4141/P98-098

Schuman, G.E., Janzen, H.H., Herrick, J.E., 2002. Soil carbon dynamics and potential carbon sequestration by rangelands, in: Environmental Pollution. pp. 391–396. https://doi.org/10.1016/S0269-7491(01)00215-9

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. Ecol. Appl. 9, 65–71. https://doi.org/10.1890/1051-0761(1999)009[0065:IOGMOT]2.0.CO;2

Schuster, M.Z., Pelissari, A., de Moraes, A., Harrison, S.K., Sulc, R.M., Lustosa, S.B.C., Anghinoni, I., Carvalho, P.C.F., 2016. Grazing intensities affect weed seedling emergence and the seed bank in an integrated crop–livestock system. Agric. Ecosyst. Environ. 232, 232–239. https://doi.org/10.1016/j.agee.2016.08.005

Schwinning, S., Parsons, A.J., 1996. Analysis of the Coexistence Mechanisms for Grasses and Legumes in Grazing Systems. J. Ecol. 84, 799. https://doi.org/10.2307/2960553

Sean Clark, M., Gage, S.H., 1996. Effects of free-range chickens and geese on insect pests and weeds in an agroecosystem. Am. J. Altern. Agric. 11, 39–47. https://doi.org/10.1017/s0889189300006718

Sekaran, U., Kumar, S., Luis Gonzalez-Hernandez, J., 2021. Integration of crop and livestock enhanced soil biochemical properties and microbial community structure. Geoderma.

https://doi.org/10.1016/j.geoderma.2020.114686

Setälä, H., McLean, M.A., 2004. Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. Oecologia. https://doi.org/10.1007/s00442-003-1478-y

Setia, R., Gottschalk, P., Smith, P., Marschner, P., Baldock, J., Setia, D., Smith, J., 2013. Soil salinity decreases global soil organic carbon stocks. Sci. Total Environ. 465, 267–272. https://doi.org/10.1016/j.scitotenv.2012.08.028

Sexstone, A.J., Revsbech, N.P., Parkin, T.B., Tiedje, J.M., 1985. Direct Measurement of Oxygen Profiles and Denitrification Rates in Soil Aggregates. Soil Sci. Soc. Am. J. 49, 645–651. https://doi.org/10.2136/sssaj1985.03615995004900030024x

Shahbaz, M., Kuzyakov, Y., Sanaullah, M., Heitkamp, F., Zelenev, V., Kumar, A., Blagodatskaya, E., 2017. Microbial decomposition of soil organic matter is mediated by quality and quantity of crop residues: mechanisms and thresholds. Biol. Fertil. Soils. https://doi.org/10.1007/s00374-016-1174-9

Shariff, A.R., Biondini, M.E., Grygiel, C.E., 1994. Grazing intensity effects on litter decomposition and soil nitrogen mineralization. J. Range Manag. 47, 444–449. https://doi.org/10.2307/4002994

Silva, L.S., Laroca, J.V. dos S., Coelho, A.P., Gonçalves, E.C., Gomes, R.P., Pacheco, L.P., Carvalho, P.C. de F., Pires, G.C., Oliveira, R.L., Souza, J.M.A. de, Freitas, C.M., Cabral, C.E.A., Wruck, F.J., Souza, E.D. de, 2022. Does grass-legume intercropping change soil quality and grain yield in integrated crop-livestock systems? Appl. Soil Ecol. https://doi.org/10.1016/j.apsoil.2021.104257

Silveira, M.L., Liu, K., Sollenberger, L.E., Follett, R.F., Vendramini, J.M.B., 2013. Short-term effects of grazing intensity and nitrogen fertilization on soil organic carbon pools under perennial grass pastures in the southeastern USA. Soil Biol. Biochem. 58, 42–49. https://doi.org/10.1016/j.soilbio.2012.11.003

Sinsabaugh, R.L., Moorhead, D.L., Xu, X., Litvak, M.E., 2017. Plant, microbial and ecosystem carbon use efficiencies interact to stabilize microbial growth as a fraction of gross primary production. New Phytol. https://doi.org/10.1111/nph.14485

Siri-Prieto, G., Reeves, D.W., Raper, R.L., 2007. Tillage systems for a cotton-peanut rotation with winter-annual grazing: Impacts on soil carbon, nitrogen and physical properties. Soil Tillage Res. 96, 260–268. https://doi.org/10.1016/j.still.2007.06.010

Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil Tillage Res. https://doi.org/10.1016/j.still.2004.03.008

Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. Plant Soil. https://doi.org/10.1023/A:1016125726789

Six, J., Elliott, E.T., Paustian, K., 2000. Soil macroaggregate turnover and microaggregate formation: A mechanism for C sequestration under no-tillage agriculture. Soil Biol. Biochem. 32, 2099–2103. https://doi.org/10.1016/S0038-0717(00)00179-6

Six, J., Elliott, E.T., Paustian, K., Doran, J.W., 1998. Aggregation and Soil Organic Matter Accumulation in Cultivated and Native Grassland Soils. Soil Sci. Soc. Am. J. 62, 1367–1377. https://doi.org/10.2136/sssaj1998.03615995006200050032x

Six, Johan, Feller, C., Denef, K., Ogle, S.M., De Moraes Sa, J.C., Albrecht, A., 2002. Soil organic matter, biota and aggregation in temperate and tropical soils - Effects of no-tillage.

Agronomie 22, 755–775. https://doi.org/10.1051/agro:2002043

Smith, P., Smith, J.U., Powlson, D.S., McGill, W.B., Arah, J.R.M., Chertov, O.G., Coleman, K., Franko, U., Frolking, S., Jenkinson, D.S., Jensen, L.S., Kelly, R.H., Klein-Gunnewiek, H., Komarov, A.S., Li, C., Molina, J.A.E., Mueller, T., Parton, W.J., Thornley, J.H.M., Whitmore, A.P., 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. Geoderma 81, 153–225. https://doi.org/10.1016/S0016-7061(97)00087-6

Smith, R.G., Ryan, M.R., Menalled, F.D., 2015. Direct and Indirect Impacts of Weed Management Practices on Soil Quality, in: Soil Management: Building a Stable Base for Agriculture. pp. 275–286. https://doi.org/10.2136/2011.soilmanagement.c18

Snapp, S., 2017. Agroecology: Principles and Practice, in: Agricultural Systems: Agroecology and Rural Innovation for Development: Second Edition. https://doi.org/10.1016/B978-0-12-802070-8.00002-5

Snyder, C.S., Bruulsema, T.W., Jensen, T.L., Fixen, P.E., 2009. Review of greenhouse gas emissions from crop production systems and fertilizer management effects. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2009.04.021

Soane, B.D., Dickson, J.W., Campbell, D.J., 1982. Compaction by agricultural vehicles: A review III. Incidence and control of compaction in crop production. Soil Tillage Res. 2, 3–36. https://doi.org/10.1016/0167-1987(82)90030-7

Sokol, N.W., Bradford, M.A., 2019. Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. Nat. Geosci. https://doi.org/10.1038/s41561-018-0258-6

Sokol, N.W., Kuebbing, S.E., Karlsen-Ayala, E., Bradford, M.A., 2019. Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. New Phytol. 221, 233–246. https://doi.org/10.1111/nph.15361

Soussana, J.F., Lemaire, G., 2014. Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and crop-livestock systems. Agric. Ecosyst. Environ. 190, 9–17. https://doi.org/10.1016/j.agee.2013.10.012

Souza, E.D. de, Costa, S.E.V.G. de A., Anghinoni, I., Carvalho, P.C. de F., Oliveira, E.V.F. de, Martins, A.P., Cao, E., Andrighetti, M., 2010. Soil aggregation in a crop-livestock integration system under no-tillage. Rev. Bras. Ciência do Solo 34, 1365–1374. https://doi.org/10.1590/s0100-06832010000400033

Sparling, G.P., 1992. Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. Aust. J. Soil Res. https://doi.org/10.1071/SR9920195

Spayd, S.E., Wample, R.L., Evans, R.G., Stevens, R.G., Seymour, B.J., Nagel, C.W., 1994. Nitrogen fertilization of White Riesling grapes in Washington. Must and wine composition. Am. J. Enol. Vitic.

Stahlheber, K.A., D’Antonio, C.M., 2013. Using livestock to manage plant composition: A meta-analysis of grazing in California Mediterranean grasslands. Biol. Conserv. 157, 300–308. https://doi.org/10.1016/j.biocon.2012.09.008

Steinbeiss, S., Beßler, H., Engels, C., Temperton, V.M., Buchmann, N., Roscher, C., Kreutziger, Y., Baade, J., Habekost, M., Gleixner, G., 2008. Plant diversity positively affects short-term soil carbon storage in experimental grasslands. Glob. Chang. Biol. 14, 2937–2949. https://doi.org/10.1111/j.1365-2486.2008.01697.x

Sulc, R.M., Franzluebbers, A.J., 2014. Exploring integrated crop-livestock systems in different ecoregions of the United States. Eur. J. Agron. 57, 21–30. https://doi.org/10.1016/j.eja.2013.10.007

Sun, T., Wang, Y., Hui, D., Jing, X., Feng, W., 2020. Soil properties rather than climate and ecosystem type control the vertical variations of soil organic carbon, microbial carbon, and microbial quotient. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2020.107905

Tamburini, G., Bommarco, R., Wanger, T.C., Kremen, C., van der Heijden, M.G.A., Liebman, M., Hallin, S., 2020. Agricultural diversification promotes multiple ecosystem services without compromising yield. Sci. Adv. https://doi.org/10.1126/SCIADV.ABA1715

Tanaka, D.L., Karn, J.F., Scholljegerdes, E.J., 2008. Integrated crop/livestock systems research: Practical research considerations. Renew. Agric. Food Syst. 23, 80–86. https://doi.org/10.1017/S1742170507002165

Tautges, N.E., Chiartas, J.L., Gaudin, A.C.M., O’Geen, A.T., Herrera, I., Scow, K.M., 2019. Deep soil inventories reveal that impacts of cover crops and compost on soil carbon sequestration differ in surface and subsurface soils. Glob. Chang. Biol. 25, 3753–3766. https://doi.org/10.1111/gcb.14762

Teague, R., Grant, B., Wang, H.H., 2015. Assessing optimal configurations of multi-paddock grazing strategies in tallgrass prairie using a simulation model. J. Environ. Manage. 150, 262–273. https://doi.org/10.1016/j.jenvman.2014.09.027

Teague, R., Provenza, F., Norton, B., Steffens, T., Barnes, M., Kothmann, M., Roath, R., 2008. Benefits of multi-paddock grazing management on rangelands: Limitations of experimental grazing research and knowledge gaps, in: Grasslands: Ecology, Management and Restoration.

Teague, W.R., Dowhower, S.L., 2003. Patch dynamics under rotational and continuous grazing management in large, heterogeneous paddocks. J. Arid Environ. 53, 211–229. https://doi.org/10.1006/jare.2002.1036

Teague, W.R., Dowhower, S.L., Baker, S.A., Haile, N., DeLaune, P.B., Conover, D.M., 2011. Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. Agric. Ecosyst. Environ. 141, 310–322. https://doi.org/10.1016/j.agee.2011.03.009

Team, R.C., 2021. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput.

Temperton, V.M., Mwangi, P.N., Scherer-Lorenzen, M., Schmid, B., Buchmann, N., 2007. Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. Oecologia 151, 190–205. https://doi.org/10.1007/s00442-006-0576-z

Thiessen, S., Gleixner, G., Wutzler, T., Reichstein, M., 2013. Both priming and temperature sensitivity of soil organic matter decomposition depend on microbial biomass - An incubation study. Soil Biol. Biochem. 57, 739–748. https://doi.org/10.1016/j.soilbio.2012.10.029

Tian, F.P., Zhang, Z.N., Chang, X.F., Sun, L., Wei, X.H., Wu, G.L., 2016. Effects of biotic and abiotic factors on soil organic carbon in semi-arid grassland. J. Soil Sci. Plant Nutr. 16, 1087–1096. https://doi.org/10.4067/S0718-95162016005000080

Tian, L., Dell, E., Shi, W., 2010. Chemical composition of dissolved organic matter in agroecosystems: Correlations with soil enzyme activity and carbon and nitrogen mineralization. Appl. Soil Ecol. 46, 426–435. https://doi.org/10.1016/j.apsoil.2010.09.007

Tindula, G.N., Orang, M.N., Snyder, R.L., 2013. Survey of Irrigation Methods in California in

2010. J. Irrig. Drain. Eng. https://doi.org/10.1061/(asce)ir.1943-4774.0000538

Tisdall, J.M., Smith, S.E., Rengasamy, P., 1997. Aggregation of soil by fungal hyphae. Aust. J. Soil Res. 35, 55–60. https://doi.org/10.1071/S96065

Tobin, C., Singh, S., Kumar, S., Wang, T., Sexton, P., 2020. Demonstrating Short-Term Impacts of Grazing and Cover Crops on Soil Health and Economic Benefits in an Integrated Crop-Livestock System in South Dakota. Open J. Soil Sci. https://doi.org/10.4236/ojss.2020.103006

Tracy, B.F., Davis, A.S., 2009. Weed biomass and species composition as aff ected by an integrated crop-livestock system. Crop Sci. 49, 1523–1530. https://doi.org/10.2135/cropsci2008.08.0488

Tracy, B.F., Frank, D.A., 1998. Herbivore influence on soil microbial biomass and nitrogen mineralization in a northern grassland ecosystem: Yellowstone National Park. Oecologia. https://doi.org/10.1007/s004420050480

Tracy, B.F., Zhang, Y., 2008. Soil compaction, corn yield response, and soil nutrient pool dynamics within an integrated crop-livestock system in Illinois. Crop Sci. 48, 1211–1218. https://doi.org/10.2135/cropsci2007.07.0390

UNFCCC, 2015. Report of the Conference of the Parties on its twenty-first session, held in Paris from 30 November to 13 December 2015 [WWW Document]. Addendum-Part two action Tak. by Conf. Parties. URL http://unfccc.int/resource/docs/2015/cop21/eng/10a01.pdf

van Bavel, C.H.M., 1950. Mean Weight-Diameter of Soil Aggregates as a Statistical Index of Aggregation. Soil Sci. Soc. Am. J. https://doi.org/10.2136/sssaj1950.036159950014000c0005x

Van Groenigen, K.J., Six, J., Hungate, B.A., De Graaff, M.A., Van Breemen, N., Van Kessel, C.,

2006. Element interactions limit soil carbon storage. Proc. Natl. Acad. Sci. U. S. A. 103, 6571–6574. https://doi.org/10.1073/pnas.0509038103

Vilela, L., Martha, G.B., Macedo, M.C.M., Marchão, R.L., Guimarães, R., Pulrolnik, K., Maciel, G.A., 2011. Sistemas de integração lavoura-pecuaria na região do Cerrado. Pesqui. Agropecu. Bras. 46, 1127–1138. https://doi.org/10.1590/S0100-204X2011001000003

Wade, J., Culman, S.W., Hurisso, T.T., Miller, R.O., Baker, L., Horwath, W.R., 2018. Sources of Variability that Compromise Mineralizable Carbon as a Soil Health Indicator. Soil Sci. Soc. Am. J. https://doi.org/10.2136/sssaj2017.03.0105

Wade, M.H., Carvalho, P.C. de F., 2009. Defoliation patterns and herbage intake on pastures., in: Grassland Ecophysiology and Grazing Ecology. https://doi.org/10.1079/9780851994529.0233

Wagg, C., Hautier, Y., Pellkofer, S., Banerjee, S., van der Heijden, M.G., 2020. Diversity and asynchrony in soil microbial communities stabilizes ecosystem 1 functioning 2 3. bioRxiv.

Walker, T.S., Bais, H.P., Grotewold, E., Vivanco, J.M., 2003. Root exudation and rhizosphere biology. Plant Physiol. https://doi.org/10.1104/pp.102.019661

Wang, B., An, S., Liang, C., Liu, Y., Kuzyakov, Y., 2021. Microbial necromass as the source of soil organic carbon in global ecosystems. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2021.108422

Wang, Z., Yuan, X., Wang, D., Zhang, Y., Zhong, Z., Guo, Q., Feng, C., 2018. Large herbivores influence plant litter decomposition by altering soil properties and plant quality in a meadow steppe. Sci. Rep. https://doi.org/10.1038/s41598-018-26835-1

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van Der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science (80-.).

https://doi.org/10.1126/science.1094875

Wasserstein, R.L., Schirm, A.L., Lazar, N.A., 2019. Moving to a World Beyond “$p < 0.05$.” Am. Stat. https://doi.org/10.1080/00031305.2019.1583913

Waters, C.M., Orgill, S.E., Melville, G.J., Toole, I.D., Smith, W.J., 2017. Management of Grazing Intensity in the Semi-Arid Rangelands of Southern Australia: Effects on Soil and Biodiversity. L. Degrad. Dev. 28, 1363–1375. https://doi.org/10.1002/ldr.2602

Wei, Y., Zhang, Y., Wilson, G.W.T., Guo, Y., Bi, Y., Xiong, X., Liu, N., 2021. Transformation of litter carbon to stable soil organic matter is facilitated by ungulate trampling. Geoderma. https://doi.org/10.1016/j.geoderma.2020.114828

Weiss, M.S., Abele, U., Weckesser, J., Welte, W., Schiltz, E., Schulz, G.E., 1991. Molecular architecture and electrostatic properties of a bacterial porin. Science (80-.). https://doi.org/10.1126/science.1721242

Wheeler, S.J., Pickering, G.J., 2003. Optimizing grape quality through soil management practices. Food, Agric. Environ.

White, R., Balachandra, L., Edis, R., Chen, D., 2007. The soil component of terroir. J. Int. des Sci. la Vigne du Vin. https://doi.org/10.20870/oeno-one.2007.41.1.860

Whitehead, D., 2020. Management of Grazed Landscapes to Increase Soil Carbon Stocks in Temperate, Dryland Grasslands. Front. Sustain. Food Syst. https://doi.org/10.3389/fsufs.2020.585913

Wiesmeier, M., Hübner, R., Barthold, F., Spörlein, P., Geuß, U., Hangen, E., Reischl, A., Schilling, B., von Lützow, M., Kögel-Knabner, I., 2013. Amount, distribution and driving factors of soil organic carbon and nitrogen in cropland and grassland soils of southeast Germany (Bavaria). Agric. Ecosyst. Environ. 176, 39–52.

https://doi.org/10.1016/j.agee.2013.05.012

Wilson, C.H., Strickland, M.S., Hutchings, J.A., Bianchi, T.S., Flory, S.L., 2018. Grazing enhances belowground carbon allocation, microbial biomass, and soil carbon in a subtropical grassland. Glob. Chang. Biol. https://doi.org/10.1111/gcb.14070

Wolkovich, E.M., 2016. Reticulated channels in soil food webs. Soil Biol. Biochem. https://doi.org/10.1016/j.soilbio.2016.06.021

Wong, V.N.L., Greene, R.S.B., Dalal, R.C., Murphy, B.W., 2010. Soil carbon dynamics in saline and sodic soils: A review. Soil Use Manag. https://doi.org/10.1111/j.1475-2743.2009.00251.x

Wu, G.L., Liu, Y., Tian, F.P., Shi, Z.H., 2017. Legumes Functional Group Promotes Soil Organic Carbon and Nitrogen Storage by Increasing Plant Diversity. L. Degrad. Dev. 28, 1336–1344. https://doi.org/10.1002/ldr.2570

Wu, H., Dannenmann, M., Fanselow, N., Wolf, B., Yao, Z., Wu, X., Brüggemann, N., Zheng, X., Han, X., Dittert, K., Butterbach-Bahl, K., 2011. Feedback of grazing on gross rates of N mineralization and inorganic N partitioning in steppe soils of Inner Mongolia. Plant Soil. https://doi.org/10.1007/s11104-010-0575-z

Xu, S., Eisenhauer, N., Ferlian, O., Zhang, J., Zhou, G., Lu, X., Liu, C., Zhang, D., 2020. Species richness promotes ecosystem carbon storage: evidence from biodiversity-ecosystem functioning experiments. Proceedings. Biol. Sci. https://doi.org/10.1098/rspb.2020.2063

Xu, X., Schimel, J.P., Janssens, I.A., Song, X., Song, C., Yu, G., Sinsabaugh, R.L., Tang, D., Zhang, X., Thornton, P.E., 2017. Global pattern and controls of soil microbial metabolic quotient. Ecol. Monogr. https://doi.org/10.1002/ecm.1258

Xun, W., Yan, R., Ren, Y., Jin, D., Xiong, W., Zhang, G., Cui, Z., Xin, X., Zhang, R., 2018.

Grazing-induced microbiome alterations drive soil organic carbon turnover and productivity in meadow steppe. Microbiome. https://doi.org/10.1186/s40168-018-0544-y

Yang, Q., Wang, X., Shen, Y., 2013. Comparison of soil microbial community catabolic diversity between Rhizosphere and bulk soil induced by tillage or residue retention. J. Soil Sci. Plant Nutr. https://doi.org/10.4067/s0718-95162013005000017

Zatta, A., Clifton-Brown, J., Robson, P., Hastings, A., Monti, A., 2014. Land use change from C3 grassland to C4 Miscanthus: Effects on soil carbon content and estimated mitigation benefit after six years. GCB Bioenergy 6, 360–370. https://doi.org/10.1111/gcbb.12054

Zhalnina, K., Louie, K.B., Hao, Z., Mansoori, N., Da Rocha, U.N., Shi, S., Cho, H., Karaoz, U., Loqué, D., Bowen, B.P., Firestone, M.K., Northen, T.R., Brodie, E.L., 2018. Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. Nat. Microbiol. https://doi.org/10.1038/s41564-018-0129-3

Zhang, T., Li, F.Y., Shi, C., Li, Y., Tang, S., Baoyin, T., 2020. Enhancement of nutrient resorption efficiency increases plant production and helps maintain soil nutrients under summer grazing in a semi-arid steppe. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2020.106840

Zhao, Y., Tian, Y., Gao, Q., Li, X., Zhang, Y., Ding, Y., Ouyang, S., Yurtaev, A., Kuzyakov, Y., 2022. Moderate grazing increases newly assimilated carbon allocation belowground. Rhizosphere 22, 100547. https://doi.org/https://doi.org/10.1016/j.rhisph.2022.100547

Zhen Teng, Fan, W., Wang, H., Cao, X., Xu, X., 2020. Monitoring Soil Microorganisms with Community-Level Physiological Profiles Using Biolog EcoPlates^{TM} in Chaohu Lakeside Wetland, East China. Eurasian Soil Sci. https://doi.org/10.1134/S1064229320080141

Zheng, Q., Hu, Y., Zhang, S., Noll, L., Böckle, T., Richter, A., Wanek, W., 2019. Growth explains microbial carbon use efficiency across soils differing in land use and geology. Soil Biol. Biochem. 128, 45–55. https://doi.org/10.1016/j.soilbio.2018.10.006

Zheng, S., Lan, Z., Li, W., Shao, R., Shan, Y., Wan, H., Taube, F., Bai, Y., 2011. Differential responses of plant functional trait to grazing between two contrasting dominant C3 and C4 species in a typical steppe of Inner Mongolia, China. Plant Soil 340, 141–155. https://doi.org/10.1007/s11104-010-0369-3

Zheng, W., Lehmann, A., Ryo, M., Vályi, K.K., Rillig, M.C., 2020. Growth rate trades off with enzymatic investment in soil filamentous fungi. Sci. Rep. https://doi.org/10.1038/s41598-020-68099-8

Zhou, G., Zhou, X., He, Y., Shao, J., Hu, Z., Liu, R., Zhou, H., Hosseinibai, S., 2017. Grazing intensity significantly affects belowground carbon and nitrogen cycling in grassland ecosystems: a meta-analysis. Glob. Chang. Biol. 23, 1167–1179. https://doi.org/10.1111/gcb.13431

Zhu, X., Jackson, R.D., DeLucia, E.H., Tiedje, J.M., Liang, C., 2020. The soil microbial carbon pump: from conceptual insights to empirical assessments. Glob. Chang. Biol. https://doi.org/10.1111/gcb.15319

Zhu, Z.L., Chen, D.L., 2002. Nitrogen fertilizer use in China - Contributions to food production, impacts on the environment and best management strategies. Nutr. Cycl. Agroecosystems 63, 117–127. https://doi.org/10.1023/A:1021107026067